Point by point response to all reference comments

Dear Editor and reviewers,

We are thankful for the valuable comments you and both reviewers made for our manuscript. In the following, you can find our point-by-point reply to all the comments. Since most of the comments are already answered in our published response during the open discussions. This reply then aims to give the details of what changes we have made during the revision. Besides, we would like to highlight the following three major changes we made during the revision.

First, we further conducted global sensitivity analysis for all the newly P parameter and some N relevant parameters for the Coup-CNP model. The details of the approach and results are given as a Supplement. The global sensitivity analysis results show the importance of P and N availability in determining the C, N and P cycling in forests ecosystems in Sweden. This confirms our major conclusions in the main paper but also justifies our key parameter sensitivity analysis reported in the paper. The simulation files for global sensitivity analysis are archived at Zenodo (https://doi.org/10.5281/zenodo.4291963).

Second, we thoroughly rewrite most of the introduction and presentation of the model as suggested by both referees.

Third, before submission, the revised paper and newly added supplement have been language checked by professional English language proofing company. Hence, some formulation below might slightly change.

We hope our revised paper now to be satisfactory for publishing.

Sincerely,

Hongxing He (on behalf of the author team)

Reply to Anonymous Referee #1

We thank Anonymous Referee #1 for your positive comments and constructive suggestions to our manuscript. Here are our changes made to address the comments. The referee comments are given in normal font and our responses in italics.

The paper by He et al. presented the integration of the phosphorus (P) cycle into the CoupModel and evaluation of the new model, Coup-CNP, against four regions in Sweden that differ in climate and fertility. It is overall a very interesting paper, particularly with the novel setup of both NP cycles and mycorrhiza. The results are well presented, and the discussion is clear and well organized; the authors have put much effort into compiling the information of the model development both in the paper and appendix. Overall I think the paper is in good shape and contributes to advances in the modeling community.

- *We are glad the referee appreciates the science and novelty value of this new model development. We appraise that our P cycle and mycorrhiza model has a good potential to contribute to improved understanding of and insights into current ongoing discussion of nutrients impacts on C cycle. We also pleased that the referee finds the presentation of the results and discussions are in a good shape.*

However, the current quality of the paper needs to be improved before final acceptance. First of all, I found the quality of English writing an obstacle for me to keep focusing on the scientific content of the paper. I would recommend the authors to go for a professional editing service with the paper. I listed some obvious mistakes in the detailed comments, mostly before the results section, since I stopped to do that for the rest of the paper simply due to the heavy load of scientific information.

- *We have thoroughly rechecked the texts of the paper, also rewritten the whole model description (now section 2) and description of the region (now section 3). The language of the revised manuscript and the newly added supplement had been edited by professional editing service in UK. We believe the language has been much improved now.*

Secondly, this study lacks a proper sensitivity analysis. The authors did a simple sensitivity test on the fungal organic uptake rates of N and P and presented the result in the appendix. As far as I see from the description in this paper, Coup-CNP is a heavily parameterized model with a huge number of parameters. It is extremely important to run a proper sensitivity analysis with multiple parameters, not only to see the effects of parameterization on model outputs but also to test the stability and robustness of the model.

- *We have now conducted global sensitivity tests including all the P parameters and few N related parameter (n=34). The tested parameters, model approach and sensitivity analysis results, including parameter sensitivity for different selected model variables, are given in the newly added supplement (details see section 1-2 in supplement).*
- *Briefly, the global sensitivity results (i.e., Table S.2; Table S.3; Table S.4) show that parameter importance/sensitivity differs in terms of selected out variables, also in terms*

of studied region. Overall, the most crucial parameters (ranked by the correlation coefficient, r between parameter and model output) in controlling the C, N and P outputs is the initial soil organic P in humus, then followed by the short-cut N/P uptake rates (renamed to replace 'organic uptake' in previous version) and non-symbiosis microbe C/P ratio both of which directly regulating the availability of N and P; then followed by the plant growth and photosynthesis related parameters (e.g. leaf optimal/threshold C/P ratios for photosynthesis); then followed by the fungi related parameters, and the least importance is the weathering and partitioning of inorganic P parameters. All parameters show importance, in determining the output (note only, r ≥0.2 or ≤ -0.2 reported in Table S.2, S.3, S.4). Our global sensitivity analysis thus confirms the stability and robustness of the model (see section 3 in supplement).

- *More importantly, the global sensitivity analysis results also show the importance of P and N availability in determining the C, N and P cycling in forests ecosystems in Sweden. This confirms our major conclusions in the main paper but also justifies our key parameter sensitivity analysis (initial soil organic P, short-cut N/P uptake coefficients) reported in the paper.*
- *We have now added a separated section in the main paper, "Section 3.5 sensitivity analysis" to briefly describe the global sensitivity analysis and links to the key parameter sensitivity analysis reported in the paper as following: "We conducted a global sensitivity analysis of the new Coup-CNP model to its parameterization (n=34) using a Monte-Carlo based sensitivity analysis method to assess the stability and robustness of the model with respect to its parameter values. The sampled parameters and their ranges (Table S.1), model design and global sensitivity results (Table S.2, S.3, S.4) were reported in detail in the supplement. Based on these simulations and parameter sensitivity rankings, we select three most important parameters (n=3), which has a strong effect on the model outcome to further form a new set of model runs, which are used for the model sensitivity analysis presented in this paper. The selected three parameters are initial soil humus P, short-cut N uptake rate and short-cut P uptake rate (Table S.2, S.3), all strongly regulates the soil N and P availability."*

Thirdly, apart from a sensitivity test, I would also recommend the authors to conduct a few model experiments to see the model responses to alternative model assumptions or changing climatic/environmental conditions. For example, the authors introduced the plant growth response to P stress based on leaf C/P ratio (Eq.9), which is novel and interesting but at the same time debatable. I personally would really like to see the effect of this mechanism on the predicted GPP/NPP and biomass. Another example is the role of mycorrhiza uptake and the so-called organic uptake of N and P. I found that the authors made some very strong assumptions regarding the uptake competition (the sequence of uptake) between plant, fungal and adsorption, and it would be interesting (and fundamental) to see the effect of these strong assumptions.

- *We have conducted global sensitivity analysis for two regions with different environmental conditions: one for the northernmost 64^{o}N region with N limitation (Table S.2; Fig.S.1; Fig.S.2) and the southernmost 56^{o}N region with P limitation (Table S.3; Fig.S.3; Fig.S.4). We further conducted an additional global sensitivity analysis in 64^{o}N region by removing the identified dominant impacts of the three parameters (i.e. initial soil organic P in humus pool, and short-cut N/P uptake* *coefficients) to better show the sensitivity of the other parameters (Table S.4). Thus, overall three extra model experiments have been conducted (details see section 1-3 in supplement).*

- *The parameters show different sensitivity to the different region. For the northernmost 64°N region, C and N change in plant and soil is mostly sensitive to the short-cut N uptake rate ($o_{uptNhumus}$) (Table S.2). This is expected as the region is identified as being N limited. For the southernmost 56°N region, C and N change in plant and soil is more sensitive to the initial soil organic P in humus (Table S.3). This is also expected, as the region is P limited. Other global sensitivity analysis results see supplement section 3 and response above.*
- *Our global sensitivity analysis show high sensitivity of the P response to GPP to the leaf C/P optimal parameter, $p_{cp,opt}$. Similarly, N response to GPP is sensitive to leaf C/N parameters (Table S.2, S.3, S.4). However, leaf C/P optimal parameter does not shown high sensitivity to the simulated plant C change, likely due to dominant of other parameters that regulates the N and P availability (short-cut uptake rates, e.g. $o_{uptNhumus}$, $o_{uptPhumus}$), plant allocation, p_{fopt} etc. (Table S.2, S.3). The additional sensitivity analysis for the N limited 64°N region in Table S.4 show the importance of leaf C/N threshold parameter, $n_{cn,th}$ in determining plant C change and total C harvest.*
- *Our global sensitivity analysis show parameters relevant to plant P demand, short-cut uptake rate, fungi related parameters, and partitioning in the soil are all sensitive in regulating the plant and soil P cycle (see supplement section 3). Within our tested parameter ranges, the parameter sensitivity rankings show, the most crucial parameter is the soil organic P, followed by the short-cut uptake rates for N and P, then the fungi parameters then lastly is the partitioning (i.e. adsorption).*
- *Please note the changing climatic/environmental model experiments were already conducted by applying the new Coup-CNP model on four regions with varying climate (annual temperature between 0.7-7.1 C) and fertility (with the soil C/N and C/P ratios between 19.8-31.5 and 425-633, respectively) along a gradient from South to North Sweden.*

Detailed comments

1. Abstract and Introduction

Line18: make "which explicitly consider mycorrhizal interactions" a relative clause after "The extended Coup-CNP"

- *Changed accordingly.*

Line 26: what is "a steady state in P availability"? I don't find "P availability" from the P budget

- *We have changed to "The simulated P budgets revealed that southern forests are losing P, while northern forests have their P budget in balance"*

Line 40: "nutrient cycling" is not a biochemical reaction

- *We have changed to "Phosphorus (P) is an essential element for all photosynthesizing plants in terrestrial ecosystems, with the P cycle coupled to Carbon (C) and Nitrogen*

(N) fluxes especially through processes such as decomposition of soil organic matter and nutrient uptake"

Line 50: it is true that N inputs to the atmosphere increased due to human activity, but for terrestrial ecosystems, the important process is the N deposited from the atmosphere

- *Revised to "atmospheric N deposition"*

Line 52: mechanisms can not be amplified, right? Second paragraph: I think it is a brilliant idea to review the literature of the P cycle in current models, but the organization of information needs to be much improved in this paragraph. I also have some disagreements with the authors about the interpretations of some cited publications, and would like to discuss with the authors about them.

- *We have removed "mechanisms". We shorten the literature P model review and thoroughly recheck the cited publications to ensure they are cited correctly. The reference to the reviewed P models is revised by referring to the more recent model description paper (e.g. Groenendijk et al., 2005). Papers which are published during open discussions are also added (e.g. Du et al. 2020).*

Line 56-65: I think this part is irrelevant to the overall discussion and conclusion of this study. I would recommend to remove or to shorten it.

- *We shortened this model review part in to "Nevertheless, the P cycle is seldom incorporated into ecosystem model structures. Incorporating the P cycle is essential in improving global models as a tool for assessment of climate-C cycling interactions (Reed et al., 2015). Most of the process-based models that can simulate P cycling were specifically developed for agricultural systems and focus on the soil processes, e.g., EPIC (Jones et al., 1984, Gassman et al., 2005), ANIMO (Groenendijk et al., 2005), and GLEAMS (Knisel and Turtola, 2000). A few catchment-scale models focus on surface water quality, e.g. SWAT (Arnold et al., 2012), HYPE (Arheimer et al., 2012), and INCA-P (Jackson-Blake et al., 2016)."*

Line 72: there are some more P-enabled ESMs, e.g. Zhu et al. 2016 Biogeosciences, Goll et al. 2017 GMD, Thum et al. 2019 GMD.

- *Added accordingly*

Line 75: Zaehle et al. 2014 does not support your statement here

- *Deleted.*

Line 76-92: The interpretation of these studies is a bit imprecise and vague. I found it difficult to jump from one study to another one; maybe it is better to reorganize all the studies with some intrinsic links, such as common problems or findings. What I will recommend is to focus on the role and effect of plant P uptake in different model studies. Yu et al. only included the P cycle into the ForSAFE model. I would not phrase it as "developed the model", which causes confusion

- *We reorganized and revised the texts for the reviewed modelling studies*

- *We have changed "developed the model" to "included the P cycle into" for ForSAFE statement.*
- *We have now added the "implicitly or explicitly of symbiotic mycorrhiza and other soil microbes" after "these P enabled models differ in how they described soil P dynamics" to be more specific.*

Line 99: whose interaction with soil mycorrhizal fungi?

- *Revised to "interaction between plants and mycorrhizal fungi"*

Line 100: I don't fully agree with the interpretation of the references here. These data driven meta-analyses do not really explain "how P availability affects plant growth", and if this mechanism is influenced by mycorrhizae-plant interactions. They are more of "a proof" than "an explanation" to me

- *We have changed to "Global meta-analysis studies highlighted that symbiosis between plants and soil mycorrhizal fungi strongly influences plant P availability that further affects plant growth" to avoid confusion.*

Line 109-111: please restructure the sentence

- *We have changed sentence into "To the best of our knowledge, only Orwin et al. (2011) have presented an ecosystem model that consider C, N and P together with symbiotic fungi. They found that considering organic nutrient uptake by symbiotic fungi in an ecosystem model can significantly increase soil C storage, with this effect more pronounced under nutrient-limited conditions. The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with mycorrhizal fungi or root exudates"*

Line 132: soil organic matter is a more commonly used term than "soil organics"

- *Changed accordingly.*

Line 134: there is little evidence for organic P uptake of plants and microbes, as far as I know

- *We have added the following in the introduction section to explain the organic nutrient uptake concept better in Coup-CNP: "The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with mycorrhizal fungi or root exudates (e.g. Schachtman et al., 1998, Gärdenäs et al. 2011, Richardson et al. 2005). However, in Orwin's model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored. Our model (Eckersten and Beier, 1998; He et al., 2018) also includes a nutrient-short-cut uptake as a process in the rhizosphere. The assumption is that nutrients released by biochemical mineralization are instantly taken up by the symbiotic microbes and/ or the plants, thereby by-passing the soil matrix solution."*
- *The section 2.2.3 further describe the concepts and calculations as "Biochemical mineralization, on the other hand, describes the release of P_i through extracellular enzymatic releases (e.g., phosphatases by root exudates), which are driven by plant*

demand for nutrients (Richardson and Simpson, 2011). In Coup-CNP, biochemical mineralization is conceptually included in the nutrient short-cut uptake (called organic uptake in earlier CoupModel publications) and assumed to be driven by the unfulfilled plant P demand after P_{ilab} *root uptake (equ A.8) but regulated by the availability (i.e. short-cut uptake coefficients in equ A.4)."*

- *Further, to avoid confusion with the uptake of organic molecules, we rename the organic P/N uptake into "short-cut P/N uptake" in the entire paper.*

2. Model structure and description of processes linked to the phosphorus pool

Please rename the title, maybe "Model structure and phosphorus process description"? Another piece of advice is linking the process description of Section 2.2 with the equation number in Section 3 and Appendix A. It is much easier for the readers to track information in this way.

- *We retitled this section to "Description of model structure and phosphorus model".*
- *We have merged previous section 2 and 3 and substantially rewritten the entire section. We have changed the model description organization by starting with describing the new P model concepts and defining its pools and assumptions in section 2.2. Then starting the detailed process and equation description in sub-sections 2.2.1-2.2.6. "Soil inorganic phosphorus dynamics and nutrient short-cut uptake" has now been moved to section 2.2.3. We have briefly described the processes that detailed described in appendix, and added linkages (i.e. equation numbers, sections in appendix) to the appendix when possible to make it easier for readers to follow.*

Line 142: what does "flexible" model mean?

- *Removed.*

Line 145: please check the grammar

- *We have changed to "The main model structure is a one-dimensional, vertical layered soil profile. The core of the model consists of five sets of coupled partial differential equations, one for water, heat, C, N, and P cycles (the later one in v6.0), respectively"*

Line147: maybe already mention the normal time step and the smaller time step here?

- *We have added the time step "daily" here as suggested.*

Line 149: "crucial"??? what and why?

- *Removed. We have further described what we mean "crucial" here by "In this application, we used a daily time step for all five, but a smaller time step was applied for the water and heat calculations during specific events with peaks in water and/or heat flow such as during snow melting to ensure the numerical stability and accuracy".*

Line 151: why the radiation forcing has to be "global"???

- *Reworded this to "global, i.e. sum of direct and diffuse shortwave incoming radiation".*

Line 153: compete for light??? Not "light interception"?

- *Corrected.*

Line 161: strange sentence structure, please consider adjusting it

- *Reworded into "We developed the P model in a way that 1) focus on the key P processes for biogeochemical cycling, e.g., dynamic plant growth and P leaching, and 2) follows the conceptual structure of CoupModel as closely as possible.".*

Line 164: "can differ" => differs, or do you mean that there are two options for time step???

- *Deleted this sentence since the same time step was used in this study.*

Line 166: difficult to understand the sentence

- *Revised to "For simplicity, the equations are given in a form that reflects one time step and one of the layers that represent the entire soil profile. The symbols in this paper were designed to conform the CoupModel nomenclature in the following way: uppercase P means state variables, lowercase p means parameters related in P processes"*

Line 171: there is not a common definition of "mineral P", please distinguish it from other inorganic P forms

- *We have re-described the pools as "The soil inorganic P has new and renewed state variables. New is the soil solid inorganic* P_{solid}*, a lumped pool containing primary and secondary mineral compounds containing P such as apatite (and occluded P) (Smeck, 1985; Wang et al., 2007).* P_{ilab} *is the sum of phosphate ions absorbed and those in soil solutions, analog to the mineral pool in salt tracer representation in CoupModel (Gärdenäs et al., 2006). Instantaneous equilibrium between adsorbed and soil solution are assumed. Plant and microbes take up phosphate ions from the* P_{ilab}*.* P_{isol} *can be compared with the sum of N state variables* NH_4^+ *and* NO_3^- *while being an intrinsic part of* P_{ilab} *(Fig. 1)."*
- *We have renamed the previous mineral P pool as "soil solid inorganic* P_{solid}*" in the entire paper to avoid confusion*

Line 174: "inorganic-phosphorus", why a hyphen here?

- *Removed*

Line 176-180: I don't see the connection between the model definition and Hedley fractionation. Please elaborate.

- *Removed*

Line 183: "which contains"=> "for"

- *We have deleted this sentence, since only one litter pool was used in this study.*

Line 185: which decomposition rate is used for the combined litter pool?

- *We have deleted this sentence, since only one litter pool was used in this study.*

Line 185-200: If I understand correctly, Coup-CNP applied a three-pool structure for soil inorganic P, which is different from most other P models. One thing that is particularly different in this study is that the role of adsorption/desorption is greatly neglected by most biochemical processes since Pisol is only relevant to transport and Pilab is relevant for other processes, such as deposition, weathering, plant/fungal uptake and etc.. It is a very interesting setup, but I think it needs to be better explained. Particularly, the statement that "These Pi ions are normally loosely adsorbed to surfaces and can thus easily re-enter the Pilab pool through the desorption process (McGechan and Lewis, 2002)." is wrong. There is plenty of evidence for the strong adsorption of phosphate, which is also the main reason for the extremely low soluble inorganic P concentration in the soil water. The main reason that plant and microbe can take up enough P in such a low P concentration is probably the fast replenishing of soluble P in soil water, which are the consequences of desorption/diffusion and biological mobilization (mineralization). Please see Buenemann et al. 2016, SBB and Pistocchi et al. 2018, SBB, and the references therein for more information.

- *We have redescribed and defined the soil P pools more clearly in section 2.2: "The soil inorganic P has new and renewed state variables. New is the soil solid inorganic* P_{solid}*, a lumped pool containing primary and secondary mineral compounds containing P such as apatite (and occluded P) (Smeck, 1985; Wang et al., 2007).* P_{ilab} *is the sum of phosphate ions absorbed and those in soil solutions, analog to the mineral pool in salt tracer representation in CoupModel (Gärdenäs et al., 2006). Instantaneous equilibrium between adsorbed and soil solution are assumed."*
- *We also make our assumptions more clearly. The assumption between the soluble P and the labile P is described in section 2.2.2: "the soluble (*P_{isol}*) and adsorbed P reach equilibrium in less than 1 hour (Cole et al., 1977; Olander and Vitousek, 2005). We assume that the* P_{isol} *and adsorbed part of* P_{ilab} *are always in equilibrium as daily timestep is used (equ 5). The modified Langmuir isotherm (Barrow, 1979) was used to model the fast and reversible sorption process within* P_{ilab}*"*
- *We have deleted the "These Pi ions are normally loosely adsorbed to surfaces and can thus easily re-enter the Pilab pool through the desorption process (McGechan and Lewis, 2002)." to avoid confusion.*

Line 214: what is mobile P and N? this is a very strong assumption that plants can capture nutrients from litterfall, and I wonder how sensitive are the model outputs to this assumption.

- *The following section was added in A4 plant litterfall to describe the pool and assumption more clearly "During litterfall seasons, plants can reallocate P and N from leaves to an internal, mobile storage to prepare for rapid growth in the spring, a known mechanism to increase efficient use of nutrients (e.g. Aerts, 1996; Niemien and Helmisaari, 1996) (also see* m_{retain} *in Table S.1 in supplementary)".*
- *Note the* m_{retain} *is also included in the global sensitivity analysis and showed the modeled ecosystem C change is sensitive to this parameter in Table S.4*

Line 221: what are the enzymatic processes? Please be specific. Btw, phosphatase is not a process

- *Reworded to "phosphatase released by the root exudates"*

Line 222-225: well, this is another astonishing assumption, which needs to be properly tested. And the hidden hypothesis that it only occurs after inorganic P uptake when plant P demand is not fully met is also quite strong from my personal feeling. It basically means that there are no interactions (feedback/competition) between soil organic and inorganic P cycling processes, all the feedback mechanisms have to go through the plant growth & litterfall pathway. I wonder how the model will perform in an extremely P limited ecosystem.

- *We realize the previous description of P uptake may be unclear thus we have revised this to make it clearer and described our assumptions more clear. We first added the following in introduction to motivate and describe the background of the short-cut uptake concepts: "The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with mycorrhizal fungi or root exudates (e.g. Schachtman et al., 1998, Gärdenäs et al. 2011, Richardson et al. 2005). However, in Orwin's model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored. Our model (Eckersten and Beier, 1998; He et al., 2018) also includes a nutrient-short-cut uptake as a process in the rhizosphere. The assumption is that nutrients released by biochemical mineralization are instantly taken up by the symbiotic microbes and/ or the plants, thereby by-passing the soil matrix solution."*
- *We have put "soil inorganic phosphorus dynamics and nutrient short-cut uptake" as a separate section 2.2.3. This is to better describe the soil inorganic and organic processes, also to highlight the interaction of soil organic and inorganic P cycling processes.*

Line 229: how is the DOM redistributed between layers? Is it described in the paper?

- *We have added the following into the A2. Section to describe the DOM redistribution more in detail: "The redistribution is done following that of water flow, as the DOM is assumed to have full mobility with water. The formation of DOM is from litter and humus. The dissolved organic matter can be fixed by humus via adsorption, precipitation, etc. A fixation coefficient,* d_{DOD}*, which varies between layers, was introduced (Kalbitz et al., 2000; Kaiser and Kalbitz, 2012). Parameterization from Svensson et al. (2008) were used in this study."*

3. Equations describing key phosphorus processes/fluxes and their parameterization

One major trouble to me is that the use of both uppercase and lowercase P (p) in the equations. It is extremely difficult sometimes, please consider replacing one of them with another letter. Another major issue is that I could not find information on how leaf P content is calculated, which is essential to understand some results

- *We have revised the symbols of the equations where could lead to possible confusion and double-check consistency in the entire paper. For instance, we have changed the "soil mineral P_m"into "soil solid inorganic P_{solid}". We have changed the symbols for three soil organic pools, soil litter, soil humus, dissolved organic P into P_{Litter} and P_{Hmus} and P_{DOP} for easier to understand, and so on.*
- *To avoid confusion, we have added the following explanation texts in the main texts (section 2.2) just before the equation sections to explain the rule of the symbol to make it easier to follow: "For simplicity, the equations are given in a form that reflects one time step and one of the layers that represent the entire soil profile. The symbols in this paper were designed to conform the CoupModel nomenclature in the following way: uppercase P means state variables, lowercase p means parameters related in P processes."*
- *We have updated the leaf C/P ratio description (under section 2.2.4) with the following to make it clear the leaf C/P is a variable that calculated at each time step: "The leaf C/P ratio is calculated at each time step with the leaf state variables C and P."*

Line 243: judging from Eq.4, I don't think "proportional" is the right word here

- *We have changed this sentence into "The weathering rate depends on soil pH and temperature (Guidry and Machenzie, 2000) and is calculated as".*

Line 247: how does erosion affect weathering rate? I cannot find it in the paper

- *We have added "the erosion affect the weathering rate by reducing the pool size of P_{solid}, (equ. A. 14)" in 2.2.1 weathering description.*

Line 254: there is a potential problem that diffusion is also considered as weathering. how uncertain is it to assume diffusion and weathering has the same temperature response? This is even a bigger problem for pH response as there is no evidence that pH affects diffusion

- *First, the weathering in Coup-CNP is independent of the mobile part of P in our model structure. We have revised our model concept description in section 2.2 and now renamed the previous soil mineral pool into "soil solid inorganic P_{solid}".*
- *However, again our aim was to build a simple yet realistic P net weathering flux. We compared to the current net weathering flux to a more detailed and rigorous geochemical model PROFILE, but not a dynamical model; that is more widely used for weathering estimates and current P flux estimates were rather similar (see discussion).*

Line 295: I am not sure if this theory is applicable to leaf CP ratio since P is not as essential as N for photosynthesis and the role of leaf P in photosynthesis is not well understood yet. As I mentioned before, it will be interesting to conduct model experiments to test this theory. Additionally, I did not find the information on how CoupCNP calculates leaf P content.

- *Please see our response above*

Line 303: The mycorrhiza module??? This sentence is confusing to me

- *We have removed the sentence "P fungi processes analog to N processes (He et al., 2018) are found in appendix A" as the fungi P processes are described in main text. Hopes that answer the reviewer question as we are not completely sure we got it right.*

Line314: Eq.9 seems the only place that soluble P concentration is used except leaching, how realistic is it to take this assumption directly from N, given the fact that P concentration is much lower than N?

- *We have revised to "analogue to the N response function" instead of the same.*

Line 316: "wais" => was

- *Corrected.*

Line 317: the piavail is another very problematic assumption, and I cannot find any theory or evidence to support it. Since the soluble P concentration is not used to calculate the plant P uptake, I could foresee that if labile P is freely taken up by the plant, the model might end up with no P limitation and the labile P might get depleted very soon. If there is no theory or literature to support this parameter, at least it should be tested in the sensitivity analysis

- *We have included this parameter p_{iavail} in the global sensitivity analysis. This parameter show sensitivity to plant and soil N change in Table S.4 in supplement. The conceptual meaning of p_{iavail} is that only a fraction defined by this parameter that could be available for plant uptake at the time step of calculation. Please also see our response above on the plant uptake concepts and rationale.*

Line 405: where is f(Piavail) used? which equation?

- *We have added "equ (A.8)"in the texts to point out where it was used.*

3. Description of the region used for simulation and model setup

It seems the same study regions have been tested with the previous version of CoupModel before, and it is unclear from this section if the new Coup-CNP model is recalibrated in this study. Please state it clearly in the paper how the model is parametrized and why some parameter values differ from previous studies (I assume that is the case)

- *We have re-described the regions and model setup. Major changes include added two separate sections of 3.4 Model forcing, initial and boundary conditions and section 3.5 sensitivity analysis to described these into more detail.*
- *We added the following to describe how the parameter values were determined in the reference model run: "The C and N parameters for these regions in CoupModel were previously tested and calibrated in a number of studies (Svensson et al., 2008) and those of fungi by (He et al., 2018) (Table 2). The surface cover parameters and litterfall rates of understory vegetation were modified from Svensson et al. (2008) to achieve a more realistic understory dynamics in those regions (Table 3). Most of the default values of the newly introduced P parameters were derived from literature (Table 2, 3). For instance, the optimal leaf C/P ratios for forest growth, C/P ratios of individual*

plant components were obtained from empirical measurements from Swedish forests (e.g. Thelin et al., (1998; 2002)). The weathering and surface runoff parameters were defined according to laboratory empirical data (e.g. Guidry and Machenzie, (2000)). "

Line 420: kg N ha-1 yr-1, right?

- *Corrected.*

Line 423: please cite the most recent FAO standard

- *We have revised into the more recent FAO 2006 guideline*

Line 443-446: difficult to follow the sentence

- *We have reworded to "The simulated rotational period was 120, 110, 90 and 70 years from the north to south region, respectively. Two thinnings were conducted for the two north region with three thinnings for the two south regions" to be more clear.*

Line 449-450: The model was spun up for 10 years, and then a clear cut is simulated??? How do you determine the initial SOM content and soil stoichiometry? How big are the effects of initial SOM status?

- *We have described the model design and setup in the beginning of section 3.3 "The results were based on simulated forest development with daily resolution over a rotation period from stand age 10 years until 10 years after final harvesting. The 10 years after final harvest were included to cover the potential nutrient leaching during the regeneration phase as in Gärdenäs et al. (2003). The trees in all regions were assumed to be planted in 1961, and the period 1961 to 1970 was used as a spin-up period."*
- *The initial conditions for both plants and soil have been described in more detail in the newly added section 3.4 as following: "The two vegetation layers were initialized as bare ground with a small amount of C, N and P mass in seedling to start vegetation growth. Initial conditions for solid inorganic P content, soil organic matter content, soil stoichiometry were reported in Table 1. Initial soil organic P pools (Table 1) were partitioned between soil litter (5%) and humus pools (95%) analog to N partition in Svensson et al. (2008), and total amount of soil organic P decreased exponentially with depth (Fransson and Bergkvist, 2000). Litter was assumed to be distributed down to 0.5 m while humus down to 1 m depth. The initial labile P_i concentrations were set according to previous data from similar Swedish forest sites (Kronnäs et al., 2019; Fransson and Bergkvist, 2000). Soil pH was set according to the NSFI data and kept constant over the simulation period (Table 1). The initial value of soil organic P for the soil profile was estimated by the available measurements of soil organic matter N/P ratios, performed at the same forest monitoring sites of the Swedish Forest Agency (Wijk, 1995; Akselsson et al., 2015) where leaf nutrient content were sampled. However, only the organic N/P ratio at the O horizon was measured at most sites. Thus, in our calculations of the total stock of soil organic P, we assumed that the mean N/P ratio measured for the O horizon also extends to the other horizons in the default model run. Model uncertainties associated with this assumption were assessed by including a range in the soil N/P ratios, 10-25, in the sensitivity analysis (e.g. Fig. 5)."*

Line 450-452: difficult to follow. Unclear to me what are the plant components and how are they treated

- *We have changed this into "Following general forest management guidelines, it was assumed that during thinnings 20% of the stem is removed while 5% transforms into litter (Swedish Forest Agency, 2005). For leaves and roots, it was assumed that 25% transforms into litter. For all of the regions, one clearance – during which 60% of the stands is removed - was applied at the end of the stand age year 10 after spin-up. During final felling, 5% of trees are remained intact, and it is assumed that 90% of the stem is harvested and 5% becomes litter, while all leaves and roots become litter. " to be more clear.*

Line 470: "chronicle"? I am not sure that is the right word here???

- *Changed to "describe".*

Line 477: This is a very unrealistic assumption; please see Yu et al. 2020 GMD

- *We have now added a new section 3.4 to describe the initial conditions for both plants and soil.*
- *We also added some few additional soil N and P content at the humus layer where leaf N and P content were measured into Table 1. However, still lacks soil P content of the layers below.*
- *We further clearly stated what assumptions we made, and how we made an sensitivity analysis to address the uncertainty raised by this assumption as following: "The initial value of soil organic P for the soil profile was estimated by the available measurements of soil organic matter N/P ratios, performed at the same forest monitoring sites of the Swedish Forest Agency (Wijk, 1995; Akselsson et al., 2015) where leaf nutrient content were sampled. However, only the organic N/P ratio at the O horizon was measured at most sites. Thus, in our calculations of the total stock of soil organic P, we assumed that the mean N/P ratio measured for the O horizon also extends to the other horizons in the default model run. Model uncertainties associated with this assumption were assessed by including a range in the soil N/P ratios, 10-25, in the sensitivity analysis (e.g. Fig. 5)."*

Line 485-487: One specific question to Table 2 is that, why the decomposition and uptake rates for different latitudes are different, given that the temperature response function already accounts for the difference in temperature? If they are calibrated separately, what is the meaning for choosing a climatic gradient??? Table 3: I would recommend running a full sensitivity test with parameters in this table

- *We have now made a few global sensitivity analysis with all the newly added P parameters and some N relevant parameters, and documented those in detail in supplement to the paper.*
- *We have added Svensson et al. 2008 and He et al. 2018 in the main texts.*

Line 519-521: difficult to follow the sentence

- *We have changed into "Thus, the measured P leaching also contains the P leaching from upstream. DOP were not measured for the regions. Thus the so call measured DOP was calculated as the difference between the measured total P and PO_4. This* *means the "measured DOP" may contain both our simulated fractions DOP and particular phosphorus." to be easier to follow what we mean.*

4. Results

Line 561: confusing, please rephrase

- *We have revised into "The total N uptake of the short-cut uptake from the organic N pools decreased from North to South (Table 4)." to make it more clear*

Line 564: why the new Coup-CNP C sequestration rates are so different from previous studies of the same regions?

- *We thank referee's comment on soil sequestration rate but we respectively disagree with the interpretation of these C sequestration rates. First, Previous model results did not consider P, and we had discussed our newly introduced P cycle has clear impacts on C sequestration rates (Fig 5b). Second, we also had different set up with previous settings (see response above), thus a different C sequestration rate could be expected, given the soil sequestration rate were a net result of a number of C fluxes. However, the general trends were the same where an increasing soil C sequestration rate moving towards the south and we consider these results were rather in according with previous results not differs.*

Line 573-575: I only see that the P leaching is very small, which may infer that it has a small effect. But the fact that P leaching accounts for 30% of P deposition does not lead to the conclusion that "a small effect on the system". I guess the key point here is that both P deposition and P loss are very small compared to other fluxes, e.g. plant P uptake

- *We agree and the intention was to compare to the outflow flux to the internal flow. We have revised the texts to "The data show that P losses through leaching were small compared to the internal fluxes, i.e., they account for approximately one-third of the annual deposition input".*

Section 5.2: the rotation period,10 years to10 years after the final felling, makes it a bit difficult to understand the results in figure 4, particularly the plant growth and change in plant in panel A. For me it is very difficult to judge how much of the changes in plant and soil pools are due to the very short spin-up time (10 years)? Is it possible to run a real spin-up to ensure a more stable state of the soil pool? Also, I did not fully understand why the pool size of 10-year-old trees differ so much in N and P size, to me it seems to be the effect of model initialization and spin-up.

- *We have made it clear about our model design and its rational at the beginning section of 3.3: "The 10 years after final harvest were included to cover the potential nutrient leaching during the regeneration phase as in Gärdenäs et al. (2003)."To avoid misunderstanding, we also added "Plant growth in a) represent the net primary production." In Fig.4 captions to explain the figure more in detail.*
- *For spin up, see response above*
- *For initialization, we have a new section 3.4 model forcing, initial and boundary conditions to describe those in more detail, also see response above*

5. Discussion

Section 6.1: all the studies that are compared to in the section are modeling studies, which should be made very clear.

- *We have added "other modelling studies" in the section title to make clear that are modelling studies compared.*

Section 6.2: In general, the discussion is interesting and the findings are encouraging. However, I do have an understanding problem regarding the soil N/P ratio. From the description in the method part, the soil N/P ratio seems to be a parameter in the sensitivity analysis. But its value is not reported in Table 3, and it seems that it is also not a constant value from Figure 3d. A more methodological problem is, only three parameters were tested in the sensitivity analysis, and the result for one parameter was presented. How could one conclude that this one is the most important parameter for the ecosystem? As I mentioned before, if this is the first study of the Coup-CNP, a better-designed sensitivity test should be performed. I am very convinced by the authors that soil N/P is an important indicator of Swedish forests, but I am convinced by the way it was accidentally chosen in this study.

- *We have now conducted global sensitivity analysis for all the newly parameters and summarized the results in the supplement. Please also see the response above for the sensitivity and extra model experiments comments.*
- *The global sensitivity analysis show the initial soil organic P (thus soil N/P ratio), together with the short-cut N and P uptake coefficients show the highest importance in determining the modelled C, N and P cycling (see supplement section 3).*
- *We have now added a separated section in the main paper, "Section 3.5 sensitivity analysis" to briefly describe the global sensitivity analysis and links to the key parameter sensitivity analysis reported in the paper as following: "We conducted a global sensitivity analysis of the new Coup-CNP model to its parameterization (n=34) using a Monte-Carlo based sensitivity analysis method to assess the stability and robustness of the model with respect to its parameter values. The sampled parameters and their ranges (Table S.1), model design and global sensitivity results (Table S.2, S.3, S.4) were reported in detail in the supplement. Based on these simulations and parameter sensitivity rankings, we select three most important parameters (n=3), which has a strong effect on the model outcome to further form a new set of model runs, which are used for the model sensitivity analysis presented in this paper. The selected three parameters are initial soil humus P, short-cut N uptake rate and short-cut P uptake rate (Table S.2, S.3), all strongly regulates the soil N and P availability."*

Line 676: where does this conclusion come from? increasingly P limited with time or latitude, or another gradient?

- *We have added with "decreasing latitude" to make it more clear*

Line 682: have you checked if the threshold is the same for pine and spruce? if not, please be specific about tree species

- *We have now added the tree species in the main texts: "In Swedish spruce forests (Picea abies L. Karst.), leaf N/P ratios below 7 are normally considered an indicator of N limitation, while ratios above 12 signal P limitation (Rosengren-Brinck and Nihlgård, 1995; Yu et al., 2018). Linder (1995) has previously reported an optimal N/P ratio of 10 for spruce forests in northern Sweden. Similar optimal N/P ratio for pine forest (Pinus silvestris) (Ingestad, 1979; Tarvainen et al., 2016).".*

Reply to Anonymous Referee #2

We thank Anonymous Referee #2 for your positive comments and constructive suggestions to our manuscript. Below are our changes made to address the comments; The referee comments in normal font and our response in italics.

The paper of He et al., brings us a model that couples P into an existing CN model. It is an interesting study with special focus on mycorrhizal fungi, which is important in P dynamics, but has yet to be adequately represented in current literature. My major concern though, is that the model is heavily parameterised with great details and many parameters, but the model performance is systematically biased. Figure 2 and Table 4 evaluated modelled tree biomass, leaf C:N, leaf C:P, leaf N:P and P leaching against measurements. First of all, for a model that covers many aspects of C, N, P dynamics, variables evaluated here are not adequate to show the model performance. Secondly, the model systematically overestimate leaf C:P (all sites) and leaf C:N (3 out of 4 sites), and underestimate P leaching (all sites). I am not convinced that the model does a good job in capturing the system. Additional work and data are needed to understand the model dynamics and thoroughly assess the model performance.

- *We have now conducted global sensitivity tests including all the P parameters and few N related parameter (n=34). The tested parameters, model approach and sensitivity analysis results, including parameter sensitivity for different selected model variables, are given in the newly added supplement (details see section 1-2 in supplement). Briefly, the global sensitivity results (i.e., Table S.2; Table S.3; Table S.4) show that parameter importance/sensitivity differs in terms of selected out variables, also in terms of studied region. Overall, our global sensitivity analysis show the stability and robustness of the model (see section 3 in supplement). More importantly, the global sensitivity analysis results further elucidate the model behavior and demonstrate the model ability of capturing the system response to the four regions. Specifically, C and N change in plant and soil is shown to be mostly sensitive to the short-cut N uptake rate ($o_{uptNhumus}$) (Table S.2) for the northernmost 64°N region,. This is expected as the region is identified as being N limited. But for the southernmost 56°N region, C and N change in plant and soil is shown to be more sensitive to the initial soil organic P in humus (Table S.3), as the region is P limited. This confirms our results from the previous model default runs and solidate that the model can capture the system response to the four regions.*
- *We have now revised the datasets for model evaluation section 3.2 to describe the data more in detail, "Thus, the measured P leaching also contains the P leaching from upstream. DOP were not measured for the regions. Thus the so call measured DOP was calculated as the difference between the measured total P and PO_4. This means the "measured DOP" may contain both our simulated fractions DOP and particular phosphorus."*
- *Again we would like to highlight our aim was to demonstrate model behavior and the implication of the newly added P in the model structure. The intention was not to make a site-specific detailed model calibration.*

In addition, I feel it is quite difficult to follow the model description. Sometimes there are logical issues related to terminology and the separation among system compartments (please see detailed comments below). Sometimes it is due to lack of critical information in P cycling in the main text, for example, P dynamics in vegetation (allocation, resorption etc.), through mineralization etc. It might be better to put part of the information in the appendix into the main text, or at least have some overall description of these processes in the main text and point to the appendix for detailed information. The goal is to give the reader a complete picture of P cycling the model tracks.

- *We have merged previous section 2 and 3 and substantially rewritten the entire section. We have changed the model description organization by starting with describing the new P model concepts and defining its pools and assumptions in section 2.2. Then starting the detailed process and equation description in sub-sections 2.2.1-2.2.6. "Soil inorganic phosphorus dynamics and nutrient short-cut uptake" has now been moved to section 2.2.3. We have briefly described the processes that detailed described in appendix, and added linkages (i.e. equation numbers, sections in appendix) to the appendix when possible to make it easier for readers to follow.*

The novel part of this model, from my perspective, is related to symbiotic mycorrhizal fungi. I did not find any observations to initialise, evaluate model performance or constrain model parameters related to this part. It is also not clear what is the advantage of incorporating detailed symbiotic mycorrhizal fungi, how it affects system dynamics, what are the novel model behaviours due to this part? I feel these questions are worth answering to persuade the reader that the model is advantageous and worth the great details..

- *We have added the following in the introduction section to briefly summarize the theory and few previous model studies that highlights the important of symbiotic fungi. This is also used to explain and motivate the organic nutrient uptake concept (closely linked with fungi module) in Coup-CNP: "The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with mycorrhizal fungi or root exudates (e.g. Schachtman et al., 1998, Gärdenäs et al. 2011, Richardson et al. 2005). However, in Orwin's model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored. Our model (Eckersten and Beier, 1998; He et al., 2018) also includes a nutrient-short-cut uptake as a process in the rhizosphere. The assumption is that nutrients released by biochemical mineralization are instantly taken up by the symbiotic microbes and/ or the plants, thereby by-passing the soil matrix solution."*
-

Detailed comments:

BeforeLine65-70, CMIP6 model results are openly available now. One model (probably the only one) that has land P component is from CSIRO, Australia. The name of the earth system model is ACCESS and land component is CABLECNP.

- *We have deleted this sentence but rephrased the sentence into the following to be precise "Nevertheless, the P cycle is seldom incorporated into ecosystem model* *structures. Incorporating the P cycle is essential in improving global models as a tool for assessment of climate-C cycling interactions"*

Lines70-75, whether CNP models from Goll et al., 2012; Wang et al., 2010; Yang et al., 2014 are simplified are context dependent. As far as I know, these models incorporated key processes in C, N, P, water and energy dynamics and take into account coupling and interactions across spatial-temporal scales. They are not necessarily simpler than the model presented here.

- *We have deleted the misleading word "simple", and also have added the missing references of the global vegetation models that have phosphorus cycle.*

Line 75-80. Models in Medlyn et al 2016 are not earth system models per se. They are process-based vegetation models. ESMs have coupled land, atmosphere, ocean etc. Some models might be used as the land component of some ESMs. Some models may not be directly coupled.

- *We will changed to "global vegetation model" to be precise.*

Line 80-85. Low eco2 response do not imply "In other words, the vegetation is rather inflexible to increase P uptake". There are many factors come into play. Without CNP, the models have difficulties in capturing nutrient limitation on CO2 response. In nutrient limited locations, nutrient limitation is likely to reduce eco2 responses. And it is not only about the uptake capability. It is also related to nutrient availability.

- *We have deleted the misleading statements and keep it as: "The CNP models that explicitly considered the P dependency of C assimilation predicted the lowest* eCO_2 *response".*

Line 140-150, "The main model structure is a one-dimensional, vertical layered soil profile including plants." This sentence is confusing. How vertical soil profile could include plants ?

- *We have rephrased this into "The main model structure is a one-dimensional, vertical model, with one or two layers of vegetation (for example a tree and field layer as in this application) on a multi-layered soil profile".*

Line 150-155, the concept of "big leaf" model assumes canopy carbon fluxes have the same relative responses to the environment as any single unshaded leaf in the upper canopy. You have two layers, trees and understory. Normally when people talk about "big leaf" model, it does not simulate light competition between up- vs. understory plants.

- *We have reworded this into "Multiple-big leaves" model concept, i.e. two vegetation layers, trees and understory plants was used.*

Line 170-171, the naming convention is quite confusing. By common definition, inorganic P is part of soil mineral P.

- *We have re-described the pools as "The soil inorganic P has new and renewed state variables. New is the soil solid inorganic* P_{solid}*, a lumped pool containing primary and secondary mineral compounds containing P such as apatite (and occluded P) (Smeck,* *1985; Wang et al., 2007). P_{ilab} is the sum of phosphate ions absorbed and those in soil solutions, analog to the mineral pool in salt tracer representation in CoupModel (Gärdenäs et al., 2006). Instantaneous equilibrium between adsorbed and soil solution are assumed. Plant and microbes take up phosphate ions from the P_{ilab}. P_{isol} can be compared with the sum of N state variables NH_4^+ and NO_3^- while being an intrinsic part of P_{ilab} (Fig. 1)."*

- *We have renamed the previous mineral P pool as "soil solid inorganic P_{solid}" in the entire paper to avoid confusion*

Line 180. The description of different P pools is rather confusing. If "soil mineral P is the total soil P without organic Po and labile P", how could you estimate it with total P content and bulk density. When we measure bulk density, we do not exclude the contribution from the organic matter.

- *We have revised the naming of the different P pools and clarified that we mean. Please also see response above. The calculation was given by using equ 2 and the content in Table 1.*

Line 180-185. What do you mean by "fresh plant residues"? If plant residue that stays above soil, but it is not fresh (e.g., it is from the last year), do you exclude it from litter?

- *We have redescribed the soil organic pools as: "Soil organic P is divided into three state variables by litter (P_{Litter}), humus (P_{Humus}), and dissolved organic (P_{DOP}) in every soil layer analog to C and N in CoupModel v2.0 (Fig. 1)".*

Line 180-185, "In CoupModel, soil litter could be further divided into two litter pools: one which contains readily decomposing materials (e.g., plant leaves and fine roots) and another for decomposition-resistant litter (e.g., stems and coarse roots)". If you do not represent these in your model, please skip these texts to reduce confusion.

- *We deleted this to reduce confusion.*

Line 190-195. Do you take into account the hysteresis in P adsorption/desorption?

- *No, we assume instant equilibrium between the labile and soluble P. We have described this assumption in section 2.2.2*

Line 170-205, you talked about litter pool, how do you treat soil organic matter/P pool? Do you only have humus pool? If so, non-symbiotic soil microbes are classified as litter in your model?

- *We have revised our definition of soil organic matter pools in section 2.2. "Soil organic P is divided into three state variables by litter (P_{Litter}), humus (P_{Humus}), and dissolved organic (P_{DOP}) in every soil layer analog to C and N in CoupModel v2.0 (Fig. 1). In this study, non-symbiosis microbes is included in the litter."*

Lines 210-215, "During certain seasons, plants can also capture mobile P (as well as mobile N) to prepare for rapid growth in the spring". What do you mean here? You mean plants take up more P in other seasons other than Spring, store it and use it in Spring? How does it occur? What do you mean by mobile P(N)?

- *The following section was added in A4 plant litterfall to describe the pool and assumption more clearly "During litterfall seasons, plants can reallocate P and N from leaves to an internal, mobile storage to prepare for rapid growth in the spring, a known mechanism to increase efficient use of nutrients (e.g. Aerts, 1996; Niemien and Helmisaari, 1996) (also see* m_{retain} *in Table S.1 in supplementary)".*
- *Note the* m_{retain} *is also included in the global sensitivity analysis and showed the modeled ecosystem C change is sensitive to this parameter in Table S.4*

Lines 220-225, I don't understand what do you mean by "In Coup-CNP, biochemical mineralization is defined as organic uptake". Biochemical mineralization and organic uptake are different processes.

- *We have added the following in the introduction section to explain the organic nutrient uptake concept better in Coup-CNP: "The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with mycorrhizal fungi or root exudates (e.g. Schachtman et al., 1998, Gärdenäs et al. 2011, Richardson et al. 2005). However, in Orwin's model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored. Our model (Eckersten and Beier, 1998; He et al., 2018) also includes a nutrient-short-cut uptake as a process in the rhizosphere. The assumption is that nutrients released by biochemical mineralization are instantly taken up by the symbiotic microbes and/ or the plants, thereby by-passing the soil matrix solution."*
- *The section 2.2.3 further describe the concepts and calculations as "Biochemical mineralization, on the other hand, describes the release of* P_i *through extracellular enzymatic releases (e.g., phosphatases by root exudates), which are driven by plant demand for nutrients (Richardson and Simpson, 2011). In Coup-CNP, biochemical mineralization is conceptually included in the nutrient short-cut uptake (called organic uptake in earlier CoupModel publications) and assumed to be driven by the unfulfilled plant P demand after* P_{ilab} *root uptake (equ A.8) but regulated by the availability (i.e. short-cut uptake coefficients in equ A.4)."*
- *Further, to avoid confusion with the uptake of organic molecules, we rename the organic P/N uptake into "short-cut P/N uptake" in the entire paper.*

Line 316, "wais" to "was"

- *Corrected.*

Line 535 – 540 and Figure 2. From Figure 2, the model systematically over-estimate Leaf C/P and leaf C/N ratio (except one site). Is it because an over-estimation of the leaf biomass? If there are coherent bias for all or most sites, it is not a neglectable issue. Figure 4. Why do you plot plant growth in C flux but change in plant for P flux, please be coherent and consistent. Table 6, systematically underestimation of P leaching

- *To avoid misunderstanding, we also added the following texts "Plant growth in a) represent the net primary production." in Fig.4 captions to explain the figure more in detail.*
- *We have now revised the datasets for model evaluation section 3.2 to describe the compared leaching data more in detail, and make it clear that the leaching data also contains P leaching from upstream more. The texts have been modified into following: "Thus, the measured P leaching also contains the P leaching from upstream. DOP were not measured for the regions. Thus the so call measured DOP was calculated as the difference between the measured total P and* PO_4*. This means the "measured DOP" may contain both our simulated fractions DOP and particular phosphorus."*
- *For model performance, see response above.*

Reply to editor comments

We thank editor for your positive comments and constructive suggestions to our manuscript. Here are our responses to the comments; The editor comments are in normal font and our response in italics.

Thanks for preparing a revised version of the manuscript addressing my previous comments. I will accept now the manuscript for publication in the discussion forum and formally start the peer review process. However, your answer to my question on the type of dynamic update, with your respective answer about coupled partial differential equations, suggests that your presentation of equations in the text is not adequate, and that you would have to rewrite many of the equations to make explicit the use of partial differential equations. You also would have to state more explicitly the boundary conditions and the initial conditions since these are factors that strongly influence the solution of the system of equations.
I accept the current version for the review process, but keep this comment in mind when preparing a revised version addressing reviewers' comments.

- *The equations in current paper is given in a form that reflects one time step and one of the layers that represent the entire soil profile. We think current forms have the advantage of being easier to follow. Therefore, we have added the following texts in the main texts at section 2.2 to describe the presentation of the equations, "For simplicity, the equations are given in a form that reflects one time step and one of the layers that represent the entire soil profile."*
- *We have further added texts to describe how CoupModel solve the partial differential equations in section 2.1 and give reference where more information is available as "They are numerically solved using an explicit forward difference model scheme (Euler integration, for more details see pp 400-401 in Jansson and Karlberg (2011)). Explicit forward difference model means that at current time step, the size of a state variable is updated with the fluxes to and from the state variable during previous time step."*
- *We have now added a separate sections of 3.4 Model forcing, initial and boundary conditions to describe these into more detail. The initial conditions for soil and plant and the boundary conditions for water and heat are all given, if not then refer to the previous studies.*

CoupModel (v6.0): an ecosystem model for coupled phosphorus, nitrogen, and carbon dynamics – evaluated against empirical data from a climatic and fertility gradient in Sweden

Hongxing He[1], Per-Erik Jansson[2], Annemieke I. Gärdenäs[1]
[1]Department of Biological and Environmental Sciences, University of Gothenburg, PO~~o~~ Box 460, Gothenburg 40530, Sweden
[2]Department of Land and Water Resources Engineering, Royal Institute of Technology (KTH), 100 44 Stockholm, Sweden
Correspondence to: Hongxing He (hongxing-he@hotmail.com)~~;~~ and Annemieke Gärdenäs (annemieke.gardenas@bioenv.gu.se)

Abstract

This study presents the integration of the phosphorus (P) cycle into CoupModel (Coup-CNP). The extended Coup-CNP, ~~(~~which explicitly consider symbiosis between soil microbes and plant roots,~~)~~ ~~which explicitly consider mycorrhizal interactions~~ enables simulations of coupled carbon (C), nitrogen (N) and P dynamics for terrestrial ecosystems ~~with an explicit consideration of symbiosis between soil microbes and plant roots~~ ~~which explicitly consider mycorrhizal interactions.~~ The model was evaluated against observed forest growth and measured leaf C/P, C/N and N/P ratios in four managed forest regions in Sweden. The four regions form a climatic and fertility gradient from 64°N in the North to 56°N in South Sweden with the mean annual temperature varying between 0.7-7.1 °C and the soil C/N and C/P ratios between 19.8-31.5 and 425-633, respectively. The growth of the southern forests was found to be P-limited, with harvested biomass representing the largest P loss over the studied rotation period. The simulated P budgets revealed that southern forests are losing P, while northern forests have their P budget in balance~~are close to in balance for P~~~~are close to a steady state in P availability~~~~close to in balance for P~~. Symbiotic~~Mycorrhizal~~ fungi account for half of the total plant P uptake across all four regions, which highlights the importance of fungal-tree interactions in Swedish forests. Sensitivity analysis results demonstrated that the highest forest

growth occurs at a soil N/P ratio of 15 to 20. A soil N/P ratio above 15-20 resulted in decreased soil C sequestration and~~ total~~ P leaching, but significantly increased N leaching. With the ~~The development and ~~evaluation of the new Coup-CNP model, we demonstrated that P fluxes need to be further considered in studies of how climate change can~~will ~~influence C turnover and ecosystem responses. We conclude that the ~~potential P limitation of terrestrial ecosystems highlights the need of a proper consideration of the P cycle in biogeochemical models. The~~ inclusion of the P cycle is necessary ~~in order ~~to make biogeochemical models more reliable tools for assessing long-term impacts of climate change and N deposition on C sequestration and nutrient~~N~~ leaching.

1 Introduction

Phosphorus (P) is an essential element for all photosynthesizing plants ~~life~~ in terrestrial ecosystems, with the P cycle coupled to Carbon (C) and Nitrogen (N) fluxes especially through ~~biochemical reactions such as ~~processes such as ~~photosynthesis ~~decomposition of soil organic matter and ~~and through~~ ~~soil~~ nutrient ~~availability~~uptake~~ cycling~~ ~~in terrestrial ecosystems ~~(Lang et al., 2016; Vitousek et al., 2010). A steep increase in the anthropogenic release of C and N to the atmosphere relative to P release has altered plant and soil nutrient stoichiometry, leading to new forcing conditions (Elser et al., 2007; Penuelas et al., 2013). For instance, numerous monitoring studies have revealed increasing N/P ratios in plants and soils, especially in forests from North America (Crowley et al., 2012; Gress et al., 2007; Tessier and Raynal, 2003) and Central and Northern Europe (Braun et al., 2010; Jonard et al., 2015; Talkner et al., 2015). Such trends are generally assumed to indicate that these ecosystems are shifting from being N limited to either co-limited by both N and P or P limited (Elser et al., 2007; Saito et al., 2008; Vitousek et al., 2010; Du et al. 2020). Human activities are expected to continue increasing the atmospheric N ~~inputs ~~deposition. ~~to~~~~from the atmosphere and,~~ A~~a~~s such~~,~~ P availability and its dynamics will become progressively more important in~~to~~ regulating the biogeochemistry of terrestrial ecosystems and amplifying feedback~~ mechanism~~s relevant to climate change, e.g. limiting the growth response of plants to increased temperature (Deng et al., 2017; Fleischer et al., 2019; Goll et al., 2017).

Nevertheless, the P cycle is seldom incorporated into ecosystem model structures. Incorporating the P cycle is essential in improving global models as a tool for assessment of climate-C cycling interactions (~~Flato et al., 2013; ~~Reed et al., 2015). ~~The few models that include a P module vary greatly with respect to scale, scope and ecosystem type. M~~Most of the process-based models that can simulate P cycling were specifically developed for agricultural systems and focus on the soil ~~ecosystem~~processes, e.g., EPIC (Jones et al., 1984, Gassman et al., 2005), ANIMO (~~Groenendijk and Kroes, 1999/~~ Groenendijk et al., 2005), and GLEAMS (Knisel and Turtola, 2000). A few catchment-scale models ~~that~~ focus on surface water quality, e.g. SWAT (Arnold et al., 2012), HYPE (Arheimer et al., 2012), and INCA-P (Jackson-Blake et al., 2016)~~, aim to simulate how crop management influences P leaching and thus, consider processes such as nutrient retention, leaching, and transport~~. However, none of these models explicitly consider dynamics of plant litter inputs, nutrient mineralization, or how nutrient uptake may ~~echanisms~~ influence photosynthesis. ~~Until recently, global vegetation models that were integrated into Earth System Models (ESMs) largely ignored carbon-phosphorus cycle interactions, e.g. only one model of present Coupled Model Intercomparison Project (CMIP 56) ESMs do not include the P cycle (Flato Eyring et al., 20163).~~ However, the C response to P limitation has recently been studied through several empirical and field studies (Van Sundert et al., 2019; Du et al., 2020). For example, Van Sundert et al. (2019) showed that ~~there is a strong correlation between~~ the productivity of European beech (*Fagus sylvestris*) forests ~~and~~ is negatively related to the soil organic carbon concentrations and mineral C/P ratios. A few global vegetation models have ~~started to~~ included a ~~simplified~~ P cycle to study how it affects the C cycle (Goll et al., 2012, 2017; Wang et al., 2010; Yang et al., 2014; Zhu et al., 2016; Thum et al., 2019). ~~However, t~~These P enabled models differ in how they describe soil P dynamics (implicitly or explicitly of symbiotic mycorrhiza and other soil microbes), plant P use and acquisition strategies, which results in considerable uncertainty in the C response (Fleischer et al., 2019; Medlyn et al., 2016; Reed et al., 2015~~; Zaehle et al., 2014~~). Medlyn et al. (2016) applied six ~~ESMs~~ global vegetation models including two coupled Carbon-Nitrogen-Phosphorus (CNP) models (CABLE and CLM4.0-CNP) to study the response to elevated CO_2 (eCO_2) of the C cycle of the Eucalyptus-Free-Air CO_2 Enrichment experiment and found large variations, ranging from 0.5 to 25%, in predicted net primary productivity. The CNP models that explicitly considered the ~~how~~ P dependency of C assimilation~~can limit photosynthesis~~ predicted the lowest eCO_2 response. ~~The P cycle is assumed to be relatively closed, meaning that the input (i.e. deposition and weathering) and output (i.e. leaching) fluxes are small. In other words, the vegetation is rather inflexible to increase P uptake.~~ Yu et al. (2018) ~~developed~~ included the P cycle into the field-scale biogeochemical model – ForSAFE and applied the model to study the P budget of a southern Swedish Spruce forest site. They concluded that the P supply by weathering ~~total P flow into the forest~~ was small compared to the internal turnover by~~. Plant P uptake was attributed more to~~ mineralization of soil organic matter~~ than the weathering of minerals~~. Fleischer et al. (2019) demonstrated that four CNP models, when applied to the Amazon forest, provide up to 50% lower estimates of the eCO_2-induced biomass increment than the 10 coupled C-N models. They ~~attributed these variations to the contrasting plant P use and acquisition strategies considered in the models, and~~ suggested that the inclusion of flexible tissue stoichiometry and enhanced plant P acquisition could improve C-P cycle coupling in terrestrial ecosystem models.

Most terrestrial plants live in symbiosis with mycorrhizal fungi to increase uptake capacity of P, among other nutrients (Smith and Read, 2008). Several studies have shown that the depletion zone around plant roots, which is caused by plant uptake and the immobile nature of mineral P, increases when a plant interacts with mycorrhizal fungi (Bolan, 1991; Schnepf and Roose, 2006; Smith, 2003). ~~It is also well known that mycorrhizal fungi acquire P from organic sources that are not directly available to the plant roots, e.g., phytic acid and nucleic acids (Schachtman et al., 1998).~~ Global meta-analysis studies highlighted that ~~interaction between~~ symbiosis between plants and ~~with~~ soil mycorrhizal fungi strongly influences ~~how~~ plant P availability that further affects plant growth (Terrer et al., 2016; ~~Terrer et al.,~~ 2019). Previous research showed that mycorrhizal fungi can receive between 1 and 25% of the plants' photosynthates and constitute as much as 70% of the total soil microbial biomass; this symbiont thus has a major impact on soil C sequestration (Averill et al., 2014; Clemmensen et al., 2013; Staddon et al., 2003). Even though there is a well-established link between mycorrhizal fungi and plant P nutrition (Bucher, 2007; Read and Perez-Moreno, 2003; Rosling et al., 2016), this factor is seldom included in ecosystem models (Smith and Read, 2008). To the best of our knowledge, only Orwin et al. (2011) have presented an ecosystem model ~~of how~~that consider C, N and P together with symbiotic~~mycorrhizal~~ fungi ~~influence soil C dynamics that considers both N and P~~. They found that considering organic nutrient uptake by symbiotic~~mycorrhizal~~ fungi in an ecosystem model can significantly increase soil C storage, with this effect more pronounced under nutrient-limited conditions. The organic nutrient uptake in their model was to mimic the additional pathway that plant can utilize organic nutrients by biochemical mineralization either in symbiosis with -mycorrhizal fungi or root exedutes ~~acquire P from organic sources that are not directly available to the plant roots, e.g., phytic acid and nucleic acids~~ (e.g. Schachtman et al., 1998, Gärdenäs et al. 2011, Richardson et al. 2005). However, in Orwin's model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored. ~~*There are some empirical studies (e.g. Jayachandran et al. 1992; Fox et al. 2010) that show mycorrhizal fungi may be able to acquire P from organic sources that are not available directly to the plant (e.g. phytic acid and nucleic acids). Also see, Lindahl et al. () and Johnson and Gehring (2007).*~~ Our model (Eckersten and Beier, 1998; He et al., 2018) also includes a nutrient-short-cut uptake as a process in the rhizosphere. The assumption is that nutrients released by biochemical mineralization are instantly taken up by the symbiotic microbes and/or the plants, thereby by-passing the soil matrix solution~~us (Eckersten and Beier, 1998; He et al., 2018).~~ ~~However,~~ in ~~in this model, plant growth was static; thus plant-soil or plant-environment interactions were largely ignored.~~ He et al. (2018) integrated the MYCOFON model (Meyer et al., 2009) into CoupModel v5 to ensure that symbiosis between plant roots and mycorrhiza~~l interactions~~ would be sufficiently considered, and compared the results with a previous implicit representation of N uptake in forest ecosystems with limited N availability. CoupModel v5 assumes that carbohydrates provided by plants are the primary driver of mycorrhizal responses to N availability, and that fungal uptake of N will influence host plant photosynthesis. We argued that terrestrial ecosystem models which explicitly consider mycorrhizal interactions should also take into account P cycling, especially due to the significant role of symbiont mycorrhiza for P uptake in P-limited environments and thus, developed a new version of CoupModel that includes the P cycle.

The overall objective of this study was to improve the current understanding of C, N and P cycle interactions in forest ecosystems by presenting a new scheme for modelling P dynamics. More specifically, the study had the following aims: 1) to present the new CoupModel v6.0 that explicitly includes the P cycle and interactions between the N and P cycles; 2) to estimate the regional C, N, and P budgets of Swedish forests along a climatic and fertility gradient; and 3) to demonstrate how soil N and P availability influence growth, soil C and nutrient leaching. For this reason, we present a new version of CoupModel (v6.0), hereafter referred to as Coup-CNP, which explicitly simulates the P cycle. The key features of the new Coup-CNP model are: 1) coupled C, N, and P dynamics; 2) explicit symbiosis between plant roots and mycorrhizal, and implicit non-symbiotic microbes~~plant-mycorrhizal~~ representations ~~–~~to describe N and P uptake from the soil; 3) flexible CNP stoichiometry for plant components, soil organic matter~~s~~, and symbiosing~~mycorrhizal~~ microbes~~fungi~~; 4) dynamic nutrient demand and uptake, photosynthesis and growth rates regulated by N and P availability; and 5) simultaneous uptake of nutrients to roots or symbiosing mycorrhizae from both ~~organic and~~x inorganic and organic (nutrient short-cut) pools. The Coup-CNP model was evaluated using four forest regions situated along a climatic and fertility gradient in Sweden that has earlier been considered by He et al. (2018) and Svensson et al. (2008).

2 Description of m~~M~~odel structure and ~~description of~~ phosphorus model ~~processes description linked to the phosphorus pool~~

2.1 Brief description of CoupModel (v5)

The CoupModel platform (coupled heat and mass transfer model for soil–plant–atmosphere systems) is a ~~flexible~~ process-based model designed to simulate water and heat fluxes, along with C and N cycles, in terrestrial ecosystems (Jansson, 2012). The main model structure is a one-dimensional, vertical model, with one or two layers of vegetation (for example a tree and field layer as in this application) on ~~vertical~~ a multi-layered soil profile~~, commonly 10 soil layers when using daily time steps.~~ ~~including plants~~. The core of the model consists of five sets of coupled partial differential equations, one for ~~each of~~ water, heat, C, N, and P ~~fluxes~~ cycles (the later one in v6.0), respectively. They are numerically solved using an explicit forward difference model scheme (Euler integration, for more details see pp 400-401 in Jansson and Karlberg (2011)). Explicit forward difference model means that at current time step, the size of a state variable is updated with the fluxes to and from the state variable during previous time step. In this application, we used a daily ~~default common~~ time step for all five, but a smaller time step was applied for the water and heat calculations during specific events with peaks in water and/or heat flow such as during snow melting ~~crucial~~ to ensure the numerical stability and accuracy. The model is driven by climatic data – precipitation, air temperature, relative humidity, wind speed, and global, i.e. sum of direct and diffuse short-wave incoming radiation – and can simulate ecosystem dynamics with daily resolution. Vegetation is described using the “multiple-big leaves~~f~~” concept, i.e. two vegetation layers, trees and understory plants, are simulated taking into account mutual competition for light interception, water uptake and soil N (Jansson and Karlberg, 2011). The model and technical description (Jansson and Karlberg (2011) is freely available at www.coupmodel.com. A presentation of CoupModel use, calibration and validation is given in Jansson (2012).~~A general structural and technical overview of the CoupModel can be found in Jansson and Karlberg (2011) and Jansson (2012)~~. He et al. (2018) introduced an explicit plant-mycorrhizal representation ~~scheme into~~ (CoupModel v5).

2.2 Phosphorus cycle representation in CoupModel (v6.0)

CoupModel (v6.0), hereafter called Coup-CNP, was extended with P cycle representation to enable simulations of coupled C, N and P dynamics for terrestrial ecosystems with an explicit consideration of symbiosis between soil microbes and plant roots.~~This study describes the inclusion of the P cycle in the CoupModel, resulting in v6.0~~. ~~In~~ Coup-CNP has P state variables and fluxes representing different plant parts, symbiotic microbes, soil organic P forms (P_o, P that is bound to organic C in the soil) and soil inorganic P, P_i, forms (Figure 1). For clarity of the coupling between C, N and P cycles, also the C and N state variables and major N and N+P fluxes are given in Figure 1.

P in the plants is partitioned into grain, leaf, stem, coarse root, fine root, and P in symbiotic microbes, analog as for C and N in CoupModel v5.0 (Fig. 1). In this paper, we use mycorrhizal fungi as the role model of plant-microbe symbiosis, the same concept is also applicable for other symbiosis microbes. Soil organic P is divided into three state variables by litter (P_{Litter}), humus (P_{Humus}), and dissolved organic (P_{DOP}) in every soil layer analog to C and N in CoupModel v~~x~~2.0 (Fig. 1). In this study, non-symbiosis microbes is included in litter. The soil inorganic P has new and renewed state variables. New is the soil solid inorganic P_{solid}, a lumped pool containing primary and secondary mineral compounds containing P such as apatite (and occluded P) (Smeck, 1985; Wang et al., 2007). P_{ilab} is the sum of phosphate ions absorbed and those in soil solutions, analog to the mineral pool in salt tracer representation in CoupModel (Gärdenäs et al. 2006). Instantaneous equilibrium between adsorbed and soil solution are assumed. Plant and microbes take up phosphate ions from the P_{ilab}. P_{isol} can be compared with the sum of N state variables NH_4^+ and NO_3^- while being an intrinsic part of P_{ilab} (Fig 1.)

~~Coup-CNP, soil phosphorus is conceptually divided into inorganic P (P_i, phosphate ions, e.g., H_3PO_4, $H_2PO_4^-$, HPO_4^{2-}, PO_4^{3-}), soil solid mineral P (P_m) and soil organic P (P_o, P that is bound to organic C). Overall, three inorganic P pools (soluble (P_{isol}), labile (P_{ilab}), and soil mineral (P_m)) and three organic P pools (litter ($P_{olitLitter}$), humus ($P_{ohumHumus}$), and dissolved organic (P_{dop})) are used to represent the soil P (Fig. 1). The labile P_{ilab} defines the available P_i for plants including the readily P_i exchanges with soil solutions, P_{isol}. Soluble pool (P_{isol}) is thus a part of labile pool (P_{ilab}) that are dissolved and not adsorbed. The soil solid mineral P_m is defined as the total soil P without organic P_o and labile P_{ilab} (Hedley and Stewart, 1982). Thus, soil solid mineral P_m is a lumped pool containing primary and secondary mineral compounds containing P such as apatite (and occluded P) (Smeck, 1985; Wang et al., 2007). The three organic P pools follow the division of the C and N cycles as that in Svensson et al. (2008). Soil litter consists of plant residues (both current year and years before) and non-symbiotic microbes, while humus is the organic residue from litter decomposition. A fraction of the P_o in the $P_{olitLitter}$ and $P_{ohumHumus}$ pools may also form the dissolved P_{dop} (Fig. 1).~~

~~P in the plants is partitioned into grain, leaf, stem, coarse root, fine root and symbiotic microbe pools, similarly as C and N (Fig. 1). In this paper, we use mycorrhizal fungi as the role model of plant-microbe symbiosis, the same concept is also applicable for other symbiosis microbes.~~

~~The mycorrhiza describes a symbiotic association between fungus and the plants' fine roots: as such, it consists of C, N, and P pools that are separate from those of the plant. The mycorrhiza is further distinguished into the mycelia, which is responsible for N and P uptake (both in inorganic forms and nutrient short-cut from organic pools), and the fungal mantle, which covers the fine-root tips (He et al., 2018). Through plant litterfall, P is recycled and released back into the soil through mineralization. During litterfall seasons, plants can also capture mobile P (as well as mobile N) to prepare for rapid growth in the spring (also see m_{retain} in Table S.1 in supplementary). The mobile P pool (not shown in Fig. 1) act as an internal storage in the plant. Coup-CNP use the mobile pool to mimic the nutrient reallocation or retranslocation process, a known mechanism to reduce dependence on nutrient uptake and increase nutrient recycle (e.g. Aerts, 1996; Niemien and Helmisaari, 1996).~~

-We developed the P model in a way that 1) focus~~concentrates~~ on the key P ~~processes that are most relevant~~ processes for biogeochemical cycling~~assessmentsdynamics~~, e.g., dynamic plant growth and P leaching, and 2) follows the conceptual structure of CoupModel as closely as possible. The key P processes are described in detail below. In appendix A are described processes that are analogous to those of the N cycle, e.g., atmospheric deposition, fertilization (A.1), mineralization-immobilization (A.2), plant growth and uptake (A.3), litterfall (A.4), leaching and surface runoff (A.5), and removal of plant harvest (A.6). ~~The P model runs at the same time step as the models for C and N cycles, which can differ from the time step of the models for water and heat~~. ~~The discretization of the soil includes common compartments thatfor P are linked follows that of to all elements C and N and abiotic conditions.~~ For simplicity, the equations are given in a form that reflects one time step and ~~For simplicity, the following description of the model concerns~~ one of the layers that represent the entire soil profile. The symbols in this paper were designed to conform the CoupModel nomenclature in the following way: uppercase P means state variables, lowercase p means parameters related in P processes. ~~Processes that are analogous to those of the N cycle, e.g., atmospheric deposition, fertilization (A.1), mineralization-immobilization (A.2), plant growth and uptake (A.3), litterfall (A.4), leaching and surface runoff (A.5), and removal of plant harvest (A.6), are detailed described in Appendix A. For simplicity, the equations are given in a form that represent one time step for each soil layer.~~

~~2.2.1 Inorganic and organic soil phosphorus~~

~~Soil phosphorus can be divided into inorganic P (P_i, phosphate ions, e.g., H_3PO_4, $H_2PO_4^-$, HPO_4^{2-}, PO_4^{3-}), soil mineral P (P_m) and soil organic P (P_o, P that is bound to organic C). Overall, three inorganic P pools (soluble (P_{isol}), labile (P_{ilab}), and soil mineral (P_m)) and three organic P pools (litter (P_{olit}), humus (P_{ohum}), and dissolved organic (P_{dop})) are used to represent the soil P (Fig. 1). In Coup-CNP, the soil inorganic phosphorus pools are defined according to the classic Hedley fractionation method (Hedley and Steward, 1982), in which labile P_{ilab} determines the available P_i for plants including the readily P_i exchanges with soil solutions, P_{isol}. The soil mineral P_m is defined as the total soil P without organic P_o and labile P_{ilab} (Hedley and Stewart, 1982). Thus, soil mineral P_m is a lumped pool containing primary and secondary mineral P compounds containing P such as apatite (and occluded P) (Smeck, 1985; Wang et al., 2007), and can be estimated using total P content and bulk density data. The three organic P pools follow the division of the C and N cycles. Soil litter consists of fresh plant residues and non-symbiotic microbes while humus is the organic residue from litter decomposition. In CoupModel, soil litter could be further divided into two litter pools: one which contains readily decomposing materials (e.g., plant leaves and fine roots) and another for decomposition-resistant litter (e.g., stems and coarse roots). For simplicity, only one soil litter pool was used in this study.~~

~~Soil mineral P_m, which mostly exists in the form of apatite, may be transformed into labile P_{ilab} through the weathering process (Fig. 1). Part of the P_{ilab} pool would quickly be adsorbed by soil water and colloids (Buendía et al., 2010; Stewart and Tiessen, 1987). These P_i ions are normally loosely adsorbed to surfaces and can thus easily re-enter the P_{ilab} pool through the desorption process (McGechan and Lewis, 2002). The adsorption/desorption of P_i in the P_{ilab} pool is thus modelled as a continuum of fast reversible exchange reactions of the phosphate groups with water or hydroxyl groups (Bünemann, 2015). Both Cole et al. (1977) and Olander and Vitousek (2005) showed that when P is added to a soil ecosystem, the soluble (P_{isol}) and labile (P_{ilab}) P pools reach equilibrium in less than 1 hour. As the CoupModel provides daily resolution, we can assume that the P_{isol} and P_{ilab} pools are always in equilibrium (Barrow, 1979). In our model, the slow P_i diffusion process into the soil matrix (e.g. adsorption/desorption to the secondary minerals) is implicitly included in the weathering flux.~~

~~If mineral P_i fertilizer is applied at the soil surface, the P_i first enters an undissolved fertilizer pool, after which P_i from this pool gradually dissolves into the labile P pool following a decay-type function. P could also be added as an external organic substrate (faeces or manure). In this~~

~~case, P moves from the surface faeces (P_{ofae}), litter ($P_{olitLitter}$), and labile (P_{ilab}) P pools according to the composition of the manure. Atmospheric P deposition is assumed to directly flow to the P_{ilab} pool in the uppermost soil layer. P_i in the P_{isol} pool can be transported by water flows between layers or from a layer to a drainage outlet. The soil surface layer may also lose mineral P_m by erosion, which is driven by surface runoff.~~

~~2.2.2 Phosphorus fluxes in plant and symbiotic fungi~~

~~Plants take up P_i from the P_{ilab} pool through roots and symbiotic microbe association and then partition the P_i into grain, leaf, stem, coarse root, fine root and symbiotic microbe pools (Fig. 1). In this paper, we use mycorrhizal fungi as the role model of plant-microbe symbiosis, the same concept is also applicable for other symbiosis microbes. Through plant litterfall, P is recycled and released back into the soil through mineralization. During certain seasons, plants can also capture mobile P (as well as mobile N) to prepare for rapid growth in the spring. This will increase the litter C/P and C/N ratios, respectively. In the Coup-CNP, P mineralization is conceptually divided into biological and biochemical mineralization following McGill and Cole (1981). Biological mineralization, which is regulated by temperature and moisture, represents microbe-mediated oxidation of organic matter, during which nutrients (P and N) are immobilized by implicit non-symbiotic microbes or transferred from litter to humus (Fig. 1). Biochemical mineralization, on the other hand, describes the release of P_i through extracellular enzymatic processes (e.g., phosphatases), which are driven by plant demand for nutrients (Richardson and Simpson, 2011). In Coup-CNP, biochemical mineralization is defined as organic uptake and assumed to be driven by the unfulfilled plant P demand after P_{ilab} root uptake. The assumption is that plant roots and symbiotic fungi bypass the P_{ilab} pool, and obtain mineralized P_i directly from the $P_{olitLitter}$ and $P_{ohumHumus}$ pools (Fig. 1). A fraction of the P_o in the $P_{olitLitter}$ and $P_{ohumHumus}$ pools may also form P_{dop}. This reaction has the same kinetics as having been observed for the C and N cycles (DOC, DON). The dissolved organics are characterized by a mobile and an immobile fraction, and thus, can be redistributed between layers. In addition to harvest, P could leave the ecosystem through leaching of P_{isol} and DOP (Fig. 1).~~

~~3 Model descriptions Equations describing key phosphorus processes/fluxes and their parameterization~~

~~The following section outlines the processes that are specific to the P cycle. Processes that are analogous to those of the N cycle, e.g., atmospheric deposition, fertilization, mineralization~~

~~immobilization, plant growth and uptake, litterfall, leaching and surface runoff and removal of plant harvest, are detailed described in Appendix A. At current time step, the size of the state variables are updated with from previous time step~~~~or processes at each time step with the pool size of C, N and P at one time step earlier.~~ ~~The pool size are then iterated with the inflow and outflow fluxes.~~

~~3~~2.~~1~~2.1 Weathering

~~During weathering, P_i is released from minerals through the dissolution of apatite ($Ca_5(PO_4)_3(F/Cl/OH)$) depending on the soil acidity. Organic acid exudates from plant roots also contribute to the release of P_i (Schlesinger, 1997). In our model,~~ By weathering s~~S~~oil solid mineral P_{solid}~~$_m$~~~~,~~ is~~may be~~ transformed into labile P_{ilab}~~.~~ ~~through the weathering process~~ (Fig. 1; equ 1). ~~In our model, the slow P_i adsorption process into the soil matrix (e.g. adsorption/desorption to the secondary minerals) is implicitly included in the weathering flux. the weathering process is modelled as a dissolution reaction (Brantley et al., 2008; Lasaga, 1998) in which the reaction rate at a given temperature is proportional exponentiallyproportional to the pH response of the soil water solution (Guidry and Machenzie, 2000).~~ The weathering rate depends on soil pH and temperature (Guidry and Machenzie, 2000) and is calculated as,

$$P_{solid\rightarrow ilab} = k_w \times f(T) \times f(pH) \times P_{solid} \qquad (1)$$

Where P_{solid}~~$_m$~~$_{\rightarrow ilab}$ is the flux rate of weathering ($g\ P\ m^{-2}\ day^{-1}$), k_w is a first-order integrated weathering rate coefficient (day^{-1}) which depends on lithology, rates of physical erosion and soil properties (Table 3), the erosion affect the weathering rate by reducing the pool size of P_{solid} (equ A.14). f~~$_w($~~(T_s) and f~~$_w$~~(pH) are response functions of soil temperature, T_s, and soil pH, P_{solid}~~$_m$~~ is the size of the P_{solid}~~$_m$~~ pool ($g\ P\ m^{-2}$), determined by,

$$P_{solid} = \delta_P \times \rho_{bulk} \times \Delta z_{layer} \times 10^6 \qquad (2)$$

Where δ_P is the prescribed ~~P_m~~-P_{solid} content for each soil layer ($g\ P\ g\ dry\ soil^{-1}$), with reported ranges from ~~0.1~~10^{-4} to 1.5×10^{-3} $g\ P\ g\ soil^{-1}$ (Yang et al., 2014), ρ_{bulk} is the dry bulk density for each soil layer ($g\ cm^{-3}$), and Δz_{layer} is the thickness of the simulated soil layer (m).

The temperature effect can~~could~~ be expressed as an Arrhenius function (3), where $E_{a,wea}$ is the activation energy parameter ($J\ mol^{-1}$) for minerals (i.e., apatite), available from empirical studies, R is the gas constant ($J\ K^{-1}\ mol^{-1}$), T_s is the simulated soil temperature in ºC, $T_{s,0}$ is a parameter (ºC) which normalize the function f~~$_w$~~(T_s)=1 and $T_{abszero}$ is -273.15 ºC.

$$f\left(T\right)=e^{\left(-\frac{E_{a,wea}}{R}\times\left(\frac{1}{T_s+T_{abszero}}-\frac{1}{T_{s,0}+T_{abszero}}\right)\right)} \tag{3}$$

Alternatively, the existing Ratkowsky function, O'Neill function or Q_{10} method can be used to determine the temperature response in CoupModel.

The effect of soil pH on weathering can be calculated through (equ 4), where n_H is a parameter that describes the sensitivity soil pH when it differs from an optimal value pH_{opt} for weathering (Table 3).

$$f(pH)=10^{n_H\times\left|pH_{opt}-pH\right|} \tag{4}$$

~~3~~2.2.2 Inorganic soluble phosphorus dynamics

~~The sizes of the P_{isol} and P_{ilab} pools are largely determined by chemical soil properties, e.g., anion exchange capacity and pH. The dynamics of these pools are regulated by physiochemical, e.g., adsorption/desorption, as well as biochemical processes, e.g., mineralization/immobilization. Part of the P_{ilab} pool would quickly be adsorbed by soil water and colloids (Buendía et al., 2010; Stewart and Tiessen, 1987). These P_i ions are normally loosely adsorbed to surfaces and can thus easily re-enter the P_{ilab} pool through the desorption process (McGechan and Lewis, 2002). Both Cole et al. (1977) and Olander and Vitousek (2005) showed that when~~ When P is added to a soil ecosystem, the soluble (P_{isol}) and adsorbed ~~labile (P_{ilab})~~ P ~~pools~~ reach equilibrium in less than 1 hour (Cole et al. (1977), Olander and Vitousek 2005). ~~As the CoupModel provides daily resolution, w~~We assume that the P_{isol} and adsorbed part of P_{ilab} ~~P_{ilab} pools~~ are always in equilibrium as daily timestep is used (equ 5). ~~(Barrow, 1979). The relationship between the P_{isol} and P_{ilab} pools is normally represented by empirical equations, i.e., Freundlich and Langmuir isotherms (McGechan and Lewis, 2002). In this study, t~~The modified Langmuir isotherm (Barrow, 1979) was used to model the fast and reversible sorption process within P_{ilab}.

$$P_{ilab,con}=p_{\max,ads}\times\frac{P_{isol}}{c_{50,ads}+P_{isol}} \tag{5}$$

Where $P_{ilab,con}$ is the concentration of labile pool (g P g soil^{-1}) calculated similarly by equation (2) as $P_{ilab,con}=P_{ilab}/(\rho_{bulk}\times\Delta z_{layer}\times 10^6)$ ~~calculated by using equation (2) with P_{ilab} (g P m^{-2}), ρ_{bulk} (g cm^{-3}) and Δz_{layer} (m)~~, $p_{max,ads}$ is the maximum sorption capacity of the labile pool (g P g soil^{-1}), and $c_{50,ads}$ is an empirical parameter corresponding to 50% of P saturation (g P m^{-2}) (Table 3).

2.2.3 Soil inorganic phosphorus dynamics and nutrient short-cut uptake

Atmospheric P deposition is assumed to directly flow to the P_{ilab} pool in the uppermost soil layer (equ A.1 in Appendix A). If mineral P_i fertilizer is applied at the soil surface, the P_i first enters an undissolved fertilizer pool, after which P_i from this pool gradually dissolves into the labile P pool following a decay-type function (equ A.1). P could also be added as an external organic substrate (faeces or manure). In this case, P moves to the surface faeces (P_{ofae}), litter ($P_{\cancel{olit}Litter}$), and labile (P_{ilab}) P pools according to the composition of the manure. P_i in the P_{isol} pool and dissolved organic $P_{\cancel{dop}DOP}$ can be transported by water flows between layers or from a layer to a drainage outlet (equ A. 12-13). The soil surface layer may also lose solid mineral P_{solid} by erosion, which is driven by surface runoff (equ A.14).

P mineralization is conceptually divided into biological and biochemical mineralization (equ A.2-A.6) following McGill and Cole (1981). Biological mineralization, which is regulated by temperature and moisture, represents microbe-mediated oxidation of organic matter, during which nutrients (P and N) are immobilized by implicit non-symbiotic microbes or transferred from litter to humus (Fig. 1; equ A.2). Biochemical mineralization, on the other hand, describes the release of P_i through extracellular enzymatic releases (e.g., phosphatases by root exudates), which are driven by plant demand for nutrients (Richardson and Simpson, 2011). In Coup-CNP, biochemical mineralization is conceptually included in the nutrient short-cut uptake (called organic uptake in earlier CoupModel publications~~literature~~) and assumed to be driven by the unfulfilled plant P demand after P_{ilab} root uptake (equ A.8) but regulated by the availability (equ A.4). The assumption is that under P limited conditions, plant roots and symbiotic fungi bypass the P_{ilab} pool, and obtain mineralized P_i directly from the organic $P_{\cancel{olit}Litter}$ and $P_{\cancel{ohum}Humus}$ pools (Fig. 1; equ A.4).

~~3~~2.2.4~~3~~ Plant growth under phosphorus and nitrogen limitation~~stress~~

Plant photosynthesis is modelled by a "light use efficiency" approach (Monteith, 1965, equ 6)). We adopted Liebig's law of minimum to simulate the effects of multiple nutrient stress on plant growth (Liebig, 1840)). This approach assumes that the nutrient (N, P) which has a the smallest~~smaller~~ supply relative to the corresponding plant demand will limit growth (equ. 7). ~~Plant demand was estimated through defined optimum ratios (equ A.9).~~

$$C_{a\rightarrow plant} = \varepsilon_L \times f(T_{leaf}) \times f(nutrient) \times f(\frac{E_{ta}}{E_{tp}}) \times R_S \qquad (6)$$

$$f\left(nutrient\right) = min\ \left(f\left(C/N_{leaf}\right); f\left(C/P_{leaf}\right)\right) \qquad (7)$$

Where $C_{a\rightarrow plant}$ is the plant carbon assimilation rate (g C m^{-2} day^{-1}), ε_L is the coefficient for radiation use efficiency (g C J^{-1}), $f(T_{leaf})$, $f(nutrient)$ and $f(E_{ta}/E_{tp})$ are response functions of leaf temperature, leaf nutrient status (N_{leaf}, P_{leaf}) in proportion to its C content, and water, respectively, and R_s represents radiation absorbed by the canopy (J m^{-2} day^{-1}). Details concerning $f(T_{leaf})$, $f(E_{ta}/E_{tp})$, as well as growth and maintenance respiration, can be found in Jansson and Karlberg (2011). Plant demand was estimated through defined optimum ratios (equ A.9). The nutrient response function $f(nutrient)$ which includes P is described below.

As is the case with N, the photosynthesis process responds to the leaf C/P ratio was modelled according to the work of Ingestad and Ågren (1992). Hence, below an optimum C/P ratio ($p_{CP,opt}$), ~~the~~ photosynthesis is not limited by P, while between $p_{CP,opt}$ and $p_{CP,th}$ the response function decrease as a linear function from one to zero,

$$f(C/P_{leaf}) = \begin{cases} 1 & C/P_{leaf} < p_{CP,opt} \\ 1 + (\dfrac{C/P_{leaf} - p_{CP,opt}}{p_{CP,opt} - p_{CP,th}}) & p_{CP,th} \le C/P_{leaf} \ge p_{CP,opt} \\ 0 & C/P_{leaf} > p_{CP,th} \end{cases} \qquad (8)$$

Where C/P_{leaf} is the actual leaf C/P ratio and $p_{CP,opt}$ and $p_{CP,th}$ are parameters that vary between plant species (Table 3). The leaf C/P ratio is calculated at each time step with the leaf state variables ~~pool sizes of~~ C and P. ~~The pool sizes are iterated with the inflow and outflow fluxes.~~

~~3~~2.2.~~5~~4 Symbiotic mycorrhizal fungi growth and phosphorus dynamics

~~The mycorrhiza describes a symbiotic association between fungus and the plants' fine roots: as such, it consists of C, N, and P pools that are separate from those of the plant. The mycorrhiza is further distinguished into the mycelia, which is responsible for N and P uptake (both in inorganic and organic forms), and the fungal mantle, which covers the fine-root tips (He et al., 2018).~~

The following described the fungal processes that are specific to P~~ (P processes analog to N processes (He et al., 2018) are found in appendix Ax)~~. Plant C allocation to mycorrhizal fungi is influenced by soil P_i concentrations. We thus introduce a response function $f_{a\rightarrow fungi}(P_i)$ to account for reductions in plant C allocation to mycorrhizal fungi when soil P_i concentrations are high ~~analog~~ analog to the N response function in He et al. (2018)~~ but with different coefficients and drivers~~,

$$f_{a\rightarrow fungi}(P_i) = e^{(-p_{avail} \times P_{isol}^2)^3} \qquad (9)$$

Where P_{isol} is the total soluble P_i in the soil (g P m^{-2}) (equ 5), and p_{avail} is a reduction parameter (m^4 g^{-2} P) (Table 3). According to Bahr et al., (2015), mycorrhizal fungi biomass decreases already when either N or P wa~~i~~s added, but most significantly when both N and P were added. These multiple responses were integrated into the model so that potential fungal growth would decline as a result of either increasing soil N or P.

$$C_{a\rightarrow fungi,\max} = C_{a\rightarrow root} \times p_{fmax} \times (f_{a\rightarrow fungi}(P_i) \times f_{a\rightarrow fungi}(N)) \qquad (10)$$

Where $C_{a\rightarrow fungi,max}$ is the defined maximum C flow that plants allocate to fungi (g C m^{-2} day^{-1}), $C_{a\rightarrow root}$ is the total C allocated to both root and mycorrhiza (g C m^{-2} day^{-1}) (equ A.10), p_{fmax} is a parameter that defines the maximum C fraction allocated to mycorrhiza from the total root and mycorrhiza C pool (Table 3), and $f_{a\rightarrow fungi}(P_i)$ and $f_{a\rightarrow fungi}(N)$ are response functions which regulate maximum mycorrhizal fungi growth due to soil N and P availability (equ 9). The actual growth of mycorrhizal fungi, $C_{a\rightarrow fungi}$ (g C m^{-2} day^{-1}), is limited by the defined maximum growth, $C_{a\rightarrow fungi,max}$ (equ 10) calculated as,

$$C_{a\rightarrow fungi} = \min\left\{\left[((C_{root} \times p_{fopt}) - C_{fungi}) \times \min(f(N_{\text{supply}}); f(P_{\text{supply}}))\right]; C_{a\rightarrow fungi,\max}\right\} \qquad (11)$$

Where C_{root} is the total root C content (g C m^{-2}), p_{fopt} is the defined optimum ratio parameter between fungi and root C content (Table 3), C_{fungi} is the total C content of fungi (g C m^{-2}), and $f(N_{supply})$ and $f(P_{supply})$ are response functions of fungal growth to the amount of N and P (both mineral and organic N) which are transferred from fungi to plant (equ 12). In this way, mycorrhizal fungi growth is also influenced by how efficiently the fungi transfer nutrients to the host plant (equ 11). The model follows the assumption that plants provide fungi with C as long as their investment is outweighed by the benefits (i.e., acquired N or P) (Nasholm et al., 2013; Nehls, 2008). We further assume the C investment will be limited by the minimum nutrient supply efficiency provided by fungi. $f(P_{supply})$ is calculated as,

$$f(P_{supply}) = \begin{cases} 1 & P_{fungi\rightarrow plant,th} \leq P_{fungi\rightarrow plant} \\ \dfrac{P_{fungi\rightarrow plant}}{P_{fungi\rightarrow plant} + P_{ilab\rightarrow root}} & P_{fungi\rightarrow plant,th} > P_{fungi\rightarrow plant} \end{cases} \quad (12)$$

$$P_{fungi\rightarrow plant,th} = p_{fth} \times (P_{fungi\rightarrow plant} + P_{ilab\rightarrow root}) \quad (13)$$

Where $P_{fungi\rightarrow plant,th}$ is the defined threshold rate of fungal P supply (g P m^{-2} day^{-1}), below which plant C investment is limited, p_{fth} is a threshold fraction determined by fungal and plant species (Table 3). $P_{fungi\rightarrow plant}$ is the actual mycorrhizal fungal P supply to the plant (g P m^{-2} day^{-1}) (equ 16), $P_{ilab\rightarrow root}$ describes plant uptake by roots (g P m^{-2} day^{-1}) (equ A.8).

P in the fungal biomass, P_{fungi} (g P m^{-2}), is calculated as,

$$P_{fungi} = P_{soil\rightarrow fungi} - P_{fungi\rightarrow litter} - P_{fungi\rightarrow plant} \quad (14)$$

Fungal P litter production ($P_{fungi\rightarrow litter}$, g P m^{-2} day^{-1}) is estimated from a first-order rate equation,

$$P_{fungi\rightarrow litter} = P_{fungi} \times p_{lrate} \times (1 - p_{fret}) \quad (15)$$

Where P_{fungi} stands for fungal P content (g P m^{-2}), p_{lrate} is the litterfall rate parameter (day^{-1}) (Table 3), and p_{fret} is a parameter describing the fraction of P retained in fungal tissue during senescence (Table 3).

P transfer from mycorrhizal fungi to plant, $P_{fungi\rightarrow plant}$ (g P m^{-2} day^{-1}), is driven by plant P demand (equ A.9) after root uptake (equ A.8), but regulated by P availability to fungi.

$$P_{fungi\rightarrow plant} = \begin{cases} P_{Demand} - P_{ilab\rightarrow root} & P_{Demand} - P_{ilab\rightarrow root} \leq P_{fungiavail} \\ P_{fungiavail} & P_{Demand} - P_{ilab\rightarrow root} > P_{fungiavail} \end{cases} \quad (16)$$

Where $P_{fungiavail}$ is the P that can be acquired by fungi and transferred to the plant (g P m^{-2}), calculated as,

$$P_{fungiavail} = P_{fungi} - \frac{C_{fungi}}{p_{cp\,fungi\max}} \quad (17)$$

Where P_{fungi} is fungal P content (g P m-2), $p_{cpfungimax}$ is a parameter describing the predefined maximum C/P ratio of fungal tissue (Table 3). This is based on the assumption that mycorrhizal fungi will only supply the plant with P as long as fungal C demand is fulfilled (Nehls, 2008).

~~3~~2.2.6~~5~~ Mycorrhizal fungi phosphorus uptake

Total and partial mycorrhizal fungal P uptake is calculated analog to the mycorrhizal fungal N uptake (He et al., 2018) as,

$$P_{soil \to fungi} = P_{ilab \to fungi} + P_{Litter \to fungi} + P_{Humus \to fungi} \qquad (18)$$

The mycorrhiza is further distinguished into the mycelia, which is responsible for N and P uptake (both in inorganic forms and nutrient short-cut from organic pools), and the fungal mantle, which covers the fine-root tips (He et al., 2018). Through plant litterfall, P is recycled and released back into the soil through mineralization. Uptake from the P_{ilab} pool to fungi is first limited by a potential uptake rate $P_{ilabpot \to fungi}$ (g P m^{-2} day^{-1}), determined by the biomass of fungal mycelia.

$$P_{ilabpot \to fungi} = p_{i,rate} \times C_{fungi} \times p_{fmyc} \qquad (19)$$

Where $P_{ilabpot \to fungi}$ stands for potential fungi P_i uptake rate (g P m^{-2} day^{-1}), and $p_{i,rate}$ is a parameter which describes the mycorrhizal fungal potential uptake rate of P_i per unite C_{fungi} (g P g C^{-1} day^{-1}) (Table 3), p_{fmyc} is the fraction of fungal mycelia in total fungal biomass (Table 3).

The actual uptake from the P_{ilab} pool to fungi, $P_{ilab \to fungi}$ (g P m^{-2} day^{-1}), is calculated by the potential uptake rate (equ 19), further regulated by soil P_{ilab} availability,

$$P_{ilab \to fungi} = \begin{cases} P_{ilabpot \to fungi} \times f(P_{fungidef}) & P_{ilabpot \to fungi} \le P_{ilab} \times f(P_{fungiavail}) \\ P_{ilab} \times f(P_{fungiavail}) & P_{ilabpot \to fungi} > P_{ilab} \times f(P_{fungiavail}) \end{cases} \qquad (20)$$

Where $f(P_{fungiavail})$ is the availability function that calculates the fraction of P_{ilab} that fungi can directly obtain (equ 21), and $f(P_{fungidef})$ is the function that calculates the deficiency fraction that fungi can possibly uptake, which is determined by the fungi C/P ratio (eq~~.~~u 22)

$$f(P_{fungiavail}) = p_{iavail} \times upt_{f,enh} \qquad (21)$$

Where p_{iavail} defines the fraction of P_{ilab} that can be directly obtained by roots (Table 3, also see eq~~.~~u A.~~.~~8~~ in Appendix A~~), $upt_{f,enh}$ is an enhanced uptake coefficient to account for the fact that fungal mycelia have higher uptake efficiency than roots (He et al., 2018).

The function of uptake deficiency fraction, $f(P_{fungidef})$ scales the unfulfilled capacity of fungi for P uptake, is calculated as,

$$f(P_{fungidef}) = 1 - \frac{p_{cpfungimax}}{C_{fungi} / P_{fungi}} \qquad (22)$$

Where $p_{cpfungimin}$ is the defined minimum fungal C/P ratio parameter (Table 3).

In our model, we assume that P_i derived from the enzymatic hydrolysis of organic P_o is directly taken up by fungi (termed ~~organic~~ nutrient short-cut uptake in this study). Similar to $P_{ilab\rightarrow fungi}$ (equ 20), -uptake from the $P_{\cancel{olit}Litter}$ pool to fungi is first limited by a potential uptake rate $P_{\cancel{olit}Litterpot\rightarrow fungi}$ (g P m^{-2} day^{-1}), determined by the biomass of fungal mycelia.

$$P_{Litterpot\rightarrow fungi} = p_{Litter,rate} \times C_{fungi} \times p_{fmyc} \qquad (23)$$

Where $p_{\cancel{olit}Litter,rate}$ is a parameter that describes the potential rate at which fungi mycelia acquire P from soil litter (g P g C^{-1} day^{-1}) (Table 3). The actual uptake from the $P_{\cancel{olit}Litter}$ pool to fungi, $P_{\cancel{olit}Litter\rightarrow fungi}$ (g P m^{-2} day^{-1}), is calculated by,

$$P_{Litter\rightarrow fungi} = \begin{cases} P_{Litterpot\rightarrow fungi} \times f(P_{fungidef}) \times frac_{P,lit} & P_{Litterpot\rightarrow fungi} < p_{Litterf} \times P_{Litter} \\ p_{Litterf} \times P_{Litter} \times frac_{P,lit} & P_{Litterpot\rightarrow fungi} \geq p_{Litterf} \times P_{Litter} \end{cases} \qquad (24)$$

Where $p_{\cancel{olit}Litterf}$ is the fungi ~~organic~~ nutrient short-cut uptake parameter that describes the uptake rate of soil litter $P_{\cancel{olit}Litter}$ that can be hydrolyzed and directly acquired by fungi (day^{-1}) (Table 3), $frac_{P,lit}$ is introduced to ensure that fungi nutrient short-cut~~organic~~ uptake is less than the missing plant demand after P_{ilab} uptake, as well as to avoid uptake from only one organic pool, calculated as,

$$\begin{aligned} &P_{of,max} = P_{Litter} \times p_{Litterf} + P_{Humus} \times p_{Humusf} \\ &frac_{P,lit} = \min\left\{\frac{P_{Demand} - P_{ilab\rightarrow plant}}{P_{of,max}}; \frac{P_{Litter} \times p_{Litterf}}{P_{of,max}}\right\} \end{aligned} \qquad (25)$$

Where $p_{\cancel{ohum}Humusf}$ is the fungi ~~organic~~ nutrient short-cut uptake parameter that describes the uptake rate of soil humus $P_{\cancel{ohum}Humus}$ that can be hydrolyzed and directly acquired by fungi (day^{-1}), The same approach can be used to quantify fungal P uptake from the humus pool by replacing terms that include the litter P pool with the humus P pool in equ (23), (24) and (25).

The fungal mantle prevents contact between roots and the soil, and thereby limits the rate at which roots can directly acquire nutrients from the soil. Plant root P_i uptake response to P availability and fungal mantle is calculated as,

$$f(P_{iavail}) = p_{iavail} \times e^{(-fm\times m)} \qquad (26)$$

Where p_{iavail} is a parameter that describes the maximum fraction of P_{ilab} that is available for uptake by plant roots, (equ A.8) (i.e., not covered by the fungal mantle), and fm, which is an uptake reduction parameter that describes cover by the fungal mantle. m is the mycorrhization degree, see He et al. (2018).

~~4~~3 Description of the region used for simulation and model setup

~~4~~3.1 Description of the region

The Coup-CNP model was tested on four managed forest regions, situated along a climatic, N and P deposition, and fertility gradient across Sweden – Västerbotten 64°N, Dalarna 61°N, Jönköping 57°N, and Skåne 56°N – the same four regions as in Svensson et al. (2008) and He et al. (2018). An overview of the climatic, geological, plant and soil characteristics of the four regions is provided in Table 1. In general, the four regions represent a North-South transect characterized by increasing mean air temperature (from 0.7 to 7.1 °C), precipitation (613-838 mm), and atmospheric N deposition (1.5 – 12.5 kg N ha^{-1} year^{-1}~~ha^{-1}~~). The measured annual P deposition ranges from 0.06 to 0.28 kg P ha^{-1}, with the lowest and highest deposition rates observed in the 61°N and 57°N regions, respectively. For comparison, sites dominated by Scots pine (*Pinus sylvestris*) and/or Norway spruce (*Picea abies*) and Podzol soils (~~FAO~~Jahn et al., ~~1990~~2006) were chosen for all four regions (Table 1). Soil fertility, indicated by C-to-nutrient ratios, exhibited an increasing trend from North to South, however, the highest soil organic C/P ratio (thus the poorest P content) was measured in the 61°N region (Table 1). Soil mineral P content varied with geology (Table 1). The aqua regia extraction method was used to determine total soil mineral P content from regional till samples collected by the Geological Survey of Sweden (SGU) (Andersson et al., 2014). Samples were taken from the C-horizon at a depth of approximately 0.8 m, where the till is generally not disturbed by weathering. In general, Swedish till soils belong to the youngest and least weathered soils in Europe. High total mineral P contents can be found in southern (i.e. 57 and 56°N) and northern parts of the country (i.e. 64°N), which include apatite-iron ore districts (Table 1). Total mineral P content in central Sweden (e.g., 61°N) is much lower than in other parts due to the occurrence of marine and postglacial clays that cover, for example, the Mälaren region.

~~4.2 Model design and setup~~

~~The development of managed forests was simulated in daily resolution over a rotation period from stand age class 10 until 10 years after final harvesting to cover the potential nutrient leaching during the regeneration phase as in Gärdenäs et al. (2003). The trees in all regions were assumed to be planted in 1961; thus, the period 1961 to 1970 represented the spin-up period. The harvesting intensities and rotation lengths were set specifically for each region following recommendations from SLU (2012). The management of forest stands ranged from two thinnings during a rotation period of 120 years for the least productive stands in northern regions to four thinnings during a rotation period of 70 years in the most productive stands in southern Sweden (Table 1). According to general forest management guidelines, it was~~

~~assumed that during thinnings 20% of the stem is removed while 5% transforms into litter (Swedish Forest Agency, 2005). For leaves and roots, it was assumed that 25% transforms into litter. For all of the regions, one clearance – during which 60% of the stands is removed - was applied at the end of the first year after spin-up. During final felling, 5% of trees are remained intact, 90% of the stem is removed and 5% becomes litter, while it is assumed that 95% of all other plant components become litter. The surface cover parameters and litterfall rates of understory vegetation were modified from Svensson et al. (2008) to achieve a more realistic understory in those regions (Table 2).~~

~~Historical weather data were derived from the nearby SMHI weather station data through spatial interpolation for each region. Projections of future weather data were generated by the climate change and environmental objective (CLEO) project, using ECHAM5 projections and bias correction of regional climatic data (Personal communication to Thomas Bosshard, SMHI). N concentration in the deposition was kept constant for each region throughout the simulation as in Svensson et al. (2008) and Gärdenäs et al. (2003).~~

~~Literature data, both soil and biomass, were compiled from sites with coniferous forests on Podzols soil within the major moisture classes (mesic and moist), according to the Swedish National Forest Soil Inventory (NFSI) (Olsson et al. 2009, Stendahl et al., 2010.) The corresponding forest biomass data were based on measured standing stock volumes of different age classes presented in the Swedish Forest Inventory (SFI) data (SLU, 2003), for more details, see Svensson et al. (2008).~~

~~Part of the model design and setup such as soil physical properties, soil depth (1 m), initial soil C content and C/N ratio followed what was reported by Svensson et al. (2008), who in turn had NSFI as the main source. He et al. (2018) additionally described explicit mycorrhizal fungi settings. The following section will only chronicle the setup for the newly developed P model, as well as describes parts of the model that differed from the aforementioned studies (Svensson et al., 2008, He et al., 2018).~~

~~The P content in soil organic matter, i.e., soil organic matter C/P ratios, was based on measurements performed at the sites during a Swedish Throughfall Monitoring Network (SWETHTRO) project (Pihl Karlsson et al., 2015). Only the organic C/P ratio at the O horizon was measured at most sites. Thus, in our calculations of the total stock of soil organic P in the soil profile, we assumed that the C/P ratio measured for the O horizon also extends to the other horizons (uncertainties associated with this assumption will be assessed by including a range in the soil N/P ratios, 10-25, in the sensitivity analysis). The initial labile P_i concentrations were set according to previous data from similar Swedish forest sites (Kronnäs et al., 2019; Fransson~~

~~and Bergkvist, 2000). Soil pH was set according to the NSFI data. Initial soil organic P pools were partitioned between soil litter (5%) and humus pools (95%) analog to N partition in Svensson et al. (2008), and decreased exponentially with depth (Fransson and Bergkvist, 2000). The sensitivity of plant growth, soil C and leaching loss responses to soil N and P availability was assessed by varying the soil N/P ratio from 10 to 25 for the study regions (see Table 2 and Figure 5). These ranges were set according to previously published Swedish forest soil data (Lagerström et al., 2009; Giesler et al., 2002; Kronnäs et al., 2019). Previous modelling studies (Eckersten et al., 1995; He et al., 2018) have reported that the parameter 'fungal organic N uptake rate' strongly affects N availability. For this reason, both fungal N and P uptake rates were included in the sensitivity analysis so that we could determine how fungal N and P uptake influence the response to soil N and P availability between soil N/P ratio 10 to 25 (Table 2). The range between the regional lowest and highest values of fungal organic uptake rates for the four regions was used for the sensitivity analysis (Table 2). The newly introduced parameters of P processes were mostly based on values from the literature (Table 3). For instance, the optimal leaf C/P ratios for forest grow~~Previous order is more logic~~th, C/P ratios of individual plant components were obtained from empirical measurements from Swedish forests (e.g. Thelin et al., (1998; 2002)). The weathering and surface runoff parameters were defined according to laboratory empirical data (e.g. Guidry and Machenzie, (2000)). The fungi related parameters were mainly obtained from the previous CoupModel calibrations for the same regions (He et al., 2018).~~

~~4~~3.~~3~~ 2 Datasets for model evaluation

Literature data of tree biomass, leaf nutrient content as well as water flow and P leaching~~, both soil and biomass,~~ were compiled from sites with coniferous forests on Podzols soil within the major moisture classes (mesic and moist), according to the Swedish National Forest Soil Inventory (NFSI) (Olsson et al. 2009, Stendahl et al., 2010.) The corresponding forest biomass data were based on measured standing stock volumes of different age classes presented in the Swedish Forest Inventory (SFI) data (SLU, 2003), for more details, see Svensson et al. (2008). ~~Data used to evaluate the newly developed model include SFI biomass values from forest stands aged 10 to 100 years (SLU, 2003).~~

~~The measured leaf nutrient data used in the evaluation were obtained from managed forests sites from Swedish Forest Agencywithin the SWETHTRO project (Pihl Karlsson et al., 2011; Pihl Karlsson et al., 2015)~~ The measured leaf nutrient data used in the evaluation were obtained from managed forests sites within the forest monitoring sites of the Swedish Forest Agency

(Wijk, 1997; Akselsson et al. 2015) in the studied regions (some forest sites are also part of the ICP FOREST LEVEL II monitoring program, www.icp-forests.org). Data used in the North 64°N region include two Scots pine stand sites, Gransjö (N 64°30, E17°24) and Brattfors (N64°29', E18°28'). For the 61°N region, two sites with Scots pine stands - Kansbo (N61°7', E 14°21') and Furudalsbruk (N61°12', E15°11') were used. Data describing the Fagerhult (N57°30', E15°20') site, dominated by Norway spruce, and the Gynge Scots pine stand (N57°52', E14°44') were used in the 57°N region. Three sites, including a Scots pine stand in Bj~~ä~~ärsgård (N56°10', E13°8'), a Norway spruce stand in Västra Torup (N56°8', E13°30') and a European Beech stand in Kampholma (N56°6', E13°30'), represented the 56°N region.

To compare model outputs with measured P leaching, PO_4 and total P data in stream water were obtained from the open database of environmental monitoring data (MVM, https://miljodata.slu.se/mvm/). Thus, the measured P leaching also contains the P leaching from upstream. DOP ~~data~~ were not ~~available~~ measured for the regions. ~~thus i~~Thus the so call measured DOP ~~t~~ was calculated as the difference between the measured total P and PO_4. ~~Thus~~ This means the "measured DOP" may contain both~~s~~ our simulated fractions DOP and~~but also~~ particular phosphorus. We used measured water outflow rates from the regional outlet from the Swedish Meteorological and Hydrological Institute (SMHI, https://vattenwebb.smhi.se/station/) to convert the concentrations into fluxes.

3.3 Model design and setup

The results were based on simulated forest development with~~of managed forests was simulated in~~ daily resolution over a rotation period from stand age ~~class~~ 10 years until 10 years after final harvesting. The 10 years after final harvest were included to cover the potential nutrient leaching during the regeneration phase as in Gärdenäs et al. (2003). The trees in all regions were assumed to be planted in 1961, and ~~thus,~~ the period 1961 to 1970 was used as ~~represented the~~ a spin-up period. The harvesting intensities and rotation lengths were specified~~set specifically~~ for each region following recommendations from SLU (2012). The simulated rotational period was 120, 110, 90 and 70 years from the N~~n~~orth to S~~s~~outh region, respectively. Two thinnings were conducted in~~for~~ the two northern region and~~with~~ three thinnings in~~for~~ the two southern regions (Table 1). Following~~According to~~ general forest management guidelines, it was assumed that during thinnings 20% of the stem is removed while 5% transforms into litter (Swedish Forest Agency, 2005). For leaves and roots, it was assumed that 25% transforms into litter. For all of the regions, one clearance – during which ~~9~~60~~60~~% of the stands is removed - was applied at the end of the stand age year 10 after spin-up. During final felling, 5% of trees are remained intact, and it is assumed that 90% of the stem is harvested and 5% becomes litter, while all leaves and roots become litter. ~~dynamics~~

3.4 Model forcing, initial and boundary conditions

Historical weather data were derived from the nearby SMHI weather station data through spatial interpolation for each region. Projections of future weather data were generated by the climate change and environmental objective (CLEO) project, using ECHAM5 projections and bias correction of regional climatic data (Personal communication ~~to~~with Thomas Bosshard, SMHI). For the P deposition, the measured P deposition rate from each region (Table 1) was kept constant over the simulation period, similar as that for N deposition.

An 11.3-meter deep soil profile of 20 layers were simulated for all the four regions as that in Svensson et al. (2008). An assumed constant heat flow was used to define the lower boundary condition for heat and no water flow was assumed at the bottom soil layer. Part of the model setup and initial conditions such as soil physical properties, drainage, initial soil C content and C/N ratio followed what was reported by Svensson et al. (2008), who in turn had NSFI as the main source. He et al. (2018) additionally described explicit mycorrhizal fungi settings. The following section will only describe the initial conditions for the newly developed P model.

The two vegetation layers were initialized as bare ground with a small amount of C, N and P mass in seedling to start vegetation growth. Initial conditions for solid mineral P content, soil organic matter content, soil stoichiometry were reported in Table 1. Initial soil organic P pools (Table 1) were partitioned between soil litter (5%) and humus pools (95%) analog to N partition in Svensson et al. (2008), and total amount of soil organic P decreased exponentially with depth (Fransson and Bergkvist, 2000). ~~The l~~Litter was assumed to be distributed down to 0.5 m while~~but the~~ humus down to 1 m depth. The initial labile P_i concentrations were set according to previous data from similar Swedish forest sites (Kronnäs et al., 2019; Fransson and Bergkvist, 2000). Soil pH was set according to the NSFI data and kept constant over the simulation period (Table 1). The initial value of soil organic P for the soil profile was estimated by the available measurements of soil organic matter N/P ratios, performed at the same forest monitoring sites of the Swedish Forest Agency (Wijk, 1995; Akselsson et al. 2015) where leaf nutrient content were sampled.

~~sites from Swedish Forestry Agency~~. However, only the organic N/P ratio at the O horizon was measured at most sites. Thus, in our calculations of the total stock of soil organic P, we assumed that the mean N/P ratio measured for the O horizon also extends to the other horizons in the default model run. Model uncertainties associated with this assumption were~~will be~~ assessed by including a range in the soil N/P ratios, 10-25, in the sensitivity analysis (~~Appendix x and~~e.g. Fig.~~ure X~~5).

3.5 ~~Model calibration and s~~Sensitivity analysis~~to parameters~~

The C and N p~~P~~arameters for these regions in CoupModel were previously tested and calibrated in a number of studies (Svensson et al., 2008) and those of fungi by~~;~~ (He et al., 2018) (Table 2). The surface cover parameters and litterfall rates of understory vegetation were modified from Svensson et al. (2008) to achieve a more realistic understory dynamics in those regions (Table 3). ~~Parameters were subjectively calibrated using the Coup-CN model to the regional biomass data in Svensson et al. (2008) study. He et al. (2018) employed a formal Bayesian calibration to the four regions with Coup-CN but with newly developed fungi model. Thus, most C-N related parameters were previously calibrated.~~ Most of the newly introduced P parameters were derived from literature (Table 2, 3)~~ if not then a subjective calibration was made to fit the observed data~~. For instance, the optimal leaf C/P ratios for forest growth, C/P ratios of individual plant components were obtained from empirical measurements from Swedish forests (e.g. Thelin et al., (1998; 2002)). The weathering and surface runoff parameters were defined according to laboratory empirical data (e.g. Guidry and Machenzie, (2000)).~~ The fungi related parameters were mainly obtained from the previous CoupModel calibrations for the same regions (He et al., 2018)~~.

We conducted a global sensitivity analysis of the new Coup-CNP model to its parameterization (n=34) using a Monte-Carlo based sensitivity analysis method to assess the stability and robustness of the model with respect to its parameter values. The sampled parameters and their ranges (Table S.1), model design and global sensitivity results (Table S.2, S.3, S.4) were reported in detail in the supplement. Based on these simulations and parameter sensitivity rankings, we select three most important parameters (n=3), which has a strong effect on the model outcome to further form a new set of model runs, which are used for the model sensitivity analysis presented in this paper. The selected three parameters are initial soil humus P, short-cut N uptake rate and short-cut P uptake rate (Table S.2, S.3), all strongly regulates the soil N and P availability. The sensitivity of plant growth, soil C and leaching loss responses to soil N and P availability was then assessed by varying the soil N/P ratio from 10 to 25 for the study regions (see Table 2 and Figure 5). These ranges were set according to previously published Swedish forest soil data (Lagerström et al., 2009; Giesler et al., 2002; Kronnäs et al., 2019) and the additional soil P data from Swedish Forestry Agency inventory (Table 1). The ranges of short-cut uptake coefficient for N and P were based on the regional lowest and highest values of short-cut uptake rates for the four regions (Table 2).

~~In the sensitivity analysis, tsimulations comparedfor evaluation (see x) eresimulation.~~

~~The sensitivity of plant growth, soil C and leaching loss responses to soil N and P availability was then assessed by varying the soil N/P ratio from 10 to 25 for the study regions (see Table 2 and Figure 5). These ranges were set according to previously published Swedish forest soil data (Lagerström et al., 2009; Giesler et al., 2002; Kronnäs et al., 2019) and the additional soil P data from Swedish Forestry Agency inventory (Table 1). Furthermore previous modelling studies (Eckersten and Beier, 1998; He et al., 2018) have reported that the parameter 'fungal short-cut N uptake rate' strongly affects N availability. High sensitivity of this parameter was again shown in our comprehensive parameter sensitivity analysis (Fig. S1, S.3 in the supplementary). Thus, both fungal N and P uptake rates were included in the sensitivity analysis so that we could determine how fungal N and P uptake influence the response to soil N and P availability between soil N/P ratio 10 to 25 (Table 2). The range of fungal N and P uptake rates was based on the regional lowest and highest values of fungal short-cut uptake rates for the four regions (Table 2).~~

~~Finally, we ed 150% expressedThe sensitivity of plant growth, soil C and leaching loss responses to soil N and P availability was then assessed by varying the soil N/P ratio from 10 to 25 for the study regions (see Table 2 and Figure 5). These ranges were set according to previously published Swedish forest soil data (Lagerström et al., 2009; Giesler et al., 2002; Kronnäs et al., 2019) and the additional soil P data from Swedish Forestry Agency inventory (Table 1). Previous modelling studies (Eckersten and Beier, 1998; He et al., 2018) have reported that the parameter 'fungal short-cut N uptake rate' strongly affects N availability. High sensitivity of this parameter was again shown in our comprehensive parameter sensitivity analysis (Fig. S1, S.3 in the supplementary). Thus, both fungal N and P uptake rates were included in the sensitivity analysis so that we could determine how fungal N and P uptake influence the response to soil N and P availability between soil N/P ratio 10 to 25 (Table 2). The range between the regional lowest and highest values of fungal short-cut uptake rates for the four regions was used for the sensitivity analysis (Table 2).~~

~~5~~ 4 Results

~~5~~4.1 Model assessment

The new Coup-CNP model was able to reproduce the observed development of forest tree biomass (SLU, 2003) over the rotation period well (Fig. 2). Note that the dips in the simulated biomass are related to the timing forestry operations in the model that is not represented in the measured. The regional biomass data show an increasing trend from North to South, which the model captured clearly (Fig. 2). However, when the predictions were compared with observed plant biomass prior to final harvesting, the model showed a slight underestimation (12%) for the northern 61°N region and slight overestimations for the other regions (7%, 13% and 1% for the 64, 57 and 56 °N regions, respectively).

The simulated leaf C/P ratios agree fairly well with the available Swedish Forest Agency data (Wijk, 1997; Akselsson et al. 2015)~~SWETHTRO data (Pihl Karlsson et al., 2011; Pihl Karlsson et al., 2015)~~, despite general overestimation of 10%, 32%, 30% and 21% from North to South. The average measured leaf C/P ratio in the four regions was 396 (standard deviation, 48), 398 (59), 355 (45) and 396 (72), respectively. The model found that the 56 and 61 °N regions have higher C/P ratios than the other regions, which was also noticed in the observational data (Fig. 2). The average measured leaf C/N ratios were 44 (4), 41 (3), 36 (5) and 31 (7), respectively. The model was accurate in simulating leaf C/N ratios, and identified a similar decreasing leaf C/N trend from North to South. The exception was a slight leaf C/N overestimation for the 57 °N region (Fig. 2). For leaf N/P ratios, the average of the observations from North to South were 9.1 (1), 9.6 (1.3), 9.9 (1.4) and 13.4 (3.8), respectively. The Coup-CNP model was also able to accurately reproduce the measured leaf N/P ratios, as well as reveal an increasing leaf N/P trend with decreasing latitudes (Fig. 2). Of the climate variables, the radiation absorbed by tree canopy increased from the North to the South, while the temperature and water limitation of Gross Primary Production (GPP) declined from the North to the South (Table 4). N was the most limiting nutrient at the 64 °N and 57 °N, while P was the most limiting nutrient at the 61 °N region and 56 °N (Table 4). The limiting effect of P availability could be seen in the predicted relatively high N/P ratios, as the 56 °N region – and, to a lesser extent, the 61 °N region as this region is also N limited (Fig. 2).

Total annual plant N and P uptake rates in the northernmost region were modelled to be 3.7 g N m^{-2} $year^{-1}$ and 0.4 g P m^{-2} $year^{-1}$, respectively. The southernmost region demonstrated three times higher N uptake rates and two times higher P uptake rates than the northernmost region (Table 4). The total N uptake of the short-cut ~~U~~uptake from the organic N pools ~~of the organic fraction of total N~~ decreased from North to South (Table 4). The modelling results also indicated that the short-cut ~~uptake of organic~~uptake of P is necessary to satisfy the demands of the plant. However, ~~uptake of~~ the ~~organic~~ fraction of total P uptake from the short-cut pathway was not found to be associated with latitude or the C/N ratio. Instead, it is regulated by soil C/P ratio and geology (Tables 1 and 5). The contribution of ~~amount of N in the~~ fungi ~~litter fraction of~~ to total ~~plant~~ N litter production decreased from North to South, but this was not the case for P, as the ~~amount~~ contribution of ~~P~~ fungi P litter remained stable in the corresponding fraction (Table 4).

The simulated annual soil C sequestration rates were 2, -2, 9, and 15 g C m^{-2} year^{-1} from North to South (Figs. 3a, 4a, Table 5). Thus, the soil C stock was generally in a steady-state over the forest rotation period, with slightly higher C sequestration rates predicted for the southern regions (Figs. 3a, 4a). The soil C/N ratios of all of the regions were in a steady-state over the forest rotation period. In contrast, the C/P ratios and N/P ratios showed a slightly increasing trend over the rotation period, with the exception of the soil N/P ratio in the 64 °N region (Fig. 3b, c, d).

The modelled P leaching generally reflected the observational data, however, the mean estimated concentrations were often lower than the measurements available for each region (MVM, https://miljodata.slu.se/mvm/, Table 6). Note the observed stream P concentration contains also sources of P from the whole watershed but our model contains only the upstream. The data show that P losses through leaching ~~have~~ were ~~a~~ small ~~effect on the system~~compared to the internal fluxes, i.e., they account for approximately one-third of the annual deposition input, while DOP losses were more dominant in the northern systems (Table 6). However, the simulated proportion of DOP in total losses through leaching was much lower than what had been measured, and the decreasing trend from North to South identified in the simulations was not supported by the observational data (Table 6).

~~5~~4.2 Modelled forest C, N and P budgets

Regarding C assimilation, the average plant growth over the rotation period was predicted to be three times higher in the southernmost region than that in the northernmost region (Fig. 4a). Most of the forest productivity was harvested, the change in plant C was small as simulation started when plants were 10 years old and ended when they were 10 years old. Regarding the N budget, the northernmost ecosystem showed a slight loss while the southern ecosystems showed N gains. The N sequestration rates generally increased towards the southern latitude (Fig. 4b). The P budget shows an opposite pattern, as the northernmost ecosystem was in balance while the other three ecosystems showed P losses, with total losses increasing from North to South (Fig. 4c).

Most of the C captured from the atmosphere was the harvested plants (Fig. 4a). Our model predicted small losses of DOC through leaching, and the forest soil in all of the regions was found to be in a quasi-steady-state with generally low sequestration. An exception was the region with the lowest P-availability (61 °N), which showed soil C losses (Tables 1, 5).

Our results identified atmospheric deposition as the main N input. When accounting only for harvested N, 60%, 53%, 35% and 36% of the deposited N was removed from the 64, 61, 57 and 56 °N regions, respectively (Fig. 4b). The N accumulated in standing plants and harvested plants accounted for 104%, 80%, 54% and 55% of the annual N deposition in the 64, 61, 57 and 56 °N regions, respectively. The model results show that soils in the two northern regions will lose N while soils in the two southern regions will accumulate N. Annual average losses through leaching were predicted to increase from North to South, and ranged from 0.09, 0.19, 0.27, 0.47 g N m^{-2} from North to South, which corresponds to 60%, 45%, 21%, 41% of the annual N deposition, respectively (Fig. 4b).

The simulated annual P weathering fluxes ranged from 0.009 to 0.025 g P m^{-2} $year^{-1}$, and showed similar magnitudes as the deposition inputs (Fig. 4c). The most significant source of P losses over the rotation period was plant harvest, which removed 89%, 255%, 108% and 167% of the deposited P from the 64, 61, 57 and 56 °N regions, respectively (Fig. 4c). When the P that accumulated in standing plants and harvested plants is considered together, this accounts for 85%, 147%, 90% and 114% of the total P input through deposition and weathering for the 64, 61, 57 and 56 °N regions, respectively. The simulation showed that soils from all four studied regions are slightly losing P, with the annual losses ranging from 0.01 to 0.03 g P m^{-2} from North to South (Fig. 4c).

~~5~~4.3 Impacts of forest growth, soil C and leaching on soil N and P levels

Forest growth, measured through harvested biomass, increased as the soil N/P ratios increased from 10 to 15, but decreased once an optimum soil N/P ratio of around 15-20 was reached. This trend was noted for three studied regions (Fig. 5a), however getting less pronounced moving north and it was almost not detectable for the northernmost region where GPP was strongly limited by radiation (average absorbed radiation 3.89×10^{6} J m^{-2} day^{-1} at 64 °N and 6.57×10^{6} J m^{-2} day^{-1} at 56 °N, Table 4). The lowest air temperature and precipitation in 64 °N out of the four regions also contribute to the GPP limitation (temperature/water limitation of GPP 0.47/0.45 at 64 °N and 0.67/0.65 at 56 °N, Table 4). Soil C sequestration between 56-61 °N latitudes was found to be highly sensitive to soil N/P ratios, with the model predicting that soil C sequestration would consistently decrease as the soil N/P ratio increases (Fig. 5b). In addition, total P losses through leaching generally decreased as soil N/P ratios increased; an exception was the 57 °N region where they increased again for soil N/P ratios above 15-18, the same range with maximum plant harvest (Fig 5a). In contrast, total N losses through leaching were found to be positively correlated with the soil N/P ratio above 15, with this relationship more pronounced for the southern regions (Fig. 5c, d). Thus, the sensitivity analysis results indicate that strong C-N-P interactions are also prevalent in forest ecosystems (Fig. 5). Forest soils with soil N/P ratios above 15-18 were predicted to exhibit slower forest growth rates, lower soil C sequestration (potentially even losses), and high N leaching risk.

~~6~~ 5 Discussion

~~6~~5.1 Modelled P budgets and comparison with other modelling studies ~~published modelling data~~

It is important to compare our modelled P fluxes with previously reported values. In a study that applied the PROFILE model and empirical data, Akselsson et al. (2008) estimated the average weathering rate in Swedish forests (down to a depth of 0.5 m) to be 0.009 g P m^{-2} year^{-1}, ranging from 0.001 to 0.024 g m^{-2} year^{-1} (5% to 95% percentile). This can be compared with our simulated P weathering rate (down to a depth of 1 m soil depth) range of 0.009 to 0.025 g P m^{-2} year^{-1}. Both our estimations and those by Akselsson et al. (2008) were far lower than the 0.071 g P m^{-2} year^{-1} (0.5 m depth) reported by Yu et al. (2018) for a spruce forest on Podzol soil in southern Sweden. It is important to mention that Yu et al. (2018) suggested that the weathering rate they provided was an overestimation.

The modelled total plant P uptake rates in this study ranged from 0.4 to 1 g P m^{-2} year^{-1} (Table 4), which is slightly higher than the 0.5 ± 0.4 to 0.96 g P m^{-2} year^{-1} reported by Johnson et al. (2003) and Yanai (1992) for temperate forests, and the 0.5 g P m^{-2} year^{-1} reported for a southern Swedish forest by Yu et al. (2018). One explanation for this discrepancy could be that Coup-CNP explicitly considers mycorrhizal processes related to P uptake, e.g., the presented estimates revealed that mycorrhizal fungi accounted for more than half of total plant P uptake (Table 4). This highlights that mycorrhizal fungi are crucial to plant P acquisition in forest ecosystems. The estimated P uptake by fungi was - to a large extent - proportional to the rates estimated for N (Table 4). He et al. (2018) compared explicit and implicit models and found that CoupModel v5.0 predictions of plant N uptake were higher when mycorrhizal fungi were explicitly included in the model. Furthermore, it is important to note that previous accounts of empirical data (Johnson et al., 2003; Yanai, 1992), as well as the ForSAFE model (Yu et al., 2018), did not account for P uptake by understory vegetation. In this study, understory vegetation was estimated to contribute to c.a. one-third of total P uptake in northern regions and one-sixth of total P uptake in southern regions (data not shown).

Akselsson et al. (2008) reported that, in Swedish forests, whole-tree harvesting causes average P removal of 0.054 g P m^{-2} year^{-1} with a range from 0.016 to 0.13 g P m^{-2} year^{-1}. This agrees well with our modelled range (0.012 to 0.038 g P m^{-2} year^{-1}) as well as the value reported by Yu et al. (2018), 0.037 g P m^{-2} year^{-1}.

The P balances estimated for the ecosystem in this study ranged from 0 to -0.02 g P m^{-2} year^{-1} (with the negative value representing P losses). This agrees with what has been reported by Akselsson et al. (2008), i.e., an average P balance of -0.029, ranging from 0.008 g P m^{-2} year^{-1} in the North to -0.1 g P m^{-2} year^{-1} in the South. The modelling by Yu et al. (2018) yielded P accumulation of 0.004 g P m^{-2} year^{-1} over a 300-year period in South Sweden. This predicted gain in P over the simulation period, which was very low, could have been due to relatively high P inputs via weathering. Our modelled regional P budget implies that clear-felling harvesting will result in a negative P balance for most Swedish forests even when P uptake by mycorrhizal fungi in nutrient-poor forests is accounted for, with an exception being the northernmost region.

~~6~~5.2 Implications of P availability on forest C and N dynamics

Our results demonstrate that Swedish forests are increasingly P-limited with decreasing latitude, a trend that was especially noticeable at southern latitudes (Table 4). N limitation was even more severe than P limitation at 64 and 57 °N regions. Furthermore, the northernmost region had much less radiation intercepted by the canopy, which partly masks the response to nutrient limitation, they may appear less sensitive to nutrient limitation. This was supported by the observed leaf N/P ratios (average values between ca. 9-14), which are recognized to reflect the state of nutrient limitation in forest trees (e.g. Jonard et al. 2015). In Swedish spruce forests (*Picea abies L. Karst.*), leaf N/P ratios below 7 are normally considered an indicator of N limitation, while ratios above 12 signal P limitation (Rosengren-Brinck and Nihlgård, 1995; Yu et al., 2018). Linder (1995) has previously reported an optimal N/P ratio of 10 for spruce forests in northern Sweden. Similar optimal N/P ratio for pine forest (*Pinus silvestris*) (Ingestad, 1979; Tarvainen et al., 2016). Our leaf N/P ratio estimates were within these ranges, with the exception of the southernmost region (Fig. 1). The ratio of total plant P uptake to total N uptake in the southernmost region was much lower than what was measured for the other regions (Table 4), which further suggests P limitation in the southernmost region. The 61 °N region, which was characterized by the lowest P inputs among the studied regions due to geology and deposition (Table 1) (Fig. 4), was also shown to be P-limited (Table 4). This low P input also explains why this region showed the highest simulated fraction of ~~organic~~ short-cut P uptake from soil organic P (Table 4). Our modelling suggests that northern regions, which have traditionally been conceived as N-limited (Högberg et al., 2017), may experience P limitation or co-limitation by N and P. For instance, the 57 °N region showed an overall N limitation as the average value of GPP response to N, 0.30 is lower than the GPP response to P, 0.34 over the rotation period (Table 4). However, our model results further showed a lower GPP response to P, thus P limitations during the initial c.a. 10 years of stand development (data not shown). This suggests co-limitation could still occur since the nutrient limitations could potentially shift during forest development stages. For example, Tarvainen et al. (2016) reported a decrease in needle P following N fertilization in a Scots pine forest in northern Sweden. Several groundwater discharge areas were also shown to be P-limited (Giesler et al., 2002). Sundqvist et al. (2014) and Vincent et al. (2014) reported that alpine ecosystems in northern Sweden may also be P-limited.

The removal of harvest residues from final fellings for use in biofuel production is common, and expected to increase in southern and central regions of Sweden (Cintas et al., 2017, Ortiz et al., 2014; Stendahl et al., 2010). Our modelling indicates that clear-cutting or final-felling will significantly impact the forest P balance and soil C sequestration (Figs. 4c, 5b). Furthermore, it is important to note that this practice was found to affect P availability more than N availability, especially in southern Sweden (Figs. 4b, 4c). Simulations with earlier versions of CoupModel have also revealed N depletion for final-felling/clear-cutting scenarios in northern Sweden, but reported N gains for southern Sweden (He et al., 2018; Svensson et al., 2008; Gärdenäs et al., 2003).

The soil C sequestration simulated by the Coup-CNP model is generally comparable with what has been reported in previous studies (Table 5). Plants in the north will need to acquire nutrients to meet demands for growth, but the Coup-CNP model showed that plants acquire a smaller fraction of total nutrients than what was previously estimated (Coup-CN model; see Table 8 in Svensson et al. (2008)). Our results further suggest that P regulates SOC, as an increasing soil N/P ratio will decrease soil C sequestration rates (Fig. 5b).

The sensitivity analysis results found the optimum soil N/P ratio for forest production to be 15 to 20 on podzol soils for 61-56 °N regions (Fig. 5). Manzoni et al. (2010) reviewed the forest litter decomposition process and found that litter C-to-nutrient ratios decreased - towards a C/N ratio of 20 and C/P ratio of 350 (thus an N/P ratio of 17.5) - as decomposition proceeded. A synthesis of long-term decomposition studies in northern forests also showed that the N/P ratio of both fine litter and woody residues converges to c.a. 20 (Laiho and Prescott, 2004). The optimum range identified by the Coup-CNP model is thus similar to these observed convergence ratios, which generally represent the shift from immobilization during the initial decomposition phase to net mobilization (Penuelas et al., 2013; Güsewell, 2004; Cleveland and Liptzin, 2007). Lagerström et al. (2009) measured soil and microbial nutrient contents in 30 diversified forest islands in northern Sweden that vary considerably in terms of fertility. Surprisingly, they found that microbial biomass N/P ratios remained unchanged across the gradient, suggesting that nutrient availability is mainly determined by soil organic N/P ratios. The identified bell shape response of plant growth to the soil N/P ratio thus highlights the importance of nutrient stoichiometry. This implies that forests with N/P below the optimal range can benefit from N fertilization, which will stimulate forest growth and reduce the P leaching risk. In contrast, P fertilization in forests with N/P above the optimal range will stimulate forest growth, promote soil C sequestration and reduce N leaching (Figure 5). A synthesis of long-term water quality measurements from forest streams in the geochemical monitoring network (GEOMON) found total N fluxes to be tightly linked to DON/TP ratios (Oulehle et al., 2017). As such, total N leaching increased with the DON/TP ratio, a finding which agrees with the results obtained in this modelling study. The presented modelling predictions thus corroborate that decreased P availability can profoundly affect the N cycle and catchment retention.

To summarize, the presented model (CoupModel v6.0) demonstrated that considering the P cycle in ecosystem models can significantly impact estimations of forest C and N dynamics. This is an important finding in the context of climate change and forest management, as researchers need to have tools that will reliably model the C-N-P dynamics in an ecosystem. Climate change research strives to maximize C accumulation in terrestrial ecosystems, but this may currently be limited by P availability, which will be further jeopardized by the removal of forest residues for bioenergy production. The presented results show that forest growth in southern regions, which are characterized by high N deposition and already show limitation by P, will be most affected (Fig. 4c, Table 4) (Akselsson et al., 2008; Yu et al., 2018; Almeida et al., 2018).

~~7~~ 6 Conclusions

This paper describes the most recent version (6.0) of CoupModel, which explicitly considers the phosphorus cycle and mycorrhizal interactions. The simulations of the C, N, and P budgets for four forest regions were complete and accurate based on evaluation with empirical forest biomass, leaf nutrient ratio, and P leaching data. The development and evaluation of this new model demonstrate that P availability needs to be considered when studying how climate change will influence C turnover and ecosystem responses, otherwise important feedback mechanisms may be overseen and the potential land sink of C overestimated. Thus, the detailed description of all the Coup-CNP components and their interactions between the water, heat, C, N, and P cycles - are highly relevant to future studies.

Our model results showed that N was the most limiting nutrient at the 64 °N and 57 °N, while P was the most limiting nutrient at the 61 °N region and 56 °N (Table 4). The N limitation at 64 and 57 °N regions was more severe than P limitation. Furthermore, the northernmost region had less radiation intercepted by the canopy and lower temperature and precipitation, which may mask or make them less sensitive to nutrient limitation. During the simulated rotation period, southern forests showed P losses, mainly through harvest and changes in soil storage, while northern forests were close to a steady-state in P availability. Mycorrhizal fungi accounted for half of total plant P uptake in all of the regions, which highlights the crucial role of the mycorrhiza in Swedish forests. A sensitivity analysis determined that a soil N/P ratio of 15 to 20 is optimal for forest growth. Furthermore, soil N/P ratio above 15-20 decreased soil C sequestration and total P leaching, while significantly increased N leaching. The largest P outflow over the rotation period was found to be removal via final-felling.

We conclude that the potential P-limitation of terrestrial ecosystems highlights the need of a proper consideration of the P cycle in biogeochemical models. The inclusion of the P cycle enable to account for possible feedback mechanisms of importance for prediction of C sequestration and N leaching under climate change and/or elevated N deposition.

~~8~~ 7 Code and data availability

The model and extensive documentation, including tutorial exercises, are freely available from the CoupModel home page: http://www.coupmodel.com/ (CoupModel, 2019). CoupModel is written in the C++ programming language and runs with a GUI under the Windows systems, but can also be run on other platforms without GUI. Version 6.0, from 03 July 2019, was used for the presented simulations. This version is archived on Zenodo (https://zenodo.org/record/3547628#.Xn3Bc0F7lEZ), as are the simulation files including the model and calibration set-up, parameterization settings, and corresponding input and validation files.

Appendix A: Equations and parameterization regarding phosphorus processes that are analogous to those for nitrogen

The following section provides the equations for P processes that are analogous to those of N, as well as discusses parameterization aspects. The inclusion of the N cycle in CoupModel was previously described by Gärdenäs et al. (2003), Jansson and Karlberg (2011), and He et al. (2018).

A1 Deposition and fertilization

Atmospheric deposition, $P_{dep\rightarrow ilab}$ is treated as a model input using the parameter p_{dep}. In contrast to N deposition, only dry P deposition is considered since wet deposition is generally neglectable. Fertilization $P_{fert\rightarrow ilab}$ is also treated as a model input and calculated as,

$$P_{fert\rightarrow ilab} = p_{kfert}\ P_{fert} \tag{A.1}$$

Where $P_{fert\rightarrow ilab}$ is the rate of fertilizer P addition (g P m^{-2} day^{-1}) and p_{kfert} is the specific dissolution rate of commercial fertilizer (day^{-1}). The value of p_{kfert} depends on fertilizer type and moisture conditions, e.g., in our model, a value of 0.15 corresponds to a half-time of 5 days, and that 90% of the fertilizer is dissolved into the P_{ilab} pool within 15 days. If manure fertilizer is used, the organic P_o in the manure is added into a separated organic pool P_{ofae}, termed faeces. Fecal processes are similar to those of soil litter, described below.

According to a global compilation of published data, the average annual global P deposition is 0.027 g P m^{-2} year^{-1} (0.033 for Europe), which equals to 0.000074 g P m^{-2} day^{-1} (Tipping et al., 2014; Schlesinger, 1997).

A2 Mineralization-Immobilization & decomposition

The P_{ilab} pool is also controlled by biological demand and turnover (Olander and Vitousek, 2005). The P flux of biological mineralization-immobilization is calculated precisely as for N, in that C fluxes from litter (or faeces) to humus or from humus to atmosphere are driven by the microbial need for energy. The non-symbiotic microbes are implicitly simulated using a fixed microbe C/P ratio parameter. The C/P ratio for microbes (cp_m) can vary widely, ranging from approximately 25–400 (see review by Manzoni et al. 2010).

$$C_{DecomL}=k_l\times f(T)\times f(\theta)\times C_{Litter} \qquad C_{DecomL}=k_l\times f(T)\times f(\theta)\times C_{Litter}$$

$$P_{Litter\rightarrow ilab}=C_{DecomL}\left(\frac{1}{C_{litter}/P_{Litter}}-\frac{f_{e,l}}{cp_m}\right)$$

~~$P_{olit\rightarrow ilab}=C_{DecomL}\left(\frac{1}{C_{litter}/P_{litter}}-\frac{f_{e,l}}{cp_m}\right)$~~

$$P_{Litter\rightarrow \text{ Humus}}=\frac{C_{Litter\rightarrow \text{ humus}}}{cp_m} \qquad P_{olit\rightarrow \text{ ohum}}=\frac{C_{litter\rightarrow \text{ humus}}}{cp_m}$$

(A.2)

Where k_l is the decomposition coefficient for soil litter (day^{-1}), C_{litter} is the size of the litter pool (g C m^{-2}), *f(T)* and *f(θ)* are common temperature and water content response functions for decomposition, for more details see Jansson and Karlberg (2011). Humus decomposition is calculated by changing pool size and the decomposition coefficient in the previous equation into terms that describe humus. $P_{\cancel{olit}Litter\rightarrow ilab}$ is the mineralization flux from the soil litter pool to the P_{ilab} pool (g P m^{-2} day^{-1}). $P_{\cancel{olit}Litter\rightarrow\cancel{ohum}Humus}$ is the humufication flux rate. C_{DecomL} is the C decomposition flux of soil litter (g C m^{-2} day^{-1}), whereas C_{litter}/P_{litter} and cp_m are the C to P ratio in the litter pool and microbes. $f_{e,l}$ is a microbial efficiency parameter which represents the fraction of mineralized C that remains in the soil. Corresponding fluxes are calculated by changing the efficiency parameter to $f_{e,f}$ or $f_{e,h}$, along with changing the litter C/P ratio to a fecal C/P ratio or humus C/P ratio, gives the corresponding flow from the fecal pool, $P_{ofae\rightarrow ilab}$, or the humus pool, $P_{\cancel{ohum}Humus\rightarrow ilab}$, respectively. A negative value means that net immobilization takes place.

The total biological mineralization is calculated as,

$$P_{biomin}=P_{Litter\rightarrow ilab}+P_{Humus\rightarrow ilab}+P_{ofae\rightarrow ilab} \qquad \text{(A.3)}$$

The biochemical mineralization process includes the release of root exudates, e.g., efflux of protons and organic anions, phosphatase and cellulolytic enzymes required for the hydrolysis or mineralization of P_o (Richardson and Simpson, 2011; Bünemann, 2015; Hinsinger, 2001). This additional mineralization process is driven by plant demand for P (Richardson et al., 2009). Bünemann (2008) reviewed the existing enzyme addition experiments and showed, for example, that the phosphatase enzyme has low substrate specificity and that up to 60% of total organic P_o in soil can be hydrolyzed and mineralized. We, therefore, assume that biochemical mineralization can occur from both the soil litter and humus pools. The flux rate is calculated as a first-order function regulated by pool size and uptake rate. Furthermore, it is assumed that the flux rate will not exceed the remaining plant demand after root P_i uptake (equ A.8). The following equation (A. 4) is used when symbiotic microbes are implicitly simulated.

$$
\begin{aligned}
P_{Litter \rightarrow plant} &= frac_{P,litter} \times o_{uptPlitter} \times P_{Litter} \\
P_{Humus \rightarrow plant} &= frac_{P,humus} \times o_{uptPhumus} \times P_{Humus} \\
P_{bioche,\max} &= P_{Litter} \times o_{uptPlitter} + P_{Humus} \times o_{uptPhumus} \\
frac_{P,litter} &= \min\left\{ \frac{P_{Demand} - P_{ilab \rightarrow plant}}{P_{bioche,\max}} ; \frac{P_{Litter} \times o_{uptPlitter}}{P_{bioche,\max}} \right\} \\
frac_{P,humus} &= \min\left\{ \frac{P_{Demand} - P_{ilab \rightarrow plant}}{P_{bioche,\max}} ; \frac{P_{Humus} \times o_{uptPhumus}}{P_{bioche,\max}} \right\}
\end{aligned}
\qquad (A.4)
$$

Where $P_{\cancel{olit}Litter \rightarrow plant}$ and $P_{\cancel{ohum}Humus \rightarrow plant}$ represent the biochemical mineralization fluxes from the litter and humus pools (g P m^{-2} day^{-1}), assuming immediate uptake by the plant roots after mineralization. $o_{uptPlitter}$ and $o_{uptPhumus}$ are coefficient parameters that define the maximum plant uptake rates from the soil litter and humus pools, respectively. $P_{\cancel{olit}Litter}$ and $P_{\cancel{ohum}Humus}$ are the pool sizes (g P m^{-2}), $frac_{P,litter}$ and $frac_{P,humus}$ are introduced to ensure that biochemical mineralization is less than the missing plant demand after P_{ilab} uptake, as well as to ensure proportional uptake from the $P_{\cancel{olit}Litter}$ and $P_{\cancel{ohum}Humus}$. In this modelling framework, the inorganic P_i, when released by enzymatic activities acquired directly by the plants rather than entering the P_i pool.

Total biochemical mineralization is calculated as,

$$P_{biochem} = P_{Litter \rightarrow plant} + P_{Humus \rightarrow plant} \qquad (A.5)$$

The total mineralization-immobilization flux is calculated as,

$$P_{totmin} = P_{biochem} + P_{biomin} \qquad (A.6)$$

As is the case with DOC/DON, in Coup-CNP, organic P dissolution is described as a microbial decomposition process. The redistribution is done following that of water flow, as the DOM is assumed to have full mobility with water. The formation of DOM is from litter and humus (equ A.7). The dissolved organic matter can be fixed by humus via adsorption, precipitation, etc. A fixation coefficient, d_{DOD}, which varies between layers, was introduced (Kalbitz et al., 2000; Kaiser and Kalbitz, 2012). Parameterization from Svensson et al. (2008) were used in this study. The equation for DOP is similar to that for DOC, and is calculated as,

$$
\begin{aligned}
P_{Litter \rightarrow DOP} &= d_{DO,l} \times f(T) \times f(\theta) \times P_{Litter} \\
P_{Humus \rightarrow DOP} &= f(T) \times f(\theta) \times (d_{DO,h} \times P_{Humus} - d_{DOD}(z) \times P_{DOP})
\end{aligned}
\qquad (A.7)
$$

Where $d_{DO,l}$, and $d_{DO,h}$ are the dissolution rate coefficients (day^{-1}) for the litter and humus, $f(T)$ and $f(\theta)$ are common response functions for soil temperature and water content, and identical to those used for the decomposition process (equ A.2).

A3 Plant growth and P uptake

Plants can acquire P_i through both the roots and mycorrhizal fungi; for this reason, both of these processes were simulated. We assume that uptake of P_i by roots is driven by net photosynthesis and determined by plant demand, yet constrained by the P_{ilab} pool size.

$$P_{ilab\rightarrow root} = min\ (p_{iavail} \times P_{ilab};\ P_{demand}) \tag{A.8}$$

Where P_{demand} is the plant P demand, based on the C/P ratios of various plant compartments ($_{iplant}$ includes leaf, stem, fine roots and coarse roots),

$$P_{demand} = \sum_{iplant} \frac{C_{a\rightarrow iplant} - C_{iplant\rightarrow a}}{cp_{iplant\min}} \tag{A.9}$$

Where $C_{a\rightarrow iplant}$ is the photosynthesis assimilation for each compartment $_{iplant}$ (g C m^{-2} day^{-1}), $C_{iplant\rightarrow a}$ is the respiration of each compartment, and $cp_{iplantmin}$ is the defined minimum C/P ratio for each plant compartment. Empirical measurements show that the C/P ratio of leaves generally varies between 200-600, while the stem requires C/P between 1000-3000 and roots require C/P between 500-1500 (Bell et al., 2014; Tang et al., 2018). It should be noted that the compartment C/P ratio is calculated for each time step; thus, the model provides flexible stoichiometry.

In addition, increasing soil P abundance, particularly when P fertilizer is added, is known to decrease belowground C allocation (Ericsson, 1995). We assume that an increasing C/P ratio (i.e. decreasing P content) in the leaf, C/P_l, will increase belowground allocation (e.g., $frac(root)$).

$$\begin{gathered} frac_{a\rightarrow root}(C/P_l) = r_{cpc1} + r_{cpc2} \times C/P_l \\ frac\left(root\right) = frac_{a\rightarrow root}(C/P_l) \times frac_{a\rightarrow root}(C/N_l) \\ C_{a\rightarrow root} = C_{a\rightarrow plant} \times frac\left(root\right) \end{gathered} \tag{A.10}$$

Where r_{cpc1} and r_{cpc2} are the plant allocation pattern parameters, determined by plant species and a similar equation as what was used to calculate $frac_{a\rightarrow root}(C/N_l)$ (He et al. 2018). CoupModel can additionally account for the effects of water stress on plant allocation. In this study, C allocation to roots is assumed to be constrained by both N and P contents in the leaves, i.e., $frac_{a\rightarrow root}(C/N_l)$ and $frac_{a\rightarrow root}(C/P_l)$.

A4 Plant litterfall

Plant litterfall P fluxes are proportional to the corresponding C fluxes, and determined by the C/P ratio of each compartment $_{iplant}$ ($_{iplant}$=leaf, steam, grain, fine roots, and coarse roots), calculated as,

$$P_{plant\rightarrow soil} = \sum_{iplant} \frac{c_{liplant} \times C_{iplant} \times (1 - m_{retain})}{C/P_{iplant}}$$ ~~$P_{plant\rightarrow soil} = \sum_{iplant} \frac{c_{liplant} \times C_{iplant} \times (1 - c_{iplantret})}{C/P_{iplant}}$~~

(A.11)

Where $c_{liplant}$ is the litterfall rate (day^{-1}) for plant compartment $iplant$, C_{iplant} is the C stock in that compartment (g C m^{-2}), and $c_{iplantret}$ is a parameter defined as the fraction that was retained before litterfall. Total litterfall also includes inputs from mycorrhizal fungi. The litterfall flux is directly added to the surface soil litter pool, or to the layer in which it formed when it was produced by roots and fungi. The average C/P ratio of fresh litter varies widely, 100 - 4100 (Manzoni et al. 2010). The retention of nutrients prior to leaf senescence is one of the main factors that affect the C/P ratio of fresh litter. During litterfall seasons, plants can reallocate P and N from leaves to an internal, mobile storage to prepare for rapid growth in the spring, a known mechanism to increase efficient use of nutrients (e.g. Aerts, 1996; Niemien and Helmisaari, 1996) (also see m_{retain} in Table S.1 in supplementary).

A5 Leaching and surface runoff

The losses of soluble $P_{isol,loss}$ (g P m^{-2} day^{-1}) are modelled through the transport of water,

$$P_{isol,loss} = \sum_{jlayer} P_{isoldrainage,j} + P_{isolpercolation}$$

$$P_{isoldrainage,jlayer} = \frac{P_{isol,j}}{\theta_{,j} \times \Delta z_{,j}} \times q_{drainage,j} \qquad \text{(A.12)}$$

$$P_{isolpercolation} = \frac{P_{isol}}{\theta \times \Delta z} \times q_{percolation}$$

Where $q_{drainage}$ is the water flow (mm day^{-1}) due to drainage, and $q_{percolation}$ is the deep percolation flow (mm day^{-1}), $\theta_{,j}$ is the water content (volume %) at the soil layer j, and $\Delta z_{,j}$ is the layer thickness (m) at soil layer j. The vertical P_i flow between layers is calculated through a similar equation.

DOP losses from the system is calculated as,

$$P_{DOP,loss} = \frac{P_{DOP}}{\theta \times \Delta z} \times \left(\sum_{jlayer} q_{drainage,j} + q_{percolation} \right) \qquad \text{(A.13)}$$

In addition, we also accounted for particulate phosphorus (*PP*) losses, e.g., due to soil erosion, subsidence and lateral losses of secondary minerals and occluded P due to surface runoff. We assume the *PP* loss is proportional to the water flow. When surface runoff occurs, for example, during snow melting, the loss is assumed to occur only for the first soil layer (soil surface).

$$P_{solid,loss} = q_{surfacerunoff} \times k_{scale}$$
$$k_{scale} = \min(1, \frac{q_{surfacerunoff}}{q_{thr}}) \times (P_{\Delta,i} - P_{base,i}) + P_{base,i} \quad \text{(A.14)}$$

Where $q_{surfacerunoff}$ is the surface runoff flow (mm day^{-1}). An empirical scale factor k_{scale} is introduced to account for the concentration of erodible $P_{solid\cancel{m}}$ over the flow rate of surface runoff. P_{Δ} (mg P l^{-1}), P_{base} (mg P l^{-1}) and q_{thr} (mm day^{-1}) are empirical coefficients.

Therefore, the total P losses are calculated as,

$$P_{totloss} = P_{isol,loss} + P_{DOP,loss} + P_{solid,loss} \quad \text{(A.15)}$$

A6 P removal during plant harvest

The removal of P during plant harvesting was calculated in a similar way as C losses through harvesting, and depends on the C/P ratio of the plant compartment.

Appendix B: Simulated annual mean P, N and C budgets, generated by varying three regional key parameters, including soil N/P ratio and the short-cut uptake rates ~~fungal organic uptake rates~~ for N and P

Table B1 Simulated annual P budget, with the associated uncertainty range (mean ± SD, g P m^{-2} year^{-1})

P budget	64°N	61°N	57°N	56°N
Weathering	0.014 (0.0002)	0.0094 (0.0002)	0.024 (0.0002)	0.025 (0.001)
Deposition	0.013	0.0065	0.028	0.023
Leaching	0.0025 (0.0003)	0.0015 (0.0003)	0.004 (0.0004)	0.006 (0.0009)
Harvest export	0.01 (0.002)	0.018 (0.003)	0.03 (0.004)	0.045 (0.01)
Change in plant	0.0125 (0.003)	0.007 (0.002)	0.018 (0.006)	0.017 (0.006)
Change in soil	-0.012 (0.005)	-0.02 (0.002)	-0.024 (0.005)	-0.045 (0.01)
Change in ecosystem	0.0005 (0.0004)	-0.013 (0.003)	-0.006 (0.003)	-0.028 (0.007)

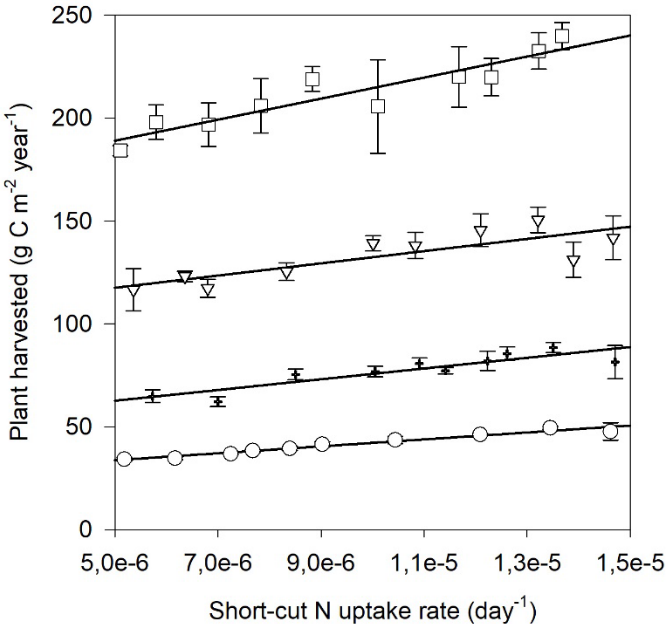
Table B2 Simulated annual N budget, with the associated uncertainty range (mean± SD, g N m^{-2} year^{-1})

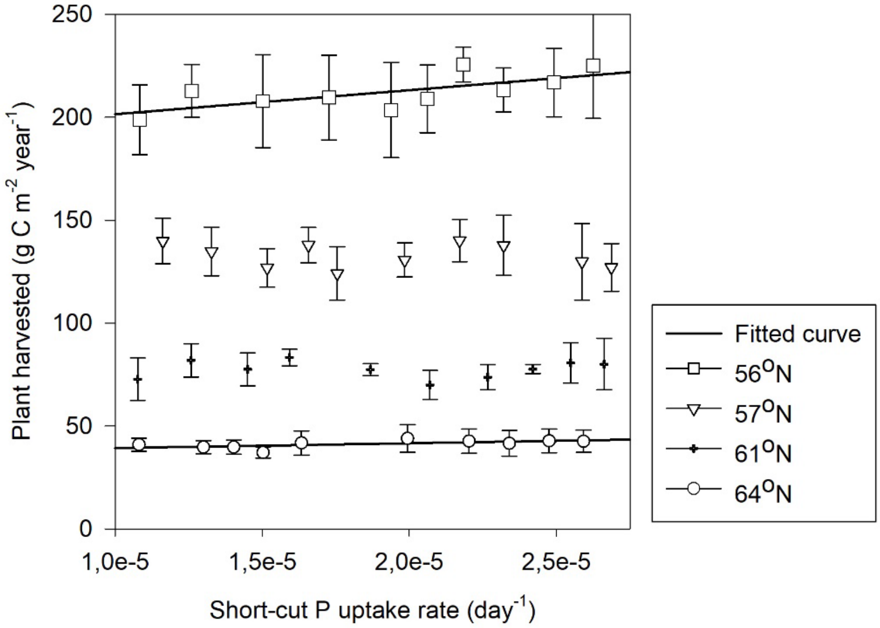
N budget	64ºN	61ºN	57ºN	56ºN
Deposition	0.15	0.35	0.78	1.26
Leaching	0.10 (0.004)	0.15 (0.02)	0.16 (0.05)	0.45 (0.15)
Harvest export	0.08 (0.01)	0.19 (0.02)	0.27 (0.04)	0.5 (0.19)
Change in plant	0.09 (0.009)	0.10 (0.008)	0.15 (0.03)	0.17 (0.01)
Change in soil	-0.12 (0.03)	-0.09 (0.02)	0.20 (0.05)	0.14 (0.03)
Change in ecosystem	-0.03 (0.005)	0.01 (0.008)	0.35 (0.03)	0.31 (0.09)

Table B3 Simulated annual C budget, with the associated uncertainty range (mean± SD, g C m^{-2} year^{-1})

C budget	64ºN	61ºN	57ºN	56ºN
Net ecosystem productivity	63 (7)	90 (10)	170 (19)	237 (21)
Leaching	0.8 (0.07)	0.6 (0.06)	0.4 (0.1)	0.3 (0.05)
Harvest export	50 (6)	81 (9)	145 (17)	201 (19)
Change in plant	10 (2)	12 (1)	18 (2)	20.7 (3)
Change in soil	2 (1)	-3.6 (6)	6.5 (4)	15 (7)
Change in ecosystem	12.2 (1)	8.4 (1)	24.5 (3)	35.7 (5)

Appendix C: Sensitivity of annual harvested biomass response to the varying short-cut uptake rates~~fungal organic uptake rates~~ for N and P


Plant harvested (g C m^{-2} year^{-1})
250
200
150
100
50
0
5,0e-6
7,0e-6
9,0e-6
1,1e-5
1,3e-5
1,5e-5
Short-cut N uptake rate (day^{-1})


Plant harvested (g C m^{-2} year^{-1})
250
200
150
100
50
0
1,0e-5
1,5e-5
2,0e-5
2,5e-5
Short-cut P uptake rate (day^{-1})
Fitted curve
56^{o}N
57^{o}N
61^{o}N
64^{o}N

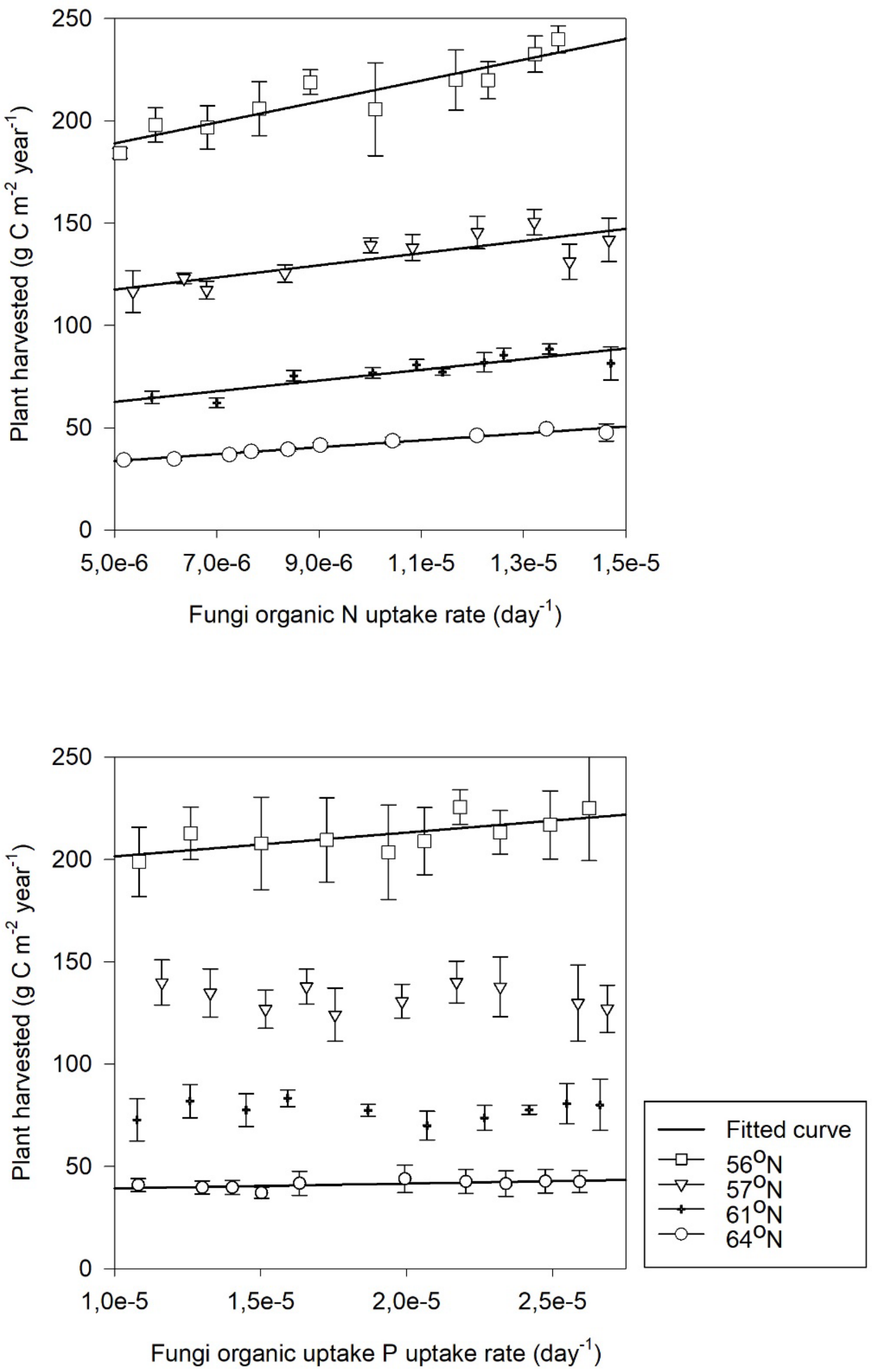


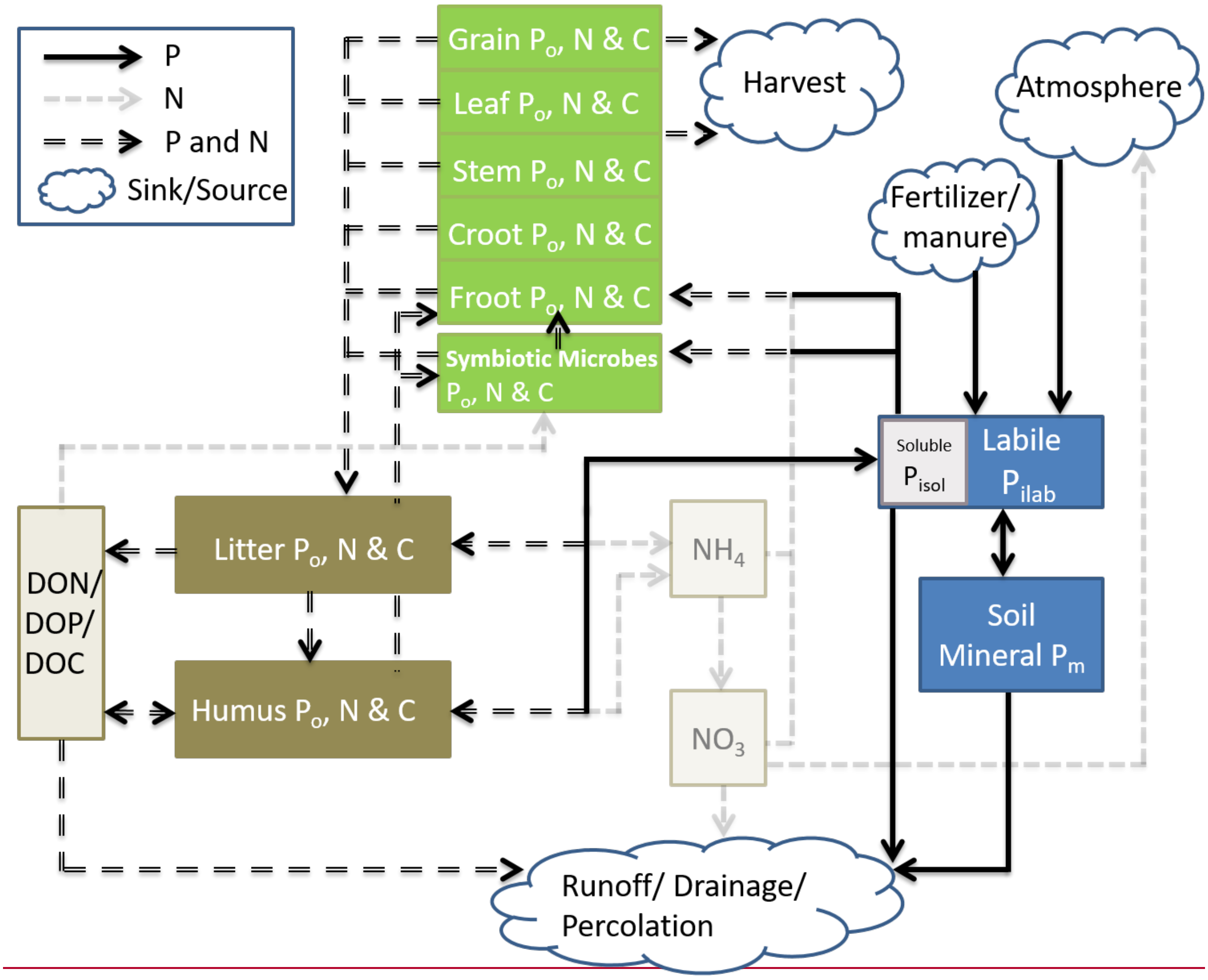
Fig. C1 Simulated annual mean (symbol) of harvested biomass response to varying short-cut uptake rates for N and P among the four regions. The bar indicates the standard deviation created by changes in the soil N/P ratio and short-cut uptake rates (Table 2)~~Simulated annual mean (symbol) of harvested biomass response to varying fungal organic uptake rates for N and P among the four regions. The bar indicates the standard deviation created by changes in the soil N/P ratio and fungal uptake rates (Table 2)~~

Author contributions. AG formulated the project, HH conducted the literature review and developed the phosphorus model concepts with AG and PEJ, HH and PEJ implemented the phosphorus cycle code into CoupModel. HH performed the simulations and analysis. HH drafted the manuscript, to which AG and PEJ contributed.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. The authors express their gratitude to all persons providing data and background information. Gunilla Pihl-Karlsson and Per-Erik Karlsson at IVL Göteborg provided regional P deposition data for the studied regions, Swedish Forest Agency (Olle Kellner) provided data on the needle P and N contents, soil P data, and regional P deposition data for the studied regions. Magnus Svensson provided the regional simulation files with CoupModel v4, and Thomas Bosshard at SMHI for the regional climate files. The Department of Aquatic Sciences and Assessment (SLU) contributed P concentrations from open water data, while the Swedish Geological Survey (SGU) provided regional mineral P content data. The Swedish Forest Soil Inventory provided soil C/N data. Cecilia Akeselson collected data for the SWETHRO project.

The Department of Biological and Environmental Sciences, University of Gothenburg and the strategic research area, along with ModElling the Regional and Global Earth system (MERGE), funded the study. MERGE provided SP project funding for “incorporating phosphorus cycle into ecosystem models”. The Formas-funded strong research environment IMPRESS. Further, we acknowledge the comments from participants of the N-P interaction workshops for the new model concepts funded by MERGE and BECC - Biodiversity and Ecosystem services in a Changing Climate.


P
N
P and N
Sink/Source
Grain P_o, N & C
Leaf P_o, N & C
Stem P_o, N & C
Croot P_o, N & C
Froot P_o, N & C
Symbiotic Microbes P_o, N & C
Harvest
Atmosphere
Fertilizer/ manure
Soluble P_{isol}
Labile P_{ilab}
Soil Mineral P_m
DON/ DOP/ DOC
Litter P_o, N & C
Humus P_o, N & C
NH_4
NO_3
Runoff/ Drainage/ Percolation

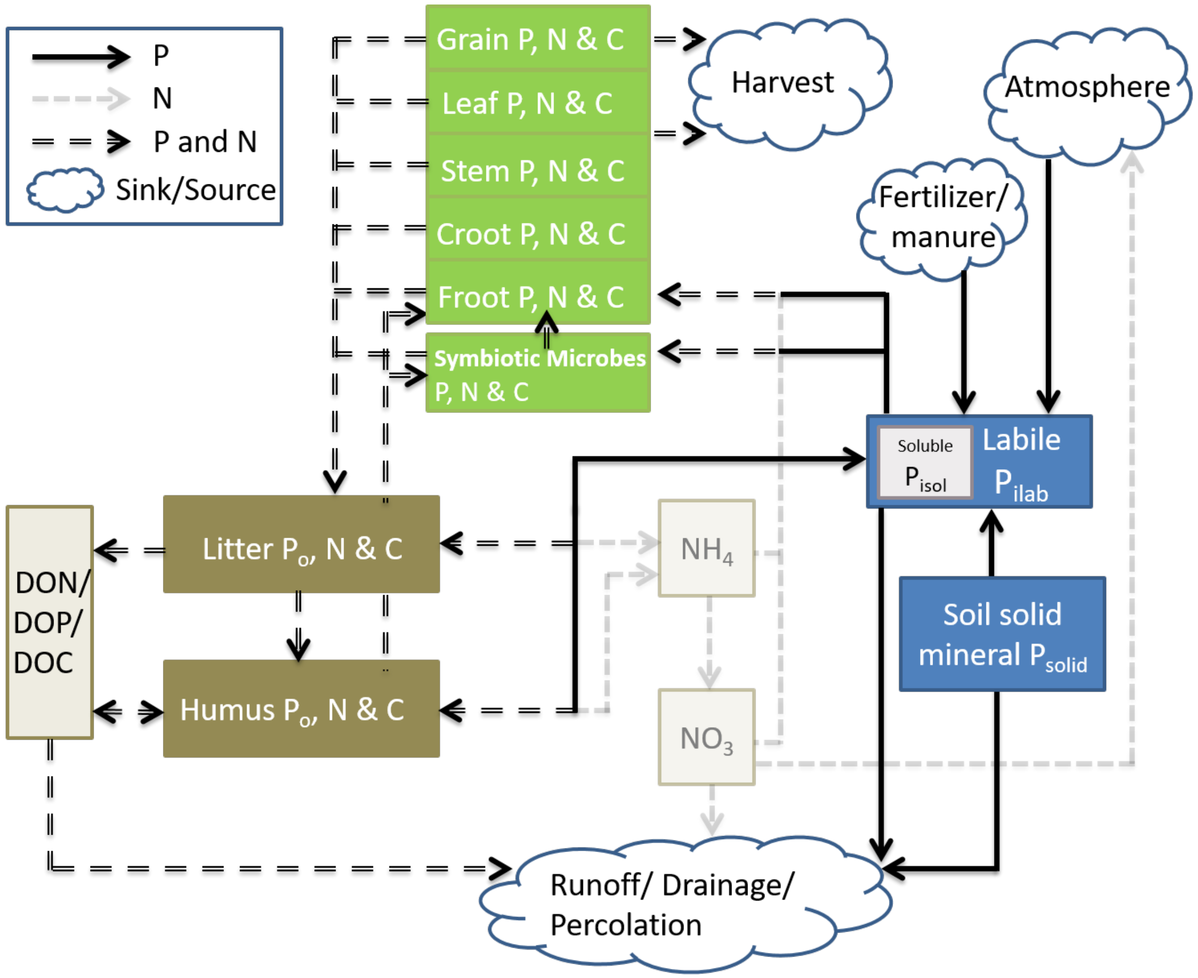


Fig. 1 Conceptual figure of simplified Coup-CNP and its link with the N cycle. Pools in green represent pools of plant-symbiotic microbes (e.g., mycorrhiza fungi), while brown represents soil organic matter, grayish-yellow represents water solutions and blue indicates the soil ~~mineral~~ inorganic P pools. Within the pools, Croot stands for coarse root and Froot stands for fine root.

Table 1 Overview of climatic, geological, plant and soil characteristics of the four forest regions

Regional characteristics	Västerbotten	Dalarna	Jönköping	Skåne
Latitude	64°N	61°N	57°N	56°N
Mean annual air temperature (°C)[a]	0.7	3.3	5.2	7.1
Mean annual precipitation (mm)[a]	613	630	712	838
Annual N deposition (kg N ha^{-1})[b]	1.5	3.5	7.5	12.5
Annual P deposition (kg P ha^{-1})[b]	0.13	0.06	0.28	0.23
Studied soil type ~~FAO (1990)~~	Podzol	Podzol	Podzol	Podzol
Quaternary deposit, SGU[c]	Glacial till	Glacial till	Glacial till	Glacial till
Bedrock geology, SGU[c]	Gneiss	Sandstone, Rhyolite~~olit~~Lit~~ter~~e	Gneiss	Gneiss
~~Mineral~~ Solid inorganic P content of till (mg kg^{-1})[d]	881	428	859	773
Major tree species Pine/Spruce/broadleaved trees (%)[f]	45/37/16	49/40/9	31/54/13	12/46/41
Rotation period, year	120	110	90	70
Thinning conducted at forest age, year (1st /2nd /3rd thinning)[h]	50/100	40/90	25/40/70	25/40/55
Measured plant biomass at 100 age class (g C m^{-2})[f]	5371	7815	10443	11501
Soil organic matter C/N (-)[e]	31.5	29.1	27.2	19.8
C/N humus[b]	43	40	31	25
Soil organic matter C/P (-)[b]	494	633	425	425
C/P humus[b]	~~Ca 325~~325	~~Ca 400~~400 ~~(320-505))~~	~~Ca 410~~410 ~~(Gynge 188)~~	~~Ca 550~~550
Soil organic matter N/P (-)	15.7	21.8	15.6	21.5
Initial Soil C (g C m^{-2})[f]	7006	8567	9995	10666
Litter C (g C m^{-2})[f]	350	428	500	533
Humus C (g C m^{-2})[f]	6655	8139	9495	10133
Initial Soil N (g N m^{-2})	223	295	367	539
Litter N (g N m^{-2})[f]	11	15	18	27
Humus N (g N m^{-2})[f]	212	280	349	512
Initial Soil P (g P m^{-2})	14.2	13.5	23.5	25.1
Litter P (g P m^{-2})[g]	0.7	0.7	1.2	1.3
Humus P (g P m^{-2})[g]	13.5	12.8	22.3	23.8
Soil pH[e]	5.1	5.1	5.1	4.9

[a] 30-year (1961 to 1991) annual average of regional SMHI stations

[b] N and P deposition data ~~and soil organic C/P ratio~~ were obtained from the SWETHTRO project and soil organic C/P ratio from Swedish Forest Agency.

[c] Geological Survey of Sweden (SGU), https://apps.sgu.se/kartvisare/

[d] according to Geochemical Atlas of Sweden. 2014, measured till samples at C horizon, c.a. 0.8 m below the soil surface

[e] calculated based on the Swedish Forest Soil Inventory data (SFSI. https://www.slu.se/en/Collaborative-Centres-and-Projects/Swedish-Forest-Soil-Inventory/)

[f] Svensson et al. (2008)

[g] assumption that 5% of the total organic pool is litter and 95% is humus, as reported for N in Svensson et al. (2008)

[h] Skogsdata (2012)

Table 2 Parameters with specific values for the different region

Region	Humus decomposition rate, k_h (day^{-1})[a]	Short-cut P uptake rate from humus pool (day^{-1})[b]~~Fungal organic P uptake rate from humus pool through biochemical mineralization (day^{-1})[b]~~	Short-cut N uptake rate from humus pool (day^{-1})[a]~~Fungal organic N uptake rate from humus pool (day^{-1})[a]~~
Västerbotten 64°N	0.00048	1.5×10^{-5}	1.5×10^{-5}
Dalarnas 61°N	0.00042	2.75×10^{-5}	1.2×10^{-5}
Jönköpings 57°N	0.0004	1.0×10^{-5}	1.0×10^{-5}
Skåne 56°N	0.00038	1.5×10^{-5}	0.5×10^{-5}

[a]: from He et al. (2018)

[b]: a high ~~fungal~~ short-cut P uptake rate was assumed for high soil organic matter C/P ratios

Table 3 Parameters **used for the default model run** for the P processes with common values of all four studied regions. Note that the same parameter values were applied for tree and understory layers if otherwise not specified.

Symbol	Parameter	Equation	Value	Unit	Reference
k_w	Integrated weathering rate	(1)	8×10^{-7}	day^{-1}	Guidry and Machenzie, (2000); Sverdrup and Warfvinge, (1993)
n_H	Weathering pH response coefficient	(4)	0.27	-	
pH_{opt}	Weathering pH response base coefficient	(4)	7	-	
$p_{max,ads}$	Langmuir max sorption capacity	(5)	0.0002	$g\ P\ g\ soil^{-1}$	Adjusted from Wang et al. (2007)
$c_{50,ads}$	Langmuir half saturation coefficient	(5)	5×10^{-5}	$g\ P\ m^{-2}$	
$p_{cp,opt}$	C/P optimal (leaf)	(8)	250	$gC\ gP^{-1}$	Thelin et al. (1998; 2002)
$p_{cp,th}$	C/P threshold (leaf)	(8)	600	$gC\ gP^{-1}$	
p_{avail}	P availability reduce C allocation coefficient	(9)	0.0009	-	Assumed
p_{fopt}	The optimum ratio between C allocation between fungi and root	(11)	0.22	-	He et al. (2018); Orwin et al. (2011)
k_{rm}	Respiration coefficient of fungi		0.01	day^{-1}	
p_{lrate}	Fungi litterfall rate	(15)	0.0045	day^{-1}	
n_{avail}	N availability reduce C allocation coefficient		0.00039	-	
$p_{i,rate}$	Potential unit fungal mycelia uptake rate PO_4	(19)	0.0001	$g\ P\ g\ C^{-1}\ m^{-2}\ day^{-1}$	Smith and Read, (2008)
$n_{NH4rate}$ / $n_{NO3rate}$	Potential unit fungal mycelia uptake rate NH_4/NO_3		0.0004	$g\ N\ g\ C^{-1}\ m^{-2}\ day^{-1}$	He et al. (2018)
$n_{\cancel{olit}Litter,rate}$ / $n_{\cancel{ohum}Humus,rate}$	Potential unit fungal mycelia uptake rate organic N,		0.00002	$g\ N\ g\ C^{-1}\ m^{-2}\ day^{-1}$	
$p_{cpfungimax}$	Fungi maximum C/P	(17)	200	$gC\ gP^{-1}$	Wallander et al. (2003); Zhang and Elser, (2017)
p_{iavail}	Maximum PO_4 uptake fraction for roots	(21)	0.008	-	
$p_{cpfungimin}$	Fungi minimum C/P	(22)	100	-	
$p_{\cancel{olit}Litter,rate}$ / $p_{\cancel{ohum}Humus,rate}$	Potential unit fungal mycelia uptake rate organic P	(23)	0.00002	$g\ P\ g\ C^{-1}\ m^{-2}\ day^{-1}$	Assumed to be the same as N
Soil organic P processes					
cp_m	C/P of non symbiotic microbes	(A.3)	350	$gC\ gP^{-1}$	Manzoni et al. (2010)

Uptake demand of P					
$cp_{leaf,\ min}$	Minimum C/P (leaf)	(A.9)	220	-	Bell et al. (2014); Tang et al. (2018)
$cp_{stem,\ min}$ / $cp_{croot,\ min}$	Minimum C/P, for stem and coarse roots	(A.9)	4000/ 800	-	
$cp_{root,\ min}$	Minimum C/P ratio (fine roots)	(A.9)	400	-	
Plant Litterfall processes					
	Leaf litterfall rate for understory		0.0015	day^{-1}	Calibrated
Plant surface cover					
	Surface maximum canopy cover, forest		0.8	$m^2\ m^{-2}$	Assumed
	Surface maximum canopy cover, understory		1	$m^2\ m^{-2}$	Assumed
Erosion					
~~P_{base}~~p_{base}	P concentration scaling coefficient for surface erosion 1	(A.14)	2.7×10^{-6}	$mg\ l^{-1}$	Assumed
~~P~~p_{Δ}	P concentration scaling coefficient for surface erosion 2	(A.14)	7×10^{-6}	$mg\ l^{-1}$	
q_{thr}	Critical surface flow rate for erosion	(A.14)	10	$mm\ day^{-1}$	

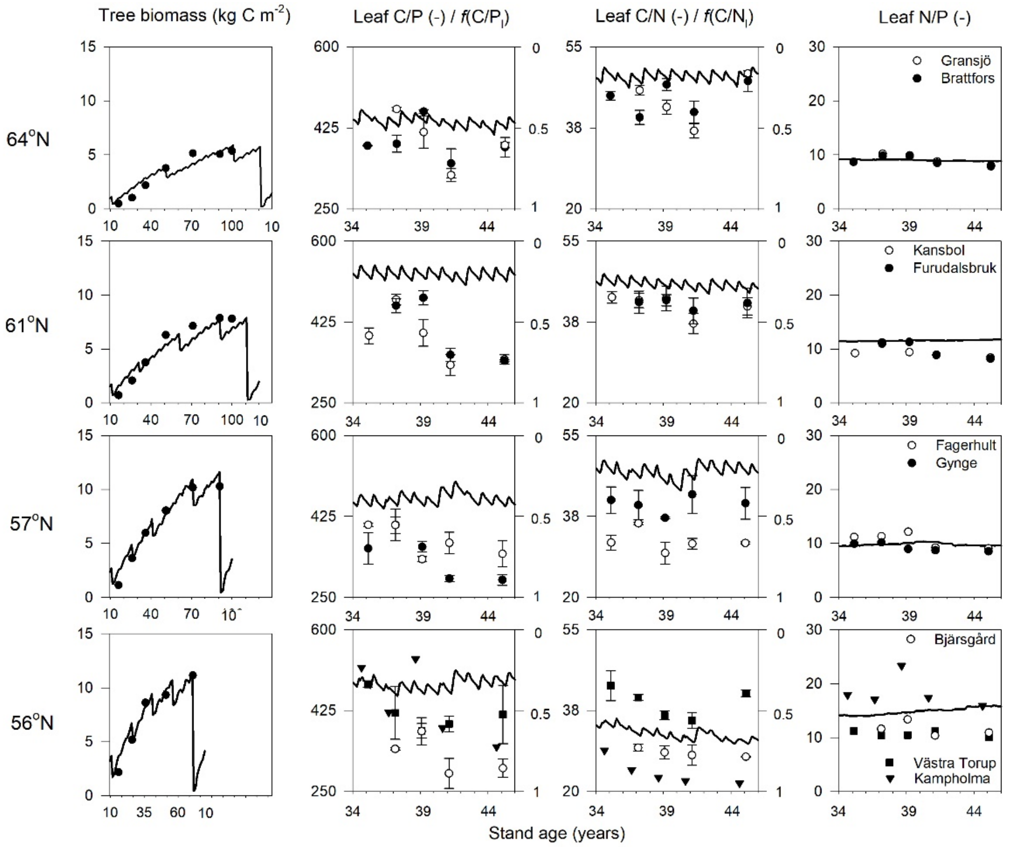


Fig. 2 Simulated (lines) and measured (symbols) plant biomass and leaf C/P, C/N and N/P ratios over the rotation period across the four regions. The x-axis is the stand age in years. The right axis in leaf C/P and C/N figure shows the minimum (*f*(nutrient)=0) and optimum (*f*(nutrient)=1) responses to gross primary production (GPP), respectively. Biomass data and leaf nutrient data were from SFI (SLU, 2003) and the ~~SWETHTRO project (Pihl Karlsson et al., 2015)~~Swedish Forest Agency.

Table 4 Summary of the plant-fungal internal C, N and P variables (shown as average values over the rotations period) of the simulated forest ecosystems. Bold values indicate a limiting response for GPP, according to the Liebig's law of minimum. The scale of response for GPP including temperature, water, N and P ranges from 0 (meaning none assimilation) to 1 (meaning optimal growth conditions).

Variable	Unit	64°N	61 °N	57 °N	56 °N
Net primary production, tree layer	g C m^{-2} $year^{-1}$	205	302	486	600
Radiation adsorbed, tree layer	×10^{6} J m^{-2} day^{-1}	3.89	5.35	6.50	6.57
Temperature response for GPP, tree layer	-	0.47	0.52	0.63	0.67
Water response for GPP, tree layer	-	0.45	0.50	0.63	0.65
Response N for GPP, tree layer	-	**0.22**	0.45	**0.30**	0.80
Response P for GPP, tree layer	-	0.56	**0.23**	0.34	**0.33**
Total plant uptake, N	g N m^{-2} $year^{-1}$	3.67	5.76	9.00	13.8
Total plant uptake, P	g P m^{-2} $year^{-1}$	0.42	0.49	0.87	1.08
~~Organic~~ Short-cut N uptake fraction (of total)	-	0.34	0.21	0.17	0.05
~~Organic~~ Short-cut P uptake fraction (of total)	-	0.14	0.23	0.10	0.14
Fungal N uptake fraction (of total)	-	0.68	0.69	0.66	0.65
Fungal P uptake fraction (of total)	-	0.56	0.57	0.56	0.56
Fungal N transfer to plant (of total)	-	0.31	0.31	0.33	0.34
Fungal P transfer to plant (of total)	-	0.44	0.43	0.43	0.43
Total plant litter, N	g N m^{-2} $year^{-1}$	3.50	5.47	8.61	13.2
Total plant litter, P	g P m^{-2} $year^{-1}$	0.40	0.47	0.82	1.02
Fungi N litter (of total ~~plant~~ litter)	-	0.38	0.40	0.35	0.33
Fungi P litter (of total ~~plant~~ litter)	-	0.13	0.15	0.14	0.13

Table 5 Simulated annual average soil C changes (g C m^{-2} $year^{-1}$, positive mean sequestration, negative mean losses), with comparisons to previous studies. Values in parentheses indicate uncertainties due to certain model parameters.

Studies	Approach	64ºN	61 ºN	57 ºN	56 ºN
Svensson et al. (2008)	Coup-CN implicit mycorrhiza	-5	-2	9	23
He et al. (2018)	Coup-CN implicit mycorrhiza	-6 (10)	-5 (11)	3 (13)	13 (13)
	Coup-CN explicit mycorrhiza	-8 (11)	-9 (12)	-5 (15)	-1 (19)
This study	Coup-CNP explicit mycorrhiza	2	-2	9	15

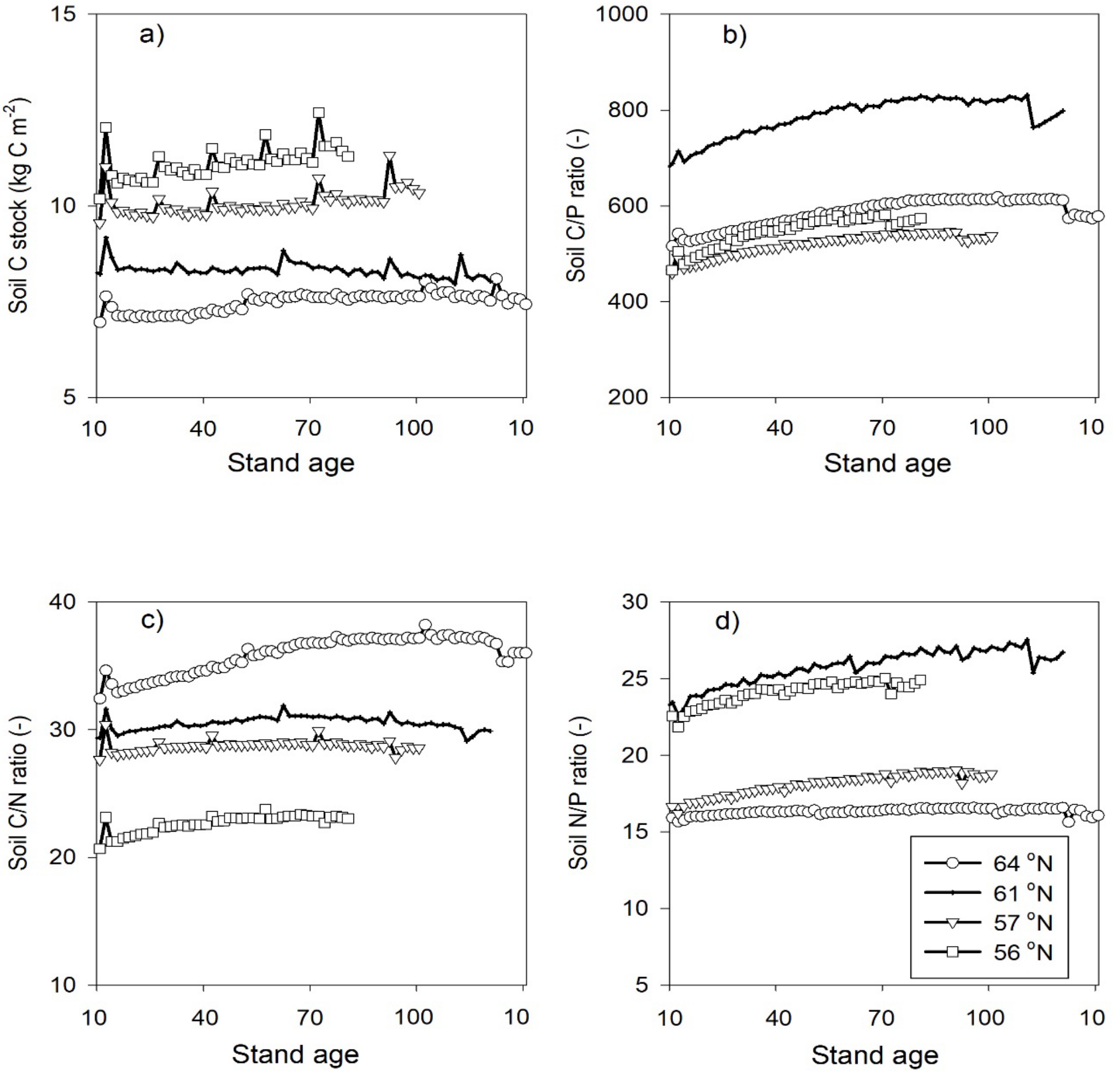


Fig 3. Simulated a) soil C stocks, b) soil C/P, c) soil C/N and d) soil N/P ratios over the rotation period from relative age 10 to 10 years after the final harvest. Rotation period increases from South to North Sweden and the small peaks in soil C were related to forest operations, which were more frequent in southern Sweden. At all latitudes, a clearance at year 10 was conducted. Thinnings varied from four in southern to two in northern Sweden.

Table 6 Simulated and measured annual P losses through leaching. Note that TP measured is more than the simulated model fraction DOP and PO4 due to the presence of particulate phosphorus and the measured value contains P leaching from upstream.

P leaching	64°N	61 °N	57 °N	56 °N
Annual regional total P leaching, measured (kg P ha^{-1})	0.04	0.02	0.09	0.08
Annual regional total P leaching, simulated (kg P ha^{-1})	0.03	0.01	0.05	0.07
Average TP concentration, measured (mg l^{-1})	0.0067	0.0066	0.03	0.02
Average PO$_4$+DOP concentration, Simulated (mg l^{-1})	0.0056	0.002	0.003	0.006
The fraction of dissolved organic P of total leaching, measured	63%	64%	83%	61%
The fraction of dissolved organic P of total leaching, Simulated	56%	74%	15%	12%

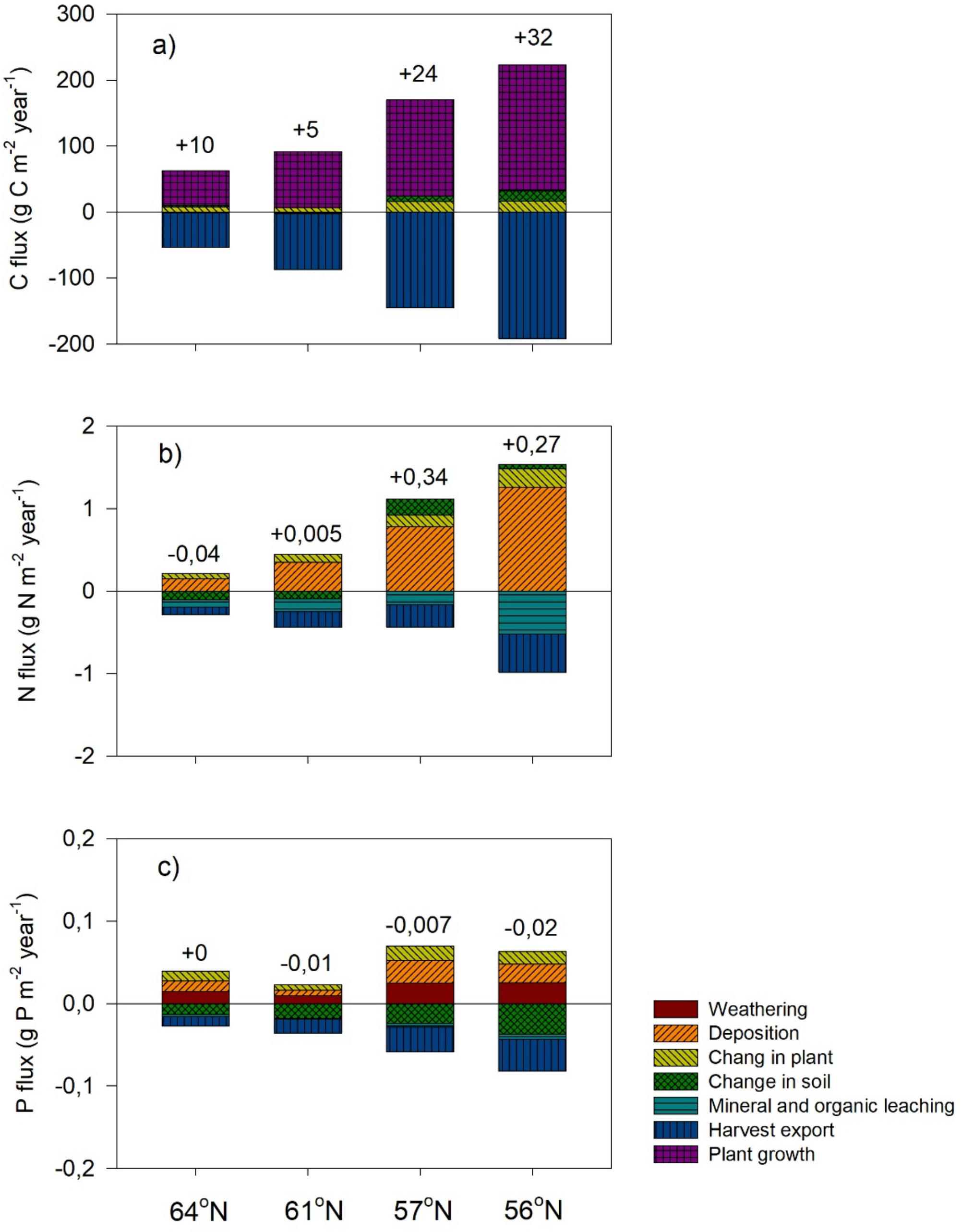


Fig. 4 Simulated annual mean major fluxes in a) C, b) N and c) P in the four regions. The numbers above the stacks indicate the annual mean change in the ecosystem. Note the

simulation period starts from year 10 and ends 10 years after final felling. Plant growth in a) represent the net primary production.

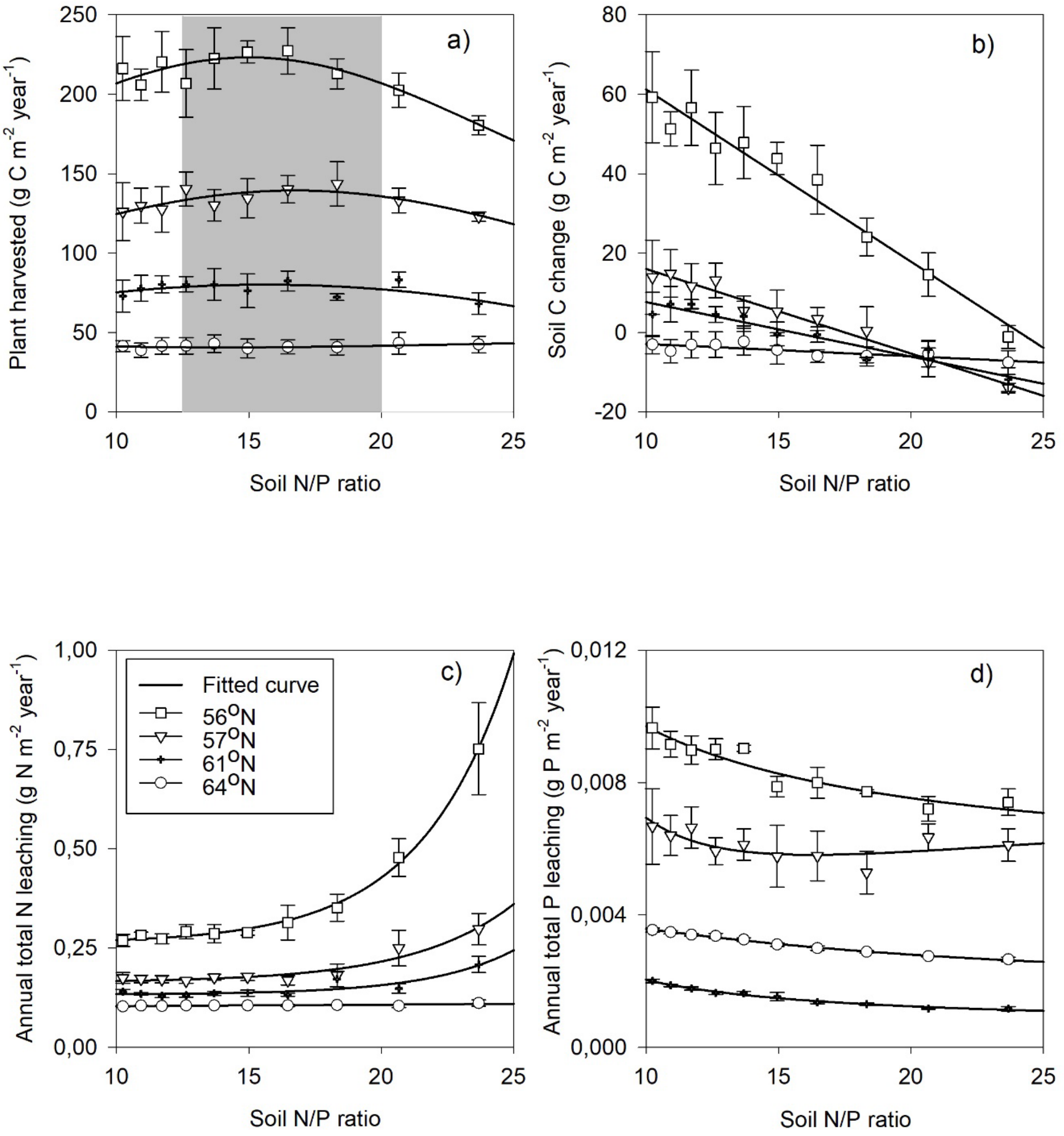


Fig. 5 Simulated annual mean (symbol) a) harvested biomass, b) soil C change (positive mean sequestration, negative mean losses), c) total N leaching and d) total P leaching response to changing soil organic N/P ratio in the four regions. The bar indicates standard deviation created by changes in short-cut uptake ~~fungal uptake~~ rates of N and P (see Table 2).

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