

Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from terrestrial ecosystems

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The biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) are fundamental to life on Earth. Because organisms require these elements in strict proportions, the cycles of C, N, and P are coupled at molecular to global scales through their effects on the biochemical reactions controlling primary production, respiration, and decomposition. The coupling of the C, N, and P cycles constrains organismal responses to climatic and atmospheric change, suggesting that present-day estimates of climate warming through the year 2100 are conservative. N and P supplies constrain C uptake in the terrestrial biosphere, yet these constraints are often not incorporated into global-scale analyses of Earth's climate. The inclusion of coupled biogeochemical cycles is critical to the development of next-generation, global-scale climate models.

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In an era of extensive environmental change, human activity – particularly the harvest of resources for food, fiber, and fuel – is substantially altering Earth's climate and its element cycles (Vitousek *et al.* 1997; Figure 1). The need for energy to support economic growth has increased atmospheric carbon dioxide (CO₂) concentrations by nearly 40% since the beginning of the Industrial Revolution (Canadell *et al.* 2007). The development of the Haber–Bosch process used in the manufacture of nitrogen (N) fertilizers has more than doubled the quan-

tity of reactive N entering the terrestrial biosphere (Galloway *et al.* 2008). Mining of phosphorus (P) for fertilizers has redistributed P across Earth's surface, substantially depleting phosphate mineral deposits (Gilbert 2009) and, in combination with N, leading to the eutrophication of aquatic ecosystems (Conley *et al.* 2009). Individually and collectively, changes in these element cycles are reorganizing biological communities, with important implications for the health of ecosystems and Earth's climate in the 21st century.

The metabolic pathways that enable life on Earth couple biogeochemical cycles to one another (Falkowski *et al.* 2008). Accordingly, a change in one element cycle invariably entrains a change in one or more different element cycles (Figure 2). This entrainment raises serious concerns about human-driven increases in atmospheric CO₂ concentrations that cause climate change and the biogeochemical consequences of vast quantities of N and P now flowing across the terrestrial landscape. To address the impacts of human activities on coupled biogeochemical cycles (herein CBCs), we first discuss the basis by which organisms couple biogeochemical cycles to one another. We then focus on the constraints CBCs impose on terrestrial productivity and the consequences these constraints may have for climate change through the 21st century.

In a nutshell:

- The coupled biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) are fundamental to life and Earth's climate system and are changing rapidly as humans increasingly extract and use food, fiber, and fuel
- Organisms couple the cycles of C, N, and P by acquiring and synthesizing essential compounds with specific ratios of C:N:P
- Climate change is likely to be more intense than predicted by the current generation of global-scale C–climate models because of the constraints on terrestrial productivity imposed by the biogeochemical cycles of N and P
- Interactions between coupled biogeochemical cycles and the biophysical properties of the land surface will strongly influence the amount of greenhouse gases released to the atmosphere as a result of warming in high-latitude ecosystems

■ Organisms, the coupling of biogeochemical cycles, and climate variability

Element ratios vary widely in nature. In the atmosphere, N is nearly 3000 times as abundant as carbon (C), and C is nearly a billion times as abundant as P (Schlesinger 1997). In the lithosphere – the Earth's crust – the order reverses: P is about twice as abundant as C and around 40 times as abundant as N. In the biosphere, however, the

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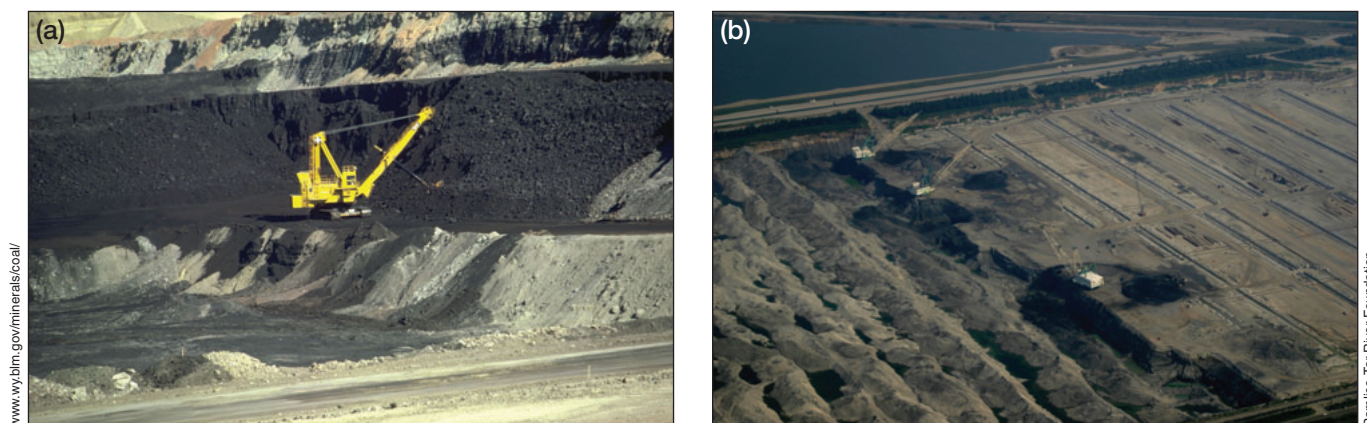


Figure 1. Examples of human activities that alter the biogeochemical cycles of C and P. (a) Vast coal reserves in Powder Ridge, Wyoming, are mined and delivered to power plants across the US. The coal is burned to generate electricity but also releases vast quantities of CO₂ to the atmosphere. (b) The mining of phosphate-bearing rock in coastal North Carolina. Mining for P fuels agricultural productivity but also transforms landscapes – in this case, a coastal wetland – and affects water quality in lakes, rivers, and the coastal ocean.

relative order is fixed, with $C > N > P$, because organisms require elements in strict proportions in order to catalyze metabolic reactions and synthesize the building blocks of life, including proteins, adenosine triphosphate (ATP), and structural compounds, each of which has specific elemental requirements (Sterner and Elser 2002). It is the strict proportions of elements required by organisms that couples biogeochemical cycles to one another.

Given that organisms have generally conservative stoichiometries, the ability to acquire C, N, and P from the environment places important limitations on organismal and community responses to variations in climate. Take, for instance, Arctic regions, which are extremely cold in the winter but warm substantially during the brief summer period; the microorganisms in these soils need to acclimate to wide temperature variations – the transition to cold soils during the fall “freeze-in” period, for example – or will otherwise die (Figure 3). To protect against mortality during the freeze-in period, microbes induce the synthesis of proteins, switch to alternative metabolic pathways, and alter the composition of their cell membranes to maintain functionality (Schimel *et al.* 2007; Hall *et al.* 2010), all of which require adequate supplies of C, N, and P, and have ecosystem-level consequences (Schimel *et al.* 2007). As soil temperatures drop toward 0°C, microbes shift from a net sink for N during the growing season to a net source of N during winter (Giblin *et al.* 1991; Schimel *et al.* 2004). Similar processes – albeit in the reverse direction – occur during the spring thaw, when microbes release many of their wintertime cell constituents, resulting in a pulse of CO₂ production and mineralized N and P. In tussock tundra in the Arctic, Schimel *et al.* (2007) estimated that CO₂ production during a single thaw pulse releases C on the order of 25% of annual aboveground net primary production and that more N is mineralized in a single thaw pulse than that mineralized annually. Though the growing microbial population in the spring may rapidly immobilize much of this N, in

alpine ecosystems this spring pulse of N fuels primary production – defined as the rate at which C from the atmosphere is converted to plant biomass per unit ground surface per unit time – during the growing season (Schmidt and Lipson 2004). Presumably, the pulsing of P into and out of microbial biomass is similar to that for N, though far less data are available on this critically important element cycle.

In addition to physiological acclimation, shifts in community composition often occur in response to climate variability. In alpine regions of Colorado, there is a fairly distinct succession in microbial communities, from those dominated by fungi in the winter to those dominated by bacteria in the summer (Schadt *et al.* 2003). This succession is due to the combination of a springtime microbial population crash, particularly in fungi, that releases labile pools of C, N, and P into the soil and the concomitant increase in the availability of labile C inputs (eg sugars, organic acids) associated with springtime root growth that favor rapidly growing bacteria (Schmidt *et al.* 2007). Because bacterial biomass turns over about 10 times per growing season, alpine plants, in symbiosis with root-colonizing fungi (ie mycorrhizae), are able to acquire some of the N and P released into the soil as cells lyse, maintaining primary production in these strongly nutrient-limited ecosystems (Schmidt *et al.* 2007).

Much like equivalent changes in the microbial world, shifts in plant species or functional-group composition are likely to have large impacts on the response of CBCs to global change (Hobbie 1996; Eviner and Chapin 2003; Hooper *et al.* 2005). Higher plant diversity in temperate grasslands is correlated with higher rates of primary production in response to both elevated CO₂ and atmospheric N deposition (Reich *et al.* 2004), suggesting that more diverse communities help mitigate climate change by storing atmospheric CO₂ and taking up excess N. Similarly, fire suppression and other changes in land management have resulted in the expansion of woody

plants in many non-forest ecosystems (Knapp *et al.* 2008). Woody plant encroachment tends to increase primary production as compared with that of grasslands as a result of greater resource-use efficiency in woody plant species that have C:N:P ratios which are much greater than those of grass leaves. And by virtue of longevity, the transition to woody plant cover also results in a redistribution of N and P from the soil to biomass pools (Berthrong *et al.* 2009).

Because plants and microbes form the base of food chains, the ecology and evolution of all higher-trophic-level organisms – herbivores, granivores, carnivores, and so forth – are intricately bound and constrained by the coupling of biogeochemical cycles. Consequently, global-change induced alterations in the functional diversity – and therefore the nutrient stoichiometry – of plant and microbial communities cascade through food webs. Plant biomass has wider C:N:P ratios than those of consumers, often limiting the growth of organisms at higher trophic levels (Sturner and Elser 2002; Hall 2009) – an effect that is amplified by chronic N deposition, which widens foliar N:P ratios and intensifies P limitation in insect herbivores (Elser *et al.* 2000). Similarly, widening of plant C:N and C:P ratios decreases the quantity of biomass consumed by herbivores, increases the quantity entering the detrital food web (Cebrian 1999), and decreases the ratio of herbivore-to-producer biomass (Cebrian *et al.* 2009). Should climate or atmospheric change alter C:N:P ratios in plant and microbial biomass, studies suggest that substantial shifts in the trophic structure of terrestrial ecosystems will result.

■ CBCs, carbon storage, and climate change

Terrestrial ecosystems in many regions of the world absorb and store atmospheric CO₂ (Dixon *et al.* 1994). The storage of C in plant biomass and in soil organic matter (SOM) is one of the most important services provided by the terrestrial biosphere. Currently, the terrestrial biosphere alone absorbs 20–30% of anthropogenic CO₂ emissions, slowing the pace at which CO₂ accumulates in and leads to the warming of Earth's atmosphere (Canadell *et al.* 2007). Most importantly, C storage is regulated by the biogeochemical cycles of N and P, because the rate of photosynthesis is proportional to the amount and activity of the N-rich enzyme ribulose biphosphate carboxylase/oxygenase in leaves (Wright *et al.* 2004) and P, in the form of biochemical energy (ie ATP, nicotinamide adenine trinucleotide

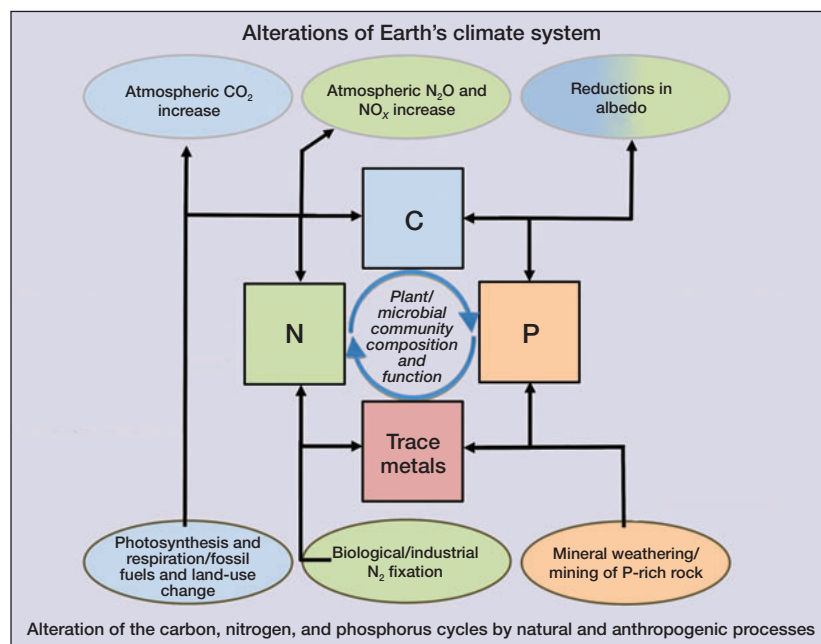


Figure 2. A diagram of human impacts on Earth's climate system and the biogeochemical cycles of carbon (C), nitrogen (N) and phosphorus (P). Although human activity tends to modify element cycles one at a time (eg releasing CO₂, fixing N, mining P), alteration of one cycle nearly always entrains alteration of other element cycles. As a result, there are complex feedbacks between human activity and the functioning of the terrestrial biosphere, feedbacks that are substantially influenced by the composition and function of plant and microbial communities.

phosphate) and in the sugar–phosphate “backbone” of DNA/RNA, is necessary for the synthesis of proteins and plant tissues.

Rising concentrations of atmospheric CO₂ are expected to increase plant growth, but results from experiments vary widely. In some ecosystems, elevated CO₂ has been shown to stimulate growth for over a decade (eg McCarthy *et al.* 2010), whereas other studies reveal only transient increases (eg Reich *et al.* 2006) or no response at all (eg Shaw *et al.* 2002). Yet the global-scale models used to predict atmospheric CO₂ concentrations and climate patterns through the 21st century assume a consistent, stimulatory effect of rising concentrations of atmospheric CO₂ on terrestrial productivity (Carter *et al.* 2007). There is therefore a clear discrepancy between empirical data and models.

Why are the responses to elevated CO₂ so variable? One answer is nutrient limitation. As with most biological systems, multiple resources simultaneously limit plant growth and ecosystem productivity (Bloom *et al.* 1985). Thus, CBCs underlie the working hypothesis for the decline in productivity under elevated CO₂; a rapidly growing biomass accumulates and stores nutrients more quickly than they can be replenished through new inputs and the decomposition of SOM (Luo *et al.* 2004).

Could nutrient constraints to growth under elevated CO₂ be alleviated? At decadal-to-centennial timescales, terrestrial C storage will likely be regulated by interactions between the C and P cycles, and N₂ fixation – the

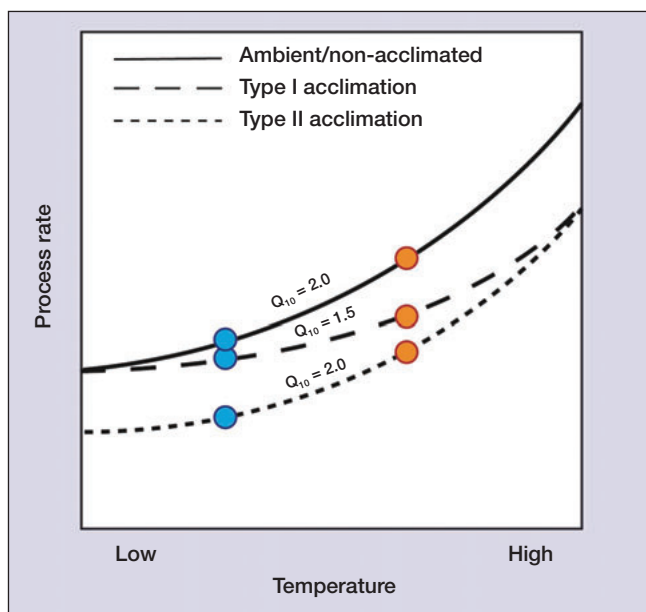


Figure 3. Potential changes in the functional response of plant or microbial communities after physiological acclimation to climate warming. In non-acclimated communities, the rate of biological processes (eg photosynthesis, respiration, mineralization) typically doubles with every 10°C rise in temperature when other resources are not limiting (referred to as “ Q_{10} ”, which in this case is equal to 2). As organisms adapt to warmer temperatures, the response of those functions can change through either (1) Type I acclimation (a decrease in the temperature sensitivity [eg Q_{10}], which results in decreased activity at higher temperatures but little or no change at lower temperatures) or (2) Type II acclimation (decreased activity at all temperatures, with no change in Q_{10} ; Atkin and Tjoelker 2003; Bradford *et al.* 2008). These acclimation responses could result from either physiological adjustments or changes in the relative abundance of different taxa within a functional community.

process by which atmospheric N_2 is converted to bioavailable forms. N_2 fixation occurs through free-living or symbiotic microbial pathways; in either case, C and P are necessary for N_2 fixation (van Groenigen *et al.* 2006). N_2 fixation is one of the most energy-demanding biological processes on Earth, thereby coupling fixation to the C cycle. N_2 fixation also requires 16 molecules of ATP per mole of N_2 fixed. ATP has a very low N:P ratio (5:3), pointing to P constraints to fixation at molecular scales, constraints that are known to occur on land, in fresh water, and in the oceans (Vitousek *et al.* 2002).

The response of N_2 fixation to atmospheric change could potentially affect Earth’s climate. A few studies have shown that fully coupled climate–C–N-cycle models predict a much warmer world by the end of the year 2100 than would be apparent in the absence of N limitations (Thornton *et al.* 2007). In a recent analysis of the fully coupled C-cycle climate models that will be used in the next Intergovernmental Panel on Climate Change (IPCC) report, Wang and Houlton (2010) estimated that global mean temperature could be 1.2°C greater than that

currently predicted for the year 2100 (Figure 4). Principal to the amount of warming is N_2 fixation and the activity of phosphatase enzymes, revealing the importance of CBCs in the planet’s future.

An equally important component of climate change is the alteration in the reflectivity of Earth’s surface with warming. Some of the most pronounced increases in temperature have been observed in high-latitude regions, particularly the Arctic, where the areal extent of summer sea ice has declined substantially over the past 40 years (Figure 5) and temperature increases have been far larger than that of the global average for the period 1850–2000 (Kaufman *et al.* 2009). In these high-latitude ecosystems (boreal forests, tundra, and their associated wetlands), decomposition is more strongly temperature- and moisture-limited than is photosynthesis, and soils store vast quantities of C – at least double that in the present-day atmosphere (Schuur *et al.* 2008; Tarnocai *et al.* 2009). The extent to which this pool of C contributes to future climate change as temperatures continue to rise depends largely on the response of CBCs to current rates of warming.

The response of CBCs to warming in high-latitude regions underlies two pathways by which positive and negative feedbacks to additional warming are possible (Figure 6). One positive feedback results from accelerated rates of decomposition and the release of greenhouse gases (GHGs) to the atmosphere. Accelerating rates of decomposition will substantially increase the flux of C back to the atmosphere as CO_2 and methane (CH_4 ; Schuur *et al.* 2008). However, CH_4 has ~21 times the global warming potential of CO_2 , making the balance between CO_2 and CH_4 critical to the amount of future warming (Christensen *et al.* 2000). The conversion of organic material to methane (ie methanogenesis) occurs in anoxic soils largely free of sulfate, highlighting the importance of two additional biogeochemical cycles – water and sulfur – for the balance between CO_2 and CH_4 production (White *et al.* 2008).

In addition to CO_2 and CH_4 , the warming-induced increase in N mineralization from detrital pools in soil is likely to accelerate the production of nitrous oxide (N_2O), a GHG with ~310 times the global warming potential of CO_2 . N_2O is produced during denitrification, a microbial process occurring under low O_2 conditions, and commonly limited by the availability of NO_3^- and labile C (ie energy). Accordingly, warming-induced increases in the oxidation of organic N to NO_3^- are likely to increase the flux of this GHG to the atmosphere. As with CO_2 and CH_4 , soil temperature, soil moisture, and freeze–thaw cycles exert considerable control over N_2O production (Repo *et al.* 2009; Elberling *et al.* 2010), and the potential for a very strong positive feedback to warming.

By contrast, a warming-induced negative feedback may be driven by changes in plant growth as a result of the increase in N and P mineralization from SOM. The supply of N and P strongly limits plant growth in high-latitude ecosystems, so the increase in nutrient availabil-

ity is likely to increase plant growth and C storage in biomass (Weintraub and Schimel 2005). Longer growing seasons in the Arctic are favoring the growth of woody plants, such as the dwarf shrubs *Betula nana* and *Salix polaris* (Weintraub and Schimel 2005). Because the C:N:P ratio of woody plant biomass is substantially higher than that of the soil, increases in C storage in Arctic regions may be sizeable.

The negative feedback to climate warming due to greater N and P availability must, however, be tempered by the biophysical and biogeochemical consequences of increasing primary production. The stems and leaves of shrubs are dark, so the expansion of shrubs into sub-Arctic and Arctic ecosystems decreases albedo and promotes warming (Weintraub and Schimel 2005). Shrub cover also increases snow pack depth, which insulates the soil from extreme cold. Microbial communities can be very active under the snow (Monson *et al.* 2006), decomposing SOM and releasing, in winter months, nutrients that are susceptible to loss in the form of CO₂, CH₄, or N₂O. Finally, warming-induced changes in decomposition and nutrient supply can result in larger C losses from the soil than the C gained in woody biomass (Mack *et al.* 2004).

■ Conclusions

This paper has reviewed some of the important interactions among organisms, CBCs, and biophysical properties of ecosystems. Many of the core ideas presented here translate, to varying degrees, to other biogeochemical cycles – as well as to aquatic ecosystems – as described in several of the other articles in this issue of *Frontiers*. Although we have learned a great deal about CBCs through observations and experiments, there remain considerable uncertainties in the interactions between CBCs, climate change, and other aspects of global change. Is there a threshold temperature (ie a tipping point) above which trace-gas losses of C and N to the atmosphere accelerate substantially faster than C gains in plant biomass, resulting in runaway global warming? Over what spatial and temporal scales will N₂-fixing organisms respond to multiple drivers of global change, including rising CO₂, atmospheric N deposition, and wildfires? What types of plant and microbial species or functional groups exhibit flexible stoichiometries that enable adaptation rather than loss from extant communities, and

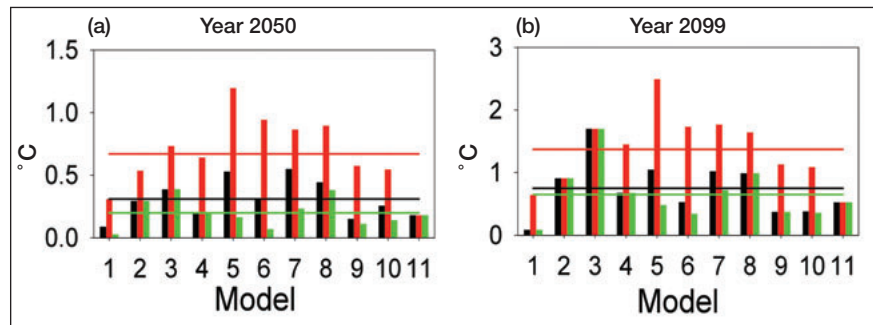


Figure 4. In a recent analysis of the fully coupled C cycle climate models that will be used in the next IPCC report, warming in the absence of N limitation (green bar) is far less than estimates correcting for widespread N limitation in terrestrial ecosystems (black and red bars represent upper and lower estimates of N₂ fixation, respectively). Horizontal lines represent the mean of 11 models for three different estimates of the additional warming. (a) Year 2050; (b) year 2099.

how would adaptation versus community change affect the resiliency of ecosystems to biogeochemical and climatic change? Answers to these questions become increasingly important in light of the expected growth of the human population – at least 2 to 3 billion more individuals this century – and the rapid pace of socioeconomic development that will result in escalating rates of CO₂ production, faster rates of climate change, and more N and P released to the environment.

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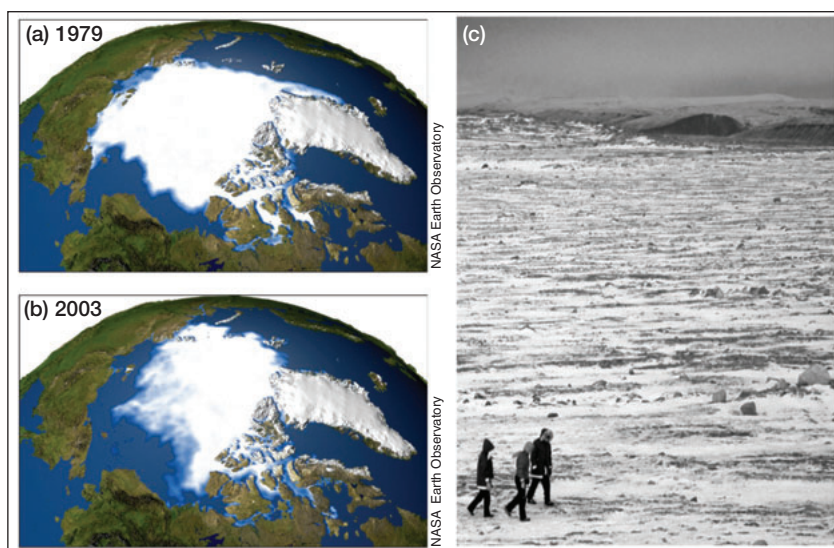


Figure 5. Satellite images of the areal extent of summer Arctic sea ice from (a) 1979 to (b) 2003. The coverage of sea ice in the summer has declined markedly. (c) Researchers study the fragile Arctic landscape in Thule, Greenland, where global change is likely to have the strongest effects on communities and ecosystems.

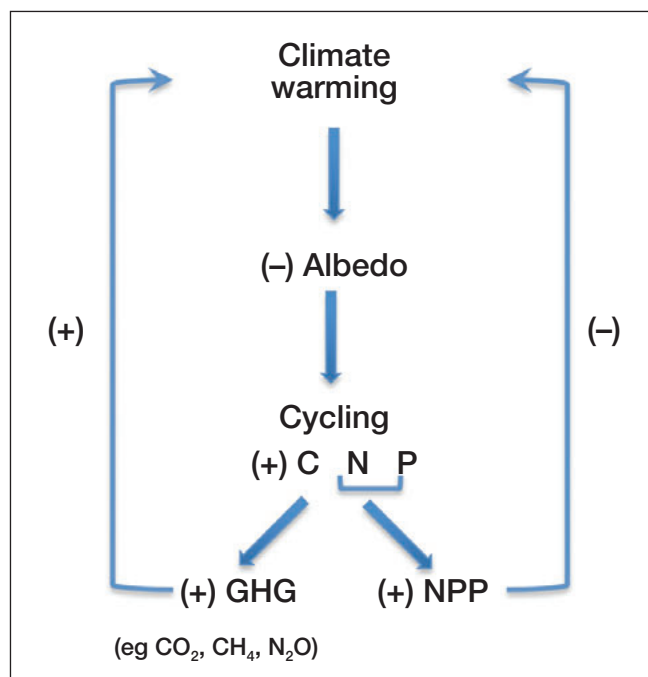


Figure 6. A diagram of the positive and negative feedbacks (indicated by “+” and “–”, respectively) between the coupled biogeochemical cycles of C, N, and P and future climate change in high-latitude ecosystems. In high-latitude ecosystems, changes in albedo are as, if not more, important as rising CO₂ in their effect on warming. Though the directions of the feedbacks are understood, the magnitude and time scales over which the feedbacks may occur remain poorly understood. NPP = net primary production; GHG = greenhouse gases.

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References

- Atkin AD and Tjoelker M. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci* 8: 343–51.
- Berthrong ST, Jobbagy EG, and Jackson RB. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecol Appl* 19: 2228–41.
- Bloom AJ, Chapin III FS, and Mooney HA. 1985. Resource limitation in plants: an economic analogy. *Annu Rev Ecol Syst* 16: 363–92.
- Bradford MA, Davis CA, Frey SD, *et al.* Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett* 11: 1316–27.
- Canadell JG, Le Quéré C, Raupach MR, *et al.* 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *P Natl Acad Sci USA* 104: 18866–70.
- Carter TR, Jones RN, Lu X, *et al.* 2007. New assessment methods and the characterisation of future conditions. In: Parry ML, Canziani OF, Palutikoff JP, *et al.* (Eds). *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Cebrian J. 1999. Patterns in the fate of production in plant communities. *Am Nat* 154: 449–68.
- Cebrian J, Shurin JB, Borer ET, *et al.* 2009. Producer nutritional quality controls ecosystem trophic structure. *PLoS One* 4: e4929, doi:10.1371/journal.pone.0004929.
- Christensen TR, Friberg T, Sommerkorn M, *et al.* 2000. Trace gas exchange in a high-Arctic valley. 1. Variations in CO₂ and CH₄ flux between tundra vegetation types. *Global Biogeochem Cy* 14: 701–13.
- Conley DJ, Paerl HW, Howarth RW, *et al.* 2009. Ecology: controlling eutrophication: nitrogen and phosphorus. *Science* 323: 1014–15.
- Dixon RK, Brown S, Houghton RA, *et al.* 1994. Carbon pools and flux of global forest ecosystems. *Science* 263: 185–90.
- Elberling B, Christiansen HH, and Hansen BU. 2010. High nitrous oxide production from thawing permafrost. *Nat Geosci* 3: 332–35.
- Elsler JJ, Fagan WF, Denno RF, *et al.* 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578–80.
- Eviner VT and Chapin III FS. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu Rev Ecol Evol S* 34: 455–85.
- Falkowski PG, Fenchel T, and Delong EF. 2008. The microbial engines that drive Earth’s biogeochemical cycles. *Science* 320: 1034–39.
- Galloway JN, Townsend AR, Erisman JW, *et al.* 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320: 889–92.
- Giblin AE, Nadelhoffer KJ, Shaver GR, *et al.* 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecol Monogr* 61: 415–35.
- Gilbert N. 2009. The disappearing nutrient. *Nature* 461: 716–18.
- Hall EK, Singer GA, Kainz MJ, and Lennon JT. 2010. Evidence for a temperature acclimation mechanism in bacteria: an empirical test of a membrane-mediated trade-off. *Funct Ecol* 24: 898–908.
- Hall SR. 2009. Stoichiometrically explicit food webs: feedbacks between resource supply, elemental constraints, and species diversity. *Annu Rev Ecol Evol S* 40: 503–28.
- Hobbie SE. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol Monogr* 66: 503–22.
- Hooper DU, Chapin III FS, Ewel JJ, *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75: 3–35.
- Kaufman DS, Schneider DP, McKay NP, *et al.* 2009. Recent warming reverses long-term Arctic cooling. *Science* 325: 1236–39.
- Knapp AK, Briggs JM, Collins SL, *et al.* 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biol* 14: 615–23.
- Luo Y, Su B, Currie WS, *et al.* 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54: 731–39.
- Mack MC, Schuur EAG, Bret-Harte MS, *et al.* 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431: 440–43.
- McCarthy HR, Oren R, Johnsen KH, *et al.* 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO₂ enrichment site: interactions of atmospheric CO₂ with nitrogen and water availability over stand development. *New Phytol* 185: 514–28.
- Monson RK, Lipson DL, Burns SP, *et al.* 2006. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* 439: 711–14.
- Reich PB, Hobbie SE, Lee T, *et al.* 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440: 922–25.
- Reich PB, Tilman D, Naeem S, *et al.* 2004. Species and functional group diversity independently influence biomass accumulation and its response to CO₂ and N. *P Natl Acad Sci USA* 101: 10101–06.
- Repo ME, Susiluoto S, Lind SE, *et al.* 2009. Large N₂O emissions from cryoturbated peat soil in tundra. *Nat Geosci* 2: 189–92.
- Schadt CW, Martin AP, Lipson DA, and Schmidt SK. 2003.

- Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* **301**: 1359–61.
- Schimel J, Balser TC, and Wallenstein M. 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* **88**: 1386–94.
- Schimel JP, Billbrough C, and Welker JA. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biol Biochem* **36**: 217–27.
- Schlesinger WH. 1997. *Biogeochemistry: an analysis of global change*, 2nd edn. New York, NY: Academic Press.
- Schmidt SK, Costello EK, Nemergut DR, *et al.* 2007. Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. *Ecology* **88**: 1379–85.
- Schmidt SK and Lipson DA. 2004. Microbial growth under the snow: implications for nutrient and allelochemical availability in temperate soils. *Plant Soil* **259**: 1–7.
- Schuur EAG, Bockheim J, Canadell JG, *et al.* 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *BioScience* **58**: 701–14.
- Shaw MR, Zavaleta ES, Chiariello NR, *et al.* 2002. Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* **298**: 1987–90.
- Sterner RW and Elser JJ. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press.
- Tarnocai C, Canadell JG, Schuur EAG, *et al.* 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem Cy* **23**, doi:10.1029/2008GB003327.
- Thornton PE, Lamarque JF, Rosenbloom NA, and Mahowald NM. 2007. Influence of carbon–nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability. *Global Biogeochem Cy* **21**, doi:10.1029/2006GB002868.
- van Groenigen KJ, Six J, Hungate BA, *et al.* 2006. Element interactions limit soil carbon storage. *P Natl Acad Sci USA* **103**: 6571–74.
- Vitousek PM, Cassman K, Cleveland C, *et al.* 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry* **57**: 1–45.
- Vitousek PM, Mooney HA, Lubchenco J, and Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* **277**: 494–99.
- Wang Y and Houlton BZ. 2010. Nitrogen constraints on terrestrial carbon uptake: implications for the global carbon–climate feedback. *Geophys Res Lett* **36**, doi:10.1029/2009GL041009.
- Weintraub MN and Schimel JP. 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *BioScience* **55**: 408–15.
- White JR, Shannon RD, Weltzin JF, *et al.* 2008. Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. *J Geophys Res-Bioge* **113**, doi:10.1029/2007JG000609.
- Wright IJ, Reich PB, Westoby M, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–27.



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