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Elevated P availability slows N recycling in northern hardwood forests

Shinjini Goswami [a], Melany C. Fisk [b,*]

[a] School of Natural and Health Sciences, Lees-McRae College, Banner Elk, NC 28604, USA
[b] Biology Department, Miami University, 700 E High St., Oxford, OH 45056, USA

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ABSTRACT

Nutrient cycling in forest ecosystems can be sensitive to disturbances that change the availability of one nutrient relative to others, altering the synchrony in nutrient cycles that is expected to develop in undisturbed systems. We asked whether the relative availabilities of nitrogen (N) and phosphorus (P) differ with forest successional age after harvest, and tested effects of adding one nutrient on availability and recycling of the other, in a factorial nitrogen (N) × phosphorus (P) fertilization study in multiple early- and mid-successional and mature northern hardwood forest stands in central NH, USA. We did not find effects of forest age on resin-available N:P ratios, which varied widely among successional forest stands and were related to net N mineralization potentials in the forest floor of each stand. P addition suppressed resin-N availability by 31 % and lowered litterfall N recycling by 10 %, but we detected no effects on net N mineralization potentials. P addition also increased nitrification potentials in the organic horizon by up to 60 %, mostly in combination with added N. The effects of added N depended on P; lower resin-P in mature stands and lower litterfall P recycling in stands of all ages were detected only when P was added with N. We conclude that P limitation influences N recycling across forest age classes in these northern hardwoods, with some indication of stronger effects in successional stands. However, net N mineralization potentials better predicted the resin-N response to added P than did stand age. Our results suggest that alleviating P limitation promotes N limitation over time, especially in more rapidly growing successional forests, by increasing biotic demand for N, reducing its recycling in litterfall, and potentially by reducing net N mineralization.

1. Introduction

Availabilities of essential nutrients can interact to influence uptake and recycling processes in forest ecosystems (Townsend et al., 2011; Vitousek et al., 2010), in ways that are thought to promote synchrony in cycling between nutrients such and N and P (Finzi et al., 2011; Rastetter et al., 2013). Central to this synchrony is that organisms require elements in stoichiometric proportion and are expected to take up and recycle nutrients in proportions that maintain balanced nutrition (Ågren, 2008; Sterner and Elser, 2002). Such balance can develop through controls by limiting nutrients on nutrient mineralization processes, on nutrient demand by plants and microbes, and on the associated feedbacks that could both accelerate (Vitousek, 2004) and lower (Fisk and Fahey, 2001) the availabilities of N and P. Recovery from any disruption of nutrient cycles, for instance by nutrient or CO_2 enrichment or large-scale disturbance such as forest harvest, depends on the net outcomes of the processes mediating the balance of nutrient supply and demand. Yet, predicting effects of the availability of one potentially limiting nutrient on the recycling of another remains difficult without a better understanding of N and P interactions in individual ecosystems.

Greater availability of one nutrient can affect available pools and recycling of another by promoting its uptake. Alleviating limitation by N or P can increase growth of plants or soil microbes, increasing demand for the other nutrient to maintain nutritional balance (Davidson and Howarth, 2007), and adding N or P has been found to promote uptake of the other nutrient and its sequestration in plant pools in many studies across ecosystems (Deng et al., 2017; Schleuss et al., 2020; Wang et al., 2022; Xia et al., 2023; Xiao et al., 2022). Subsequent recycling of the nutrient in greater demand can be slowed if its efficiency of use and retention in biomass increase, especially in forest ecosystems (Gonzales et al., 2023; Waring et al., 2015; You et al., 2018). For example, N addition depleted P pools in the organic horizon in temperate deciduous forest, and P mineralization declined in one of the two ecosystems studied (Heuck et al., 2018). Thus, increased P demand by plants following N addition could promote P limitation over time (Deng et al., 2017), perpetuating the imbalance in nutrient recycling. Alleviating P

* Corresponding author.
E-mail address: fiskmc@miamioh.edu (M.C. Fisk).

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limitation could have similar effects on N cycling.

An imbalance between N and P cycling could be offset over time if alleviating limitation by one nutrient increases the supply of the other. Greater availability of either N or P have been found to promote activity of the enzymes that mineralize the other (Allison et al., 2011; Marklein and Houlton, 2012; Olander and Vitousek, 2000; Schleuss et al., 2020, Treseder and Vitousek, 2001), but effects on nutrient supply are less consistent across ecosystems. For example, greater phosphatase activity in response to N addition was sufficient to increase P mineralization in one temperate deciduous forest ecosystem, but not in another in which P mineralization declined (Heuck et al., 2018). Meta-analyses have found that P addition increased net N mineralization (Sun et al., 2022), especially in forest systems and low pH soils (Xia et al., 2023). However, meta-analysis has also shown that P addition did not increase net N mineralization, in forest and other ecosystems, despite higher rates of gross mineralization in many cases (Wang et al., 2022). The lack of consistent outcomes suggests that ecosystem-specific work is needed to identify the contexts in which predictable N and P interactions occur.

Harvest and successional history can be important controls of nutrient cycles in forest ecosystems. Post-harvest N losses can be large (Bormann et al., 1968; Vitousek and Melillo, 1979) and can be disproportionate to those of P (Davidson et al., 2007). Following forest harvest, the immobilization of N in harvest residues can be an important nutrient sink (Vitousek and Matson, 1984), retaining N in the ecosystem but slowing its recycling. In northern hardwood forests the low N:P ratios of the branches and twigs comprising these residues and even lower N:P ratios of dead root systems (Whittaker et al., 1979) suggest that this nutrient sink should be stronger for N than for P. These combined effects are predicted by the Multiple-Element Limitation model to lower the availability of N relative to that of P early in northern hardwood forest succession, causing changes over time in recycling and limitation as N and P cycles resynchronize (Rastetter et al., 2013). Empirical tests of these predictions are needed to improve our understanding of successional variation in N relative to P cycling in forest systems, especially in the managed landscapes of the northern hardwoods experiencing ongoing environmental change.

We examined interactions between N and P availability at different successional stages in an extensive long-term N × P fertilization experiment, the Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE) study. This experiment includes eight successional and five mature forest stands, located in three sites that vary widely in N and P availabilities in central New Hampshire, USA (Ratliff and Fisk, 2016; See et al., 2015). Simulations with the Multiple Element Limitation model predicted change from N limitation of forest growth in young successional forests to P limitation in mid-age successional and maturing forests, and eventually to N-P co-limitation of productivity in the older mature northern hardwood ecosystems (Rastetter et al., 2013). These changes in the model were driven by shifting imbalances between the N:P ratio of nutrient supplies and that of tree demand, with low N relative to P availability following harvest, transitioning to low P relative to N availability in mid-succession, and eventually to the balanced N and P recycling in the mature forests (Rastetter et al., 2013). Tree growth responses measured after the first four years of nutrient treatments in the MELNHE study were mostly consistent with model predictions: Goswami et al. (2018) found that the diameter growth rates of trees in these forests increased somewhat in response to elevated N in young forests and primarily in response to elevated P in mid-successional and mature forests, with some mature stands responding to N.

In this study we tested the general hypotheses that the availability of N relative to P differs over successional time following harvest, and that alleviating limitation by one nutrient lowers the available pools and recycling of the other, over the first ten years of N × P fertilization in the MELNHE study. In the first year of fertilizing, Fisk et al. (2014) found no effects of one nutrient on resin-availability of the other but did show that adding N+P together increased the resin-available N pool more so than adding N alone. We continued to examine responses over time after this very early finding. We predicted that, independent of nutrient treatments, the ratio of available N:P is lowest in young stands, greatest in mid-age stands, and intermediate in mature stands, based on the idea that more N than P is lost immediately following forest harvest, and on model simulations (Rastetter et al., 2013) and tree growth responses to added nutrients (Goswami et al., 2018). Expecting that alleviating limitation by one nutrient increases demand for the other by trees and microbes, we also predicted that effects of adding one nutrient on the other are stronger where the added nutrient is in lower relative supply: i.e. N effects are greatest where available N:P is lowest, and P effects are greatest where available N:P is highest. We used resin-available N and P as our measures of nutrient availability, which should represent a balance between input via nutrient mineralization and removal via plant or microbial uptake or losses. Increased uptake by plants and microbes is expected to lower the resin-availability of a nutrient, assuming that plant roots and microbes are more competitive than resin strips in nutrient adsorption. A decline in nutrient mineralization should also lower resin-availability, whereas less uptake or greater mineralization would increase resin-available nutrients in the soil.

2. Methods

2.1. Site description

We studied 13 northern hardwood forest stands at three different sites located in central New Hampshire, USA; nine at the Bartlett Experimental Forest (BEF; elevation 250–500 m) and two each at Hubbard Brook Experimental Forest (HBEF; elevation 500 m) and Jeffers Brook (JB; elevation 730 m). Climate in the study region is humid continental with the mean temperatures of −9 °C in (January) and 19 °C in (July) (at 450 m elevation). The mean annual precipitation is approximately 140 cm evenly distributed throughout the year. Soils are Typic and Aquic Haplorthods overlying glacial drift originating primarily from granitic rock. The soils have thick surface organic horizons and low pH, varying from 4.2 – 4.9 in the top 10 cm of the mineral soil in the different forest stands (Ratliff and Fisk, 2016).

These 13 forests stands included three each of young-successional (young; 21–25 yr), mid-successional (mid-age; 30–40 yr) and mature (>100 yr) forests at BEF and one mid-age and one mature each in HBEF and JB (Table 1; ages given as the time between clear-cut harvest and treatment initiation). Young, mid-age, and mature forest ages were chosen to represent different stages of stand development in which supplies of N relative to P might differ (Rastetter et al., 2013).

Forest composition is typical of northern hardwood stands in each age class, mature forests having an overstory dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghniensis* Britton), with occasional white ash (*Fraxinus americana* L.), white birch (*Betula papyrifera* Marsh.) and red maple (*Acer rubrum* L.). Mid-age forests were generally dominated by white birch, yellow birch, American beech, followed by pin cherry (*Prunus pensylvanica* L.f.), red maple and bigtooth aspen (*Populus grandidentata* Michx.). Pin cherry, white birch and red maple dominated the young forests (Goswami et al., 2018). Species composition of northern hardwood forests in this region varies owing to differences in native soil fertility associated with mineralogy and texture of glacial tills and variation in hydrology and soil development (Leak, 1991), as well as to past management (Vadeboncoeur et al., 2012).

Four 50 × 50 m plots were established in each stand with the exception of the mid-age stands at HBEF and JB, which were 30 × 30 m. Plots were randomly assigned to control, N, P, and N+P fertilizer treatments within each stand. Fertilizer was applied to the entire plot area; measurements were made in the inner 30 × 30 m area (20 × 20 m for mid-age stands at HBEF and JB). Nutrient additions began in spring of 2011. N was added at a rate of 30 kg ha^{-1} year^{-1} as pelletized ammonium nitrate (NH_4NO_3) and P was added at a rate of 10 kg ha^{-1} year^{-1} as powdered or granulated sodium monophosphate (NaH_2PO_4).

Table 1
Characteristics of 13 northern hardwood forest stands in the Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HBEF) and Jeffers Brook (JB) in central New Hampshire, USA. SOM (soil organic matter) and pH were in the surface 10 cm of mineral soil; Net N mineralization (N_{min}) potentials and Nitrification (N_{itr}) as a percent of net N mineralization were in the organic horizon (forest floor). Soil and nutrient variables are control plot averages over time.

Site	Stand	Age class	Year clearcut	Elevation (m)	SOM (%)	pH	N_{min} ($mg/m^2/d$)	N_{itr} (% of N_{min})	Resin N (μg/d)	Resin P (μg/d)	Resin N:P
BEF	C1	young	1990	570	9.0	4.44	82	0.1	4.4	0.50	14.8
	C2	young	1988	340	7.8	4.44	29	0.6	3.2	0.36	11.0
	C3	young	~1982–1985	590	9.1	4.14	118	16.6	10.2	0.19	75.9
	C4	mid-age	1979	410	8.6	4.14	29	0.4	3.5	0.56	13.6
	C5	mid-age	1976	550	7.0	4.38	75	3.6	8.9	0.36	33.2
	C6	mid-age	1975	460	10.4	4.28	76	9.9	9.0	0.38	33.6
	C7	mature	1890	440	9.0	4.75	42	2.3	4.5	0.51	11.4
	C8	mature	1883	330	7.3	4.67	27	0.0	3.8	0.90	4.9
	C9	mature	1890	440	7.9	4.65	48	8.4	6.0	0.78	16.8
HBEF	HBM	mid-age	1970	500	11.4	3.85	73	36.5	4.9	0.21	25.1
	HBO	mature	1911	500	14.5	3.86	73	21.2	3.9	0.22	20.1
JB	JBM	mid-age	~1975	730	10.8	4.85	33	80.4	4.2	0.10	101.2
	JBO	mature	1915	730	10.7	4.56	74	68.5	7.0	0.34	20.6

N and P amendments were applied twice (early June and mid-July) in each of the first three years and once (early June) each year thereafter. Fertilizer was pre-weighed for 2.5 × 10 m sub-plots and spread evenly by hand. Four soil-sampling locations (approx. 5 × 5 m each) were delineated in each plot to minimize the potential over time for interpreting spatial variation as temporal variation.

2.2. Resin-available nutrients

Post-treatment inorganic soil N and P availability were tested using ion-exchange resin strips incubated in the organic horizon for approximately two weeks in summers of 2012 (the second year of treatment), 2014, 2015, 2016, 2017, 2019, and 2021 in at least six of the 13 forest stands, always including at least two each of young, mid-age and mature stands at BEF. The annual sampling period of July was chosen to be as close as possible to the peak period of N mineralization in northern hardwoods (Bohlen et al., 2001), and to allow enough time for fertilizers to dissolve and be incorporated into soil following the application. Ions from soil solution are adsorbed as they come in contact with the surface of the resins in the strip, providing comparable indices of soil solution N and P available for uptake by plant roots and microbes.

We used anion exchange resin strips (Ionics AR-204-SZRA; Maltz Sales) to quantify available PO_4^- and NO_3^-, and cation exchange resin strips (Ionics CR67-HMR; Maltz Sales) to quantify available NH_4^+ in soils. Resin strips (2 × 6 cm) were prepared by rinsing in weak HCl and deionized H_2O and then soaking in 1 M NaCl (cation strips and anion strips for NO_3^-) or alternating rinses in deionized H_2O and 0.5 M $NaHCO_3$ (anion strips for PO_4^-). All strips were rinsed with deionized H_2O immediately prior to placement in the field. We deployed resin strips by inserting them under the blade of a knife used to cut the surface organic horizon at a 30–45° angle. Eight strips per plot (2 per soil sampling location) were deployed for each nutrient. Strips were retrieved after approximately 14 days and rinsed in deionized H_2O prior to extraction for nutrient analyses. Anion exchange resins were extracted by shaking rinsed strips in 30 mL of 1 M KCl for (NO_3^-) and 30 mL of 0.5 M HCl (PO_4^-) for 1 hour each. Cation strips (NH_4^+) were extracted by shaking rinsed strips in 30 mL of 1 M KCl for 1 hour. Resin-N refers to the sum of NH_4^+ and NO_3^-. We used a phenolate-hypochlorite method to quantify NH_4^+ (method 351.2, US EPA 1983) and a cadmium reduction method to quantify NO_3^- (method 353.2, US EPA, 1983) in extracts. Extract PO_4^- concentration (resin-P) was analyzed by the ammonium-molybdate-ascorbic acid method (Murphy and Riley, 1962).

2.3. Litter nutrients

Leaf litter was collected approximately weekly from five baskets (0.234 m^2 each) per plot in each stand, throughout the autumn litterfall seasons of 2012, 2016, and 2018. Litter from each basket was oven dried (60 degrees C) and weighed for each collection time. For nutrient analysis, individual litter collections were composited over time (from late September to early November) into one single sample per basket in 2012 and were composited over two approximately equal time periods, for two samples per basket, in 2018. In 2016 we did not composite litter over time, to permit a time-sequence of nutrient analysis.

After compositing (if applicable), litter samples were finely ground, N concentrations were quantified on a Leico CHN analyzer, and P concentrations were quantified by ICP-OS following dry ash digestion in nitric acid. N and P concentration in 2018 were each averaged between the two composite samples per basket according to the fraction of total litter mass in each of the two composited samples. In 2016, nutrients were analyzed only for the collection from 15 to 22 October because of sample losses in an oven fire prior to analysis, and no litter from young stands was analyzed for P. As a consequence, 2016 litter was omitted from statistical analysis. Litter nutrient concentrations (Table S1) were multiplied by annual litterfall mass for each basket in each collection year to estimate litterfall nutrient recycling (g N or P per m^2 per year).

2.4. Soil N transformations

Net N mineralization and nitrification potentials were quantified in soil samples collected from all four plots per stand in all 13 stands in the first week of July 2012, 2014, and 2017. We extracted 3–4 soil cores (2 cm diameter) in each of the four soil sampling locations in each plot, from the forest floor in 2012 and to a depth of 10 cm in the mineral horizon in 2014 and 2017. We separated the core samples into Oe, Oa, and mineral horizons in the field using visual criteria. Decaying plant matter that appeared fibrous and reddish- to dark brown in color was considered Oe horizon and non-fibrous amorphous organic matter that was dark to black in color, with occasional mineral flecks, was identified as Oa horizon. The remaining soil was identified as the mineral horizon. Cores from the four sampling locations were pooled by horizons for one composite sample per horizon in each plot. Samples were homogenized and inorganic N was extracted from an initial subsample (t_i) within a day of collection and from a final subsample (t_f) after 21 days of incubation in the laboratory at 18–20 °C. Subsamples were shaken in 2 M KCl and the resulting solution was filtered through Whatman #1 qualitative grade paper and stored at 4°C until analysis.

We used a phenolate–hypochlorite method to quantify NH_4^+ (method 351.2, US EPA, 1983) and a cadmium reduction method to quantify NO_3^- (method 353.2, US EPA, 1983) in KCl extracts. Net N mineralization was estimated as the difference in KCl-extractable NH_4^+ and NO_3^- between initial and final incubated soil subsamples and net nitrification potential was estimated as the difference in KCl-extractable NO_3^- between initial and final incubated soil subsamples. Values were transformed from concentrations (mg/g soil) to an area basis (mg/m^2) by multiplying by the mass of each horizon and summing Oe and Oa horizons for forest floor totals. Concentrations are provided in Table S2.

2.5. Data analysis

Effects of forest age on resin-N and P availability were tested in control plots over the 10-year study period. We tested effects of forest age classes (young, mid-age, and mature) on the response variables resin-available N ($NO_3^- + NH_4^+$), P, and N:P, using a linear mixed effects model in the nlme package in R (Pinheiro et al., 2016). Forest age class and year were fixed effects and plots were nested within forest stands as random effects. Only stands in the BEF site were included in this analysis because of the lack of young stands at HBEF or JB. We also used correlation analysis in the ggpubr package in R to test the relationships of resin-available nutrients and litterfall nutrient recycling with ages of individual forest stands and with net N mineralization in the forest floor horizon. We used stand-level means of control plots over the entire study period to best represent spatial variation.

Effects of fertilization treatments on resin, soil, and litter variables were tested using a linear mixed effects model in the nlme package in R. Fixed effects included treatment (N or P addition), forest age class (young, mid-age, or mature), and year. Plots were nested within stands and stands were nested within sites as random effects. Response variables included resin-available N ($NO_3^- + NH_4^+$) and P, net N mineralization, net nitrification, leaf litter N and P concentrations, and leaf litter N and P recycling (g m^{-2} year^{-1}). N or P effects were inferred if response variables in plots receiving a nutrient differed from those in plots not receiving that nutrient. This factorial approach compares response variables in plots with N addition (i.e., N and N+P plots) to those with no N addition (i.e., control and P plots) and plots with P addition to those with no P addition and tests the interaction between N and P additions. Contrast analyses were used to test pairwise differences between individual treatments (control vs N or P; N or P vs N+P). Resin-available N and P values were log-transformed to meet the assumptions of normality of the residuals. We also calculated responses to treatments as (treatment – control) for resin N and P each year in each stand, averaged those stand-level responses over time, and tested their relationships with control plot net N-mineralization in the forest floor horizon, also averaged over time.

Forest stands in the HBEF and JB sites were sampled only in 2–3 of the six years, and did not include stands in the young age class. Therefore, in addition to the above analyses of treatment effects including all sites, we analyzed stands in the BEF site only using the above model without site as a random effect. Including HBEF and JB data does not appear to introduce bias; statistical outcomes with and without these sites were virtually the same and are presented in the Supplementary information (Tables S3, S4, S5). We present results from all sites in the main text.

3. Results

The only evidence of forest age class effects on available nutrients was greater resin-P availability in mature than successional stands (effects of age class, $p = 0.04$; Table 1 and S1), and a positive relationship between resin-P and the age of individual stands (r = 0.54, $p = 0.05$; Fig. S1A). We did not detect effects of forest age class on resin-N or N:P ($p >$ 0.36 for effects of age class). The range of variation in resin-N among individual young-successional stands completely overlapped with and exceeded that of mid-successional or mature stands (Table 1), and neither resin N:P or N were related to the age of individual stands ($p =$ 0.48 for resin-N; $p = 0.26$ for resin N:P; Fig. S1B and C). Litter N and P recycling also did not differ among forest age classes ($p > 0.84$ for age class effects; Table S1) and were not related to age of individual stands ($p > 0.20$; data not shown).

Nutrient availability and recycling were more closely related to net N mineralization than to forest age across our 13 forest stands. Both resin N:P and resin-N were positively related to forest floor net N mineralization potential across stands (r = 0.85, $p = 0.0002$ for resin N:P; r = 0.74, $p = 0.003$ for resin-N; Fig. 1A and B), whereas resin-available P tended to decline in relation to forest floor net N mineralization (r = −0.46, $p = 0.11$; Fig, 1 C). Litterfall N recycling was positively related to forest floor net N mineralization potentials (r = 0.57, $p = 0.04$), but litterfall P recycling (r = 0.09, $p = 0.78$) and litterfall NP (r = 0.35, $p =$ 0.23) were not (data not shown).

Fertilization increased the resin-availability of the added nutrient as expected (Figs. 2 and 3, Table S3), and altered that of the other nutrient, depending on stand age and time. Adding P lowered resin-available N (p <0.0001 for main effects of P), on average 31 % in plots receiving P vs those receiving no P, over the entire study period. P effects were most consistent in successional stands and depended on N addition in some years (N × P × age × year, $p = 0.0001$; Fig. 2). Resin-N was significantly lower in P compared with control plots in five of the seven years measured in successional stands, but only in two years in mature stands, and was lower in N+P compared with N in three years in successional stands and one year in the mature stands (Fig. 2). The resin-N response to added P (i.e. P plot resin N – control plot resin N) was significantly negatively related to forest floor net N mineralization potentials across stands (r = −0.54, $p = 0.05$; Fig. S2A).

Effects of added N on resin-P were detected only in a few of the

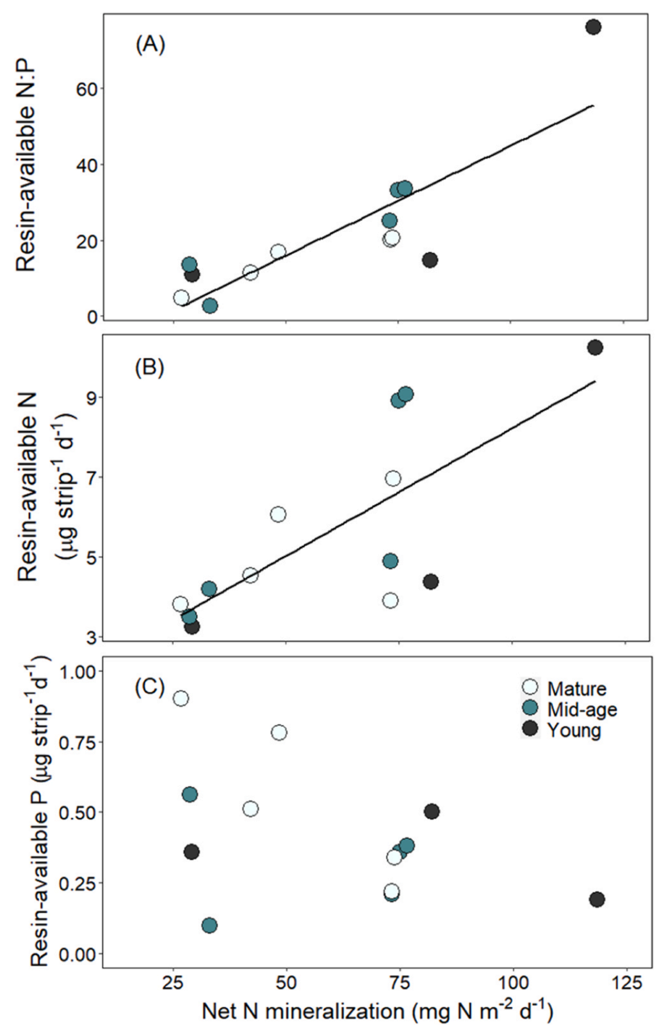

Fig. 1. Relationship of (A) resin N:P, (B) resin N, and (C) resin P with net N mineralization potential in forest floor across 13 stands. Values are means of control plots throughout the study period.

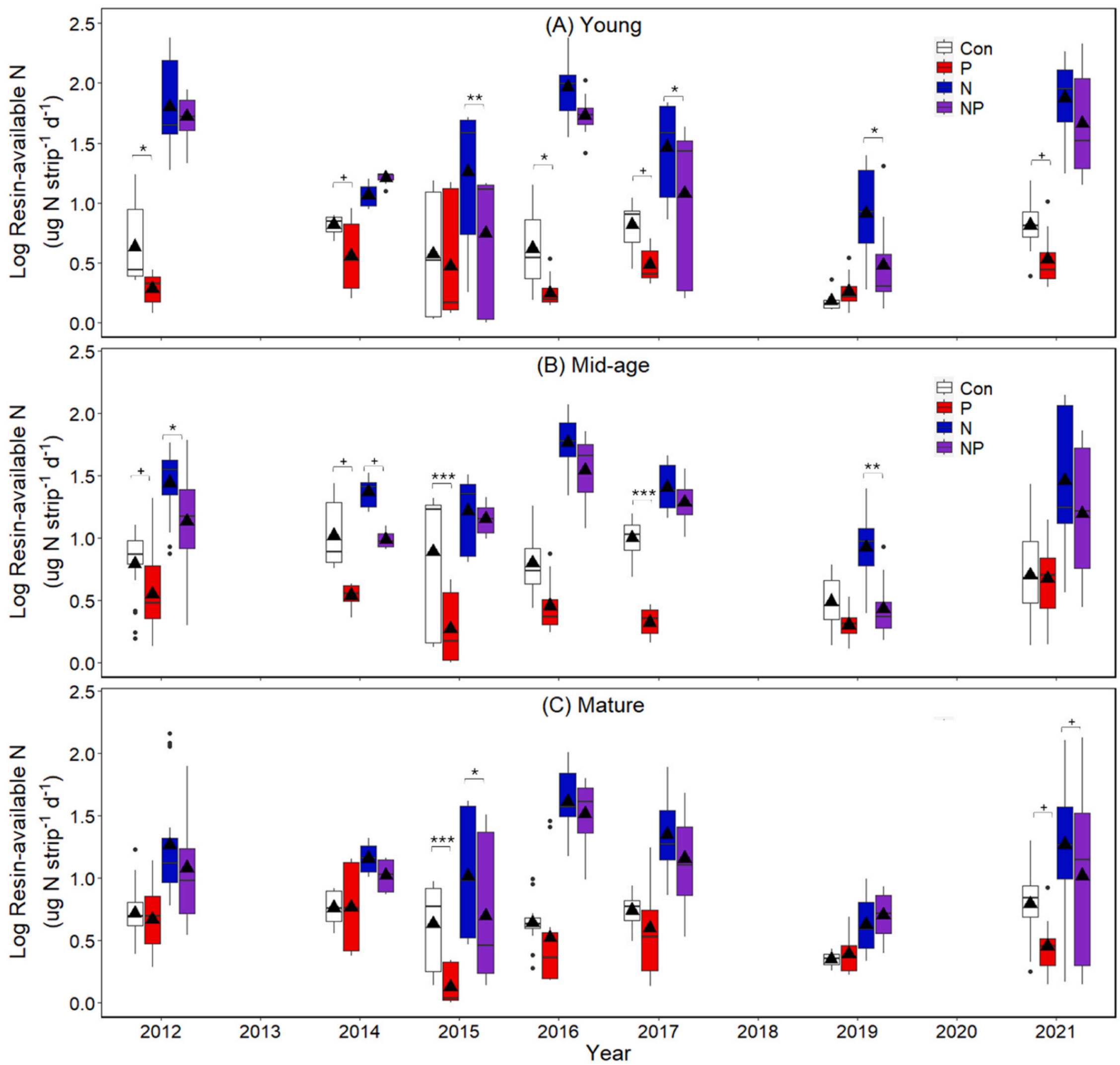

Fig. 2. Resin-available N over time in (A) young, (B) mid-age, and (C) mature forest stands in 3 central NH sites (BEF, HBEF, JB), fertilized annually with N, P, and N+P. Boxes are the interquartile ranges, whiskers are the 5th and 95th percentiles, horizontal lines are the medians, and triangles are the means. Significance of control vs P and N vs NP contrasts is indicated with brackets ($^{+}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

sample years and were less consistent than those of added P on N. Added N lowered resin-P availability only in mature stands and only when added in combination with P, by an average of 26 % over the entire study period. In contrast, adding N+P together increased resin-P more so than adding P alone in mid-age and young stands (N × P × age × year, $p < 0.02$; Fig. 3). The resin-P response to added N was not related to forest floor net N mineralization potentials across stands (Fig. S2B)

Litter N concentration increased in response to N addition and declined in response to P addition ($p < 0.0001$ for main effects of each nutrient), with effects depending on stand age and year (P × age, $p = 0.01$; N × age, $p = 0.08$; N × year, $p < 0.0001$, Tables S1, S4). Suppression of litter N concentration by P addition was greater in young than in mid-age or mature stands in all years. In the last year measured (2018) litter N concentration was lower in plots receiving P than those receiving no P by 14.2 % in young, 7.6 % in mid-age, and 9.2 % in mature stands. Similar to concentrations, litter N recycling (total annual litterfall N; g $m^{-2}yr^{-1}$) increased in response to N and declined in response to P (Fig. 4A-C). We detected main effects of N and P on litter N recycling ($p < 0.0001$ for both), but we detected no interactions with age or year (Table S4). Litter N recycling in 2018 was lower in plots receiving P than those receiving no P by an average of 9.5 % (13.7 % in young, 9.6 % in mid-age, and 11.3 % in mature stands).

Litter P concentration increased in response to P addition (main effects of P, $p < 0.0001$), but less so when N was added in combination with P (N × P interaction, $p = 0.0004$; Tables S1, S4). Litter P concentration was 8 % lower in N+P than P plots in 2012 and 24 % lower in 2018. Litter P recycling (g P $m^{-2}yr^{-1}$) also increased in response to P ($p < 0.0001$) and added N suppressed that response to P (N × P interaction $p = 0.0007$; Fig. 4D-F), by 20 % in the final year measured (2018). The reduction in litter P recycling in N+P compared with P plots was strongest in young and mature stands, but we did not detect an N × P × age interaction (Table S4).

Soil N transformations in the forest floor increased over time in response to N addition (N × year interactions $p \leq 0.0001$; Table S5). Net nitrification was more responsive than net N mineralization to N fertilization (75 % vs 24 % greater in N vs no N plots in 2017, the final year measured; Figs. 5A and 6A). We detected no effects of P on net N mineralization, whereas net nitrification was greater in plots receiving P than those receiving no P (Table S5; $p = 0.0007$ for main effects of P). Although we detected no N × P interaction, effects of both N and P on forest floor nitrification appeared to be driven mostly by greater nitrification in N+P plots compared with those fertilized with N or P alone

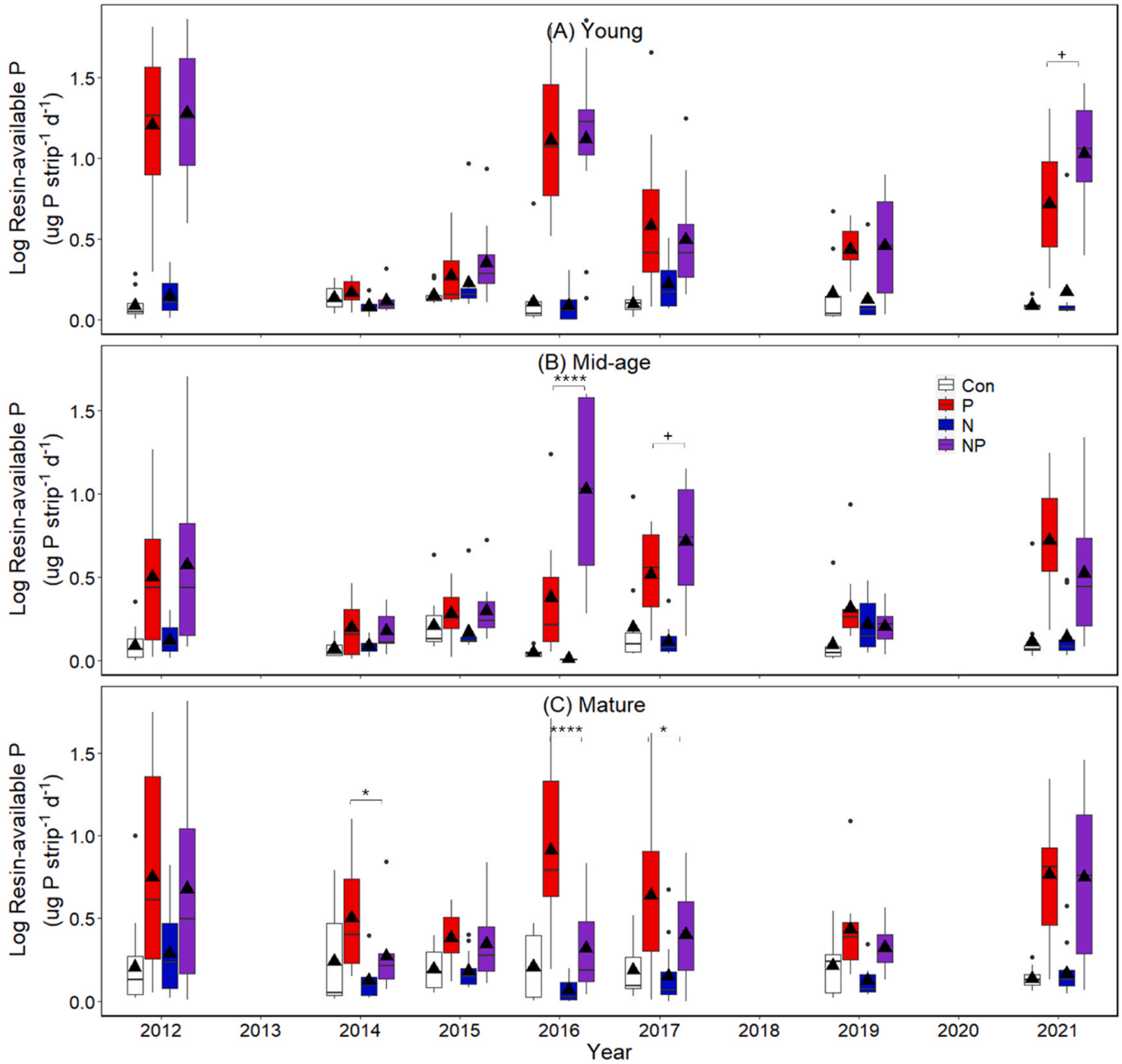

Fig. 3. Resin-available P over time in (A) young, (B) mid-age, and (C) mature forest stands in 3 central NH sites (BEF, HBEF, JB), fertilized annually with N, P, and N+P. Boxes are the interquartile ranges, whiskers are the 5th and 95th percentiles, horizontal lines are the medians, and triangles are the means. Significance of control vs N and P vs NP contrasts is indicated with brackets ($^+p < 0.10$, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

(Fig. 6A). In 2017, nitrification in N+P plots was 96 % greater than in N plots, whereas it was only 18 % greater in P plots than controls, and 30 % greater in N plots than controls.

In mineral soil, N mineralization did not respond to N (main effects of N, $p = 0.87$), and declined somewhat in response to P (main effects of P, $p = 0.10$), mostly in 2014 in N+P compared with N plots (Fig. 5B). Nitrification in mineral soil increased in response to N (main effects of N, $p = 0.01$; N × year interaction, $p = 0.07$; Fig. 6B; Table S6) but did not respond to P.

4. Discussion

Added P influenced N cycling in successional and mature northern hardwood forest by reducing resin-available N and litterfall N recycling (Figs. 2, 4). Surprisingly, effects of N addition also appeared to be controlled by added P: litterfall P recycling in stands of all ages declined in response to N only when added in combination with P (Fig. 4D-F), and the same was true of resin-available P in mature stands (Fig. 3). Thus, support for our general hypothesis that adding one nutrient lowers recycling of the other points mostly to the importance of P. This finding adds support for the idea that P controls N processes in the northern hardwoods (Gonzales et al., 2023; Salvino et al., 2019; Tatariw et al., 2018) and emphasizes that studies of N cycling in this region could benefit from simultaneously considering P as a potentially interacting limiting nutrient. Our results also are consistent with the suppression of inorganic N availability by P addition that has been noted in studies conducted in other regions and ecosystems (Chen et al., 2017; Sun et al., 2022; Xia et al., 2023). However, unlike those studies, we found no increase in net N mineralization or acceleration of N cycling in response to elevated P.

We did not find the predicted successional pattern of resin N:P, or any relationship with forest age. Instead, the most obvious trend was wide variation among young and mid-successional stands (Table 1). The relationship between resin N:P and forest floor net N mineralization suggests that forest site N status contributes to a stand-level variation in the balance of N and P availability. Using chronosequences to detect age-related patterns in soil processes can be problematic in northern hardwoods because of forest site variation (Fisk and Fahey, 1990); tracking changes in individual stands over the long-term would be needed to verify whether available N:P follows a systematic pattern as forests age. Nevertheless, any changes with forest age are likely to be small relative to site-level variation across these forested landscapes.

The suppression of resin-N availability by added P increased in relation to resin-available N:P, as predicted. Furthermore, it was related

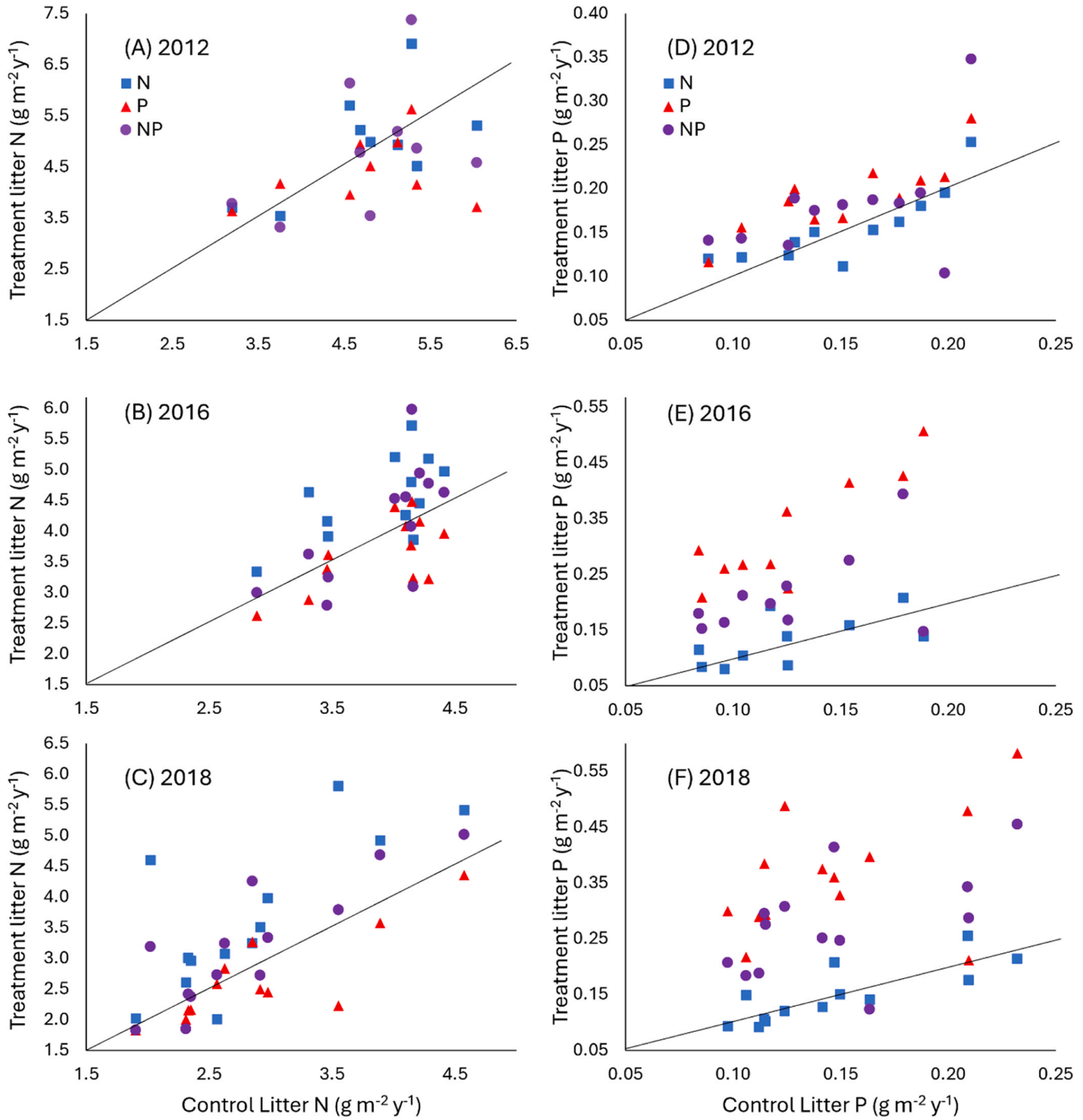

Fig. 4. Leaf litterfall N and P (g m^{-2} yr^{-1}) in 3 central NH sites (BEF, HBEF, JB), fertilized annually with N, P, and N+P. Mean litterfall N and P in each treatment plot are plotted against the corresponding control plot in each stand for 2012, 2016, and 2018; the diagonal line is the 1:1 line. Treatment effects are summarized in Table S4.

to net N mineralization, thereby indicating the importance of forest site N status. Chen et al. (2017) concluded that P controlled N processes in N-saturated but not N-limited forest, and it is noteworthy that the variation in N availability or total soil N within our region (Bae et al., 2015; Ratliff and Fisk, 2016; See et al., 2015) is wide enough to influence the effects of P. However, the effects of added P on N also depended on forest age class, suggesting that P is more limiting than N in successional stands compared with mature stands. This result agrees with greater P limitation of tree diameter growth in mid-successional stands compared with mature stands, but not with the lack of evidence of P limitation in young-successional stands (Goswami et al., 2018). Thus, successional changes following forest harvest do influence N and P interactions, partly in agreement with the tree growth responses, but appear to be of secondary importance to forest site N status.

Litter nutrient responses to treatments show a feedback to elevated P that could slow N cycling, whereas the effects of elevated N were limited by P. Reduction of annual litterfall N recycling by P addition indicates some combination of lower N uptake into foliage or greater N resorption from foliage prior to senescence. Other MELNHE studies confirm that foliar N concentration was reduced by P addition in stands of all age

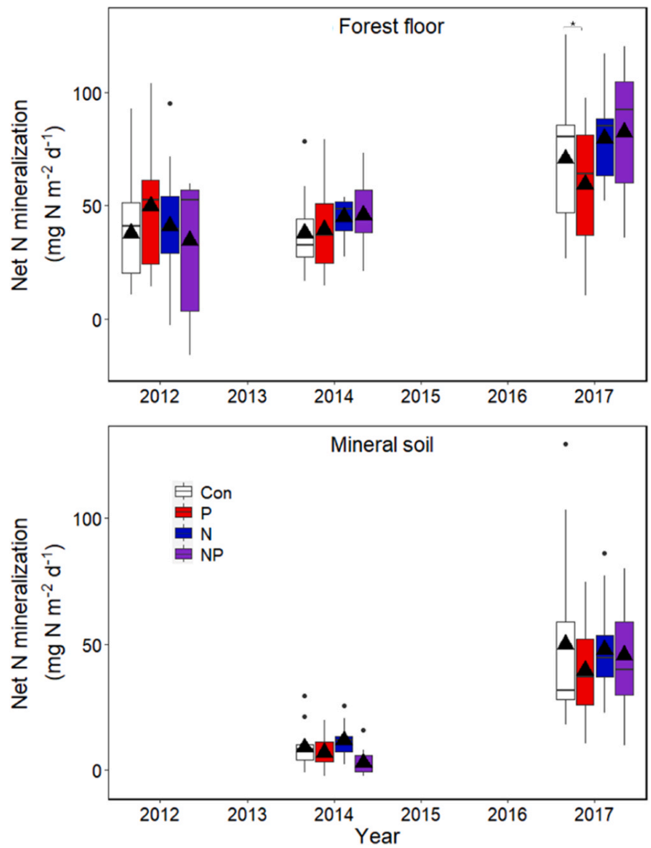

Fig. 5. Potential net N mineralization (mg N m^{-2} d^{-1}) in forest floor (FF) and mineral soil horizons in forest stands in 3 central NH sites (BEF, HBEF, JB), fertilized annually with N, P, and N+P. Significance of control vs P and N vs NP contrasts is indicated with brackets ($^{+}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

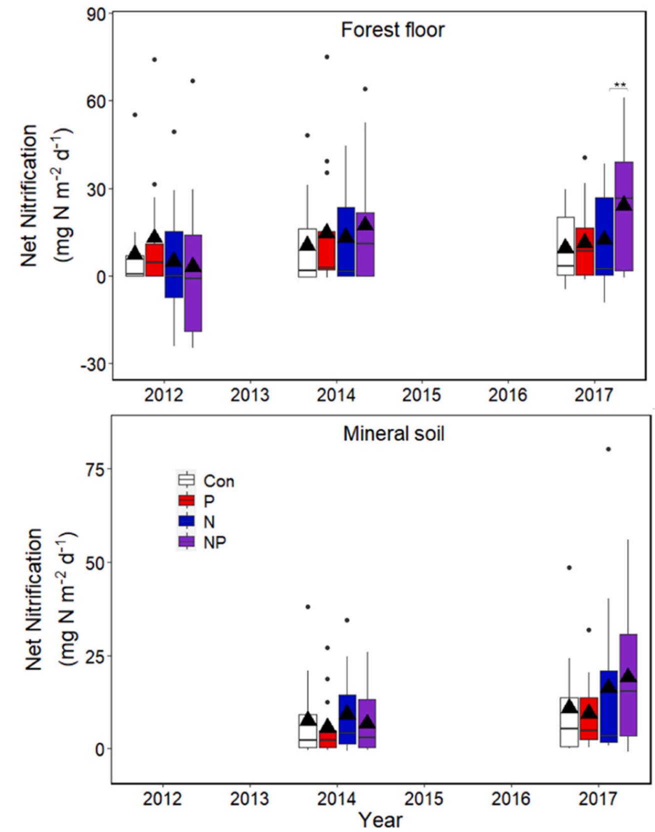

Fig. 6. Potential nitrification (mg N m^{-2} d^{-1}) in forest floor (FF) and mineral horizons in forest stands in 3 central NH sites (BEF, HBEF, JB), fertilized annually with N, P, and N+P. Significance of control vs P and N vs NP contrasts is indicated with brackets ($^{+}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

classes (Gonzales and Yanai, 2019, Gonzales et al., 2023, Hong et al., 2022), whereas N resorption increased in response to added P only in young stands (Gonzales and Yanai, 2019). That litterfall P was sensitive to N only when added in combination with P is also consistent with findings of lower foliar P (Hong et al., 2022), and with greater P resorption (Gonzales and Yanai, 2019) in response to addition of N and P together than to P alone. This control by P of the effects of added N suggest that foliar P and the resorption of P from senescing foliage are already close to a maximum under the ambient conditions in many of our forest stands, with little potential to increase even if added N enhances demand for P.

Net N mineralization increased as expected with added N, but the response to P was not as clear. The lack of stimulation of N mineralization by added P contrasts with the more common finding that added P increases net N mineralization (Chen et al., 2017; Sun et al., 2022; Xia et al., 2023). N-mineralizing enzyme activities in the forest floor increased in response to added P in our study sites (Shan, 2020), which could be expected to increase the mineralization of N. However, the high organic content of the forest floor in our northern hardwood stands may promote N immobilization when microbial P limitation is alleviated. For instance, Fisk and Fahey (2001) found lower net N mineralization owing to greater N immobilization in nearby young forest stands that had been fertilized for eight years with a balanced mix of plant macronutrients. In the current study, although we did not detect effects of P on net N mineralization in the forest floor, it was on average 44 % greater in P plots than controls in the first year (2012), but 17 % lower in P plots in the last year measured (2017; Fig. 5A). The possibility that this pattern is showing the beginning of N cycling feedbacks, either from greater microbial N immobilization and sequestration in organic matter or from lower litterfall N recycling, warrants continued attention over time.

Net nitrification in the forest floor increased in response to P as well as to N. P limitation of nitrification agrees with the previous work in which added P increased gross nitrification in our HBEF site (Minick et al., 2011), and net nitrification in Ohio hardwoods (DeForest and Otuya, 2020). Additionally, we found that nitrification increased more in response to N+P together than to either nutrient alone, indicating co-limitation. Thus, high availability of both N and P together may maximize the potential for nitrification-related N losses, via leaching or through gaseous forms. Effects of P on N_2O emissions and NO_3^- leaching are mixed (Chen et al., 2022; Cheng et al., 2018; Wang et al., 2022; Yu et al., 2017), in part because of pH effects, with suppression of N_2O production by P evident below pH 4.5 (Xia et al., 2023). At our HBEF site, where ambient N availability and nitrification are already somewhat high relative to the BEF stands (Table 1), strong soil retention of added NO_3^- (Fuss et al., 2018) and exceptionally low NO_3^- levels in streamwater (Fakhraei et al., 2020) argue against any large leaching losses in response to P, even if in combination with high N. However, gaseous losses deserve further attention as a possible consequence of elevated P in the ecosystem.

Together, our resin, litter, and soil results suggest that alleviating P limitation increased plant or microbial demand for N and decreased N recycling in litterfall, likely promoting N limitation over time. N mineralization was not reduced by added P in the initial years of the study, leaving plant or microbial uptake as a more likely explanation for the suppression of resin-N during that time. The lower foliar N in response to P found in other MELNHE studies (Gonzales et al., 2023, Hong et al., 2022), could indicate greater limitation and less uptake by trees. However, it could also indicate greater N allocation to non-leaf biomass, especially in smaller trees that can allocate preferentially to woody growth relative to foliage (Li et al., 2018), and sequestration of N in the aggrading biomass of successional forests would be expected to accompany the diameter growth response to added P found by Goswami et al. (2018).

In addition to aboveground storage, evidence of microbial P limitation and N-P colimitation of root growth in our sites points to important N sinks belowground. Scarcity of available N relative to P has been found to reduce the transfer of N from mycorrhizal associates to trees (Hasselquist et al., 2016; Näsholm et al., 2013), and the need for balanced nutrition in roots and mycorrhizal fungi is known to increase N accumulation in these pools when P is added (Blanes et al., 2012). Hence, in our system, adding P should increase N use for construction of roots or mycorrhizae, potentially lowering nutrient supply to foliage and increasing nutrient resorption. This is especially true in successional stands where root growth increased in response to P and more so to N+P together, suggesting that elevated P availability substantially intensified N demand (Butt et al., unpublished; Li et al., 2024). Greater microbial N uptake and turnover in response to P, found in northern hardwoods in Maine (Tatariw et al., 2018), would suggest a further reduction in N availability. In the MELNHE study, the idea that adding P induces N demand by microbes is supported by microbial respiratory response to added P (Fisk et al., 2015) and also by vector analysis of C, N, and P acquiring enzymes (i.e. Moorhead et al., 2016), which indicated that the activity of decomposer microbes is sequentially P- and then N-limited (Shan, 2020). The question of whether P addition increases N accumulation by soil microbes, mycorrhizae, roots, or tree biomass, deserves further attention because these sinks differ in turnover times and thus in their longer-term effects on N recycling.

In conclusion, our findings show that P limitation influences nutrient cycling in these northern hardwood forests. They also emphasize that the availability of P relative to N and the effects of elevated P are more sensitive to site N status than to the legacy of forest harvest. We suggest that alleviating P limitation increases N uptake by plants and microbes and sequesters N in biomass and organic matter, contributing to N limitation, which may be intensified over time by plant or microbial feedbacks to N mineralization. These effects are consistent with the idea that sequential N and P co-limitation occurs in this ecosystem (Goswami et al., 2018), and identifying the pools in which sequestered N is retained will be important for explaining long-term effects on the cycling of N relative to P.

CRediT authorship contribution statement

Melany Fisk: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Shinjini Goswami:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Competing Interest

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

Data availability

Data in this manuscript are available in the Environmental Data Initiative repository in the following:

Fisk, M. 2023. Resin-available nutrients in the O horizon in the MELNHE study at Hubbard Brook Experimental Forest, Bartlett Experimental Forest and Jeffers Brook, central NH USA, 2011- ongoing ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/3b4a83378686decca2c2d5c1f0709444.

Fisk, M. 2023. Multiple Element Limitation in Northeast Hardwood Ecosystems (MELNHE): Net N mineralization at Hubbard Brook Experimental Forest, Bartlett Experimental Forest and Jeffers Brook, central NH USA, 2009 - 2017 ver 4. Environmental Data Initiative. https://doi.org/10.6073/pasta/826e44994e01aba173fae30115478584.

Fisk, M.C., R.D. Yanai, S.D. Hong, C.R. See, and S. Goswami. 2022. Litter chemistry and masses for the MELNHE NxP fertilization experiment ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/8b2975a3a02cbcfb1b0a12ac954576d4.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122203.

References

Ågren, G.I., 2008. Stoichiometry and nutrition of plant growth in natural communities. Ann. Rev. Ecol. Evol. Syst. 39, 153–170. https://doi.org/10.1146/annurev.ecolsys.39.110707.173515.

Allison, S.D., Weintraub, M.N., Gartner, T.B., Waldrop, M.P., 2011. Evolutionary-economic principles as regulators of soils enzyme production and ecosystem function. In: Shukla, G., Varma, A. (Eds.), Soil Biology, Soil Enzymology. Springer Verlag, Berlin, pp. 230–243. Vol. 22.

Bae, K., Fahey, T.J., Yanai, R.D., Fisk, M.C., 2015. Soil Nitrogen Availability Affects Belowground Carbon Allocation and Soil Respiration in Northern Hardwood Forests of New Hampshire. Ecosystems 18, 1179–1191. https://doi.org/10.1007/s10021-015-9892-7.

Blanes, M.C., Emmett, B.A., Viñegla, B., Carreira, J.A., 2012. Alleviation of P limitation makes tree roots competitive for N against microbes in a N-saturated conifer forest: A test through P fertilization and ^{15}N labelling. Soil Biol. Biochem 48, 51–59. https://doi.org/10.1016/j.soilbio.2012.01.012.

Bohlen, P.J., Groffman, P.M., Driscoll, C.T., Fahey, T.J., Siccama, T.G., 2001. Plant–soil–microbial interactions in a northern hardwood forest. Ecology 82, 965–978.

Bormann, F.H., Likens, G.E., Fisher, D.W., Pierce, R.S., 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. Science 159, 882–884.

Chen, H., Zhang, W., Gurmesa, G.A., Zhu, X., Li, D., Mo, J., 2017. Phosphorus addition affects soil nitrogen dynamics in a nitrogen-saturated and two nitrogen-limited forests. Eur. J. Soil Sci. 68, 472–479. https://doi.org/10.1111/ejss.12428.

Chen, Y., Yin, S., Shao, Y., Zhang, Q., Zhang, K., 2022. Greenhouse gas fluxes from riparian forest soil depend on the responses of microbes to nitrogen and phosphorus additions. Appl. Soil Ecol. 173, 104365 https://doi.org/10.1016/j.apsoil.2021.104365.

Cheng, Y., Wang, J., Sun, N., Xu, M., Zhang, J., Cai, Z., Wang, S., 2018. Phosphorus addition enhances gross microbial N cycling in phosphorus-poor soils: a ^{15}N study from two long-term fertilization experiments. *Biol. Fert. Soils* 54, 783–789.

Davidson, E.A., Howarth, R.W., 2007. Environmental Science: Nutrients in synergy. Nature 449, 1000–1001.

Davidson, E.A., de Carvalho, C.J.R., Figueira, M., Ishida, F.Y., Ometto, J.P.H.B., Nardoto, G.B., Sabá, R.T., Hayashi, S.N., Leal, E.C., Vieira, I.C.G., Martinelli, L.A., 2007. Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. Nature 447, 995–998.

DeForest, J.L., Otuya, R.K., 2020. Soil nitrification increases with elevated phosphorus or soil pH in an acidic mixed mesophytic deciduous forest. Soil. Biol. Biochem 142, 1–4. https://doi.org/10.1016/j.soilbio.2020.107716.

Deng, Q., Hui, D., Dennis, S., Reddy, K.H., 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: A meta-analysis. Glob. Ecol. Biogeogr. 26, 713–728. https://doi.org/10.1111/geb.12576.

Fakhraei, H., Fahey, T., Driscoll, C., 2020. The Biogeochemical Response of Nitrate and Potassium to Landscape Disturbance in Watersheds of the Hubbard Brook Experimental Forest, New Hampshire, USA. In: Levia, D.F., Carlyle-Moses, D.E., Iida, S., Michalzik, B., Nanko, K., Tischer, A. (Eds.), Forest-Water Interactions. Ecological Studies, vol 240. Springer, Cham, pp. 537–563. https://doi.org/10.1007/978-3-030-26086-6_22.

Finzi, A.C., Austin, A.T., Cleland, E.E., Frey, S.D., Houlton, B.Z., Wallenstein, M.D., 2011. Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from terrestrial ecosystems. Front. Ecol., Env. 9, 61–67. https://doi.org/10.1890/100001.

Fisk, M.C., Fahey, T.J., 1990. Nitrification potential in the organic horizons following clear felling of northern hardwood forests. Soil Biol. Biochem. 22, 277–279.

Fisk, M.C., Fahey, T.J., 2001. Microbial biomass and nitrogen cycling response to fertilization and litter removal in young northern hardwood forests. Biogeochemistry 53, 201–223.

Fisk, M.C., Ratliff, T.J., Goswami, S., Yanai, R.D., 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. Biogeochemistry 118, 195–204.

Fisk, M.C., Santangelo, S., Minick, K., 2015. Carbon mineralization is promoted by phosphorus and reduced by nitrogen addition in the organic horizon of northern hardwood forests. Soil Biol. Biochem. 81, 212–218.

Fuss, C.B., Lovett, G.M., Goodale, C.L., Ollinger, S.V., Lang, A.K., Ouimette, A.P., 2018. Retention of nitrate-N in mineral soil organic matter in different forest age classes. Ecosystems 22, 1280–1294.

Gonzales, K., Yanai, R.D., 2019. Nitrogen–phosphorous interactions in young northern hardwoods indicate P limitation: Foliar concentrations and resorption in a factorial N by P addition experiment. Oecologia 189, 829–840. https://doi.org/10.1007/s00442-019-04350-y.

Gonzales, K.E., Yanai, R.D., Fahey, T.J., Fisk, M.C., 2023. Evidence for P limitation in eight northern hardwood stands: Foliar concentrations and resorption by three tree species in a factorial N by P addition experiment. For. Ecol. Manag 529, 1–7. https://doi.org/10.1016/j.foreco.2022.120696.

Goswami, S., Fisk, M.C., Vadeboncoeur, M.A., Johnston, M., Yanai, R.D., Fahey, T.J., 2018. Phosphorus limitation of aboveground production in northern hardwood forests. Ecology 99, 438–449.

Hasselquist, N.J., Metcalfe, D.B., Inselsbacher, E., Stangl, Z., Oren, R., Näsholm, T., Högberg, P., 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. Ecology 97, 1012–1022.

Heuck, C., Smolka, G., Whalen, E., Frey, S., Gundersen, P., Moldan, F., Fernandez, I., Spohn, M., 2018. Effects of long-term nitrogen addition on phosphorus cycling in organic soil horizons of temperate forests. Biogeochemistry 141, 1–15. https://doi.org/10.1007/s10533-018-0511-5.

Hong, D.S., Gonzales, K.E., Fahey, T.J., Yanai, R.D., 2022. Foliar nutrient concentrations of six northern hardwood species responded to nitrogen and phosphorus fertilization but did not predict tree growth. PeerJ 10, e13193.

Leak, W.B., 1991. Secondary forest succession in New Hampshire, USA. For. Ecol. Manag. 43, 69–86.

Li, S., Fisk, M.C., Yanai, R.D., Fahey, T.J., 2024. Co-limitation of Fine Root Growth by Nitrogen and Phosphorus in Early Successional Northern Hardwood Forests. Ecosystems 27, 33–44. https://doi.org/10.1007/s10021-023-00869-7.

Li, Y., Tian, D., Yang, H., Niu, S., 2018. Size-dependent nutrient limitation of tree growth from subtropical to cold temperate forests. Funct. Ecol. 32, 95–105.

Marklein, A.R., Houlton, B.Z., 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. N. Phyt 193, 696–704.

Minick, K.J., Fisk, M.C., Groffman, P.M., 2011. Calcium and phosphorus interact to reduce mid-growing season net nitrogen mineralization potential in organic horizons in a northern hardwood forest. Soil Biol. Biochem. 42, 271–279.

Moorhead, D.L., Sinsabaugh, R.L., Hill, B.H., Weintraub, M.N., 2016. Vector analysis of ecoenzyme activities reveal constraints on coupled C, N and P dynamics. Soil Biol. Biochem. 93, 1–7.

Murphy, J., Riley, J.P., 1962. A modified single solution method for determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36.

Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S.G., Campbell, C., Hurry, V., Linder, S., Högberg, M.N., 2013. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? N. Phyt 198, 214–221.

Olander, L.P., Vitousek, P.M., 2000. Regulation of soil phosphatase and chitinase activity by N and P availability. Biogeochemistry 49, 175–190.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R. Core Team 2016. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128, http://CRAN.R-project.org/package=nlme.

Rastetter, E.B., Yanai, R.D., Thomas, R.Q., Vadeboncoeur, M.A., Fahey, T.J., Fisk, M.C., Kwiatkowski, B.L., Hamburg, S.P., 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecol. Appl. 23, 621–642.

Ratliff, T.J., Fisk, M.C., 2016. Phosphatase activity is related to N availability but not P availability across hardwood forests in the northeastern United States. Soil Biol. Biochem. 94, 61–69.

Salvino, C.J., Patel, K.F., Fernandez, I.J., Gruselle, M.C., Tatariw, C., MacRae, J.D., 2019. Soil Sci. Soc. Am. J. 83, 1209–1218. https://doi.org/10.2136/sssaj2019.02.0043.

Schleuss, P.M., Widdig, M., Heintz-Buschart, A., Kirkman, K., Spohn, M., 2020. Interactions of nitrogen and phosphorus cycling promote P acquisition and explain synergistic plant-growth responses. Ecology 101, e03003. https://doi.org/10.1002/ecy.3003.

See, C.R., Yanai, R.D., Fisk, M.C., Vadeboncoeur, M.A., Quintero, B.A., Fahey, T.J., 2015. Soil nitrogen affects phosphorus recycling: foliar resorption and plant–soil feedbacks in a northern hardwood forest. Ecology 96, 2488–2498.

Shan, S. 2020. The controls of nutrient limitation on resource allocation belowground. PhD dissertation. Miami University, Oxford OH USA. https://etd.ohiolink.edu/.

Sterner, R.W., Elser, J.J. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press.

Sun, Y., Wang, C., Chen, X., Lui, S., Lu, X., Chen, H.Y.H., Ruan, G., 2022. Phosphorus additions imbalance terrestrial ecosystem C:N:P stoichiometry. Glob. Change Biol. 28, 7353–7365. https://doi.org/10.1111/gcb.16417.

Tatariw, C., MacRae, J.D., Fernandez, I.J., Gruselle, M.C., Salvino, C.J., Simon, K.S., 2018. Chronic nitrogen enrichment at the watershed scale does not enhance microbial phosphorus limitation. Ecosystems 21, 178–189. https://doi.org/10.1007/s10021-017-0140-1.

Townsend, A.R., Cleveland, C.C., Houlton, B.Z., Alden, C.B., White, J.W.C., 2011. Multiple element regulation of the tropical forest carbon cycle. Front. Ecol. Env 9, 9–17.

Treseder, K.K., Vitousek, P.M., 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. Ecology 82, 946–954.

, 1983US EPA, 1983. Methods for chemical analysis of water andwastes EPA-600/4-79-020.

Vadeboncoeur, M.A., Hamburg, S.P., Cogbill, C.V., Sugimura, W.Y., 2012. A comparison of presettlement and modern forest composition along an elevation gradient in central New Hampshire. Can. J. For. Res. 42, 190–202.

Vitousek, P.M. 2004. Nutrient cycling and limitation: Hawai'i as a model System. Princeton University Press.

Vitousek, P.M., Matson, P.A., 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. Science *225*, 51–52.

Vitousek, P.M., Melillo, J.M., 1979. Nitrate losses from disturbed forests: patterns and mechanisms. For. Sci. 25, 605–619.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecol. Appl. 20, 5–15.

Wang, R., Bicharanloo, B., Hou, E., Jiang, Y., Dijkstra, F.A., 2022. Phosphorus supply increases nitrogen transformation rates and retention in soil: a global meta-analysis. e2021EF002479 Earth'S. Future 10. https://doi.org/10.1029/2021EF002479.

Waring, B.G., Becknell, J.M., Powers, J.S., 2015. Nitrogen, phosphorus, and cation use efficiency in stands of regenerating tropical dry forest. Oecologia 178, 887–897. https://doi.org/10.1007/s00442-015-3283-9.

Whittaker, R.H., Likens, G.E., Bormann, F.H., Easton, J.S., Siccama, T.G., 1979. The Hubbard Brook Ecosystem Study: Forest Nutrient Cycling and Element Behavior. Ecology 60, 203–220.

Xia, S., Jiang, J., Lui, F., Chang, Z., Yu, M., Liu, C., Wang, Y.P., Yan, J., 2023. Phosphorus addition promotes plant nitrogen uptake mainly via enhancing microbial activities: a global meta-analysis. *Appl. Soil Ecol.* 188, 1–10 doi.org/10.1016/j.apsoil.2023.104927.

Xiao, J., Dong, S., Shen, H., Li, S., Zhi, Y., Mu, Z., Ding, C., 2022. Phosphorus addition promotes nitrogen retention in alpine grassland plants while increasing N deposition. Catena 210, 105887. https://doi.org/10.1016/j.catena.2021.105887.

You, C., Wu, F., Yang, W., Xu, Z., Tan, B., Yue, K., Ni, X., 2018. Nutrient-limited conditions determine the responses of foliar nitrogen and phosphorus stoichiometry to nitrogen addition: A global meta-analysis. Environ. Poll. 241, 740–749. https://doi.org/10.1016/j.envpol.2018.06.018.

Yu, L., Wang, Y., Zhang, X., Dorsch, P., Mulder, J., 2017. Phosphorus addition mitigates N2O and CH4 emissions in N-saturated subtropical forest, SW China. *Biogeosciences* 14, 3097–3109. https://doi.org/10.5194/bg-14-3097-2017.