

Increased plant growth from nitrogen addition should conserve phosphorus in terrestrial ecosystems

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Inputs of available nitrogen (N) to ecosystems have grown over the recent past. There is limited general understanding of how increased N inputs affect the cycling and retention of other potentially limiting nutrients. Using a plant–soil nutrient model, and by explicitly coupling N and phosphorus (P) in plant biomass, we examine the impact of increasing N supply on the ecosystem cycling and retention of P, assuming that the main impact of N is to increase plant growth. We find divergent responses in the P cycle depending on the specific pathway by which nutrients are lost from the ecosystem. Retention of P is promoted if the relative propensity for loss of plant available P is greater than that for the loss of less readily available organic P. This is the first theoretical demonstration that the coupled response of ecosystem-scale nutrient cycles critically depends on the form of nutrient loss. P retention might be lessened, or reversed, depending on the kinetics and size of a buffering reactive P pool. These properties determine the reactive pool’s ability to supply available P. Parameterization of the model across a range of forest ecosystems spanning various environmental and climatic conditions indicates that enhanced plant growth due to increased N should trigger increased P conservation within ecosystems while leading to more dissolved organic P loss. We discuss how the magnitude and direction of the effect of N may also depend on other processes.

nitrogen cycle | nitrogen inputs | phosphorus cycle | phosphorus retention

Human activities have caused increased nitrogen (N) inputs to ecosystems through atmospheric deposition, fertilizers, and spread of N-fixing plants (1–3). The effects of N enrichment have been considered with respect to the N cycle and in relation to carbon (C) storage (4–6), yet there is limited general understanding of how increased N inputs affect the cycling and retention of other important nutrients, such as phosphorus (P) (7). N and P are important for ecosystem functioning because both nutrients commonly limit production of plant biomass (8). The response of plant production to atmospheric deposition, climate change, and other modern human influences will therefore be mediated by changes in the availability of these elements. However, essential elements do not cycle through the ecosystem independently. Through growth and metabolism, plants couple N and P and other required elements in relatively constrained ratios (9, 10), causing nutrient cycles to be linked at the scale of entire ecosystems (11). Although recent studies have focused on the impact of increased N on ecosystem C balances (5, 6), the question of how increased N affects the internal distribution, cycling, and forms of P loss from systems remains largely unexplored, except for a few experimental studies (12, 13). Given the importance of P in regulating ecosystem processes, such as plant production or decomposition, sometimes in combination with N (8, 14, 15), and potentially governing long term ecosystem dynamics (16), a general understanding of P response to N addition would be invaluable. Here, we introduce a simple model of N and P biogeochemistry that can provide mechanisms behind observed responses to N addition by taking into account nutrient coupling in an analytical manner.

Our simple plant–soil nutrient model for the ecosystem scale explicitly couples N and P in plant biomass. It incorporates losses of nutrients from ecosystems in forms that are both available and unavailable for plant uptake. In the first instance, we highlight the impact of N addition due to increased plant growth, later extending our analysis to discuss the likely impact of other effects of N addition on P cycling processes. We specifically examine how increasing the supply of one potentially limiting element (N) affects the distribution, cycling, and retention of the other nutrient (P). Our analytical approach complements more complicated simulation models that have been developed to investigate nutrient dynamics in ecosystems, such as the Century model (17) or the very recent model of Wang *et al.* (18). Our approach allows general insights to be drawn as to the potential mechanisms behind ecosystem responses (19), in our case to increased N availability.

Model Structure. We introduce in Fig. 1 and [supporting information \(SI\) Appendix](#) a simple ecosystem model in which N and P are explicitly coupled in plant biomass. Both nutrients exist in three functionally distinct pools (20, 21): nutrients dissolved in solution that are available for plant uptake, including ammonium, nitrate, and directly available amino acids for N (22, 23), and phosphate for P; nutrients stored in live plant biomass; and nutrients that are bound in dissolved and solid form to soil organic matter. Fluxes between the pools define the biotic nutrient cycle: The available nutrients are assimilated by plants; plant tissue loss transfers nutrients from the plant biomass to the unavailable soil organic pool; and organic matter decomposition, through biological or biochemical mineralization pathways (24), allows the transfer of plant unavailable organic nutrients into the plant available pool.

Nutrients are lost from the plant rooting zone via two functionally distinct paths (7, 21): loss of plant available nutrients through leaching, together with denitrification in the case of N, and loss of organically bound unavailable nutrients through leaching of dissolved organic matter and particulate organic matter. We ignore particulate loss of P from the reactive pool, later discussing how qualitative conclusions remain unchanged where this loss pathway is included. The inclusion of the differing loss mechanisms incorporates the recent observation of significant export of dissolved organic nutrients from terrestrial soils (25), lacking in some coupled models (17, 18), although more recent versions of the Century model incorporate organic loss. We assume nutrients enter the ecosystem in available form from atmospheric and weathering sources (26, 27); unavailable organic inputs are negligible. As discussed later, including a biological N fixation input, which may

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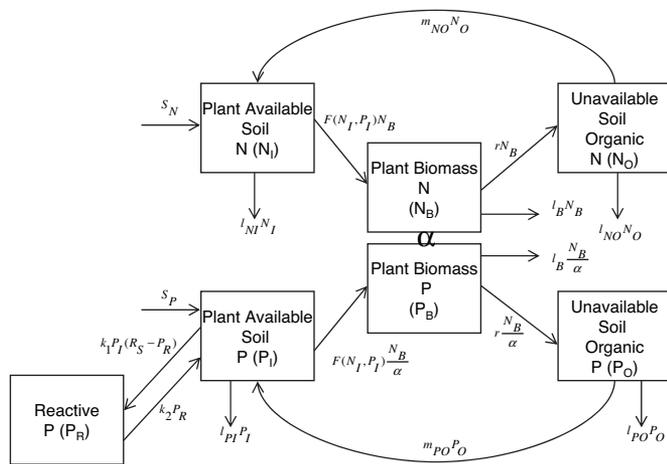


Fig. 1. General coupled ecosystem model for N and P. Both N and P are found in the ecosystem in three functionally distinct pools: in plant biomass with a constant stoichiometric ratio of α ; in plant available (both organic and inorganic) forms in the soil; and unavailable organic forms in the soil. P is also found in a reactive pool, which is in dynamic equilibrium with plant available P.

be an important N source in some systems (28), potentially leaves our qualitative conclusions unchanged.

We include an additional P pool, “reactive P,” representing otherwise available P loosely bound on both organic and inorganic soil particles through chemisorption processes (29). This pool is in dynamic equilibrium with the plant available P (30). Incorporation of this pool allows investigation of different buffering capacities for P within soils (31) by altering the density of sorption sites and the kinetics of the adsorption–desorption reaction. Where the density of sorption sites is low, leading to a low equilibrium reactive P pool, or adsorption is highly favoured relative to desorption, there is little capacity in the soil to buffer decreases in plant available P.

Our model is modified from the traditional presentations for P in ecosystems that usually include occluded and/or apatite P pools (e.g., 32, 33). At the relatively short timescales considered here these pools can be considered a constant and their explicit dynamics can reasonably be ignored. We incorporate supply of apatite P within the term for available P input and assume that its supply remains constant through the timescale considered here. We discuss later the implications of increasing available P supply through internal and external mechanisms with increased N input. Including a loss from the reactive pool to take account of supply to an occluded pool does not qualitatively alter the conclusions we draw, as we discuss later.

Results

Impact of Sustained Increases in Nitrogen on Total Ecosystem Phosphorus. Plants cannot survive at equilibrium if the supply of nutrients from outside the system is below a persistence threshold (shown in *SI Appendix*). In very nutrient-poor systems, plant persistence may require some active foraging for nutrients to increase nutrient supply above the persistence threshold. We consider the general case of N and P colimitation of plant growth and also assess the extremes: single-nutrient limitation by N or P. In the case of N sufficiency, addition of N has no effect on P dynamics, because plant growth and P demand is unresponsive to increased N loading. When N is limiting growth, either alone or in tandem with P, we find that sustained addition of N causes an unexpectedly diverse set of potential responses in ecosystem P cycling (Table 1).

The direction of the response in the plant available, plant, and soil organic P pools combined depends on the mechanism of nutrient loss from the ecosystem. In particular, the direction depends on the relative magnitudes of the loss rate constants for available versus

unavailable losses of P from the ecosystem (l_{PI} vs. l_O). The rate constant for unavailable losses l_O is a combination of l_B and l_{PO} (Eq. 4). It is the fraction of P that is lost from the system as it cycles through the plant biomass and soil organic pools divided by the residence time for P in these two unavailable compartments. When the rate constant for plant available P loss is greater than that for unavailable losses, N addition causes the conservation of P within these three compartments of the plant–soil system. In contrast, when the rate constant for unavailable losses is greater than that for available loss, P in the system declines in response to N addition. This response occurs even though, at the equilibrium with higher N addition, the input of P is equal to output.

We show in Fig. 2 how the internal P pools respond to a sustained fivefold increase in external N supply from 10 to 50 kilograms of N per hectare per year. Plant and soil organic pools combined (Fig. 2, light gray line) increase in response to N addition in all cases, as long as N remains limiting to growth. The pool of plant available P in soils (dark gray line) decreases in all cases to attain new equilibria. The overall combined response (black line) differs markedly depending on the exact pathway of P loss: total ecosystem P stores, excluding the reactive pool, increase if the propensity for P loss is greatest for plant available paths (Fig. 2a) but decrease if the propensity is greatest for unavailable organic paths (Fig. 2b).

In both scenarios, the observed dynamics imply that total losses of unavailable P will increase, and available P will decrease, as the system develops toward a new equilibrium. When the rate constant for plant available loss is greater than that for unavailable losses, losses of P from the ecosystem are effectively minimized through efficient plant uptake of P from the available pool, combined with the subsequent build-up of P in plant and soil organic pools. Inputs remain greater than the combined outputs and P is thus conserved until the system reaches a new equilibrium (Fig. 2a).

In contrast, when the rate constant for unavailable losses is greater than that for available losses, internal cycling of P through the organic pools causes losses of P from the system to exceed P inputs from external sources. This pattern is determined by the propensity for P in the soil organic pool to be irrevocably exported from the system, reducing the total P available for internal recycling. The ecosystem responds to added N by increasing plant growth, which, in turn, increases P export from the soil organic pool. The implication of this feedback is that P is lost from the system compared with the unperturbed state until a new steady state develops (Fig. 2b).

Extending our analysis, we determined that the response of the system at equilibrium may be sensitive to the buffering pool of reactive P (Table 1 and *Materials and Methods*). Where soil P buffering capacity is low, the reactive pool will not act as a significant P source for plants, which will not affect increases in plant and soil organic P in response to added N. In contrast, where the soil P buffering ability is high, the reactive pool supplies some or all of the P required to support the plant response to N. As a result, P retention in the ecosystem as a whole (including the reactive pool) does not necessarily increase, even though P increases in both organic pools.

We have determined a minimum counteracting buffering capacity for the soil (CBC_{min} ; see *Materials and Methods*). An equilibrium reactive P pool size above this minimum buffering capacity may act to offset any potential increase in total ecosystem P, depending on the kinetics of the equilibrium reaction. A reactive P pool below this size cannot offset any increase, whatever the kinetics of the equilibrium reaction. In summary, whole ecosystem retention of P after N addition may be prevented where the soil has a sufficiently high buffering capacity, by virtue of the reactive P pool’s dynamic equilibrium with plant available P.

Implications of Response in Phosphorus for Nutrient Limitation. Retention of P in the ecosystem may be expected to have implications for the limitation status of the ecosystem, usually measured by how

Table 1. Effect of N addition on P in the system at equilibrium depending on limitation status of the ecosystem, relative loss rate constants, and potential size and kinetics of a reactive P pool

Conditions		Equilibrium outcome			
Effect of increased availability of N on plant growth	Relative loss rate constants*	Sum of all pools except reactive pool (Eq. 3)	Reactive Pool (Eqs. 7–11)		
			Adsorption rate >> desorption rate	Other kinetics	Total P
No change (e.g. P limitation)	All cases	No change	No change	No change	No change
Increase (i.e. N limitation, including colimitation)	$\frac{l_{PI}}{l_O} < 1$	Decrease	No change	Decrease	Decrease
Increase (i.e. N limitation, including colimitation)	$\frac{l_{PI}}{l_O} > 1$	Increase	No change	Decrease	Increase when adsorption >> desorption OR reactive pool sufficiently small† OTHERWISE Undetermined/Decrease‡

*Loss rate constants are defined as the amount of loss from a pool (typically measured in $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) divided by the pool size (typically measured in $\text{kg}\cdot\text{ha}^{-1}$) and are therefore in dimensions of per unit time (year^{-1}). The rate constant for unavailable losses (l_O) is defined in *Materials and Methods*.

†The minimum counteracting buffering capacity (CBC_{\min}) of the reactive pool below which there is an increase in phosphorus in the system overall with nitrogen addition is derived in *Materials and Methods*.

‡A decrease is observed when desorption is much greater than adsorption and the equilibrium reactive pool size is above CBC_{\min} ; otherwise the response is undetermined.

plant biomass responds to continued additions of nutrients. In the colimited case, the status of ecosystem limitation is determined by both N and P. Continued N addition increases plant available N and decreases available P at equilibrium. The strength of N limitation is therefore relieved as P limitation becomes more significant in determining plant growth. In cases where the propensity for loss leads to conservation of P within the ecosystem, plant biomass stops responding at equilibrium to continued N addition at a higher rate of N supply (Fig. 3 in *SI Appendix*). In contrast, in cases where N addition leads to loss of P from the system, biomass stops responding to continued increases in N supply at a lower level as P limitation strengthens. Systems with a propensity for unavailable losses might therefore be expected to stop responding to added N at a lower level of elevated N. Having accurate estimates of loss rate constants would indicate the susceptibility of systems to switching primary limitation status with continued heightened N availability.

Expected Outcome of Sustained Nitrogen Addition for Phosphorus in Forest ecosystems. To evaluate the most likely scenario for natural ecosystems, we parameterized our model, using published data from temperate and tropical forest ecosystems. Although empirical estimates of N and P loss rate constants have not been generally

attempted, we were able to derive them for sites in Hawaii (7, 34), the Hubbard Brook Experimental Forest (35, 36), and the Coweeta Long-Term Environmental Research Site (37, 38) (see *SI Appendix*). As a first approximation, we assumed reported inorganic losses to be of plant available nutrients, organic losses to be unavailable, and particulate organic P loss to be negligible. In all cases (Table 2), we estimated available loss rate constants to be larger than the unavailable soil organic loss rate constants. Therefore, we expect P to be conserved in these systems with increased N availability, provided that the direct plant loss rate constant is equal to or less than the constant estimated for the unavailable soil organic pool and contingent on sustained N limitation and the buffering capacity of the soil in the ecosystem.

We have attempted to estimate the buffering capacity of these soils. Notwithstanding the difficulties in comparing idealized mathematical scenarios with potentially biologically meaningful pools obtained through chemical fractionation, we estimated the potential reactive P pool sizes and CBC_{\min} for these sites, using parameters described in *SI Appendix*. Although such estimates are uncertain, and the analysis is therefore preliminary, results indicated that the buffering capacity of these soils may be too low to change the expected effect of increased N, which is to conserve P.

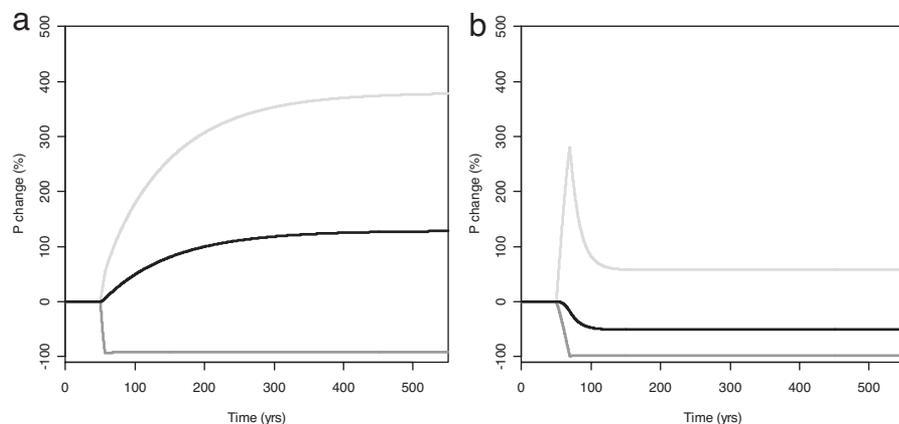


Fig. 2. Percentage response of P pools in the system through time to a sustained increased availability of N, from a background scenario of 10 kilograms of N per hectare per year to 50 kilograms of N per hectare per year at $t = 50$ years and thereafter. (a) Available loss rate constant greater than rate constant for unavailable losses. (b) Rate constant for unavailable losses greater than available loss rate constant. The black line indicates total P in the system excluding the reactive pool, the light gray line the combined response of the organic P pools, and the dark gray line the response of the plant available P pool. See *SI Appendix* for parameters used in generating these graphs.

Table 2. Parameters that determine the response of P in a system, following sustained N addition, for a variety of forested ecosystems

Site	Limitation Status*	Ratio* (I_P/I_{PO})	Predicted effect of N addition on total P in the ecosystem		
			CBC_{min}^*	P_R^*	
Hawaii					
Thurston	N	46	1,490	92	Increase
Laupahoehoe	N + P	5	910	641	Increase
Kokee	P	5	1,303	825	No effect
Hubbard Brook	N?	1,125	910	394	Increase?
Coweeta	P?	57	644	32	No effect if P limited Increase if N limited

In all cases, the available loss rate constant is greater than the unavailable organic loss rate constant; i.e. the ratio I_P/I_{PO} is > 1 . Total P in the plant-available, plant, and soil-unavailable organic pools is expected to increase with N addition, providing N is limiting growth and the direct loss rate constant from the plant pool is equal to or less than the unavailable organic loss rate constant. CBC_{min} denotes the minimum counteracting buffering capacity. In all cases, the estimated reactive pool size (P_R) is less than CBC_{min} , so the buffering capacity is not sufficient to counteract the expected increase in total P with N addition.

*See *SI Appendix*, Estimating parameters.

Discussion

We have presented a simple baseline model of N and P interactions in an ecosystem where plants alone are able to respond to N addition. We have shown that the response of P in the whole system to sustained increases in available N input depends on the limitation status of plant growth, the propensity for loss of P through functionally different pathways, and the buffering capacity of a reactive P pool. In particular, we have highlighted the importance of including an unavailable loss pathway in determining the overall ecosystem P response to increased N.

Our model predicts decreased available P pools after increased plant growth due to additional N whether or not P is conserved in the system as a whole. Studies of a variety of ecosystems have confirmed such a decrease (12, 13). Our model also predicts increased unavailable organic P losses with N addition, whether or not P is conserved in the system as a whole. These losses may be of significance for downstream ecosystems (39) depending on where organic P compounds are mineralized along the downstream flow path. To our knowledge, there are few experimental investigations of whether this increased organic P loss has been observed in otherwise undisturbed systems after increased available N input. Williams and Silcock (12) showed that N had little impact on dissolved organic P loss from a peat bog, although available losses decreased as our model predicts. These contradictory results may be because total dissolved losses varied with the addition of N whereas our model predicts that overall P loss at equilibrium would be equal between perturbed and unperturbed systems. Results from agricultural settings show equivocal responses to N addition of organic P lost through leaching (40), probably because P export from the plant pool is increased because of cropping and/or because soil organic P export takes time to increase as the organic pool accumulates in response to additional N. Organic P loss may also not necessarily increase because N has other dynamic impacts on P in ecosystems beyond increasing plant growth.

Other dynamic impacts of N on ecosystem P fluxes include changing pH, potentially altering the kinetics of the reaction between the reactive and plant available P pools (41), and increasing the rate of weathering of apatite P. Additional N may also increase phosphatase enzyme production (42, 43). In such scenarios, the external and internal supply of available P may therefore not be independent of N input. We have investigated the concurrent impact of N on P mineralization and on plant growth (see *SI Appendix*). Our analysis shows that the loss pathways and the

buffering capacity of the reactive pool still determine ecosystem P response, in generally the opposite way to the simple results presented in Table 1. In essence, a prediction of N addition leading to P conservation when considering an effect on plant growth alone may be tempered or reversed if increased N sufficiently increases the mineralization of P. Therefore, our model suggests that accurate predictions of the impact of N on ecosystems, e.g., in determining the amount of C storage, may be compromised by the variety of potential impacts of N addition and the potential for reciprocal feedbacks between N and P availability and C storage (44). Other mechanisms may increase the “external” supply of available P: Acidification may increase weathering, and plants may exude acids, bases, and chelating agents that release more recalcitrant P (45). If the P released by these mechanisms is not taken up by the plants, which is unlikely given active plant foraging, available P losses could increase. The overall amount of P in the system at equilibrium, given heightened supply, would increase as predicted by our model.

One of our most interesting findings is that the ecosystem response to N addition is highly sensitive to the exact pathway and dynamics by which P already in mineral form is made available for plant uptake within the soil. We explored this mechanism generally by using a “reactive pool” of P, which was linked by standard exchange kinetics to the plant available pool. This pool represents otherwise available P loosely bound on both organic and inorganic soil particles through chemisorption processes. In effect, this allowed us to explore the importance of a buffering pool as a general mechanism for influencing P availability to plants. In reality, however, soil P pools and soil P dynamics are more complex. We ignored explicit dynamical treatment of occluded and apatite forms of P, based on the assumption that change in these pools is negligible over the timescales we consider.

Our findings point to the critical nature of the exchangeable pool of mineral P in the soil and its interaction with plant uptake. In our model, the number of adsorption sites available, determined by the mineralogy of the soil, determines how much reactive P is present. We expect that to be the major driver for the size of the reactive P pool across ecosystems. However, in a given environment, our conclusions regarding the impact of N addition on P in the ecosystem, and its dependence on loss pathways, would remain unchanged, provided that only plant growth, and not the nature of the exchange reaction, is affected. Any effect of N addition on the chemical exchange reactions could potentially lead to dramatic effects on P pools and availability, but they remain to be demonstrated.

In some ecosystems, the majority of P might be found in forms not presented in our model (e.g., 46). However, the pools and fluxes that we do consider take account of the majority of P present in the parameterized systems (*SI Table 3*): between 50 and 70% of soil P, except for Thurston, where 83% of P is apatite. Organic P makes up $\approx 33\%$ of the total soil P in the systems examined. Even in Hubbard Brook, which is a temperate system, organic P makes up 36% of total soil P. Therefore, we argue that the impact of N on P forms and fluxes could be far from trivial; only experiments can tell.

We have not considered losses of reactive P from the model, through particulate and erosional loss or through strong binding to soil minerals (occlusion). Incorporating this loss would not change the qualitative results: N addition in N limited systems would decrease the size of the reactive pool leading to less loss from this pool and enhancement of P conservation provided that the rate constant for unavailable losses is less than the available loss rate constant. The buffering capacity of the reactive pool would also be reduced, again enhancing the P conservation effect of N addition.

Particulate losses can be an important loss pathway in some ecosystems, particularly agricultural ones (47, 48). These can be from the organic pool, as we proposed in our model formulation, and from the reactive pool. In the systems we investigated, we assumed that organic particulate losses were of small magnitude, and thus P conservation was predicted from continued N addition.

However, in natural systems possessing high amounts of organic matter with a propensity for erosional flux, e.g., peat bogs or some sites in Hawaii (49), the opposite trend with N addition may be predicted, i.e., N addition could lead to loss of P from the system, because the unavailable loss rate constant, with the incorporation of organic particulate losses, is greater than the available loss rate constant.

Our model also does not consider direct biological nitrogen fixation, either by vascular plant symbioses or by heterotrophic bacteria, a potentially important ecosystem N source (28), the magnitude of which may depend on P availability (50). Incorporating biological N fixation into the model does not qualitatively change our conclusions. Heterotrophic fixation would be an increased supply to the available N pool from outside of the system, as argued by Baisden and Amundson (19), whereas symbiotic N fixation would be an input into plant biomass N. Such input would leave our conclusions unchanged so long as N addition results in increased plant growth in the ecosystem overall. Our conclusions would only be changed if plant growth was depressed as a result of N addition, which could arise through toxic effects (51).

Our model makes clear predictions and can thus be subjected to direct field tests. Our discussion shows that the model's predictions may prove to be robust to additional factors, such as N fixation, pH changes, active foraging for P, and reactive P losses, unless plant growth is depressed with the additional N. However, only additional field tests can test this assertion. N addition may lead to a system that is P limited at the perturbed equilibrium. Conservation would still occur compared with the unperturbed N limited ecosystem. Conclusions would be altered in systems with greater unavailable losses than available losses, possibly in systems with high organic particulate losses. Conclusions would also be reversed if P foraging leads to a greater effect on P mineralization than on plant growth.

We argue that our model provides a baseline for deriving general insights into the myriad impacts of N on ecosystem P cycling. Our analytical approach suggests that predictions of the likely impacts of N addition may be made difficult given the range of potential responses even when only a very few ecosystem P processes are considered. More broadly, our analysis suggests that conclusions drawn about the impacts of N on C fixation need to take account of feedbacks between limiting nutrients such as N and P and their impacts on plant growth and organic matter dynamics. The potential impacts for P in ecosystems, given the near-ubiquity of terrestrial N enrichment, warrant further theoretical, experimental, and empirical investigation. The results of our model reinforce the requirement to understand losses and supply pathways in determining the response of other important nutrients to increased N availability.

Materials and Methods

Model Specification. The model in Fig. 1 is described in *SI Table 4*. We solved the model equations at equilibrium, by setting the rates of change to 0, as shown in *SI Appendix*. The model generally converges to equilibrium provided that persistence conditions are met (see *SI Appendix*). In certain instances, plant extinction is possible even though persistence conditions are met. This occurs when the reactive pool is highly competitive for available P, out-competes plants for this P and prevents plants from surviving. The reactive pool is highly competitive when it is relatively empty, there is a high density of reactive sites, and the adsorption rate (k_1) is high compared with desorption (k_2).

Equilibrium Amounts of Phosphorus with Increasing Nitrogen Addition. We analyze the effects of N addition on total P, by examining all compartments apart from the reactive pool, and then include the reactive pool. The total amount of P in the ecosystem at equilibrium (P_{Tot}^*) is equal to:

$$P_{Tot}^* = P_B^* + P_O^* + P_I^* + P_R^* \quad [1]$$

Condition for Increase in Plant Available, Plant, and Soil Organic Phosphorus Pools Combined. Ignoring the reactive pool, and expressing the remaining pools in terms of N_B^* , the change in P, in the plant available, plant, and soil organic pools combined (P_{BO}^*), with respect to N addition, is given by:

$$\frac{dP_{BO}^*}{dS_N} = \frac{1}{\alpha} \frac{dN_B^*}{dS_N} \left(1 + \frac{r}{l_{PO} + m_{PO}} - \left(\frac{l_B}{l_{PI}} + \frac{r l_{PO}}{(l_{PO} + m_{PO}) l_{PI}} \right) \right) \quad [2]$$

Because $dN_B^*/dS_N > 0$, where N is limiting growth (*SI Appendix*), the sign in the parentheses determines whether P increases or decreases in the plant available, plant, and soil organic pools combined. For an increase of P in plant available, plant, and soil organic pools combined with N addition, it is necessary that:

$$\frac{l_{PI}}{l_O} > 1 \quad [3]$$

where l_O is the rate constant for unavailable losses:

$$l_O = \frac{\varphi}{T_{res}} \quad [4]$$

φ is the fraction of nutrient lost along the plant pathway:

$$\varphi = \frac{l_B}{l_B + r} + \frac{r}{l_B + r} \left(\frac{l_{PO}}{l_{PO} + m_{PO}} \right) \quad [5]$$

T_{res} is the organic residence time:

$$T_{res} = \frac{1}{l_B + r} + \frac{r}{l_B + r} \left(\frac{1}{l_{PO} + m_{PO}} \right) \quad [6]$$

Eq. 3 states that for an increase of P in this part of the system with N addition, the plant available loss rate constant has to be greater than the rate constant for unavailable losses (l_O). Where losses from the plant pool are negligible, conservation of P is more likely provided that the available loss rate constant is greater than the unavailable soil organic loss rate constant.

Deriving the Minimum Counteracting Buffering Capacity. The buffering capacity of the reactive pool depends on its size and the kinetics of its reaction with the available P pool. We derived the minimum counteracting buffering capacity (CBC_{min}) of the reactive P pool by considering two kinetically limiting cases for the effects of N deposition:

$$k_1 P_I^* \gg k_2, \quad [7i]$$

the rate of adsorption of plant available P on to reactive P pool sites is far greater than the rate of desorption; and the converse case:

$$k_1 P_I^* \ll k_2 \quad [7ii]$$

In Eq. 7i, the reactive pool size at equilibrium is determined by the density of sorption sites for plant available P, $P_R^* \approx R_S$. We assume that this is independent of N addition. In other words, the buffering capacity of the reactive P pool in Eq. 7i is equal to 0.

In Eq. 7ii, $P_R^* \approx \theta P_I^*$, i.e., the size of the reactive P pool is proportional to the plant available P pool. The proportion is denoted by θ , where $\theta = k_1 R_S / k_2$. Provided that N limits plant growth, and, therefore, the plant available P pool is depleted after N addition, the reactive pool is necessarily depleted at equilibrium, too. The conservation of P in the ecosystem, given the necessary loss rate condition (Eq. 3), may therefore be counteracted.

In Eq. 7ii, total P at equilibrium is given by:

$$P_{Tot}^* = (1 + \theta) \frac{S_P}{l_{PI}} + \frac{N_B^*}{\alpha} \cdot \left(1 + \frac{r}{l_{PO} + m_{PO}} - (1 + \theta) \left(\frac{l_B}{l_{PI}} + \frac{r l_{PO}}{(l_{PO} + m_{PO}) l_{PI}} \right) \right) \quad [8]$$

The derivative of total P with respect to N input is given by:

$$\frac{dP_{\text{Tot}}^*}{dS_N} = \frac{1 dN_B^*}{\alpha dS_N}$$

$$\cdot \left(1 + \frac{r}{l_{PO} + m_{PO}} - (1 + \theta) \left(\frac{l_B}{l_{PI}} + \frac{r l_{PO}}{(l_{PO} + m_{PO}) l_{PI}} \right) \right) \quad [9]$$

Because $dN_B^*/dS_N > 0$ with N limitation, and, after simplification, an increase in total P in the system with N addition requires that θ is less than some value (θ_{crit}) where:

$$\theta < \theta_{\text{crit}} = \frac{l_{PI}}{l_O} - 1 \quad [10]$$

Eq. 10 allows the derivation of CBC_{min} :

$$CBC_{\text{min}} = \theta_{\text{crit}} P_I^* \quad [11]$$

This indicates the smallest size of the reactive P pool at which N addition may counteract any propensity of the ecosystem to conserve P. Where an equilibrium reactive P pool size in an ecosystem is below this value, there is not sufficient buffer capacity to alter the effect of N addition on the ecosystem.

In cases where the available P loss rate constant is greater than the rate constant for unavailable losses, N addition will lead to an increase of P in the system, provided that the buffering capacity is sufficiently small. In other cases, the right-hand side of Eq. 10 will be less than or equal to 0 and therefore cannot be true. In such scenarios, increasing N availability will lead to decreased P in the ecosystem, contingent on N limitation of plant growth.

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