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Using research networks to create the comprehensive datasets needed to assess nutrient availability as a key determinant of terrestrial carbon cycling

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Abstract

A wide range of research shows that nutrient availability strongly influences terrestrial carbon (C) cycling and shapes ecosystem responses to environmental changes and hence terrestrial feedbacks to climate. Nonetheless, our understanding of nutrient controls remains far from complete and poorly quantified, at least partly due to a lack of informative, comparable, and accessible datasets at regional-to-global scales. A growing research infrastructure of multi-site networks are providing valuable data on C fluxes and stocks and are monitoring their responses to global environmental change and measuring responses to experimental treatments. These networks thus provide an opportunity for improving our understanding of C-nutrient cycle interactions and our ability to model them. However, coherent information on how nutrient cycling interacts with observed C cycle patterns is still generally lacking. Here, we argue that complementing available C-cycle measurements from monitoring and experimental sites with data characterizing nutrient availability will greatly enhance their power and will improve our capacity to forecast future trajectories of terrestrial C cycling and climate. Therefore, we propose a set of complementary measurements that are relatively easy to conduct routinely at any site or experiment and that, in combination with C cycle observations, can provide a robust characterization of the effects of nutrient availability across sites. In addition, we discuss the power of different observable variables for informing the formulation of models and constraining their predictions. Most widely available measurements of nutrient availability often do not align well with current modelling needs. This highlights the importance to foster the interaction between the empirical and modelling communities for setting future research priorities.

Abbreviations

Research infrastructures

ANAEE	Analysis and experimentation on ecosystems (https://anaee.com/)
ICOS	Integrated carbon observation system (https://icos-ri.eu/)
LTER	Long term ecological research (https://lternet.edu/)
NEON	National ecological observatory network (https://neonscience.org/)
CZO	Critical zone observatory (http://criticalzone.org/national/)

Research networks

ClimMani	Climate change manipulation experiments in terrestrial ecosystems: networking and outreach (http://climmani.org/)
DroughtNet	Network of drought experiments (http://drought-net.colostate.edu/)
Fluxnet	Global network of meteorological sensors measuring atmospheric state variables, like temperature, humidity, wind speed, rainfall, and atmospheric carbon dioxide.
INTERFACE	An integrated network for terrestrial ecosystem research on feedbacks to the atmosphere and climate (https://bio.purdue.edu/INTERFACE/experiments.php)
LIDET	Long-term inter-site decomposition experiment team (https://andrewsforest.oregonstate.edu/sites/default/files/lter/pubs/webdocs/reports/lidet.htm)
NutNet	Nutrient Network (http://nutnet.umn.edu/)
TERN	Australia's land ecosystem observatory http://tern.org.au/
INCyTE	Investigating Nutrient Cycling in Terrestrial Ecosystems (NSF network)

1. Introduction

More than a century of research has shown that availability of nutrients, such as nitrogen (N) and phosphorus (P), is a key determinant of ecosystem community composition, diversity, architecture, and functioning (von Liebig 1841, Chapin 1980, Elser *et al* 2000, Peñuelas *et al* 2013, Borer *et al* 2014). Nutrient availability can influence, plant activity and growth (Vitousek *et al* 2010, Fay *et al* 2015, Verlinden *et al* 2018), as well as microbial activity (Janssens *et al* 2010), and consequently has a strong influence on terrestrial carbon (C) cycling (De Vries *et al* 2009). Nutrient availability is also an important modulator of the effect of environmental changes on terrestrial ecosystems, and hence the terrestrial feedback to anthropogenic climate change (Melillo *et al* 2011, Sardans and Peñuelas 2012). For example, nutrient availability has been shown to have a fundamental control over plant responses to elevated CO_2 (De Graaff and Van Groenigen 2006). Despite the critical role of nutrients in terrestrial C cycling, however, we still lack comprehensive, comparable datasets to fully unravel the influence of nutrients and the varied mechanisms through which they interact with environmental change to influence ecosystem functioning (box 1). The lack of coordinated assessments of multiple elements in concert not only limits our fundamental understanding of the role of nutrients, but also hinders model evaluation and development.

The strong evidence for nutrient effects on C cycling in terrestrial ecosystems has motivated their explicit representation in process-based terrestrial biogeochemistry (BGC) models, (Thornton *et al* 2007, Medvigy *et al* 2009, Wang *et al* 2010, Zaehle and Friend 2010, Parton *et al* 2010, Smith *et al* 2014, Reed *et al* 2015). Taking nutrient limitations into account, these models generally simulate a reduced sensitivity of plant growth to increasing CO_2 and strongly reduced C uptake by the terrestrial biosphere under future climate and atmospheric CO_2 concentration scenarios (Thornton *et al* 2007, Zaehle and Dalmonech 2011, Peñuelas *et al* 2013, Wang *et al* 2015, Wieder *et al* 2015a, Achat *et al* 2016). This is in line with evidence from manipulation experiments and remote sensing results, which imply that allowable emissions to keep global warming below a given target are much lower than emission estimates from models without C-nutrient interactions (Zaehle *et al* 2010, 2014a, Ciais *et al* 2013, Zhang *et al* 2014, Smith *et al* 2015). However, detailed

Box 1. A need for a coordinated assessment of coupled biogeochemical cycles.

Targeted measurements of specific nutrient pools and fluxes performed across a range of locations can directly inform a unified understanding of how variation in nutrients helps dictate ecosystem structure and function. Yet, relatively few synthesis studies on terrestrial C cycling have taken nutrient availability into account, and those that exist, have typically focused on N—the element often considered most limiting for plant growth outside the tropics (LeBauer and Treseder 2008, Augusto *et al* 2017)—using a single indicator for N availability (e.g. N addition in van Groenigen *et al* 2006, C:N ratio in Alberti *et al* 2015, or total N stock in Stevens *et al* 2015). In an attempt to create a more comprehensive understanding of the role of nutrient availability in mediating ecosystem carbon cycling and its responses to environmental perturbations, a coarse classification was developed based on the sparsely available data and on expert knowledge (Vicca *et al* 2012, Fernandez-Martinez *et al* 2014, Alberti *et al* 2015, Campioli *et al* 2015, Terrer *et al* 2016). These data syntheses provided powerful insight into the ways nutrients influence ecosystem responses to environmental changes, but they also revealed that our understanding of the role that nutrients play in the terrestrial C cycle is hampered by the limited comparability of datasets where soil nutrient information was provided. While carbon cycle data are increasingly becoming available, and the comparability of these data among sites and networks is improving, standardized assessment of ecosystem nutrient dynamics are less common (figure 1). These data gaps hinder inter-site comparison of the influence of nutrient availability on ecosystem processes and their responses to environmental change.

	n
Sand%	81
Silt%	81
Clay%	89
BD	56
SOM	26
Soil N	96
Soil C:N	90
Soil pH	36
CEC	42
TEB	38
Olsen P	5
Bray P	2
Total P	17

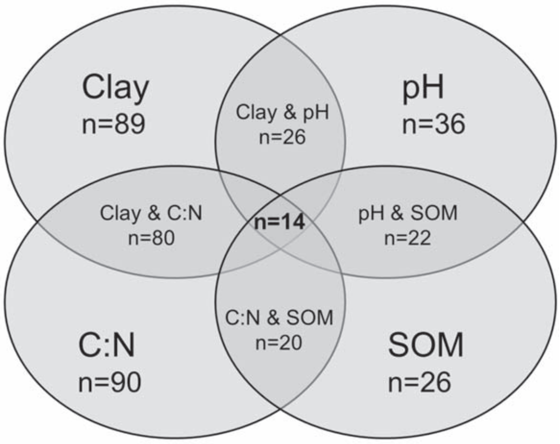

Figure 1. The availability of data for 13 soil variables in a global dataset of 125 forests and a Venn diagram showing the overlapping availability for four of these variables. These four variables were chosen because of their complementary information regarding nutrient availability and because they are among the most commonly measured soil properties in the database. The number of sites providing any single variable is shown by *n*, some combination of two of these variables is shown by *n* where two polygons overlap, and the combination of all four is shown in bold text. Abbreviations are for bulk density (BD), soil organic matter (SOM), cation exchange capacity (CEC), and total exchangeable bases (TEB). For SOM, *n* includes also sites that provided soil organic carbon (SOC) instead of SOM, and pH includes measurements performed using H_2O, $CaCl_2$ or KCl solutions. For both SOM and pH, the variable of interest can be obtained through conversion (Ahern *et al* 1995, Pribyl 2010). All data are provided in table S1.

comparisons of models with interactive C and N cycles against field experiments revealed that key mechanisms determining the uptake and recycling of nutrients are poorly simulated by the current generation of BGC models (Piao *et al* 2013, Zaehle *et al* 2014b, Medlyn *et al* 2015) and the uncertainty arising from missing empirical data and poor process understanding remains a serious limitation for model projections (Thomas *et al* 2013, Meyerholt and Zaehle 2015, Meyerholt *et al* 2016). Information on soil properties, nutrient availability, allocation and plant stoichiometry, along with site-level terrestrial C cycle data, is therefore critical to inform the formulation of models and to establish new benchmarks.

A range of large scale research infrastructures (e.g. ICOS, ANAEE, NEON, LTER, TERN, CZO) and research networks (e.g. Fluxnet, ClimMani, INCyTE, INTERFACE, LIDET, NutNet, DroughtNet, TERN) have been initiated to collect empirical data from terrestrial ecosystem monitoring and manipulation experiments with a focus on characterizing the cycling of C and its response to environmental change (Hinckley *et al* 2016, Richter *et al* 2018). While ample data are commonly available for accompanying measurements of meteorological variables, background climate, vegetation cover, and soil moisture, an assessment of how nutrient cycling may modulate terrestrial C cycling across networks and in experiments is often missing. Here, we argue that the additional provision of coherent and comprehensive observations of nutrient availability, soil properties, and plant stoichiometry would greatly enhance the power of these networks and experiments to generate mechanistic insights for understanding how and why nutrient availability interacts with ecosystem functioning and structure to shape their response to global environmental change.

To support the coupling of nutrient cycling measurements with those being made for C in large scale cross-site infrastructures and global change experiments, we highlight research gaps and the types of measurements that could be particularly valuable for: (1) developing a solid empirical basis and identifying general patterns of how nutrient availability interacts with C cycling; and (2) parameterizing and evaluating BGC models, especially their representation of mechanisms by which nutrients affect C cycling and ecosystem feedbacks to climate and environmental change. We first focus on how to characterize and compare the nutrient status and propose combining a set of complementary measurements to assess nutrient availability among sites and experiments. Subsequently, we discuss the power of different variables of ecosystem nutrient cycling to inform and evaluate process-based BGC models. A primary aim of this work is to raise awareness about the need for comparable nutrient cycling measurements. To facilitate a wide implementation, we focus on common biogeochemical measurements that are relatively easy to make and interpret. We focus on N and P as nutrients shown to strongly affect C cycling (although we recognize other nutrients have poorly represented importance as well (Kaspari and Powers 2016)).

2. Integrated assessment of nutrient availability

Comparing nutrient availability among sites remains challenging due to the large variability in edaphic properties that modify nutrient availability (e.g. soil pH) and due to varying plant strategies of nutrient acquisition (e.g. cluster roots, mycorrhizal fungi). This complicates the interpretation of chemical assays used to assess N and P availability (Binkley and Hart 1989, Holford 1997, Neyroud and Lischer 2003, Inselsbacher and Näsholm 2012, DeLuca *et al* 2015, Darch *et al* 2016). Nonetheless, characterizing and comparing nutrient availability within and among sites can be accomplished by combining key soil properties with indicators of N and P availability. The simultaneous measurement of multiple aspects of nutrient cycling can help reduce the caveats associated with any single measurement. Such integrated metrics could provide a broad indication of site nutrient availability and provide new insights into how it influences C cycling.

Qualitative estimates of nutrient availability across sites can be made using relatively common metrics. This integrative approach was applied in a few synthesis studies that used a nutrient availability classification (Vicca *et al* 2012, Fernandez-Martinez *et al* 2014, Campioli *et al* 2015) and could help bring quantitative capacity to coupled biogeochemical perspectives. However, large data gaps persist. For example, figure 1 shows the availability and overlap of a few of the most commonly measured soil variables that are available for a set of 125 forest sites, including sites that are part of networks such as Fluxnet and LTER (Luyssaert *et al* 2007, Vicca *et al* 2012, Campioli *et al* 2015). Here, we used all forests for which aboveground primary production data were available (table S1 is available online at stacks.iop.org/ERL/13/125006/mmedia). Although some soil data (especially texture and soil C:N ratio) were available for the majority of the sites, overlap in the combination of soil variables providing complementary information was very limited. Using these sparse data (see figure 1), Vicca *et al* (2012) developed a nutrient availability classification based on information such as soil texture, soil organic matter (SOM), pH, C:N ratio, and cation exchange capacity (CEC). This categorical classification explained significant differences in biomass production efficiency and ecosystem carbon use efficiency across forests (Vicca *et al* 2012, Fernandez-Martinez *et al* 2014). Hence, integrated assessments of ecosystem nutrient availability could provide a means to assess nutrient effects on broad differences in ecosystem function and productivity. Such classifications would become more accurate and powerful if more comprehensive and comparable datasets were available, such that the same set of variables can be considered for all sites.

Adding to this qualitative approach, quantitative metrics that integrate information about key soil properties and nutrients can be used in inter-site comparisons. For example, Fischer *et al* (2012) and Van Sundert *et al* (2018) developed site fertility indices from commonly used measurements to broadly assess nutrient availability. Briefly, these metrics consider three or four soil factors that influence nutrient availability (attributes like SOM, pH, texture, C:N ratio, total exchangeable bases (TEB, i.e. the sum of K, Ca, Mg and Na)). Each attribute included in the metric received a rating that decreases as it diverges from a predefined optimal range. Thus, nonlinear relationships and interactions among attributes are taken into account. For example, at low pH, differences in N availability may be less influential than at optimal pH because at pH < 4.5 plant growth is commonly limited by Al toxicity and/or P deficiency (Cross and Schlesinger 1995, Chapin *et al* 2002). This approach requires further investigation, development, and testing, as its potential for wider applications requires the establishment of comprehensive datasets of soil properties and nutrients (Van Sundert *et al* 2018). In future availability of a larger number of data for multiple edaphic factors and nutrient availability measurements, along with C cycle variables, may enable machine learning-based approaches to identify such patterns from the data alone.

As illustrated by the variables included in both the nutrient availability classification and in quantitative nutrient metrics, some soil characteristics seem consistently indicative of site nutrient status and can help to estimate ecosystem nutrient availability (Andrianarisoa *et al* 2009, Van Sundert *et al* 2018). These include SOM, CEC and TEB, texture, bulk density, and pH. SOM is a source of nutrients and both organic matter and clay colloids are important exchange sites for nutrients (Schroeder 1984, Roy *et al* 2006). CEC represents the capacity of soil to avoid leaching of essential nutrients, including N (Robertson *et al* 1999). Bulk density indicates the porosity of the soil and is particularly relevant where gravel and stones reduce the 'fine earth' volume from which plants acquire essential nutrients. Bulk density is also necessary to convert concentration data into stocks. Soil pH is a critical determinant of nutrient availability, especially for P, and also has strong relationships with soil microbial communities (Fierer and Jackson 2006). Thus, these relatively straightforward soil assays are useful for developing proxies of nutrient availability across sites (see also box 1).

Pairing these simple assays of soil characteristics with direct, targeted measurements of ecosystem N and P availability provides additional information about nutrient-carbon cycle interactions from monitoring programmes, networks, and global change experiments. An indicator of N availability that is comparable across a wide range of environmental conditions is the soil C:N ratio (e.g. Andrianarisoa *et al* 2009, Wang *et al* 2014, Alberti *et al* 2015). The soil C:N ratio has the advantage of being fairly straightforward to determine and it does not change on short temporal scales, thus the timing of measurements is less influential. This variable was also included in the metric developed by Van Sundert *et al* (2018). A high soil C:N ratio indicates a relatively low N availability, and several studies have reported a significantly negative relationship between soil C:N ratio and N mineralization rates (Andrianarisoa *et al* 2009, Yan *et al* 2012), plant biomass (Grau *et al* 2017), organic matter decomposition, and plant productivity (Yan *et al* 2012, Van Sundert *et al* 2018). Similarly, assessment of foliar N and P stoichiometry suggests broad scale indicators of relative nutrient limitation in plants (Vitousek 1984, McGroddy *et al* 2004, Reich and Oleksyn 2004). Although caution in inferring nutrient limitation from stoichiometry is warranted (e.g. because of a strong phylogeny effects; Townsend *et al* 2007, Asner *et al* 2014, Sardans *et al* 2015, Zechmeister-Boltenstern *et al* 2015), we contend that these metrics offer powerful indicators of ecosystem nutrient availability, especially when paired with other measurements.

Ecosystem P status regulates productivity and ecosystem function at multiple spatial and temporal scales (Vitousek *et al* 2010, Cleveland *et al* 2011, Peñuelas *et al* 2013). Despite the central role of coupled C–N–P dynamics, a reliable, widely applicable indicator for P availability for inter-site comparisons is challenging to suggest, as the accuracy of different indicators of P availability depends strongly on soil properties (especially pH) and on the dominant P acquisition strategy (e.g. carboxylate-releasing cluster roots, roots releasing phosphatase enzymes, or mycorrhizal fungi; Raven *et al* 2018, Zemunik *et al* 2018). We therefore advocate that inter-site comparisons (e.g. in meta-analyses) and models should always take the P-acquisition strategy of plants into account, and combine this with data on total soil P and the most suited extraction methods for the study soils (Olsen P, Bray P, Colwell P (Colwell 1963), Resin P (Turner and Romero 2009)) (table 1). These extraction methods have been widely applied (Colwell 1963, Bolland 1997, Dalling *et al* 2016, Turner *et al* 2018a, b). While Olsen P is considered to best reflect P extractability in soils of alkaline to neutral pH (Olsen *et al* 1954), Bray P and Colwell P provide a more accurate estimate of extractable P at lower pH (Wolf and Baker 1985). We recommend prioritizing the Resin-P extraction method, as it measures P that is in solution, independent of soil pH. P in the soil solution is available for all plants, but because species with P-mining strategies have access to a greater pool (Lambers *et al* 2018), we advise measuring also other P indicators most relevant to the system (e.g. total P, Olsen P, Bray P).

Except for the P extraction methods, the measurements of soil properties and indicators of N and P availability suggested above are all relatively stable at short time scales. While this is advantageous for a nutrient availability characterization of different sites (avoiding confounding effects of the time of sampling), these measurements may miss short-term responses to natural or imposed environmental changes. A particularly useful method that can be added to capture short-term dynamics are resin membranes, with which the availability of a suite of nutrients that can be estimated in an integrated fashion through time. Resin membranes (or bags) absorb anions and/or cations that are in the soil solution, and hence provide an estimate of the relative availabilities ('supply rates') of various ions during the time resins are in the soil (Qian and Schoenau 2002). These membranes also provide unique information about the relative abundance of different elements in soil solution, a measure that is comparable among study sites. Nonetheless, the potential for comparing changes in nutrient availability among sites and in response to environmental perturbation is challenging, in part because supply rates depend on soil moisture and temperature (Qian and Schoenau 2002), and the units (e.g. μg N cm^{-2} membrane^{-1} burial time^{-1}) differ from those of fluxes actually occurring in the ecosystem. Nevertheless, relative differences in measured supply rates among treatments or sites provide valuable information, useful for interpreting observations (Dijkstra *et al* 2010, 2012) and for informing models. Overall, ion

Table 1. List of suggested soil measurements to characterize sites in terms of nutrient availability and additional data needs for model development and evaluation. Foliar stoichiometry refers to the ratios of the elements: C, N, P, Ca, Mg, K, Zn, Fe, Mn, S.

		Primary advantage
Edaphic soil properties	pH	Generalist and integrative indicators of soil nutrient availability
	Texture	
	Bulk density	
	Organic matter concentration	
	Cation exchange capacity	
Targeting specific plant and soil nutrients	Total N	Indicative of the stock size and availability of individual nutrients
	C:N ratio	
	Total P	
	P extraction[a]	
	Total exchangeable bases (K, Ca, Mg, Na)	
	Resin membranes	Ability to capture short-term changes
	Foliar stoichiometry	
Additional model data needs	Belowground C allocation	Improving mechanistic understanding of nutrient cycling and its relationship with C cycling
	Plant nutrient uptake rates	
	Net mineralization rates	
	N fixation	
	Nutrient resorption coefficients	
	Inorganic nutrient pools (NO_3^-, NH_4^+, PO_4^{3-})	

[a] P extraction refers to Resin P, Olsen P, Bray P, Colwell P, etc depending on the soil condition (see text).

exchange resins can offer a good additional measurement for comparing nutrient availability among treatments within a site, as well as the elemental ratios among sites, and for indicating strong differences in individual nutrient availabilities among sites.

In table 1, we summarize the measurements that we consider of primary relevance for inter-site comparison—in addition to (already available) data on major C pools and fluxes of ecosystems (e.g. net C exchange fluxes, plant and soil C stocks, microbial respiration). We focus on measurements that are comparable across a wide range of environmental conditions, that provide complementary information, and that are relatively simple to make. We suggest that, for the aim of inter-site comparison, variables with low seasonal variability are preferred over variables that exhibit considerable variability at short temporal and spatial scales, as the latter require high spatial and temporal resolution of measurements or spatial and seasonal integrations, and would substantially complicate robust comparisons across biomes and climatic regions. Of course, the measurements in table 1 can be complemented by other measurements that help advance process understanding of nutrient cycling or fit specific project goals.

This article focusses on the type of data that are needed, without providing or discussing specific protocols for sample timing, depth or spatial representation. However, standardized measurement protocols are critical for enabling comparability of data across sites. Concerted research within multi-site networks offers an opportunity for designing and disseminating common protocols. This has been put into practice within some networks (see e.g. NutNet http://nutnet.org/methods and NEON https://neonscience.org/data-collection/protocols-standardized-methods). In future, more effort should be made to adopt standard protocols more widely and harmonize them across networks. In addition, publicly accessible and usable datasets from monitoring and experimental sites and networks is needed to greatly enhance the power of data synthesis as well as model development and evaluation.

3. Data and process understanding for model development and evaluation

Data from research networks and experimental manipulations are already critical for developing and evaluating BGC models (Luo *et al* 2012, Schaefer *et al* 2012, Zaehle *et al* 2014b, Hinckley *et al* 2016). Expanded measurements that facilitate the characterization and comparison of nutrient status among different sites would also enable additional insights into the representation of nutrient controls on biogeochemical cycles in models. BGC models provide process-based representations of BGC and vegetation dynamics and are the primary tool for integrating knowledge about the functioning of the terrestrial C cycle and its interaction with nutrient cycles. Here we provide a brief overview of the development of C-nutrient interactions in BGC models and summarize data-model linkages that would be enabled by systematic, targeted data collection across existing

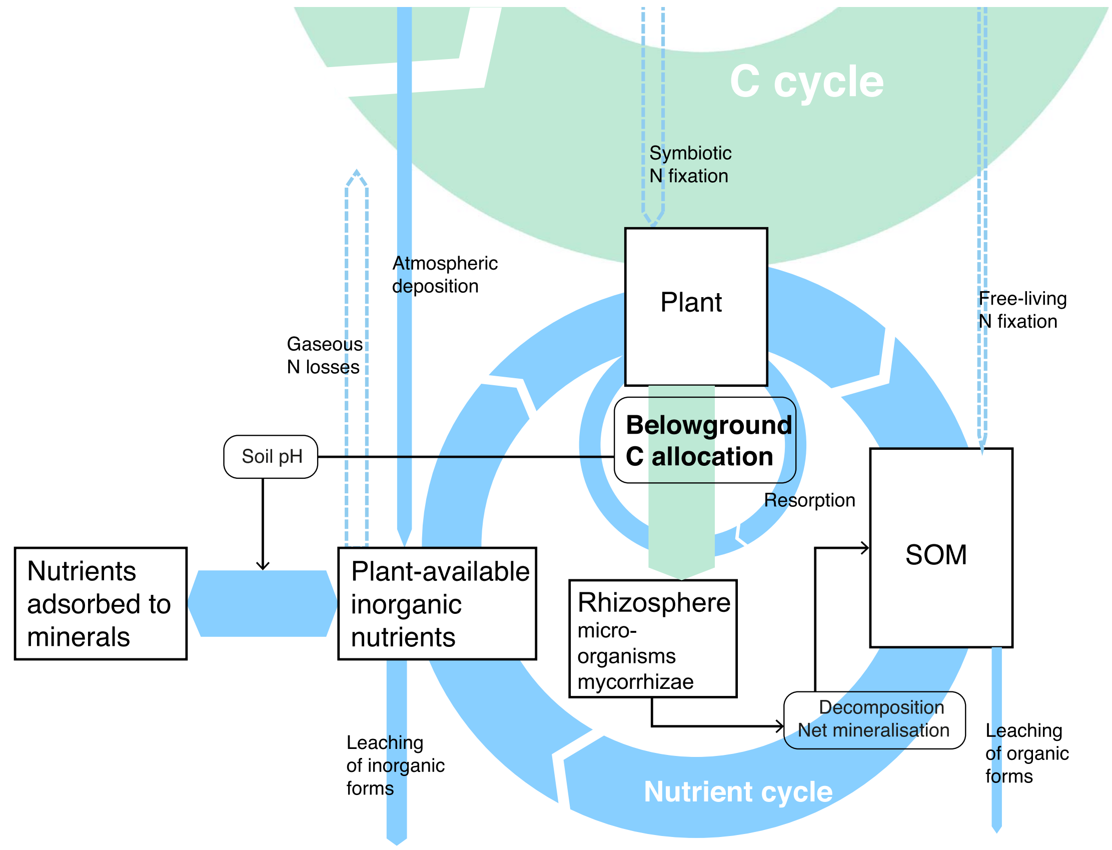

Figure 2. Schematic representation of the link between carbon and nutrient cycles as considered in biogeochemistry models. 'Belowground C allocation' subsumes different components and functions, including fine root production, fine root respiration, export to mycorrhizae and symbiotic bacteria (e.g. rhizobium for N fixation), and exudation of labile C compounds into the rhizosphere. The thickness of arrows approximately indicate the relative magnitudes of the fluxes. Blue arrows indicate nutrient fluxes, green arrows indicate carbon fluxes. Fluxes specific to nitrogen are given by arrows with a dashed outline. Boxes indicate pools.

research infrastructures. An overview of the interplay of relevant processes and fluxes is given in figure 2.

3.1. Carbon-nutrient relationships in terrestrial BGC models

While the explicit representation of C and N interactions is becoming common in BGC models, and recent developments have been aimed at explicitly simulating P cycling (Wang *et al* 2010, Yang *et al* 2014, Achat *et al* 2016, Goll *et al* 2017), other nutrients and additional soil properties that modulate nutrient availability to plants (e.g. pH, CEC, texture) remain largely ignored by the suite of models available today. This historical legacy resulted from the origin of these models, which were developed and applied mainly with the aim of simulating C cycle changes and their feedbacks with climate. The motivation for including effects of nutrients has primarily been to increase confidence in model projections of future C cycle trajectories in response to environmental change (Hungate *et al* 2003, Zaehle *et al* 2014a, Wieder *et al* 2015a). However, substantial uncertainties remain in how to adequately represent ecological processes that determine C-nutrient cycle interactions in global-scale models (Brovkin and Goll 2015, Meyerholt and Zaehle 2015, Wieder *et al* 2015b, 2015c). This challenge also presents new opportunities to test alternative hypotheses and refine ecological understanding of how nutrients shape the C cycle at centennial time scales and across the globe (Fowler *et al* 2015, Medlyn *et al* 2015, Tian *et al* 2018).

The key mechanistic relationships between C and nutrient cycles represented in models are related to allocation and stoichiometry. Allocation defines the partitioning of assimilated C into different plant organs and functions. Key for simulating C-nutrient interactions in BGC models is the partitioning into above- and belowground biomass pools (foliage and wood versus roots). The size of these pools is related to the efficiency at which above- and belowground resources are acquired. Stoichiometric relationships in models define particular C:nutrient ratios in simulated ecosystem pools. Despite widespread observational evidence for adaptive flexibility in plant C allocation and stoichiometry in response to nutrient availability and environmental manipulations, appropriately simulating these changes remains a significant challenge (Zaehle *et al* 2014b, Ghimire *et al* 2016, Terrer *et al* 2018). This challenge is particularly acute for belowground processes, where allocation and stoichiometry affect root function and plant-soil interactions that control nutrient uptake (figure 2). While many BGC models only have a rudimentary representation of functional relationship between roots and nutrient uptake, recent model developments have been aimed at better resolving this process (Iversen *et al* 2017, McMurtrie and Näsholm 2018). Despite this progress, significant knowledge and data gaps persist.

3.2. Data-model linkages

To address knowledge and data gaps, we call on existing research infrastructure and networks to collect data that help to clarify and quantify key functional relationships between allocation, stoichiometry and ecological function that are to be represented in models. Broadly, measurements are needed: (1) to reveal insights into allometric and stoichiometric changes and how they vary across ecosystems, over time, and under experimental manipulations; and (2) to link observed plant adaptations with observed variations in nutrient availability. We acknowledge a significant disconnect between suggested measurements for characterization of the nutrient status (section 3) and modelling needs (see below), which underscores opportunities to better align future research activities. Below we briefly summarize the approach commonly taken to simulate nutrient limitations in global models and discuss the power of different observable variables for informing and evaluating modelled relationships.

Belowground C allocation is directly affected by nutrient availability and the balance between above- (light, CO_2) and belowground (water, nutrients) resource availabilities (Poorter *et al* 2012). The magnitude of belowground C allocation indicates how much of the assimilated C is spent on nutrient and water acquisition. Without explicitly resolving how much C is allocated to different nutrient uptake mechanisms and plant-soil interactions, total belowground C allocation is the most relevant quantity for providing information on overall C costs of nutrient uptake (Gill and Finzi 2016) and can directly be related to variables simulated in BGC models (Shi *et al* 2016). Therefore, we highly recommend a strengthened focus on measuring belowground C pools and its change under experimental treatments and along environmental gradients (Iversen *et al* 2017). In the field, belowground C allocation is commonly estimated by subtracting litterfall and the changes in SOM pool from the soil CO_2 efflux (Davidson *et al* 2002, Litton *et al* 2007). Direct estimates of root production are rarely available since they are highly labour-intensive. However, root mass estimates can be more easily obtained by soil core sampling, and may be used as alternative proxy for total belowground C allocation under some simplifying assumptions (Terrer *et al* 2018). Instead of relying on absolute estimates of root mass, relative differences across sites and experimental manipulations may be a useful constraint on the model sensitivity of root allocation to environmental conditions (Terrer *et al* 2018). Interpretation of relationships between belowground C allocation and nutrients has to take into account that belowground C allocation and root biomass are affected by water availability, especially where deep rooting is a common plant strategy to access water stored in deep layers during prolonged dry periods.

Plant tissue stoichiometry and its response to nutrient availability is critical for the degree to which nutrient uptake limits plant growth. Particularly critical is to appropriately simulate the flexibility in leaf stoichiometry in response to environmental change. Current N-enabled BGC models explicitly resolve the C:N stoichiometry in plant tissue (Ghimire *et al* 2016). An evaluation by Zaehle *et al* (2014b) showed that available models generally overestimate the flexibility in tissue stoichiometry in response to elevated CO_2. This ensemble of models also simulated a feedback of increased foliar C:N under elevated CO_2 which (erroneously) tended to induce a progressively enhanced N limitation effect on plant growth due to greater N immobilization at high C:N ratios of litter inputs. Empirical data documenting how stoichiometry varies with experimental treatments and across environmental gradients is therefore important as a constraint for models and model-data evaluations should be extended to investigate P-related stoichiometry.

Soil C:N is typically prescribed in models for different SOM compartments (e.g. slow and fast turnover SOM). Hence, it is treated as constant in time and independent of environmental factors. Therefore, although soil C:N emerges as a good indicator for explaining variations in C cycling in observational datasets (see section 2), it cannot be used as a direct observational constraint on simulated nutrient dynamics in models. Furthermore, prescribed soil C:N ratios do not directly determine N availability in models. Until the complex nature of soil C:N as both a predictor and result of coupled ecosystem C and N cycling is accurately simulated by a next generation of models, its use for constraining current BGC models remains limited.

Plant nutrient uptake rates from the soil are useful for quantifying the 'return' on a given 'investment' of belowground C allocation (Terrer *et al* 2018). While these fluxes cannot directly be observed, field data can be obtained indirectly, based on litterfall, biomass increment, and tissue nutrient concentration data (Finzi *et al* 2007). Hence, the power of such data and the usefulness as an independent model benchmarking variable is limited. Nevertheless, comparing modelled and observation-derived nutrient uptake rates may serve as a practical way for model evaluation and has previously generated valuable insights (Zaehle *et al* 2014b).

Net mineralization rates represent the balance between gross mineralization from organic matter and the simultaneous immobilization in microbial biomass. While gross mineralization and immobilization are usually simulated separately by models, these are not readily measurable quantities in the field (Schimel and Bennett 2004). Net mineralization rates quantify the total nutrient 'throughput' through the system (figure 2) and are used to estimate nutrient availability for plants in the field (Gill and Finzi 2016). However, the use and interpretability of net mineralization data is not straightforward due to large seasonal variations, requiring repeated measurements, and due to the varying importance of nutrient losses (leakage and gaseous N loss) in confounding the relationship between net mineralization rates and nutrient availability. The value of net mineralization data for models therefore lies primarily in constraining simulated nutrient cycling rates and, in combination with estimates of nutrient inputs or losses and resorption, they can indicate the openness of nutrient cycling (Cleveland *et al* 2013).

N fixation is an important component of the ecosystem N balance and provides information about the degree of biological control on N availability and therefore on the potential of plants and the ecosystem as a whole to relieve limiting effects of low N availability, especially in global change scenarios (Menge *et al* 2014, Wieder *et al* 2015c, Meyerholt *et al* 2016). N fixation is increasingly recognized as a key variable that should be modelled based on the balance between N availability in the soil and plant demand (Medlyn *et al* 2015). Reliable measurements are therefore crucial for constraining models, but extrapolations based on field measurements and isotopic data produce varied estimates of global N fixation rates that still lack spatial or temporal resolution (Vitousek *et al* 2013). While estimates of ecosystem-level N fixation rates are difficult to achieve, especially where contributions from diverse N-fixing processes are substantial (e.g. free-living microbes, bryophytes; Reed *et al* 2011), information about relative differences in fixation rates or the fraction of N in biomass derived from N fixation (Schneider *et al* 2004) can also be used as a valuable constraint for models.

Resorption coefficients are typically prescribed and constant parameters in models (but see Shi *et al* 2016). Since they are thus not internally predicted, they cannot directly be used as an observational constraint. Nonetheless, a wider availability of observational data can provide a solid empirical basis for how resorption coefficients vary along environmental gradients (Reed *et al* 2012) and are therefore important for robust model parameterizations and as a target for future modelling efforts, where resorption coefficients may be treated as an internally predicted quantity.

Atmospheric deposition of nutrients is a key quantity that determines ecosystem nutrient balances and the degree to which nutrients limit or support additional C sequestration (De Vries *et al* 2009). CN-models commonly use prescribed spatial data of atmospheric deposition derived from large-scale atmospheric chemistry and transport models (Mahowald *et al* 2008, Lamarque *et al* 2011, 2013). However, these global datasets have a relatively coarse resolution spatially and temporally, may not resolve all local processes affecting deposition velocities, and comparisons to local measurements indicate a tendency for underestimated rates in global datasets (Sutton *et al* 2011), at least partly owing to challenges in estimating dry N deposition rates. This underlines the value of using specific measurements of deposition rates for interpreting results in empirical studies and as model forcing for site-level simulations.

The sizes of inorganic soil nutrient pools (NO_3^-, NH_4^+, PO_4^{3-}) are often simulated explicitly in models and typically determine plant uptake and loss rates. The temporal dynamics of inorganic nutrient pools are highly variable and subject to different biotic and abiotic factors. Hence, reliable model-data comparisons require frequently repeated sampling and standardized measurement protocols. However, the response of these pools to experimental manipulations and environmental changes yield insights into how nutrient pools, and therefore nutrient availability, change and how these changes relate to C cycling. More robust and accurate measurements, integrated over relevant timescales may be obtained from resin membrane methods (see above). These methods are particularly useful for assessing relative differences among sites or experiments that can be highly informative for network syntheses and for model-data comparisons. Field estimates typically quantify the inorganic pool size per unit soil volume or mass. In contrast, pool size per unit surface area is typically, but not always (Koven *et al* 2013), simulated in models. Quantities integrated over the entire soil profile are generally difficult to measure, suggesting that an explicit representation of the vertical distribution of SOM dynamics in models will contribute to a better capacity to evaluate models. Due to the key role of triggering plant responses and its explicit treatment and equally central role in models, we highly encourage the wide application of measurements of the size and availability of inorganic nutrient pools, and recommend methods that provide temporally integrated information (e.g. resin membranes).

Additional edaphic factors for modelling, including several soil properties (pH, CEC, texture, etc) influence soil chemistry and nutrient availability and can explain substantial additional variability of terrestrial C cycling across sites (Vicca *et al* 2012, Fernandez-Martinez *et al* 2014). These empirically based studies established the utility of using multiple edaphic factors to develop qualitative or quantitative metrics as proxies to understand ecosystem C responses across fertility gradients (section 2). Applying a similar methodology in models may help simulate cross-site variation in C cycle responses to environmental change, or the efficiency by which assimilated C is converted to biomass (Vicca *et al* 2012). To our knowledge, such a 'phenomenological' approach that accounts for multiple indicators of soil nutrient availability remains untested in BGC models. Alternatively, soil properties may serve as covariates in functions describing nutrient transformations and fluxes. For example, soil texture and pH modify transfer coefficients and C turnover times in several soil biogeochemical models, although recent analyses call into question the underlying assumptions applied in these models (Rowley *et al* 2017, Rasmussen *et al* 2018). Moreover, although it is tempting to explicitly represent fine scale soil processes and nuances, attention should be given to the main application of BGC models' to predicting large-scale biosphere dynamics and fluxes, especially under global change scenarios. The aim of using edaphic properties in conjunction with models should be to identify robust patterns in these relationships and will be important to guide future model developments to account for additional edaphic factors. Simultaneously, these efforts should identify additional data needs or availability to better constrain novel model formulations.

The imperfect overlap between field measurement options (section 2, table 1) and current model representations (section 3) speaks to the challenges and opportunities for incorporating empirical data into models, as well as for using models to help inform our understanding of terrestrial processes that are difficult to measure. For example, many of the processes central to regulating nutrient cycling in models are not easy to gather data for in the field (e.g. belowground C allocation, gross mineralization). Moreover, many of the field measurements are not straightforward to incorporate into existing models (e.g. spatial variation in site nutrient availability). Cross-site evaluations and global change manipulations offer strong possibilities to address the lack of overlap in what is measured empirically and what is represented numerically. In particular, the physical edaphic characteristics discussed above may be a common ground where increased data collection and incorporation into models could improve both approaches and our overall understanding. Further, components of models that are difficult but not impossible to measure well in the field could be collected across sites or treatments in an organized way, knowing the data would be critical for model evaluation. Improved knowledge of coupled C and nutrient cycles from separated empirical and modelling approaches will advance understanding, but joining these approaches through data collection, analysis, and interpretation would be the strongest way forward.

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