Soil Biology and Biochemistry 165 (2022) 108489

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Sporadic P limitation constrains microbial growth and facilitates SOM accumulation in the stoichiometrically coupled, acclimating microbe–plant–soil model

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ARTICLE INFO

Keywords:
Stoichiometry
Modeling
Microbial physiology
Tundra
Climate change

ABSTRACT

Requirements for biomass carbon (C), nitrogen (N), and phosphorus (P) constrain organism growth and are important agents for structuring ecosystems. Arctic tundra habitats are strongly nutrient limited as decomposition and recycling of nutrients are slowed by low temperature. Modeling interactions among these elemental cycles affords an opportunity to explore how disturbances such as climate change might differentially affect these nutrient cycles. Here we introduce a C–N–P-coupled version of the Stoichiometrically Coupled Acclimating Microbe-Plant-Soil (SCAMPS) model, "SCAMPS-CNP", and a corresponding modified CN-only model, "SCAMPS-CN". We compared how SCAMPS-CNP and the modified SCAMPS-CN models project a moderate (RCP 6.0) air warming scenario will impact tussock tundra nutrient availability and ecosystem C stocks. SCAMPS-CNP was characterized by larger SOM and smaller organism C stocks compared to SCAMPS-CN, and a greater reduction in ecosystem C stocks under warming. This difference can largely be attributed to a smaller microbial biomass in the CNP model, which, instead of being driven by direct costs of P acquisition, was driven by variable resource limitation due to asynchronous C, N, and P availability and demand. Warming facilitated a greater relative increase in plant and microbial biomass in SCAMPS-CNP, however, facilitated by increased extracellular enzyme pools and activity, which more than offset the metabolic costs associated with their production. Although the microbial community was able to flexibly adapt its stoichiometry and become more bacteria-like (N-rich) in both models, its stoichiometry deviated further from its target value in the CNP model because of the need to balance cellular NP ratio. Our results indicate that seasonality and asynchrony in resources affect predicted changes in ecosystem C storage under warming in these models, and therefore build on a growing body of literature indicating stoichiometry should be considered in carbon cycling projections.

1. Introduction

Organisms must navigate a complex web of trade-offs to survive. One key constraint on both the survival and composition of plant and microbial communities is stoichiometry (Sterner and Elser, 2002), or the ratio of elements such as carbon (C), nitrogen (N), and phosphorus (P) in organisms and their environment. Disturbances such as elevated CO_2, warming, drought and fire can differentially-affect these elemental cycles (Buckeridge and Grogan, 2008, 2010; Bret-Harte et al., 2013), potentially leading to stoichiometric imbalance. Given the increasing frequency of these disturbances in the Arctic, there is a growing need for a mechanistic understanding of how changes to the C, N, and P cycles will drive changes in ecosystem C stocks in tundra ecosystems. Microbes are likely to be central to this response; they form the backbone of all biogeochemical cycles (Falkowski et al., 2008) and can recycle nutrients locked up in soil organic matter (SOM) back into plant-available forms. Microbes are increasingly being explicitly included in C cycling models (Allison, 2012; Wieder et al., 2014), but rarely do they include both multiple elements and an adaptable microbial community (Sistla et al., 2014; Kyker-Snowman et al., 2020). Modeling the competition and collaboration between plants and microbes for access to elements and the capacity of these organisms to flexibly allocate elemental resources according to need might allow researchers to explore the nuanced responses of tundra ecosystems to climate change (Sistla et al., 2014).

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https://doi.org/10.1016/j.soilbio.2021.108489
Received 9 May 2021; Received in revised form 29 September 2021; Accepted 3 October 2021

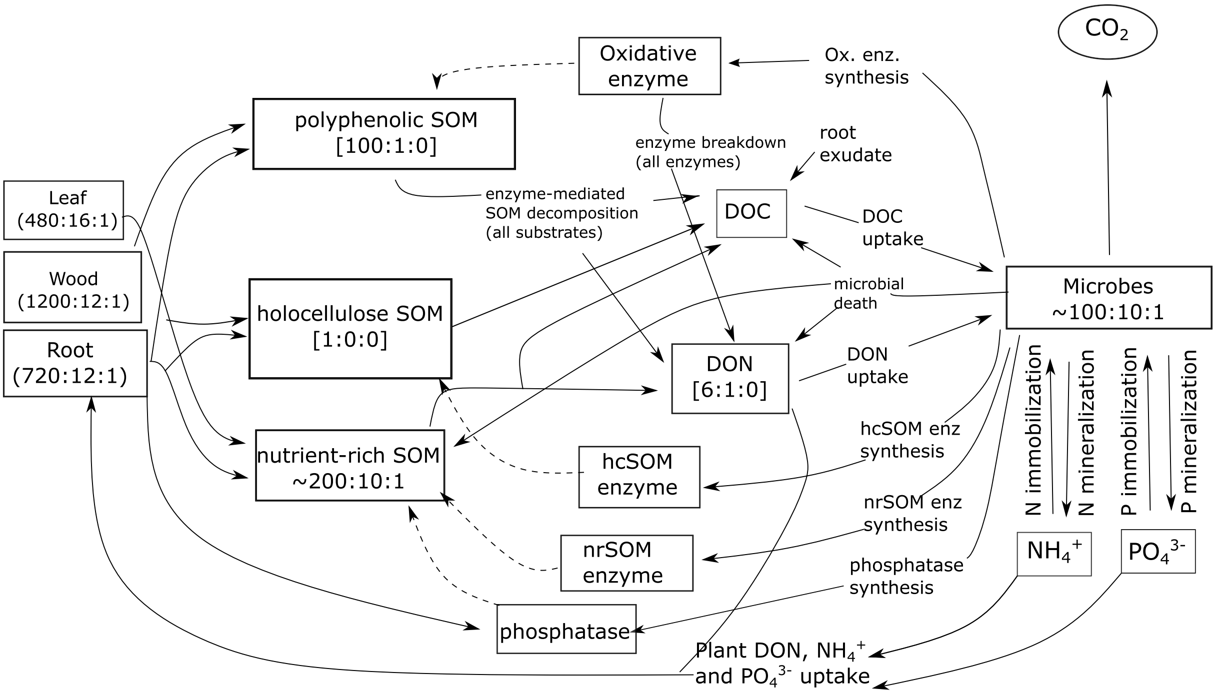

Fig. 1. Outline of the SCAMPS-CNP biogeochemical cycling model. Boxes denote pools of carbon (C), nitrogen (N), and phosphorus (P), and text without boxes denote processes contributing to these pools. Solid arrows denote transfer of mass, and dashed arrows denote the process of enzymes acting on substrates. Numbers in boxes denote C:N:P ratios; square brackets denote pools with strictly maintained stoichiometry, round parentheses denote target ratios with some deviation, and values without parentheses denote initial stoichiometries of pools with flexible stoichiometries. There are three classes of soil organic matter and four microbially produced extracellular enzymes targeting these SOM pools (phosphatase just cleaves P from nutrient-rich SOM and leaves the organic portion intact). The microbial community C:N ratio is either fixed at 10 or acclimates between a more bacteria-like (lower biomass C:N target (4), faster turnover) and fungal-like community (higher C:N (16), slower turnover) according to soil organic matter and dissolve resource conditions. Plants dynamically allocate N (and P) to wood, leaf, and root growth based on N uptake. Resorption of nutrients over winter ensures that litter inputs to soil are less nutrient-rich than remaining "green" plant biomass. DOC leaching is not shown for space reasons.

Plasticity of organismal- and community-level C:nutrient balance ("stoichiometric flexibility") regulates both the extent and mechanisms by which an ecosystem responds to altered nutrient availability and is relevant for projecting ecosystem C storage potential. This flexibility is scale dependent (Sistla and Schimel, 2012); the stoichiometry of macromolecules such as DNA or phospholipids are fixed within a relatively narrow range, but cells can change their macromolecular composition through the production and catabolism of storage compounds such as ribosomes, polyphosphate, starch and polyhydroxyalkanoates granules as needs change (Wilkinson, 1963; Zundel et al., 2009, Akbari et al., 2021). Multicellular organisms might also change their stoichiometry by allocating resources to organs with different resource requirements, such as N- and P- poor wood versus N- and P- rich leaves. Finally, stoichiometric flexibility can occur at the community-level through changes in community composition, such as increases in C-rich woody species over nutrient-rich herbaceous species, or C-rich fungi over nutrient-rich bacteria (Cleveland and Liptzin, 2007; Mouginot et al., 2014).

There is considerable uncertainty in the relative importance of these scales of acclimation in ecosystem C dynamics (Schade et al., 2005; Sistla and Schimel, 2012). However, changes in the relative allocation of biomass to nutrient-rich versus nutrient-poor tissues and in the relative abundance of nutrient-rich vs. nutrient-poor species appear to be more important than within-organ shifts in C:N:P ratio for tundra plant community response to altered nutrient availability (Hobbie and Chapin, 1998; Bret-Harte et al., 2013; Sistla et al., 2013). No matter the scale of adaptation assumed, all stoichiometric ecosystem models assume that organism growth depends on the ability to manage differences between the environment and themselves, and to obtain sufficient quantities of the most limiting nutrients to survive. The pursuit of nutrients by organisms and the ability to attain those nutrients then drives changes in ecosystem C, N, and P stocks and the flow of nutrients in and out of these pools.

Tundra habitat biogeochemistry is particularly susceptible to warming disturbance because low temperatures historically inhibited decomposition (Shaver et al., 2006) and C stocks equivalent to twice the C in the atmosphere have accumulated in the soil (Tarnocai et al., 2009). As soil thaws and the organic matter is no longer protected by low temperatures, decomposition can accelerate and release N and P that were historically unavailable to plants and microbes. Tundra habitats also receive minimal external N or P inputs; tight internal nutrient cycling is an essential regulator of plant growth, and catastrophic loss of nutrients because of rapid thaw events such as thermal erosion might have dramatic and long-lasting impacts on primary production (Pearce et al., 2015). Additionally, tundra plant communities are very sensitive to climate warming, as evidenced by both widespread arctic greening driven by increasing shrub abundance with higher C:N ratios than the non-woody plants they replace (Shaver and Chapin, 1991), and browning following frost, fire, and drought (Myers-Smith et al., 2020). Because our knowledge of coupled C, N, and P cycle responses to warming in arctic systems is patchy (Pold et al., 2021), modeling linkages among these cycles allowed us to explore potential warming scenarios in the tussock tundra.

The Stoichiometrically Coupled Acclimating Microbe-Plant-Soil (SCAMPS) (Sistla et al., 2014) model simulates how changes in resource allocation strategies and organism stoichiometry drive tussock tundra response to climate warming. Here we developed a version of SCAMPS that includes P ("SCAMPS-CNP") and compared the changes it predicts in C and N cycling under warming to those predicted by a modified version of the originally published "C–N only" version of the model. We hypothesized that (1) additional growth constraints— such as the presence P in SCAMPS-CNP compared to SCAMPS-CN — limit the ability of plants and microbes to adjust their stoichiometry in response

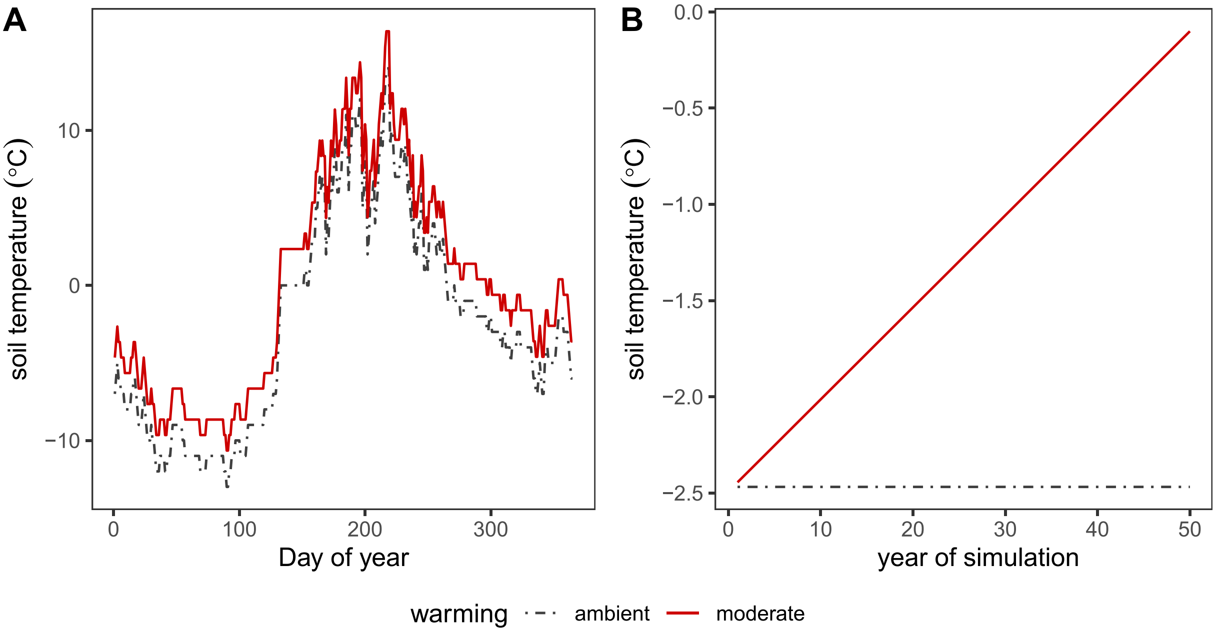

Fig. 2. Plot A on the left shows daily soil temperature in the final year of the simulation. The X axis shows day of year from 0 to 365. The y axis shows soil temperature in degrees Celsius, from -12.5 to 17.5C. A black line denotes the control scenario. It shows a decrease in temperature from -5C at day zero to -10C at day 30. On day 90, the temperature starts to increase towards 0C, slowly at first and then almost vertically by day 140. The soil temperature increases irregularly to 12C by day 200, and then starts to decline again. A red line appears 2C above the black line and denotes soil temperatures in the warmed scenario.

to disturbance; and (2) plant biomass accumulation and SOM loss are more constrained under warming when P is included. These effects would be consistent with the observations that adding additional limiting resources such as N in C-only models on a global scale (Thornton et al., 2007) or P in C:N-only models in tropical sites constrains CO_2 fertilization effects in plant biomass (Fleischer et al., 2019), and that alleviating both N and P limitation in tussock tundra increases some plant species' biomass more than alleviating limitation of either element alone (Gough and Hobbie, 2003; Wang et al., 2017).

2. Methods

2.1. SCAMPS-CNP model description

SCAMPS-CNP is a stoichiometrically-coupled model in which plants and microbial decomposers interact and compete with one-another for access to nutrients (Fig. 1). The model simulates transfer of C, N, and P among organic soil, microbes and plants using a daily timestep, and is driven by temperature and day of year. The system is assumed to be closed with respect to N and P, but open with respect to C, such that C enters the system via photosynthesis and leaves the system via microbial respiration and DOC leaching, but N and P move only among the plant, soil and microbial pools.

We assume plants have unlimited access to resources other than N and P. Plant N uptake is allocated to root, leaf, and wood, with more allocated to roots and leaves under low N uptake rates and to wood under nutrient-replete ones. The allocation of P uptake parallels that of N to balance stoichiometry in the three plant organs. Plants produce phosphatase enzyme to increase available P. Plants lose C, N, and P via litterfall, during which N and P are preferentially retained in the plant (resorbed) according to limitation status and are used for new growth in the spring. This litter then becomes part of the soil organic matter pool (SOM), which consists of holocellulose (hcSOM), polyphenolic soil organic matter (ppSOM; lignin), and nutrient-rich SOM (nrSOM).

Microbes produce extracellular enzymes to break down this SOM. hcSOM and ppSOM are each broken down by one class of enzyme, but a separate enzyme cleaves P from nrSOM than cleaves C and N from it (Fig. 1). Microbes have a certain amount of resources available for extracellular enzyme production depending on their biomass, but the fraction of that resource pool is distributed between production of different enzyme classes (i.e. relative effort) according to need. More effort is allocated to synthesizing a given enzyme when its substrate is abundant and products are deficient relative to the demand for those products (Supplementary file 1, equation B.2). Demand for nutrient-rich SOM is relatively greater when microbial biomass is enriched in C compared to its target C:N ratio. The target N:P ratio is fixed at 10, but the target C:N ratio can either be parameterized as fixed at 10, or to flexibly vary between 4 and 16 depending on the relative abundance of the different SOM and dissolved nutrient pools. Low C:N (bacteria-like) and high C:N (fungus-like) communities are characterized, respectively, by slow versus high turnover and the production of more polyphenolic-SOM versus nutrient-rich SOM-targeting extracellular enzyme pools. Microbes can also attain their target C:N:P ratio through preferential uptake and mineralization. Mineralization serves as an important source of N for plants because although they can take up both organic and inorganic N, they depend primarily on inorganic N.

A modified version of the original CN-only version of SCAMPS was structured and parameterized identically to the CNP model, with the exception of P-related processes. We refer to this modified model as "SCAMPS-CN". The SCAMPS models are coded in Lazarus 1.8.4 (2018) Free Pascal. A full list of modifications to the original CN model and a rationale can be found in Supplementary File 1. The reader is directed to Sistla et al. (2014) for a more complete description of the rationale behind the model and the formulation of plant and microbial processes.

2.2. SCAMPS-CNP parameterization

We adjusted model parameterization from the original SCAMPS model so that both SCAMPS-CNP and SCAMPS-CN could both spin up under ambient climate scenarios and run under warmed scenarios. We derived P-specific parameters and pools from the literature where possible and otherwise set initial P pools to 10% of the N pool values. Parameterization was adjusted so that SCAMPS-CNP's plant, microbial, and soil C and N stocks were consistent with field observations of moist

Table 1
Carbon and nutrient stocks at the 50th year of simulations with a stoichiometrically-flexible microbial community. Numbers in parentheses indicate percent change with warming for a given model (100*(warmed – ambient)/ambient). All units are in g m^{-2}.

Variable	SCAMPS-CN ambient soil temperature	SCAMPS-CN warmed soil temperature	SCAMPS-CNP ambient soil temperature	SCAMPS-CNP warmed soil temperature
EcosystemC	3471	3182 (−8)	4973	4180 (−16)
Total soil C	2651	2112 (−20)	4558	3484 (−24)
Wood C	212	287 (35)	107	179 (67)
N	2.12	2.88 (36)	1.03	1.24 (20)
P	NA	NA	0.087	0.089 (2)
Leaf C	95	129 (36)	48	78 (63)
N	3.45	4.69 (36)	1.75	2.84 (62)
P	NA	NA	0.1	0.15 (50)
Root C	356	481 (35)	180	308 (71)
N	5.99	8.09 (35)	3.02	5.17 (71)
P	NA	NA	0.25	0.41 (64)
Root:shoot ratio	1.16	1.16 (0)	1.16	1.20 (3)
Wood:leaf ratio	2.23	2.23 (0)	2.23	2.29 (3)
Litter C	153	208 (36)	77	130 (69)
N	2.14	2.91 (36)	1.12	2.02 (80)
P	NA	NA	0.0436	0.0675 (55)
Litter C:N:P	71.5:1:0	71.5:1:0 (0)	1766:25.7:1	1926:29.9:1 (0)
Microbial C	129	139 (8)	63	101 (60)
N	14.1	16 (13)	6.4	11.1 (73)
P	NA	NA	0.63	1.11 (76)

acidic tussock tundra at the Arctic LTER (Sistla et al., 2014; Supplementary Table 1). We ran the modified SCAMPS-CN with identical drivers and parameters to SCAMPS-CNP; this enabled us to directly compare predictions from the two models. A full description of model parameters and references for their values can be found in **Supplementary File 1.**

2.3. Climate warming simulations

We ran SCAMPS-CN and SCAMPS-CNP under the "ambient" conditions the latter was initially parameterized to, corresponding to repeating a year of daily soil temperature data from Toolik Lake LTER in 2010 (Jim Laundre, personal communication), and compared results to a "warmed" scenario. The warmed scenario increased soil temperatures by 0.048 °C yr^{-1}, which corresponds to the 50 year increase in mean annual air temperatures predicted by CMIP5 downscaled to Anaktuvuk Pass, AK, USA under a moderate (RCP 6.0) emissions scenario (Van Vuuren et al., 2011; Walsh, 2018). Both ambient and moderate warming scenarios were run for 50 years following spin-up under ambient conditions (Fig. 2); while the temperature driver under ambient conditions repeated the same constant annual cycle over the comparable period. We report annual mean pool sizes over this period to describe overall warming trajectories, and the 50th year of the simulation to examine seasonal variation in nutrient pools and ecosystem processes. Figures were generated in R v. 4.04 (R Core Team, 2021) using ggplot2 v. 3.3.3 (Wickham, 2016). Where data were available, we compared our simulations to a recent meta-analysis of observations from field warming experiments to identify where the models perform comparatively well (Pold et al., 2021).

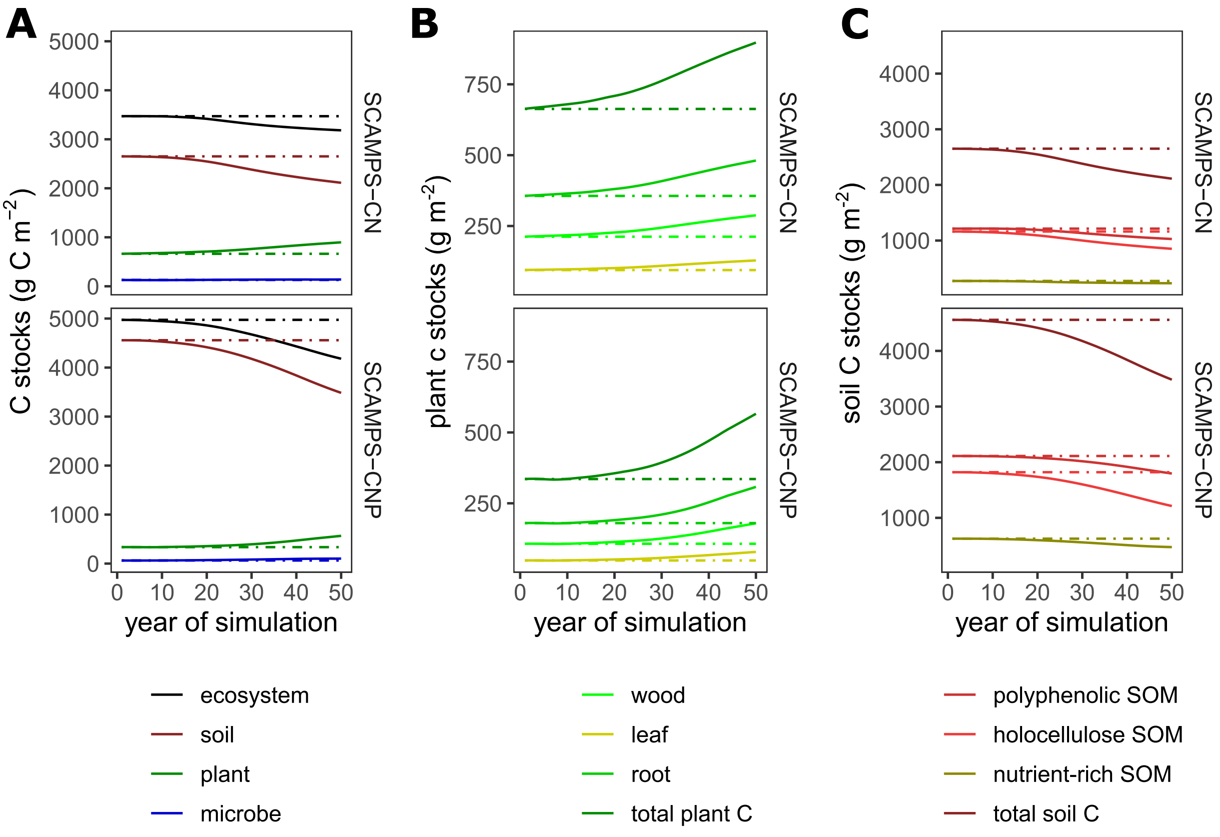

Fig. 3. Effect of simulated warming on mean annual carbon stocks. Total ecosystem C stocks and main constituent pools (a), plant organs (b) and soil organic matter pools (C). Dot-dashed lines denote ambient scenarios and solid lines the moderate warming scenario. SCAMPS-CN and SCAMPS-CNP were spun up under ambient temperature prior to the onset of warming simulations.

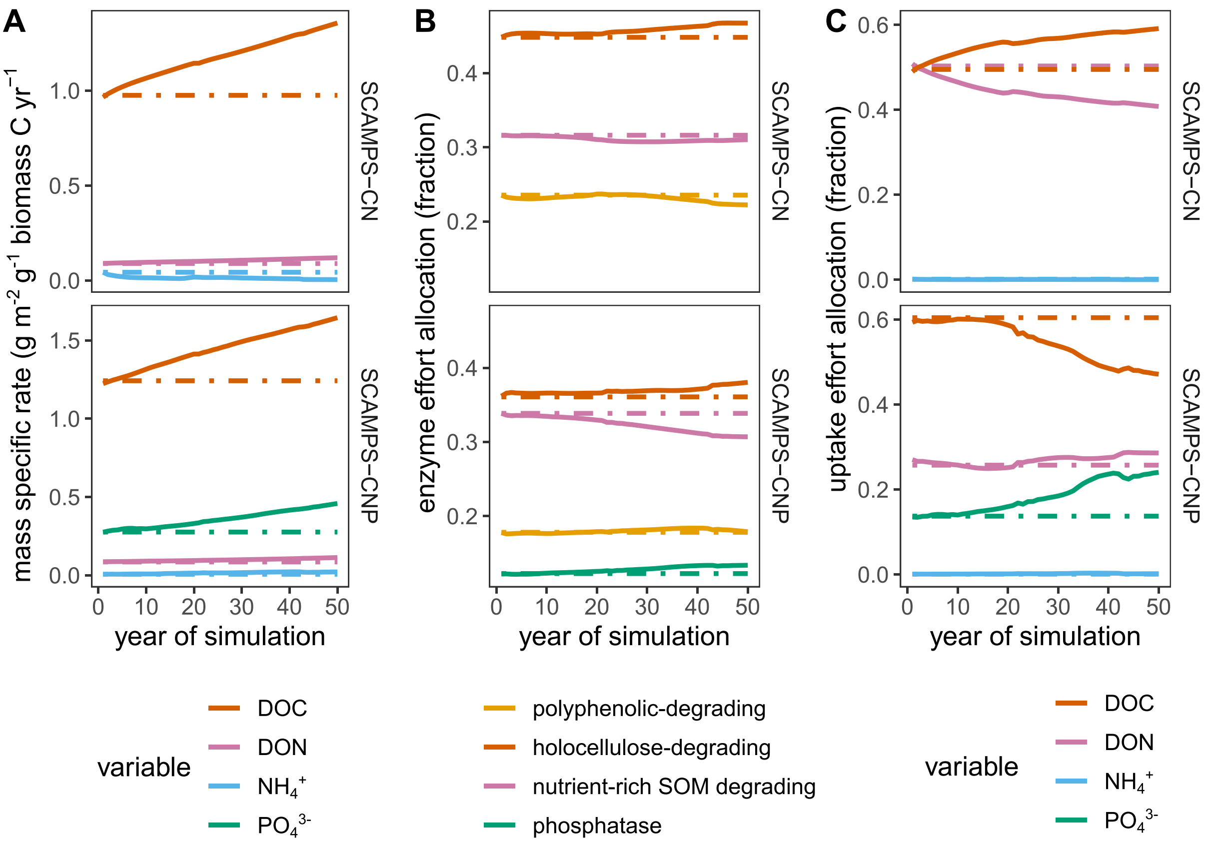

Fig. 4. Effect of moderate warming on microbial uptake rates and effort allocated to uptake of different nutrients. Mass-specific dissolved nutrient uptake (a), relative effort allocation to different enzyme classes (b), and effort allocated to uptake of different nutrients (c). Enzyme and uptake effort allocation sum to 1 and describe the fraction of total resources available for enzyme production or uptake for all substrates that is allocated to a given substrate. NH_4^+ and PO_4^{3-} uptake rates in a. were multiplied by 10 and 50, respectively, to facilitate visualization on the same axis. Dot-dashed lines denote ambient scenarios and solid lines the moderate warming scenario. SCAMPS-CN and SCAMPS-CNP were spun up under ambient temperature prior to the onset of warming simulations.

3. Results and discussion

3.1. *Effect of model structure on ecosystem C storage under ambient conditions*

Under ambient temperature conditions, total ecosystem C was greater in SCAMPS-CNP compared to SCAMPS-CN, and also preferentially accumulated in soil over plants in the former compared to the latter (Table 1 and Fig. 3). Greater SOM stocks are generally associated with higher microbial biomass across habitats (Xu et al., 2013), but this correlation was not the case here. Microbial biomass was lower in SCAMPS-CNP compared to SCAMPS-CN because of closer coupling between actual and target microbial C:N in the absence of P, rather than direct C costs associated with acquiring P. Lack of substantial direct costs associated with acquiring P are evidenced by higher DOC-specific uptake rates by microbes in the SCAMPS-CNP (Fig. 4a) despite considerable effort being allocated to P acquisition (Fig. 4b and c). On the other hand, greater ability to match microbial biomass C:N with resource conditions (i.e., smaller difference between the microbial C:N target (qmicB) and microbial biomass C:N) in SCAMPS-CN (Fig. 5a) is associated with higher carbon use efficiency (CUE; Fig. 5b) and approximately seven-times lower waste respiration in SCAMPS-CN compared to SCAMPS-CNP (Fig. 5c). Strict target microbial N:P in SCAMPS-CNP causes waste respiration to increase when either N or P is limiting, while waste respiration is exclusively regulated by N limitation in the CN only version of the model. In turn, lower microbial biomass in the CNP model allows more SOM to accumulate relative to the CN-only model.

Lower microbial biomass can also constrain plant growth by limiting the rate at which inaccessible SOM-associated N and P are transformed into plant-available forms. Although the plant biomass was also substantially reduced in SCAMPS-CNP compared to SCAMPS-CN, it appears that microbial stoichiometric imbalance led to primarily P limitation in plants. This is evidenced by the observation that SCAMPS simulates leafier plant communities under N limitation, but the wood:leaf ratio was unaffected by the introduction of P into the model (Table 1, Fig. 3b). Furthermore, although plants are often observed to resorb a greater fraction of nutrients upon senescence when growing in nutrient-limited compared to nutrient replete environments, the leaf litter was relatively more N-rich in SCAMPS-CNP compared to SCAMPS-CN (Table 1). This increase in nutrient loss upon senescence is attributable plant P limitation, which can occur in our model without also altering the plant biomass allocation to leaves vs. wood.

3.2. *Effect of model structure on ecosystem C storage under warming*

Total ecosystem C storage was reduced by warming in both models (Table 1), but SCAMPS-P projected greater ecosystem C losses compared to SCAMPS-CN after 50 years of warming (793 g C m^{-2} (16% reduction) vs. 289g C m^{-2} (8% reduction)). This decrease was driven by a loss of SOM, which was only partially compensated by an increase in total plant and microbial biomass. Such modeled SOM loss contrasts with a meta-analysis of field warming experiments showing no overall change in stocks or mass percent organic matter in soil (Pold et al., 2021), although the plant results are somewhat more consistent. Specifically, aboveground plant biomass associated with an expansion of woody shrubs has increased in parts of the Arctic as the climate warms (Sturm et al., 2001, Tape et al., 2006); only the CNP model here predicted

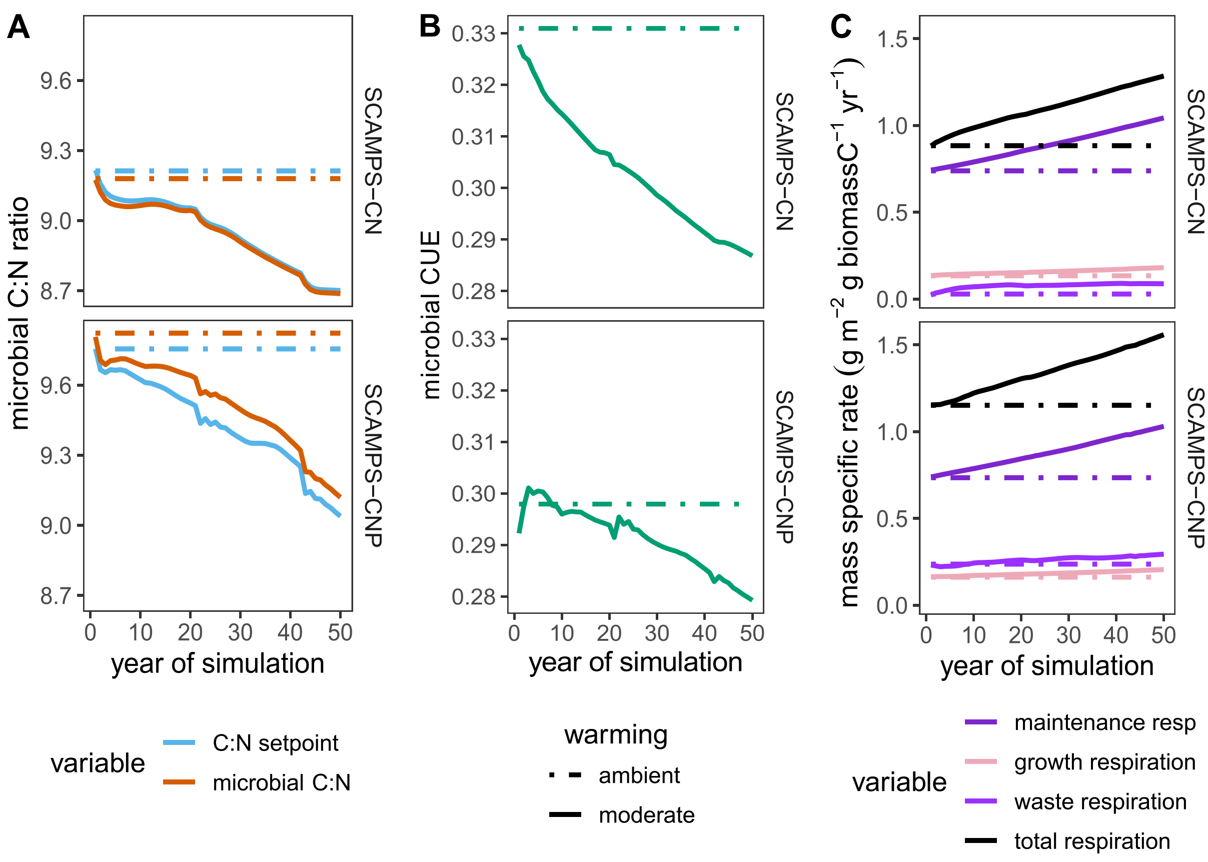

Fig. 5. Effect of warming on microbial C:N ratio and SOM-determined target C:N (a), CUE (b) and sources of mass-specific respiration (c). Dot-dashed lines and solid lines indicate the ambient and warmed scenarios (respectively) in all panels, while colors denote different variables across the plots. SCAMPS-CN and SCAMPS-CNP were spun up under ambient temperature prior to the onset of warming simulations. Note that CUE depicted in this figure includes waste respiration, while the CUE used to determine effort allocated to C uptake to maintain biomass does not. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

increased woodiness of the plant community (Table 1). More broadly, a recent meta-analysis noted that increased tussock tundra plant biomass in response to experimental warming occurs predominantly belowground (Pold et al., 2021), which, again, only the CNP model captured. Nonetheless, this model predicts only very subtle shifts in the root:leaf:wood ratio of biomass over the 50 year simulation period.

Increased plant and microbial biomass – and lower C:N ratios – in both models under warming indicate that the higher temperatures alleviated organism nutrient limitation, facilitating greater C inputs to soil but also greater decomposition. Mass-specific microbial DOC and DON uptake rates (Fig. 4a) as well as respiration (Fig. 5c, Table 2) were increased by warming in both models, indicating greater demand for organic C. This increased demand is in part due to lower CUE at higher temperatures, associated with additional carbon being allocated to maintenance respiration and extracellular enzyme production (Table 2).

3.3. Effect of P inclusion on stoichiometric response to warming

Warming increased microbial stoichiometric imbalance in both models, which drove elevated rates of mass-specific waste respiration (which is used to release excess C) and N mineralization (Table 2). However, the warming-driven increase in C mineralization was relatively greater in SCAMPS-CN, with a more than doubling of waste respiration compared to an only 25% increase in SCAMPS-CNP. By contrast, the effect of warming on N mineralization was relatively greater in SCAMPS-CNP, with a 26% increase in N mineralization compared to an only 3% increase in SCAMPS-CN (Table 2). Approximately equal increases in stoichiometrically-correcting C and N mineralization with warming in SCAMPS-CNP are possible because of strong seasonality in which nutrient is limiting. This presence of a second limiting nutrient (P) drives microbes to mineralize additional C and N to balance their stoichiometry, periodically reducing biomass in addition to limiting additional growth.

The greatest impact of warming on stoichiometric imbalance in SCAMPS-CNP was on P mineralization, which was more than seven-fold greater at the end of fifty years under elevated temperatures. Surprisingly, greater P mineralization was associated with an increase in relative effort allocation to phosphatase production by both microbes (12% vs. 13%; Fig. 4b) and plants (88 μg C g-1 biomass m^{-2} yr $^{-1}$ vs. 68 μg C g^{-1} biomass m^{-2} yr^{-1}), and in effort allocated to PO_4^{3-} uptake (24% vs. 14%). This apparent disparity between high rates of P mineralization and effort allocated to uptake can be attributed to strong seasonality in P limitation and surplus. P mineralization and high PO_4^{3-} uptake effort co-occurred in midsummer, indicating a lag between resource allocation to uptake and current stoichiometric set point as the microbial community acclimates to become more fungal (greater C:N,P Fig. 6).

3.4. Effect of warming and P on plant-microbe interactions

Particularly strong N and P mineralization responses to warming in the CNP model were associated with comparable plant biomass responses. Furthermore, total plant CN ratio only changed in response to warming in the CNP model. This pattern indicates that microbial stoichiometric imbalance is a key determinant of plant stoichiometry, and that as microbial C:N deviates further from the environmentally-regulated target – whether due to time lags or the constraints of also

Table 2
Key microbial process rates at the 50th year of simulations with a stoichiometrically-flexible microbial community. Numbers in parentheses indicate percent change with warming for a given model (100*(warmed – ambient)/ambient).

Variable	SCAMPS-CN ambient soil temperature	SCAMPS-CN warmed soil temperature	SCAMPS-CNP ambient soil temperature	SCAMPS-CNP warmed soil temperature
respiration (g C m-2 yr-1)	114	178 (56)	72	158 (119)
mass-specific waste respiration (g C g^{-1} MBC m^{-2} yr^{-1})	0.029	0.088 (203)	0.236	0.295 (25)
mass-specific maintenance respiration (g C g^{-1} MBC m^{-2} yr^{-1})	0.74	1.04 (40)	0.73	1.04 (42)
mass-specific growth respiration (g C g^{-1} MBC m^{-2} yr^{-1})	0.13	0.18 (35)	0.16	0.21 (27)
mass-specific EEA production (g C g^{-1} MBC m^{-2} yr^{-1})	0.092	0.14 (52)	0.08	0.12 (50)
mass-specific Nmin (g N g^{-1} MBC m^{-2} yr^{-1})	0.02	0.021 (5)	0.017	0.022 (29)
mass-specific Pmin (g P g^{-1} MBC m^{-2} yr^{-1})	NA	NA	0.00025	0.0021 (740)

having to balance biomass P – plant stoichiometry further responds. This pattern is associated with asynchronous peaks of plant and microbial nutrient uptake - particularly for ammonium (Fig. S1). This asynchrony led to the post-hoc hypothesis that if microbes have a fixed stoichiometry, they might mineralize more, leading to greater changes in plant stoichiometry. We tested this hypothesis by fixing the microbial C:N setpoint (qmicB) to 10, reflecting the initial conditions for microbial stoichiometry and approximating the microbial stoichiometry when SCAMPS-CNP is spun up under ambient.

Except for P under ambient conditions, fixing microbial setpoint induced microbes to mineralize more by forcing the microbial C:N,P ratio to remain higher than it would otherwise be (Table S4, Fig. S2). This increased mineralization in the fixed scenario supported greater plant biomass, particularly C-rich wood compared to the flexible scenario; the relatively lignin-poor, nutrient-rich leaf litter inputs in the flexible scenario further reduced N mineralization by favoring development of a low C:N microbial community with higher N demand. Nonetheless, increased nutrient pools in the presence of the stoichiometrically-inflexible microbial community did not consistently lead to changes in plant community stoichiometry. Plant C:N remained insensitive to warming in SCAMPS-CN (C:N of 57 for simulations with fixed and flexible microbial communities under both ambient and warmed scenarios) and responsive to warming in SCAMPS-CNP. The plant community was more C-rich and woodier under ambient conditions when microbial setpoint was fixed (plant C:N 66.9 fixed vs. 57.8 flexible), but converged somewhat under warming as it became leafier and more N-rich in the fixed scenario (C:N 65) but woodier and more C-rich in the flexible scenario (C:N 61.2). Therefore, only SCAMPS-CNP run under a flexible scenario accurately reproduced the increased shrub biomass observed under warming at Toolik (Sistla et al., 2013), which our model is parameterized for. However, plant biomass increased with warming in both SCAMPS-CN and SCAMPS-CNP because of a lengthening of the growing season, whether or not microbial setpoint was fixed.

Plant community became leafier shortly after the initiation of warming when microbial setpoint was fixed in SCAMPS-CNP, but woodier only after a few decades of warming when the setpoint was flexible (Fig. S3). This indicates some degree of disequilibrium in the latter case. Tundra soils are characterized by a “zero-curtain period” (Muller, 1947) in which soil temperature remains at 0 °C for a prolonged period even though air temperatures are above zero. Our warming scenarios eliminate the zero-curtain period, instead causing soil temperatures to remain at a temperature just above zero for a couple of weeks in spring (Fig. 1). Microbial respiration and uptake start to accelerate dramatically above 0 °C in our models, but plant nutrient uptake begins when soil temperature reaches -1 °C. This means that warming has a particularly strong effect on microbial compared to plant physiology in spring when high rates of N mineralization accompany rapidly shifting microbial stoichiometry in our model. We therefore suspected that the more rapid equilibration of plant C:N under warming when microbial setpoint is fixed might be related to less dramatic shifts in the difference between microbial C:N and its setpoint in early spring, and therefore more similar seasonal patterns of plant and microbial nutrient uptake as warming proceeds when setpoint is fixed. To test this hypothesis, we examined ammonium uptake after 10, 30, and 50 years of warming in SCAMPS-CNP with fixed and flexible microbes; we chose ammonium because it is the favored plant N source and produced exclusively by microbial stoichiometric imbalance.

Warming rapidly reduced microbial ammonium uptake during this period in both fixed and flexible microbial scenarios in SCAMPS-CN, and caused a steady increase in microbial uptake when setpoint was flexible in SCAMPS-CNP. However, warming caused a decrease then increase in microbial ammonium uptake during this period in SCAMPS-CNP when microbes were fixed (Fig. S4). This could explain the divergent plant community C:N responses to warming when microbes are fixed vs. flexible in SCAMPS-CNP because of differences in how wood obtains its nutrients compared to leaves and roots. Specifically, wood litter C:N is the same as wood C:N, but the C:N of leaf and root litter are greater than that of leaves and roots. Therefore, wood depends on N resorbed by leaves and roots for its early spring growth at a cost to leaf and root growth in our models. When plant uptake of soil nutrients can move earlier in the year as a result of warming, this reduces the importance of nutrient reallocation from leaves and roots to wood, thereby leading to an otherwise unexpected reduction in woodiness. This effect is particularly pronounced when microbes have a fixed setpoint because the spring peak ammonium pool moves earlier in the year and allows for a more nutrient-rich, leafier community. Therefore, the effect of microbial stoichiometric imbalance on plant growth and woodiness is not always straight-forward in our model and can depend on when in the year the stoichiometric imbalance occurs rather than just how severe it is. Additionally, given the propensity for springtime P-limitation induced N mineralization in our model, it would be a fruitful area of future research to explore how altering the microbial N:P setpoint affects ecosystem warming response.

4. Conclusion

The arctic tundra is one of the most rapidly warming ecosystems in the world, but also has widely divergent modeled and empirically-derived projections for ecosystem C storage as the climate warms (Wieder et al., 2019). Mechanistic modeling affords an opportunity to extend the existing data and explore hypotheses regarding the role of stoichiometric limitations to growth in biogeochemical cycling in this rapidly changing habitat. However, many models perform poorly in the Arctic, whether because of applying mechanisms of SOM stability and soil physical properties more appropriate for sub-arctic ecosystems (Wieder et al., 2019), neglecting microbial stoichiometric adaptation

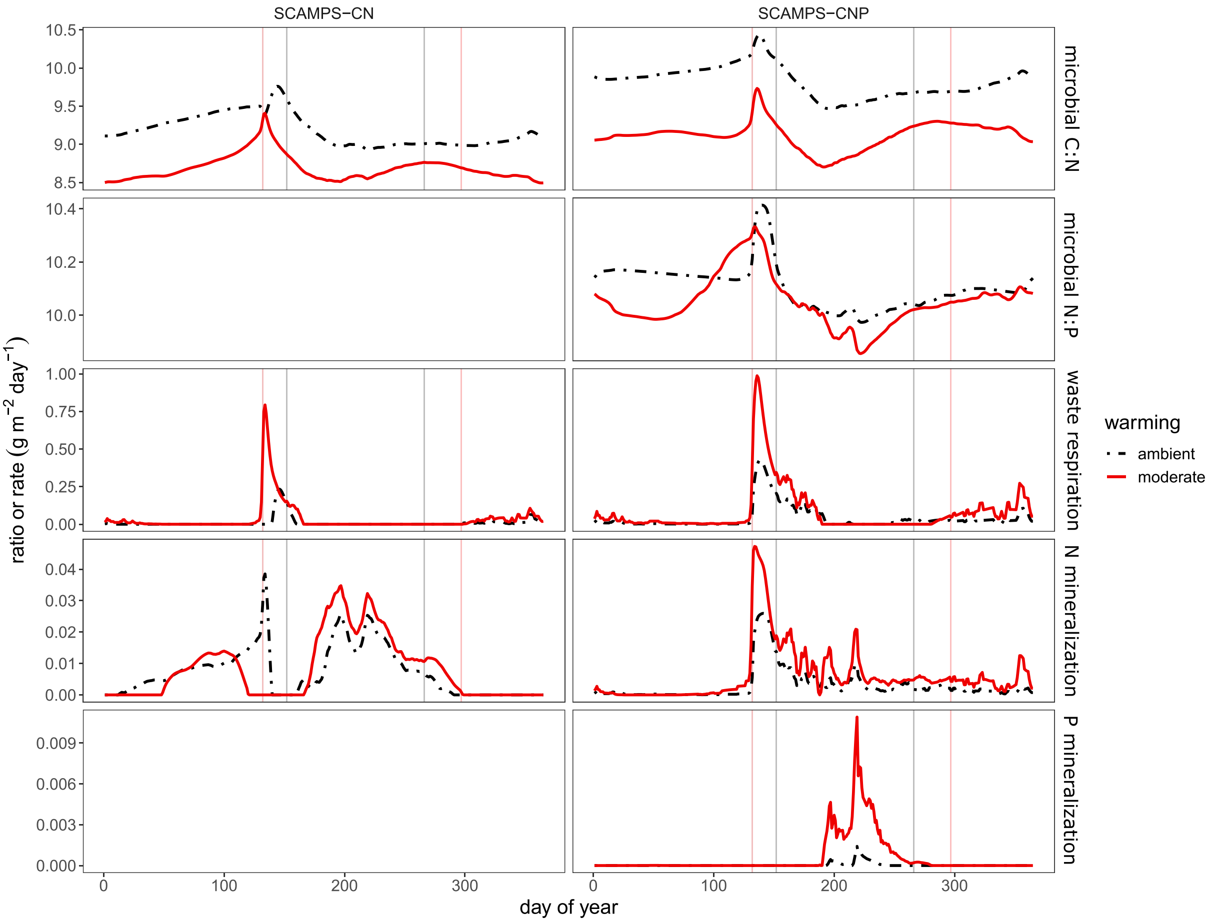

Fig. 6. Seasonality in microbial stoichiometry and mineralization for the purpose of stoichiometric correction in the 50th year of simulations. Vertical lines denote the first day in spring when soil temperatures exceed 0 °C and the first day in fall when soil temperatures are below 0 °C. Line type and color correspond to warming treatment. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Wang et al., 2010), or some combination of these factors (Schädel et al., 2018). Poor model performance in arctic tundra could also reflect neglecting the complex, seasonally dynamic plant-microbe feedbacks and tight intercoupling of biogeochemical cycles that structure arctic and alpine terrestrial systems (Lipson et al.,1999; Sistla et al., 2014).

We evaluated the effect of accounting for P acquisition and stoichiometric regulation impacts projected soil C stocks and changes in ecosystem biogeochemistry under a moderate warming scenario. Including P processes in SCAMPS causes the microbial community to be more fungal than expected based on SOM chemistry, largely because of a lag between microbial P demand and availability, rather than the direct costs associated with P acquisition. Warming alleviated nutrient limitation of the plant and microbial communities in both models, but did so slightly more in SCAMPS-CNP, leading to a larger decrease in microbial C:N and increase in plant community woodiness compared to the CN-only model. However, increased woody biomass did not fully ameliorate the warming-induced reduction in soil C observed in both models, which was almost twice as large in absolute terms in the CNP compared to CN only model because microbial SOM decomposers benefitted more from warming in the CNP model. Fixing the microbial C:N setpoint allowed plant and biomass to both increase despite generally increased stoichiometric imbalance, and lead to a more nutrient-rich plant community under warming only in SCAMPS-CNP. Together, these results indicate that rather than limiting ecosystem warming response, including P in this microbially-explicit biogeochemical cycling model exacerbates it by constraining the ability of plants to recapture lost soil C in their biomass. Given the current lack of data on coupled Arctic tundra CNP cycle responses to climate change, our results indicate a more robust understanding of arctic terrestrial P dynamics could be critical to improving projections of ecosystem C balance in this rapidly warming biome.

Data availability

The model code, climate driver, and parameter files used to generate the simulations used in this paper are available in the supplement.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thank you to the members of INCyTE RCN for fruitful discussions that helped narrow the focus of this work, as well as to the useful comments made by the reviewers and editor, which greatly helped clarify the text. This work was funded by the National Science Foundation Signals in the Soil grant number 1841610 to SAS and EBR.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108489.

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