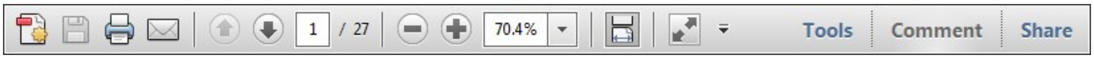
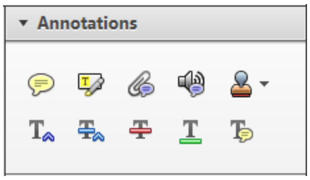
USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

Once you have Acrobat Reader open on your computer, click on the Comment tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the Annotations section, pictured opposite. We've picked out some of these tools below:

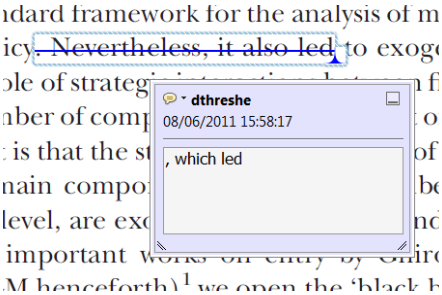


1. Replace (Ins) Tool – for replacing text.

Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the Replace (Ins) icon in the Annotations section.
- Type the replacement text into the blue box that appears.



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2. Strikethrough (Del) Tool – for deleting text.

Strikes a red line through text that is to be deleted.

How to use it

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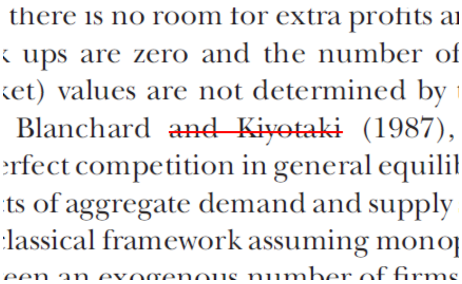
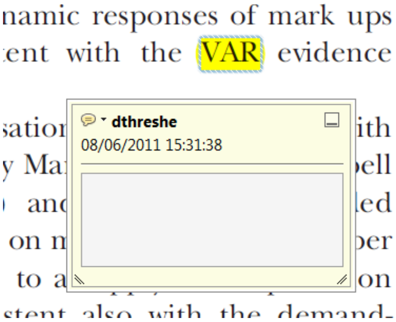


3. Add note to text Tool – for highlighting a section to be changed to bold or italic.

Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the Add note to text icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.



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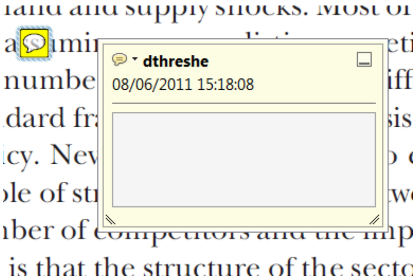
4. Add sticky note Tool – for making notes at specific points in the text.

Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the Add sticky note icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.



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5. Attach File Tool – for inserting large amounts of text or replacement figures.

Inserts an icon linking to the attached file in the appropriate place in the text.

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- Click on the Attach File icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
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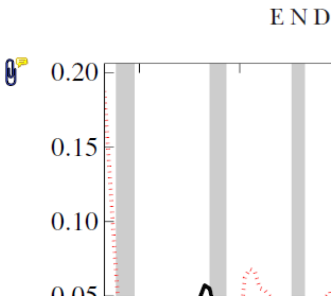
- Select the colour and type of icon that will appear in the proof. Click OK.



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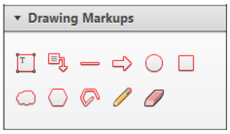

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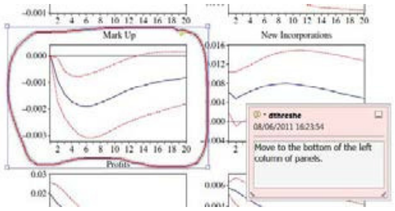
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



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Tansley insight

Incorporating phosphorus cycling into global modeling efforts: a worthwhile, tractable endeavor

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Summary

Myriad field, laboratory, and modeling studies show that nutrient availability plays a fundamental role in regulating CO_2 exchange between the Earth's biosphere and atmosphere, and in determining how carbon pools and fluxes respond to climatic change. Accordingly, global models that incorporate coupled climate–carbon cycle feedbacks made a significant advance with the introduction of a prognostic nitrogen cycle. Here we propose that incorporating phosphorus cycling represents an important next step in coupled climate–carbon cycling model development, particularly for lowland tropical forests where phosphorus availability is often presumed to limit primary production. We highlight challenges to including phosphorus in modeling efforts and provide suggestions for how to move forward.

I. Introduction

Earth system models (ESMs) represent the scientific community's best attempt at distilling the complexity of ecosystems into tractable, mathematical relationships that combine the physical, chemical, and biological components of the Earth system. These models provide the opportunity to test contemporary ideas of how climate and biogeochemistry interact, and offer a platform for predicting how ecosystems will respond to a range of global changes, such as rising atmospheric [CO_2] and increasing temperature. However, the utility and credibility of these models depend not only on their capacity to distill complexity, but also on how well they select for and capture the key drivers, processes, and relationships that regulate ecosystem function.

Here we propose that the inclusion of phosphorus (P) cycling into ESMs would significantly improve our capacity to test hypotheses and forecast interactions between biogeochemical cycles and a changing climate. It is well established that nutrient availability helps to regulate the terrestrial exchange of CO_2 with the atmosphere and imposes strong controls on carbon (C) cycling responses to global change (e.g. De Graff *et al.*, 2006; van Groenigen *et al.*, 2006; Elser *et al.*, 2007; Norby *et al.*, 2010; Fernández-Martínez *et al.*, 2014). For example, the lack of a nitrogen (N) cycle in first-generation climate–C models led to serious concerns about the models' capacity to accurately predict future climate (Hungate *et al.*, 2003) and, over the past decade, an increasing number of ESMs have incorporated prognostic N cycles and C–N interactions (Thornton *et al.*, 2007; Sokolov *et al.*, 2008; Zaehle *et al.*, 2010b). But N is not the only nutrient with the potential to greatly affect C cycling rates and response to change (e.g. Elser *et al.*, 2007). Thus, while we recognize that the power of models comes from minimizing the number of parameters included, we argue that P controls over C cycling are important enough to warrant incorporation into ESMs.

II. A need for phosphorus in global models

Compared with models that don't include a prognostic N cycle, terrestrial biosphere models that explicitly consider C–N interactions show that future land C sequestration could be reduced by 50% or more as a result of N cycle controls over C cycle responses (Sokolov *et al.*, 2008; Thornton *et al.*, 2009; Zaehle *et al.*, 2010b). Estimates of the size of this N effect vary among model projections as a result of variability in the representation of the processes that determine N controls over C storage (Zaehle *et al.*, 2014). Phosphorus is also an essential nutrient that commonly limits key C cycling processes, including plant productivity and microbial metabolism (e.g. Cleveland & Townsend, 2006; Elser *et al.*, 2007; Vitousek *et al.*, 2010; Reed *et al.*, 2011b). Unlike N, for which new N is principally supplied by biological N_2 fixation and anthropogenic deposition, the primary source of new P for terrestrial ecosystems is bedrock weathering and, sometimes, dust deposition (Fig. 1). These P inputs are uniformly low relative to plant uptake (Cleveland *et al.*, 2013). Accordingly, the P cycle may be less able to respond rapidly to increased biological demand from, for example, elevated atmospheric [CO_2]. If true, P regulation of C cycling responses to global change could become increasingly pronounced, and ignoring P's regulatory power over the global C cycle will become increasingly problematic.

Further, because of the different biogeochemical controls over N vs P cycling (e.g. McGill & Cole, 1981; Vitousek *et al.*, 2010), the two cycles may not respond in the same way to environmental change. From a modeling perspective, this means P cycle responses would not be captured by modeling the N cycle, or vice versa. Phosphorus also has notable potential to affect C cycling indirectly via interactions with N. Multiple lines of evidence suggest that increased P availability can result in increased N inputs via biological N_2 fixation (Reed *et al.*, 2011a; Batterman *et al.*, 2013) and, in turn, that changes to N could affect P availability via effects on phosphatase activity (Marklein & Houlton, 2012). Taken together, data suggest P could play a significant role in regulating C cycling responses to global change, and that improving coupled climate–C cycling models may require including P-specific drivers and mechanisms (Fig. 1).

Suggestions of P controls over global-scale C cycling stem, in part, from perceptions of P limitation of tropical lowland rain forest function. Tropical rainforests store and exchange enormous amounts of CO_2 with the atmosphere (e.g. Pan *et al.*, 2013), and our limited capacity to model tropical responses to global change may be the largest hurdle in accurately predicting Earth's future climate (Bonan & Levis, 2010; Piao *et al.*, 2013). Lowland tropical forests are common on highly weathered Ultisol and Oxisol soils (Palm *et al.*, 2007), which maintain low available and total P pools (Yang & Post, 2011). A variety of tropical C cycling processes respond to changes in P availability, and given its relative scarcity, P will almost certainly constrain the response of tropical forests to increases in atmospheric CO_2 and N deposition. Thus, improving

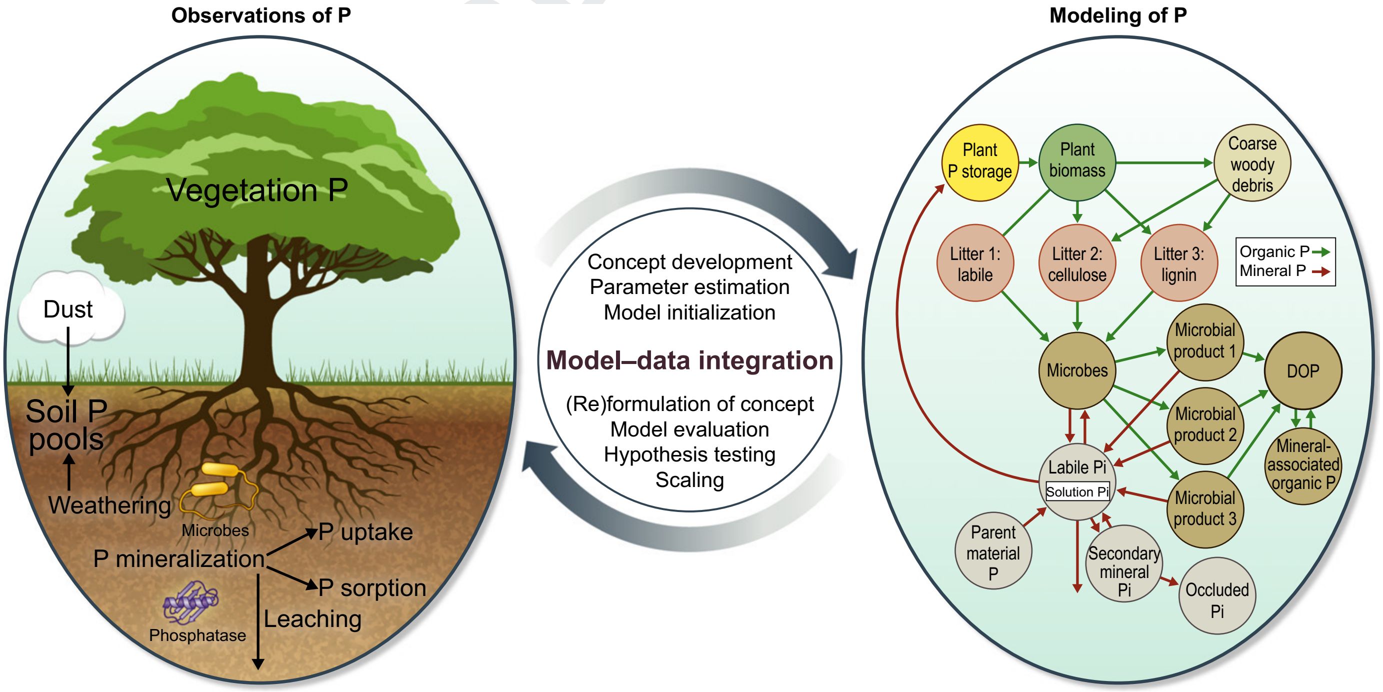

Fig. 1 Conceptual model depicting how field and laboratory research can work in concert with model development to improve our understanding of phosphorus (P) cycling in the environment and its responses to global change. Pi, ???; DOP, ???. 3

our ability to model the trajectory of these C-rich ecosystems may mandate the inclusion of P cycling.

III. Considerations for including phosphorus

Based on an understanding of P cycling and past modeling, there are four aspects of P cycling we suggest as being particularly important for inclusion in ESMs: P mineralization, P sorption, P limitation, and the stoichiometric relationships of P with C and N (Box 1; Table 1). One of the most influential components of the P cycle is P mineralization: the breakdown of organic P into mineral forms that, unless sorbed or lost via leaching, are available for plant and microbial uptake. On an annual basis, the recycling of P out of organic matter (via litter leaching or organic matter decomposition) represents the largest source of P to biota in most ecosystems (Cleveland *et al.*, 2013) and P mineralization will be central to effective modeling of P (Table 1; Yang *et al.*, 2014). In some modeling studies that examined the influence of C–N coupling on C–climate interactions, altered N mineralization as driven by warming and changing soil moisture under climate change were the factors most responsible for differences in spatial and temporal patterns of C–climate feedbacks (Thornton *et al.*, 2007, 2009; Sokolov *et al.*, 2008). Other modeling suggests that climate-driven changes in N mineralization could be offset by changes in vegetation C : N ratios, generating a smaller influence on net C flux (Zaehle *et al.*, 2010a). In either case, N mineralization is a critical underlying driver of modeled ecosystem response. Variation in C : N : P stoichiometry notwithstanding (see later), we expect that P mineralization will likewise form the process foundation for any modulation of the C–climate feedbacks driven by P cycle processes.

Differences between N and P mineralization offer important considerations for models. While C and N are stabilized together and mineralized through biological mineralization, organic P is located independently of the main organic moiety and can thus be mineralized through 'biochemical mineralization'. Biochemical mineralization is the release of inorganic P through enzymatic catalysis external to the cell membrane, and the process can be independent of organic C and N breakdown and controlled by the demand for P rather than the need for energy (McGill & Cole, 1981). Although current model representations capture the major factors controlling biochemical mineralization, the parameterization is based on a limited number of observations (Yang *et al.*,

Box 1 Xxxxxxxxxxxxx

Effectively incorporating phosphorus into modeling efforts will rely upon important decisions about how to represent and parameterize the phosphorus cycle and its interactions with the cycles of carbon and nitrogen. We suggest that empirical and modeling efforts could make large advances by focusing on improving our understanding of phosphorus mineralization, sorption, limitation, and stoichiometry (Table 1; Fig. 1).

Table 1 Phosphorus (P) cycle processes and parameters for consideration when including P in models

Process/parameter	Issues to consider
P mineralization (Biological vs biochemical)	• Multifaceted enzyme controls, particularly for phosphatase • Fate of mineralized P • C: N: P stoichiometry of microbes vs soil organic matter
P sorption	• Soil mineralogy and texture • Competition with biotic demand • Redox–Fe–P interactions • pH
P limitation to C cycle processes (e.g. plant and microbial growth and respiration)	• Where does P limit ecosystem processes, and what processes? • Relationships between limitation and P acquisition strategies • Multi-element limitation
P cycle coupling with the cycles of C and N	• Plasticity of C : N : P stoichiometry in plants, microbes, and soil organic matter and links with P-use efficiency • N effects on P enzyme activity
Soil P pools	• What is 'available P'? • Choice of soil P assay • P pools ranging in biological availability • Chemistry of different P pools
Plant/microbe P uptake	• Mechanisms used to access P • Competition among biota • Rhizosphere biogeochemistry • Root architecture
P-use efficiency	• Drivers and consequences of P-use efficiency
Bedrock P and weathering rates	• Rock P content • Role of parent material inputs across time • Relationship between bedrock P and soil P pools
Atmospheric inputs (e.g. dust, ash)	• Role of atmospheric P inputs in sustaining fertility • Global variation in P inputs
P leaching	• Loss of P through leaching • Inorganic vs organic P loss • Variation in loss of P with variation in biological demand
Topographic position	• Topographic variability in soil pedogenesis, P pools, and P limitation
Ecosystem development and successional stage	• Variation in P limitation, P cycling, and coupled biogeochemical cycles with ecosystem successional stage
Species-specific P acquisition, nutrient limitation, and effects on P pools	• Species-specific P acquisition • Species-specific P pools • Soil P structuring of community composition
Symbioses – in particular, N_2 fixation and mycorrhizas	• Symbiosis controls over P cycling and pools • P controls over symbiotic relationships • Interactions among symbionts

We highlight the first four processes/parameters in bold italics as critical for consideration. An improved understanding of P cycling rates/pool sizes, as well as responses to global change, is needed for all parameters and thus the 'issues to consider' column provides parameter-specific topics additional to this need. We provide suggestions for further reading, with full citations given, in Supporting Information Table S1.

2014). In general, more observational and experimental data are needed to quantify P mineralization rates and controls, and we encourage the scientific community to focus on improving our understanding of this fundamental process.

Phosphorus sorption – the removal of P from solution into less reactive, geochemical sinks – is an important consideration in modeling P, because in soils with strong sorption capacities (e.g. highly weathered soils) this geochemical sink effectively competes with biota for P (e.g. Sollins *et al.*, 1988). The strength, extent, and longevity of P sorption are determined in part by soil mineralogy, and traditional definitions of occluded P suggest that it is biologically unavailable, at least over decadal timescales. However, emerging evidence indicates that occluded P may enter biological pathways on shorter timescales (Richter *et al.*, 2006; Syers *et al.*, 2008; Huang *et al.*, 2014); for example, results from an aggrading forest on an Ultisol soil showed that 28 yr of Piedmont forest regrowth occurred via biological access to occluded P (Richter *et al.*, 2006). These and other data suggest that movement from geochemical to biotic pools over hourly to decadal time steps is strongly influenced by biological demand (Olander & Vitousek, 2004; Richter *et al.*, 2006), but our understanding of these competing pathways remains poor. From an ESM perspective, this means that for some soils we should account for the role of sorption in determining P availability, the potential for global change to affect sorption patterns (e.g. via O_2 controls; Table 1), and the likely necessity of measuring and considering multiple soil P pools.

Ultimately, interest in including nutrient cycles in ESMs is based on the desire to understand how nutrient availability and changes to nutrient cycles affect C cycling, and nutrient limitation is central to this consideration. While we know that increasing P availability can significantly affect rates of plant and soil C cycling, our understanding of P limitation is far from complete. For example, a variety of research suggests P limitation to fundamental aspects of tropical forest structure and function, including plant growth, soil respiration, microbial biomass growth, and plant community composition (Vitousek & Farrington, 1997; Wardle *et al.*, 2004; Cleveland & Townsend, 2006; Elser *et al.*, 2007; Reed *et al.*, 2011b; Quesada *et al.*, 2012; Condit *et al.*, 2013). That said, direct tests of tropical P limitation are rare and there is enough variability among the results to suggest we require significantly more information about how P (and other nutrients) constrains tropical forest function. For instance, data from fertilization studies suggest a role for P, but also show that the nutrient(s) limiting plant productivity in tropical rainforests can vary among ecosystems and tree species, and that different ecosystem components can be limited by different nutrients (Wright *et al.*, 2011; Alvarez-Clare *et al.*, 2013; Turner & Wright, 2014). Further, while fertilization experiments help to decipher what nutrients are limiting, from a global change perspective our questions are really centered upon what happens when P availability declines relative to demand (e.g. with increased plant uptake in the face of CO_2 fertilization; Cernusak *et al.*, 2013). Exploring this question requires a different set of field experiments.

A second challenge for including nutrient limitation centers on how limitation is represented within ESMs. Nitrogen limitation is represented either through direct down-regulation of gross primary productivity using the supply–demand approach or through the control of foliar N on photosynthesis (Thornton *et al.*, 2007; Zaehle *et al.*, 2010b). A similar approach has been adopted for representing P limitation (Wang *et al.*, 2007; Goll *et al.*, 2012; Yang *et al.*, 2014); however, unique challenges for P include foliar concentrations that are much more variable than N, and our poor understanding of how leaf P concentrations control photosynthesis. As a result, a mechanistic representation of leaf P concentration [4] on photosynthesis has not been implemented in models. Encouragingly, with increasing interest in P limitation and effect on photosynthesis, new research is addressing this need (e.g. Ellsworth *et al.*, 2015). There is also a role for stoichiometry in modeling P effects; for example, a recent effort synthesizing C–N model and field experimental results of two free-air CO_2 enrichment (FACE) studies suggests that better constraints on plant stoichiometry are pivotal in reducing model uncertainty. It follows that C : P stoichiometry would be equally important in many ecosystems.

Beyond an improved general understanding of P cycling, a central challenge to modeling P derives from a paucity of data for addressing questions of P cycling responses to global change. Because more global change experiments have been carried out in temperate and high-latitude systems, which are thought to be more strongly regulated by N availability, less research has focused on P (with important exceptions – such as Niklaus & Körner, 2004; Huang *et al.*, 2014). Thus, we have relatively few data with which to predict how elevated $[CO_2]$ and altered climate will affect P, even in lowland tropical forests where understanding the response of P may be critical to understanding ecosystem responses as a whole. However, new global change experiments with a P focus are beginning (see the following section), and provide substantial opportunities for increased understanding.

IV. Opportunities for moving forward

Each topic discussed in the previous sections can be addressed with data synthesis, the collection of new data (particularly in a global change context), evaluation of different P models (conceptual and numerical), and increased collaboration between modelers and empiricists. Global meta-analysis efforts are providing biogeochemical data relevant to P cycling and its stoichiometric relationships with C and N (e.g. Reich & Oleksyn, 2004; Cleveland & Liptzin, 2007; Reed *et al.*, 2012; Cleveland *et al.*, 2013; Table 1). These datasets advance our general understanding of P cycling, as well as our capacity to populate models, and can be used for creating products that benefit multiple P models. For example, Yang *et al.* (2013) employed a data synthesis effort to provide global maps of various P pools that can be used for multiple aspects of modeling P, including the initialization of models to include P cycling that spans millions of years.

A number of global change experiments that consider P are beginning and these offer a substantial opportunity to gain an insight into how P cycling and its interactions with other biogeochemical cycles will respond to global change. For example, a FACE experiment is under construction in a Brazilian Amazon forest (http://face.ornl.gov/AmazonFACE.html), as is a soil and understory forest warming experiment in Puerto Rico (http://www.forestwarming.org). These projects will measure numerous aspects of P cycling and its coupling to the cycles of C and N. There is also a large-scale project focused on improving our understanding of P limitation and the risks associated with a growing stoichiometric imbalance at the global scale (http://imbalancep-erc.creaf.cat/). Comparisons between field experimental and modeling results underscore the power of evaluating modeled and empirical data together, and the importance of considering both approaches before the experiment begins (e.g. Zaehle *et al.*, 2014). We urge leaders of new experiments to include a modeling perspective before finalizing the experimental design, metrics to measure, and pretreatment data collection.

Incorporation of P into global models is taking place (Wang *et al.*, 2007; Goll *et al.*, 2012; Yang *et al.*, 2014) and these models, as well as models including C–N interactions (Zaehle *et al.*, 2014), are paving the way for increased inclusion of P cycling into ESMs. The examples allow for the evaluation of different P modeling approaches and the exploration of new ways to model P in the context of global change (Table 1). A cross-model analysis could be a powerful next step in assessing how to model P at the global scale. Another opportunity for modeling P stems from the fact that ESMs are becoming increasingly modularized. While testing isolated components of models is not new, subcomponents of full models that run independently of ESMs and functional test platforms are increasingly powerful, and allow for the rapid testing of new model structure, algorithms, and parameters, as well as direct model–data comparisons (e.g. Hu *et al.*, 2014).

Increased collaboration between modelers and empiricists is a critical mechanism for improving our understanding of, and ability to model, P cycling in the context of global change. Observational, experimental, and modeling approaches have different strengths and weaknesses, and using them together offers the most powerful way forward for finding answers to longstanding P questions. Modelers can help empiricists develop and test P hypotheses, accessing spatial and temporal scales that are impossible to address in the field. In turn, empiricists can help modelers select the most relevant aspects of P cycling, and construct process representations with the greatest potential to lend insight into future C cycling and climate (Fig. 1). We encourage empiricists, particularly those in the early stages of their research careers, to seek out collaborations with modelers, and vice versa, and we applaud programs that facilitate this interaction (e.g. INTERFACE; www.bio.purdue.edu/INTERFACE). This is an exciting time to study P and its role in global change, and taking advantage of the varied tools available offers the best chance of solving the substantial puzzles presented by P cycling.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 An extended version of Table 1, with a handful of suggestions for further reading and the full citations included

Author Query Form

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During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper's edge. Please remember that illegible mark-ups may delay publication.

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1	**AUTHOR: Please confirm that given names (red) and surnames/family names (green) have been identified correctly.**	
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