**Global response patterns of plant functional traits to nitrogen and phosphorus addition are governed by additive interactions, climatic demand, and species acquisition strategy**

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**Keywords**

nutrient addition, plant functional ecology, photosynthetic capacity, meta-analysis, carbon cycle

**Abstract**

The availability of nutrients such as nitrogen and phosphorus plays a central role in shaping plant ecophysiological responses to global change. While nitrogen availability has been asserted as a key driver of plant responses to global change, the role of phosphorus – both individually and in combination with nitrogen – remains less understood due to a lack of data syntheses that precludes the development of a mechanistic framework. To address this knowledge gap, we compiled data from full-factorial nitrogen and phosphorus addition experiments across the globe and conducted a meta-analysis. We quantified the individual and interactive effects of nitrogen and phosphorus addition on leaf nutrient content, leaf photosynthetic traits, and biomass partitioning and assessed how climate and species acquisition strategy mediate these responses. Nutrient addition played a minimal role in shaping leaf-level photosynthetic traits, despite nitrogen and phosphorus addition each increasing foliar nutrient concentrations, increasing aboveground biomass, and decreasing the root:shoot ratio. Most trait responses to combined nitrogen and phosphorus addition were driven by additive interactions except for leaf N:P and aboveground biomass, which demonstrated stronger responses to combined nitrogen and phosphorus addition than the sum of the individual nitrogen and phosphorus effects. Some trait responses were mediated by climate, with foliar nitrogen responses to nitrogen addition and foliar phosphorus responses to phosphorus addition each being strongest in regions with greater demand for soil resources. Regions with greater demand for soil resources also demonstrated stronger synergistic responses of leaf N:P and aboveground biomass to nitrogen and phosphorus addition. In general, C4 species, species that could not form associations with nitrogen-fixing bacteria, and species with scavenging acquisition strategies demonstrated stronger responses to nutrient amendments than C3 species, species that could associate with nitrogen-fixing bacteria, and species with mining acquisition strategies. These findings clarify the role of phosphorus in shaping plant ecophysiological trait variation, highlight possible mechanisms governing trait responses across climatic gradients and acquisition strategies, demonstrate key traits that demonstrate synergistic responses to nitrogen and phosphorus, and ultimately provide a foundation for improving the representation of C-N-P interactions in terrestrial biosphere models.

**Introduction**

Terrestrial ecosystems are regulated by complex carbon, nitrogen, and phosphorus cycles. Recent terrestrial biosphere model development has focused on incorporating fully coupled nitrogen and phosphorus cycles, following from evidence that nutrient availability constrains primary productivity under present and future climates (Hungate *et al.*, 2003; LeBauer & Treseder, 2008; Wieder *et al.*, 2015; Fay *et al.*, 2015). Models with fully coupled nutrient cycles generally reduce the magnitude of the land carbon sink (Goll *et al.*, 2012; Wieder *et al.*, 2015; Braghiere *et al.*, 2022), and ensemble analyses often show stronger agreement with observations compared to carbon-only models (Kou-Giesbrecht *et al.*, 2023; Stocker *et al.*, 2025). However, land carbon sink trends still diverge across models, with some studies showing a stronger divergence among nutrient-coupled models than carbon-only models (Davies-Barnard *et al.*, 2020; Kou-Giesbrecht *et al.*, 2023; Stocker *et al.*, 2025). This model disparity is likely due to an incomplete understanding of how nutrient availability influences plant traits that drive ecosystem carbon and nutrient fluxes, highlighting the need for global data syntheses to resolve broad-scale patterns of nutrient effects on plant traits that are commonly used to predict the land carbon sink.

Nitrogen availability has long been recognized as an important driver of plant ecophysiological trait variation. Soil nitrogen availability is often positively correlated with leaf nitrogen content, while leaf nitrogen content is often positively correlated with photosynthetic capacity (Field & Mooney, 1986; Evans, 1989; Walker *et al.*, 2014; Firn *et al.*, 2019; Liang *et al.*, 2020). At the whole-plant level, increased nitrogen availability is commonly associated with greater biomass production, typically through stronger increases in aboveground than belowground biomass (Liang *et al.*, 2020; Stocker *et al.*, 2025). Leaf nitrogen-photosynthesis relationships arise because a large fraction of leaf nitrogen is allocated toward the maintenance and construction of photosynthetic enzymes (Evans & Seemann, 1989; Waring *et al.*, 2023), and is a primary reason why leaf nitrogen is used as a predictor of photosynthesis in many terrestrial biosphere models (Rogers *et al.*, 2017). However, correlations between soil nitrogen availability and photosynthetic capacity are often weaker than correlations between soil nitrogen availability and leaf nitrogen content (Liang *et al.*, 2020; Waring *et al.*, 2023; Perkowski *et al.*, 2025b; Stocker *et al.*, 2025), likely because investment in photosynthetic capacity is more strongly regulated by climatic factors that influence leaf-level demand for soil resources than by soil nitrogen supply (Smith *et al.*, 2019; Dong *et al.*, 2020; Peng *et al.*, 2021; Westerband *et al.*, 2023). Leaf and whole-plant responses to nitrogen availability are also shaped by climate and species identity, with stronger plant trait responses expected under conditions that increase the leaf-level demand for soil resources, in species with nutrient acquisition strategies that rely on soil inorganic nitrogen, and in species that have heightened demand for nitrogen (e.g., C3 species, annual species, etc.) (Hoeksema *et al.*, 2010; Ghannoum *et al.*, 2011; Valeria & Santiago, 2011; Kivlin *et al.*, 2013; Cleland *et al.*, 2019; Cheaib *et al.*, 2025b; Perkowski *et al.*, 2025a).

Phosphorus availability is also an important determinant of plant ecophysiological trait variation, though it has historically garnered less attention than nitrogen. Soil phosphorus availability is often positively correlated with leaf phosphorus content, and leaf phosphorus content is often positively correlated with photosynthetic capacity (Walker *et al.*, 2014; Norby *et al.*, 2017; Firn *et al.*, 2019; Ellsworth *et al.*, 2022), leading to an increase in biomass production that stems from a stronger increase in aboveground biomass than belowground biomass (Cleland *et al.*, 2019; Keller *et al.*, 2023; Yang *et al.*, 2025). Leaf phosphorus-photosynthesis relationships arise because phosphorus is required to build and maintain energy transfer compounds (e.g., ATP, NADPH), substrate (e.g., Ribulose-1,5-bisphosphate), and triose phosphate compounds that play a central role in driving the Calvin-Benson cycle. However, direct relationships between soil phosphorus availability and photosynthesis are inconsistently observed (Reich *et al.*, 2009; Mo *et al.*, 2019; Yu *et al.*, 2022; Hersch-Green *et al.*, 2024), a discrepancy that may reflect shifts in the fraction of leaf phosphorus allocated to metabolic versus non-metabolic pools across phosphorus availability gradients (Wang *et al.*, 2019; Yu *et al.*, 2022; Dong *et al.*, 2025) and complicates model predictions when photosynthesis is predicted using leaf nutrients (Rogers *et al.*, 2017). Climate and species identity also likely play an important role in determining plant trait responses to phosphorus availability, with stronger trait responses expected in regions where demand for phosphorus is high (e.g., low temperature, high aridity, high light), in species with acquisition strategies that increase phosphorus limitation (e.g., species that associate with N2-fixing bacteria), and in species with increased demand for phosphorus (e.g., C3 species, annual species) (Hoeksema *et al.*, 2010; Valeria & Santiago, 2011; Augusto *et al.*, 2013; Keller *et al.*, 2023; Yang *et al.*, 2025). However, the effects of climate and species identity on leaf and whole-plant responses to phosphorus availability have not been well-documented. Broad-scale syntheses that assess phosphorus effects on leaf and whole-plant traits would be useful for identifying mechanisms that drive phosphorus effects on leaf and whole-plant trait variation, and for advancing frameworks that predict carbon and nutrient fluxes in phosphorus-coupled terrestrial biosphere models.

Nitrogen and phosphorus often colimit primary productivity (Du *et al.*, 2020; Braghiere *et al.*, 2022), likely due to their complementary role in driving photosynthetic processes and biomass partitioning. Indeed, nitrogen supports the construction and maintenance of photosynthetic enzymes such as Rubisco, while phosphorus supplies the energy transfer compounds and substrate needed to drive the Calvin-Benson cycle. Nitrogen and phosphorus addition also each contribute to biomass production through enhanced aboveground biomass relative to belowground biomass (Cleland *et al.*, 2019; Keller *et al.*, 2023). This complementarity suggests that combined enrichment of nitrogen and phosphorus could jointly enhance leaf nutrient content, photosynthesis, and biomass production (Niinemets & Kull, 2005; Reich *et al.*, 2009; Walker *et al.*, 2014; Fay *et al.*, 2015). Indeed, some studies suggest that plants respond to combined nitrogen and phosphorus addition by increasing aboveground biomass more strongly than expected from individual effects, highlighting the likelihood that plant responses to nitrogen and phosphorus availability may be synergistic (Harpole *et al.*, 2011; Fay *et al.*, 2015; Fang *et al.*, 2024). Synergistic interactions may be particularly apparent in ecosystems where nitrogen and phosphorus co-limit growth, such as tropical ecosystems (Vitousek *et al.*, 2010; Du *et al.*, 2020). Yet, plant responses to multiple environmental change factors tend to be additive (Yue *et al.*, 2017; Ding *et al.*, 2025), and existing syntheses have only quantified nitrogen and phosphorus interactions for a subset of traits (Elser *et al.*, 2007; Harpole *et al.*, 2011; Li *et al.*, 2016; Fang *et al.*, 2024; Ding *et al.*, 2025). Beyond analyses from coordinated nutrient manipulation experiments (i.e., the Nutrient Network; Firn et al., 2019; Hersch-Green et al., 2024; Cheaib et al., 2025b), no data syntheses to our knowledge have explicitly quantified the interactive effects of nitrogen and phosphorus on leaf nutrient content and photosynthesis, representing a key knowledge gap in understanding how nutrient interactions regulate traits that are important for predicting primary productivity and the land carbon sink. Furthermore, no data syntheses have quantified whether interactions between nitrogen and phosphorus are modified by climate or species identity. Thus, broad-scale analyses that compile data from multiple full-factorial nitrogen-by-phosphorus addition experiments are needed to clarify these dynamics and to develop mechanistic frameworks for predicting how nitrogen-phosphorus interactions influence leaf and whole-plant traits.

Here, we conducted a global meta-analysis using experiments that manipulated nitrogen and phosphorus in full-factorial designs to address three primary objectives. First, we quantified the individual effects of nitrogen, phosphorus, and nitrogen+phosphorus addition on leaf nutrient content, net photosynthesis, photosynthetic capacity, leaf nitrogen and phosphorus use efficiency, biomass production, and biomass partitioning. Second, we quantified the interactive effects of nitrogen and phosphorus addition on each trait to understand whether the effects of nitrogen+phosphorus addition were the product of additive, synergistic, or antagonistic interactions. Finally, we evaluated how climate and species identity traits (e.g., photosynthetic pathway, ability to associate with nitrogen-fixing bacteria, mycorrhizal nutrient acquisition strategy) moderate trait responses to nutrient addition. We used this approach and study objectives to test the following hypotheses: (1) nitrogen and phosphorus addition will increase leaf nutrient content and biomass production, with minimal impacts on investment in leaf-level photosynthesis; (2) the effects of combined nitrogen and phosphorus addition will be no different than the sum of the individual effects (i.e. responses to nitrogen and phosphorus addition will be driven by additive interactions); (3) leaf and whole-plant responses to nutrient addition will be strongest in regions with greater demand for soil resources; and (4) leaf and whole-plant responses to nutrient addition will be strongest in species with greater demand for soil resources (e.g., C3 species) or in species that rely on acquisition strategies that directly acquire nutrients from the soil (e.g., species that do not form associations with N2-fixing bacteria or species that associate with mycorrhizal fungi that have scavenging acquisition strategies).

**Materials and Methods**

*Data compilation*

Initial data for the meta-analysis were collected using citations listed in the Manipulation Experiments Synthesis Initiative (MESI) database (Van Sundert *et al.*, 2023). Manipulation experiments that added nitrogen and phosphorus in a full-factorial design were only selected in this database to ensure that any comparisons made between nitrogen, phosphorus, and nitrogen+phosphorus addition responses were from the same subset of experiments. All data for manuscripts included in the MESI database that fit these criteria were downloaded or extracted using a plot digitizer to ensure that all relevant traits were included in the meta-analysis and undergo a round of quality control to avoid any data entry issues that may arise when using large ecological datasets (Augustine *et al.*, 2024). To supplement studies included in the MESI database, studies that reported data from Nutrient Network experiments were also included in the meta-analysis, including only measurements collected from control, nitrogen, phosphorus, and nitrogen+phosphorus addition plots. Each site in each paper that reported data from Nutrient Network experiments was treated as an independent experiment, following that the Nutrient Network is a globally distributed experiment where independent sites share the same nutrient addition and experimental design scheme (Borer *et al.*, 2014). Specifically, we added leaf nutrient data from Firn et al. (2019), biomass partitioning data from Cleland et al. (2019), and photosynthetic data from Hersch-Green et al. (2024).

To supplement MESI and Nutrient Network datasets, we added additional manipulation experiments using journal articles published on or before March 2025. We selected manipulation experiments where nitrogen and phosphorus were added in a full-factorial design. From this, we selected experiments that measured traits related to leaf photosynthesis (e.g., net photosynthesis maximum rates of Rubisco carboxylation and electron transport for RuBP regeneration), leaf nutrient content (e.g., mass- or area-based leaf nitrogen content, mass- or area-based leaf phosphorus content), resource-use efficiency (e.g., photosynthetic nitrogen- and phosphorus-use efficiencies), biomass (e.g., above-ground or belowground biomass), or biomass partitioning (e.g., root mass fraction, root:shoot ratio). Finally, we selected experiments that included explicit explanations of treatment replication schemes to accurately calculate summary statistics. We first searched for studies that followed these guidelines using citations included in the MESI and Nutrient Network papers. To supplement these studies, we also created a search query in Web of Science using similar search terms as in (Liang *et al.*, 2020). Specifically, our query mined for the following topics: (nitrogen AND phosphorus) AND (fertiliz\* OR addition) AND (effect\* OR respon\* OR affect\* OR impact\* OR increas\* OR decreas\* OR alter\* OR deposition OR enrich\*) AND (leaf nitrogen\* OR leaf phosphorus\* OR \*use efficiency OR biomass OR mass fraction OR root:shoot OR LMA OR SLA OR photosynthesis OR Vcmax OR Jmax) NOT (animal\* OR medic\* OR chemist\*).

*Data extraction*

One mean value ± standard deviation per trait per species per nutrient fertilization treatment per experimental site was considered one observation for experiments that reported results at the species level. Observations for different species from the same study were considered independent, allowing us to determine the effects of species identity traits (e.g., mycorrhizal type, photosynthetic pathway) in modifying plant responses to nutrient treatments. For experiments that reported results at the treatment level, one mean value ± standard deviation per trait per nutrient fertilization treatment per experimental site was considered one observation.

Observations were integrated into a compiled dataset through multiple pathways. First, summary statistics (mean, standard deviation, replication scheme) were calculated directly from published datasets from studies that adopted open data practices. Where possible, summary statistics were extracted from tables included in the main text or supplemental information if studies did not explicitly publish their data. If studies did not include their data or provide summary statistics in tables, we digitized plots using information about treatment and sample replication information. Plots were digitized in R (version 4.4.2) using the ‘metadigitise’ package (Pick *et al.*, 2019). Studies that did not include clear descriptions about the replication scheme were not included in the dataset. Overall, this data extraction approach rendered 4843 observations (1614 observations each for nitrogen, phosphorus, and nitrogen+phosphorus treatments) from 87 studies. Of these studies, 80 were field experiments, 6 were greenhouse experiments, and 1 was a growth chamber experiment. Of the field experiments, 168 independent sites were represented, spanning a broad global gradient with diverse climate types (Table S1). The dataset also includes data comprising 175 species from 55 families, representing diverse growth forms, growth durations, nutrient acquisition strategy, and photosynthetic pathway.

*Moderator variables*

Mean monthly temperature, precipitation, and solar radiation information spanning 1970-2000 were extracted using site latitude and longitude data for all field experiments using the Climatic Research Unit Time Series v4.09 (CRU TS v4.09) gridded data product (Harris *et al.*, 2020) downscaled to a 30 arc-second spatial resolution with WorldClim 2.1 (Fick & Hijmans, 2017). Site aridity was extracted using a complementary gridded data product (Global-AI\_PET\_v3) using the same period (1970-2000) and spatial resolution (30 arc-seconds) (Zomer *et al.*, 2022). This aridity product uses WorldClim 2.1 to calculate a monthly aridity index as a function of mean monthly precipitation per unit mean monthly potential evapotranspiration, estimating potential evapotranspiration using the Penman-Monteith approach. Given that increasing aridity index values indicate increasing wetness, we use the term “moisture index” to avoid confusion.

Mean monthly temperature (°C), mean monthly precipitation (mm), mean daily solar radiation (kJ m-2 day-1), and mean monthly moisture index (unitless) values were extracted from the grid cell containing each site using the “extract” function in the “raster” R package (Hijmans, 2010). Solar radiation values (from kJ m-2 day-1) were converted to photosynthetically active radiation (μmol m-2 s-1) assuming a conversion factor of 2.1 μmol m-2 s-1per unit W m-2. Site mean growing season temperature (*T*g; °C), growing season moisture index (*MI*g; unitless), and growing season PAR (*PAR*g; μmol m-2 s-1) were estimated using the months where mean temperature was above 0°C. All growing season climate data are reported in Table S1.

Species identity traits were included for all measurements that were collected at the species level. Specifically, we included information about species family, photosynthetic pathway (C3, C4), ability to associate with N2 fixing bacteria (N2-fixer, non-fixer), and mycorrhizal type (AM, EcM, dual AM-EcM, facultative AM, ErM, non-mycorrhizal). Mycorrhizal type was assigned from the FungalRoot database using the genus of each species (Soudzilovskaia *et al.*, 2020) and used to determine the mycorrhizal nutrient acquisition strategy following the approach of Cheaib et al. (2025a). Specifically, EcM, ErM, and dual AM-EcM species were assigned a scavenging mycorrhizal nutrient acquisition strategy while AM, facultative AM, and non-mycorrhizal species were assigned a mining mycorrhizal nutrient acquisition strategy. Ability to associate with N2-fixing bacteria was determined based on whether species were in the *Fabaceae* family.

*Determination and analysis of individual and interaction effect sizes*

We used the natural logarithm of the response ratio (ln RR) to determine the individual effects of nitrogen, phosphorus, and nitrogen+phosphorus addition on leaf and whole-plant traits. For each observation *i* (i.e., trait per species per site per experiment), we calculated the natural logarithm of the response ratio (ln RR) as:

(1)

Where is the mean value of a treatment (i.e., nitrogen, phosphorus, or nitrogen+phosphorus addition) and is the mean value of the control treatment for each observation. We determined the weighted log-response ratio () across observations as:

(2)

Where ln RRi is the log-response ratio of observation *i* given in (1), *w*i is the weight of each log-response ratio, and *k* is the total number of observations. *w*i was calculated as the inverse of the variance (*v*i) of observation *i* (that is, *w*i = 1 / *v*i). *v*i was calculated as:

(3)

Where *s*t and *s*c are the standard deviations of the treatment and control groups, respectively, and *n*t and *n*c are the sample sizes of the treatment and control groups.

Next, we used Hedge’s *d* to determine the interactive effect of nitrogen and phosphorus addition on leaf and whole-plant traits (Gurevitch *et al.*, 2000; Yue *et al.*, 2017; Ding *et al.*, 2025). For each observation *i*, the interactive effect size of nitrogen and phosphorus addition (dNPi) was calculated as:

(4)

Where ,,, and refer to the mean of the nitrogen, phosphorus, nitrogen+ phosphorus, and control treatments, respectively, for each observation *i*. *s*int\_i refers to the pooled standard deviation across treatments, calculated as:

(5)

Where *N*ci, *N*ni, *N*pi, and *N*npi refer to the sample sizes of control, nitrogen, phosphorus, and nitrogen+phosphorus treatments, respectively. *S*ci, *S*ni, *S*pi, and *S*npi refer to the sample sizes of control, nitrogen, phosphorus, and nitrogen+phosphorus treatments, respectively, for each observation. In (6), *J*int\_i refers to a correction term for small sample size bias, calculated as:

(6)

We determined the weighted interaction effect size () of each trait across experiments as:

(7)

Where *d*NPi is the interaction effect size of observation *i* given in (6), *w*dnpi is the associated weight of each interaction effect size, and *k* represents the total number of observations. *w*dnpi was calculated as the inverse of the variance (*vd*NPi) of observation *i* (that is, *w*dnpi = 1 / *vd*NPi). *vd*NPi was calculated as:

(8)

*Data analysis*

We constructed a series of mixed-effects meta-regression models to understand the individual and interactive effects of nitrogen and phosphorus addition on leaf and whole-plant traits. Three separate models were created for each trait to assess the individual effects of nitrogen, phosphorus, and nitrogen+phosphorus addition using log-response ratios and their associated variances. We created a fourth model for each trait to assess the interactive effect of nitrogen and phosphorus addition using *d*NPi values and their associated variances and weights. We also assessed the role of climate or species identity moderated the response of each trait to nitrogen, phosphorus, or nitrogen+phosphorus addition by including *T*g, *MI*g, *PAR*g, photosynthetic pathway (C3, C4), N2-fixation ability (N2-fixer, non-fixer), and mycorrhizal nutrient acquisition strategy (mining, scavenging) as moderator variables. We also assessed the role of climate and species identity on the interaction effect size of each trait. In all cases, we built mixed-effects meta-regression models using the ‘rma.mv’ function in the ‘metafor’ R package (Viechtbauer, 2010), manually specifying the weights of each observation as explained above, fitting each model using restricted maximum likelihood estimation, and including experiment as a random intercept term. We used the ‘orchaRd’ R package to assess and visualize moderator effects (Nakagawa *et al.*, 2023). We could not assess the role of climate in modifying leaf photosynthetic traits, as there was not enough data collected from field experiments to test patterns with confidence.

Interactions between nitrogen and phosphorus addition on leaf and whole-plant traits were classified into three categories: additive, synergistic, and antagonistic interactions. Null interaction effects (i.e. the 95% confidence intervals overlapped with zero) were classified as additive interactions, where the combined effect of nitrogen and phosphorus addition had similar effects as the sum of the individual effects of nitrogen and phosphorus addition. An interaction was classified as synergistic (i.e. the combined effect of nitrogen and phosphorus addition was *stronger* than predicted through individual effects) if positive individual effects of nitrogen and phosphorus addition corresponded with a significant positive interaction effect, if negative individual effects of nitrogen and phosphorus addition correspond with a significant negative interaction effect, or if mixed sign individual effects (e.g., one positive and one negative effect) corresponded with a significant negative interaction effect. An interaction was classified as antagonistic (that is, the combined effect of nitrogen and phosphorus addition was *weaker* than predicted through individual effects) if positive individual effects of nitrogen and phosphorus addition corresponded with a significant negative interaction effect, if negative individual effects of nitrogen and phosphorus addition corresponded with a significant positive interaction effect, or if mixed sign individual effects corresponded with a significant positive interaction effect.

All plots and statistics were completed using R version 4.4.2 (R Core Team, 2021). Plots visualize individual and interaction effects for each response variable as the percentage change between control and treatment groups, calculated as .

**Table 1** Summary of traits and their associated description, trait scale, and trait units

|  |  |  |  |
| --- | --- | --- | --- |
| Trait | Description | Trait type | Units |
| *M*area | leaf dry biomass per unit leaf area | leaf structure, morphology | g m-2 |
| *N*mass | leaf nitrogen content per unit leaf biomass | leaf chemistry | gN g-1 |
| *N*area | leaf nitrogen content per unit leaf area | leaf chemistry | gN m-2 |
| *P*mass | leaf phosphorus content per unit leaf biomass | leaf chemistry | gP g-1 |
| *P*area | leaf phosphorus content per unit leaf area | leaf chemistry | gP m-2 |
| Leaf N:P | ratio of leaf nitrogen content (*N*mass) to leaf phosphorus content (*P*mass) | leaf chemistry | unitless |
| *A*sat | light-saturated net photosynthesis rate | leaf photosynthesis | μmol m-2 s-1 |
| *V*cmax | maximum rate of Rubisco carboxylation | leaf photosynthesis | μmol m-2 s-1 |
| *J*max | maximum rate of electron transport for RuBP regeneration | leaf photosynthesis | μmol m-2 s-1 |
| *PNUE* | photosynthetic nitrogen-use efficiency (*A*sat/*N*area) | resource use efficiency | μmol gN-1 s-1 |
| *PPUE* | photosynthetic phosphorus use efficiency (*A*sat/*P*area) | resource use efficiency | μmol gP-1 s-1 |
| Total biomass | total biomass | biomass production | g (or g m-2) |
| AGB | aboveground biomass | biomass production | g (or g m-2) |
| BGB | belowground biomass | biomass production | g (or g m-2) |
| RMF | root mass fraction | biomass partitioning | unitless |
| Root:shoot | ratio of root biomass to shoot (aboveground) biomass | biomass partitioning | unitless |

**Results**

*Nitrogen addition*

Nitrogen addition increased *N*mass and *N*area by 13.2% and 13.4%, respectively, but decreased *M*area by 3.6% and *P*mass by 7.2% and had no effect on *P*area, leading to a 15.1% increase in the leaf N:P ratio (Table S2; Fig. 1a). Photosynthetic traits were not modified by nitrogen addition (Table S3; Fig 1b). However, nitrogen addition increased aboveground biomass by 38.5% without affecting belowground biomass, leading to a 14.6% decrease in the root mass fraction and 28.9% decrease root:shoot ratio (Table S4; Fig. 1c).

Individual effects of nitrogen addition were modified by climate. The positive effects of nitrogen addition on *N*mass, *N*area, and leaf N:P diminished with increasing growing season temperature (Table S5; Fig. 2a). Warmer temperatures were also associated with a reduction in the response ratio that explained the effect of nitrogen addition on total biomass despite no general nitrogen addition effect on total biomass (Table S6). Increasing growing season moisture index diminished the positive effect of nitrogen addition on *N*mass and marginally diminished the positive effects of nitrogen addition on *N*area and leaf N:P (Table S5; Fig. 2b). Finally, increased growing season light availability was also associated with an increase in the response ratio that explained the effect of nitrogen addition on *P*area despite no general nitrogen addition effect on *P*area across the climatic gradient (Table S5). Greater light availability also weakened the negative effect of nitrogen addition on the root mass fraction (Table S6).

Species identity modified some responses to nitrogen addition. Positive *N*mass, leaf N:P, and negative *M*area responses to nitrogen addition were only observed in species that could not associate with N2-fixing bacteria (Table S7; Fig. 2c). Nitrogen addition increased *A*sat in species that could form associations with N2-fixing bacteria despite no general nitrogen addition effect (Table S8). Positive *N*area and leaf N:P responses to nitrogen addition were also generally stronger in species with scavenging acquisition strategies, while negative *P*mass and *M*area responses to nitrogen addition were stronger in species with mining acquisition strategies (Table S9; Fig. 2d). While photosynthetic traits were modified by mycorrhizal acquisition strategy, no trait within each strategy demonstrated a significant nitrogen addition effect (Table S10; Fig. 2e). Finally, positive *N*mass responses and negative *M*area responses to nitrogen addition were strongest in C4 species, while positive *N*area responses were strongest in C3 species (Table S11; Fig. 2f). Nitrogen addition increased *PNUE* in C4 species only (Table S12).

*Phosphorus addition*

Phosphorus addition increased *P*mass and *P*area by 56.7 and 71.2%, respectively, with no effect on *M*area, *N*mass, or *N*area (Table S2; Fig 2d). These patterns reduced the leaf N:P ratio by 29.1% (Table S2; Fig. 1d). Phosphorus addition increased *J*max by 19.4%, but there was no apparent effect detected for any other photosynthetic trait (Table S3; Fig 1d). Phosphorus addition increased aboveground biomass by 21.1% without affecting belowground biomass, yielding a 16.8% increase in total biomass and 20.3% reduction in the root:shoot ratio (Table S4; Fig. 1f).

Climate shaped several trait responses to phosphorus addition. Increasing growing season temperature diminished the positive *P*mass and *P*area responses and negative leaf N:P response to phosphorus addition (Fig. 2f; Table S5). Warmer temperatures slightly diminished the positive total biomass response to phosphorus addition (Table S6). Increasing growing season moisture index marginally weakened the positive *P*mass and negative leaf N:P response to phosphorus addition (Fig. 2g; Table S5). Increasing growing season moisture index strengthened the negative root mass fraction response and increased the response of *M*area to phosphorus addition despite no general phosphorus addition effect on *M*area across the environmental gradient (Table S5-S6).

Species identity also modified some plant responses to phosphorus addition. Positive *P*mass, *P*area, and *J*max responses to phosphorus addition were stronger in species that could associate with N2-fixing bacteria, while negative *M*area responses to phosphorus addition were only observed in species that could associate with N2-fixing bacteria (Fig. 2h; Table S7-S8). Species that could associate with N2-fixing bacteria also demonstrated a positive *N*mass response and *PNUE* to phosphorus addition despite no general phosphorus addition effect (Table S7-S8), while species that could not associate with N2-fixing bacteria demonstrated a positive *V*cmax and *J*max response to phosphorus addition despite no general phosphorus addition effect (Table S8). Positive *P*mass and *P*area responses and negative leaf N:P responses to phosphorus addition were strongest in species with mining acquisition strategies (Table S9; Fig. 2i). Species with mining strategies also demonstrated a decrease in *PPUE* in response to phosphorus addition despite no general phosphorus addition effect (Table S10). Finally, positive *P*mass responses to phosphorus addition were only observed in C3 species, with no effect of photosynthetic pathway detected for any other trait response (Table S11-12; Fig. 2j).

*Nitrogen + phosphorus addition*

Nitrogen+phosphorus addition increased *N*mass, *N*area, *P*mass, and *P*area by 12.5%, 16.6%, 44.1%, and 47.6%, respectively, and decreased *M*area by 5.1% (Table S2; Fig. 1g). These responses reduced leaf N:P by 18.3% (Table S2; Fig. 1g). Among photosynthetic traits, nitrogen+ phosphorus addition increased *A*sat by 27.9% through a stronger increase in *J*max (29.9% increase) than *V*cmax (marginal 17.9% increase; Table S3; Fig. 1h). Nitrogen+ phosphorus addition also increased total biomass by 46.1% through an 87.2% increase in aboveground biomass and no change in belowground biomass, reducing the root mass fraction by 13.7% and the root:shoot ratio by 33% (Table S4; Fig. 1i).

Climate shaped some responses to nitrogen+phosphorus addition. Increasing growing season temperature diminished the positive *N*mass and *P*mass responses to nitrogen+ phosphorus addition, with positive total biomass responses marginally diminishing (Table S5-S6). Growing season moisture index had no effect on trait responses to nitrogen+phosphorus addition except for *M*area, where negative *M*area responses to nitrogen+phosphorus addition diminished with increasing moisture index (Table S5). Positive *P*mass and *P*area responses to nitrogen+phosphorus addition strengthened with increasing growing season light availability (Table S6). Greater light availability also increased the response of belowground biomass to nitrogen+phosphorus addition despite a null belowground biomass response across the climatic gradient (Table S6).

Species identity modified some plant responses to nitrogen+phosphorus addition. Positive *N*mass, *A*sat, *V*cmax, and *J*max responses to nitrogen+phosphorus addition were only observed in species that could not associate with N2-fixing bacteria, while positive *P*mass responses were only observed in species that could associate with N2-fixing bacteria (Table S7-S8). Negative leaf N:P responses to nitrogen+phosphorus addition were stronger in species that could associate with N2-fixing bacteria, while negative *M*area responses were only observed in species that could not associate with N2-fixing bacteria (Table S7). Positive *P*mass, *A*sat, *V*cmax, and *J*max responses to nitrogen+phosphorus addition were stronger in species with scavenging acquisition strategies, negative *M*area and leaf N:P responses were stronger in species with mining acquisition strategies (Table S9-S10). Finally, positive *N*mass and negative *M*area responses to nitrogen+ phosphorus addition were stronger in C4 species, while positive *N*area and *P*arearesponses were stronger in C3 species, with no apparent effect of photosynthetic pathway on leaf N:P or any photosynthetic trait (Table S11-S12).

**Figure 1**

A collage of graphs and diagrams

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**Figure 1**. Individual effects of nitrogen addition (top row of panels), phosphorus addition (middle row of panels), and nitrogen+phosphorus addition (bottom row of panels) on traits related to leaf nutrient content (left column of panels), leaf photosynthesis (middle column of panels), and biomass partitioning (right column of panels). Large points indicate the meta-analytic mean (represented as % change, calculated as), error bars indicate 95% confidence intervals, and sample sizes are reported in parentheses. Significant treatment effects are noted with asterisks next to sample sizes (based on *Z*-score; \*: *p*<0.05, \*\*: *p*<0.01; \*\*\*: *p*<0.001). All acronyms are as explained in Table 1.

**Figure 2**

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**Figure 2** Effects of growing season climate and species identity on mass-based leaf nitrogen responses to nitrogen addition (top row of panels) and leaf phosphorus responses to phosphorus addition (bottom row of panels). From left to right, the top row of panels describes the growing season temperature (a), growing season moisture index (b), ability to associate with nitrogen fixing bacteria (c), mycorrhizal nutrient acquisition strategy (d), and photosynthetic pathway effect on the leaf nitrogen content response to nitrogen addition. The bottom row of panels describes the growing season temperature (f), growing season moisture index (g), ability to associate with nitrogen fixing bacteria (h), mycorrhizal nutrient acquisition strategy (i), and photosynthetic pathway (j) effect on the leaf phosphorus content response to phosphorus addition. For climate moderator plots, grey points indicate individual data points. Solid trendlines are drawn if climate significantly modified leaf nutrient responses to nutrient addition (*p*<0.05) and dashed trendlines are drawn if climate marginally modified leaf nutrient responses to nutrient addition (*p*<0.1). For species identity traits, large points indicate the meta-analytic mean (represented as % change, calculated as ) and error bars indicate 95% confidence intervals, with significant pairwise differences noted with asterisks above brackets (based on *Z*-score; \*: *p*<0.05, \*\*: *p*<0.01; \*\*\*: *p*<0.001).

*Interaction effects*

There was no interaction effect detected for *M*area, *N*mass, *N*area, *P*area, *A*sat, *V*cmax, *J*max, *PNUE*, *PPUE*, total biomass, belowground biomass, root mass fraction, or the root:shoot ratio (Table S13; Fig. 3a-c). These additive responses indicate that the nitrogen+phosphorus addition effect was no different than the sum of the individual nitrogen and phosphorus effects. However, there was a significantly negative interaction effect for leaf N:P, a significantly positive interaction effect for aboveground biomass, and a marginal negative interaction effect for leaf *P*mass (Table S13; Fig. 3a, 3c). We expected a 14% reduction in leaf N:P (leaf N:P increased by 15.1% with nitrogen addition and decreased by 29.1% with phosphorus addition), a 59.5% increase in aboveground biomass (aboveground biomass increased by 38.5% with nitrogen addition and by 21.0% with phosphorus addition), and a 49.5% increase in *P*mass (*P*mass decreased by 7.2% with nitrogen addition and increased by 56.7% with phosphorus addition) if responses to nitrogen+phosphorus addition were driven by additive interactions. However, nitrogen+ phosphorus addition decreased leaf N:P by 18.3%, increased aboveground biomass by 87.2%, and increased *P*mass by 44.2% (Table SX). These responses indicate a stronger negative effect of nitrogen+phosphorus addition on leaf N:P and a stronger positive effect of nitrogen+phosphorus addition on aboveground biomass than the sum of individual nitrogen and phosphorus effects, highlighting a synergistic interaction. For *P*mass, these results indicate a marginally weaker positive effect of nitrogen+ phosphorus addition than the sum of individual nitrogen and phosphorus effects, highlighting an antagonistic interaction.

Climate influenced interaction effects for the two traits that demonstrated synergistic responses to nitrogen and phosphorus addition. For leaf N:P, the negative interaction effect became less negative with increasing growing season temperature but more negative with increasing light availability (Table S14; Fig. 4a-b). This pattern indicates that cooler temperatures and greater light availability increased the magnitude of the synergistic response of leaf N:P to nitrogen and phosphorus addition. The positive interaction effect for aboveground biomass became less positive with increasing growing season temperature and moisture index, suggesting that warmer and wetter conditions dampened the synergistic aboveground biomass response to nitrogen and phosphorus addition (Table S14; Fig. 4c-d).

Species identity played a limited role in shaping the interactive effects of nitrogen and phosphorus addition on plant traits. Ability to associate with N2-fixing bacteria did not modify effect sizes for any trait (Table S15). The synergistic response of *P*mass and leaf N:P were marginally stronger for species with mining strategies compared to those with scavenging strategies (Table S16). Although *M*area and *N*massresponses to nitrogen and phosphorus addition were additive, species with mining strategies exhibited significantly negative interaction effects that were indicative of a synergistic response for *M*area and an antagonistic response for *N*mass (Table S16). Photosynthetic pathway did not modify interaction effects of any trait (Table S17).

**Figure 3**

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**Figure 3**. Interaction effects of nitrogen and phosphorus addition on traits related to leaf nutrient content (a), leaf photosynthesis (b), and biomass partitioning (c). Large points indicate the meta-analytic mean (represented as % change, calculated as ), error bars indicate 95% confidence intervals, and sample sizes are reported in parentheses. Black colored points indicate additive interactions while blue colored points indicate synergistic interactions. The light red colored point for *P*mass indicates a marginally significant antagonistic interaction. Significant interaction effects are also noted with asterisks next to sample sizes (based on *Z*-score; \*: *p*<0.05). All acronyms are as explained in Table 1.

**Figure 4**

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**Figure 4** Effects of growing season climate on interaction effect sizes of leaf N:P and aboveground biomass. The top row of panels describes the effects of growing season temperature (a) and growing season light availability (b) on the interaction effect size for leaf N:P. The bottom row of panels describes the effects of growing season temperature (c) and growing season moisture index (d) on the interaction effect size for aboveground biomass. Black points indicate individual data points, represented as % change (calculated as ). Solid trendlines and 95% confidence intervals are drawn if climate significantly modified a given interaction effect size (*p*<0.05).

**Discussion**

*Nutrient addition alters leaf chemistry, leaf stoichiometry, and whole-plant traits more strongly than photosynthetic traits*

Consistent with our first hypothesis, nitrogen addition and phosphorus addition primarily increased leaf nutrient content and biomass production, with limited effects on leaf-level photosynthetic traits. Nitrogen addition increased *N*mass and *N*area, decreased *P*mass, and increased leaf N:P, but did not change *A*sat, *V*cmax, or *J*max. Similarly, phosphorus addition increased *P*mass and *P*area and reduced leaf N:P, but these patterns corresponded with a weak increase in *J*max and no change in *A*sat or *V*cmax. At the whole-plant level, both nitrogen and phosphorus addition increased aboveground biomass and did not change belowground biomass, decreasing the root:shoot ratio. These results support previous work showing weak or absent fertilization effects on photosynthetic traits despite strong effects on leaf nutrient content and biomass production (Reich *et al.*, 2009; Liang *et al.*, 2020; Yu *et al.*, 2022; Waring *et al.*, 2023; Perkowski *et al.*, 2025b,a; Stocker *et al.*, 2025). They also challenge model formulations that predict photosynthetic capacity from leaf nitrogen and phosphorus content and build on work suggesting that models using fixed leaf nutrient-photosynthesis relationships may risk overestimating leaf-level photosynthesis and, by extension, primary productivity and the land carbon sink (Rogers, 2014; Achat *et al.*, 2016; Rogers *et al.*, 2017; Smith *et al.*, 2019; Harrison *et al.*, 2021; Stocker *et al.*, 2025).

Mechanistically, stronger leaf nutrient than photosynthetic responses to nutrient additions imply that additional nitrogen and phosphorus were allocated to non-photosynthetic pools, decreasing the fractional pool allocated to photosynthesis. For nitrogen addition, this pattern is consistent with previous work (Waring *et al.*, 2023; Perkowski *et al.*, 2025a). For phosphorus addition, these patterns indicate a similar pathway where phosphorus allocation to non-metabolic pools increases in response to phosphorus addition. While the slight increase in *J*max suggests that phosphorus addition may have increased the metabolic phosphorus pool, recent work along a phosphorus availability gradient showed much stronger increases in orthophosphate, lipid, nucleic acid, and residual phosphorus pools than the metabolic pool with increasing phosphorus availability (Dong *et al.*, 2025). This result implies that the relative fraction of leaf phosphorus content allocated to metabolism may still decline even as its absolute amount increases. We attempted to quantify the effects of phosphorus addition on leaf phosphorus fractionation pools; however, a paucity of leaf phosphorus fractionation data collected from full-factorial nitrogen-by-phosphorus experiments precludes any robust conclusions.

Whole-plant responses to nutrient addition were also stronger than photosynthetic responses. This response follows patterns expected from eco-evolutionary optimality theory, where investment in leaf-level photosynthesis is expected to be more strongly determined through climatic factors (e.g., light, temperature, atmospheric CO2 concentration, vapor pressure deficit) that alter demand to build and maintain photosynthetic enzymes than soil nutrient availability (Maire *et al.*, 2015; Smith *et al.*, 2019; Paillassa *et al.*, 2020; Harrison *et al.*, 2021; Peng *et al.*, 2021; Dong *et al.*, 2022; Westerband *et al.*, 2023; Stocker *et al.*, 2025). Eco-evolutionary optimality theory posits that plants should prioritize nutrient allocation toward leaf production as a strategy for maximizing biomass production in environments where nutrient availability is sufficient for satisfying leaf-level photosynthetic demand (Liang *et al.*, 2020; Stocker *et al.*, 2025; Perkowski *et al.*, 2025a). In contrast, the theory suggests that plants should prioritize investment in leaf-level photosynthesis in environments where nutrient availability is insufficient for satisfying photosynthetic demand. Thus, when nutrients are added, the theory predicts stronger increases in photosynthesis than biomass production in nutrient-limited systems and stronger increases in biomass production than photosynthesis in nutrient-rich environments (Waring *et al.*, 2023; Perkowski *et al.*, 2025a). Here, the stronger response of biomass production to nutrient addition implies that background soil nutrient availability across experiments was, on average, sufficient for satisfying leaf-level photosynthetic demand. Furthermore, these responses indicate that leaf quantity-quality tradeoffs persist at the global scale, both for nitrogen and phosphorus, a result that is directly relevant for incorporating eco-evolutionary optimality (Harrison *et al.*, 2021; Smith *et al.*, 2024; Ren *et al.*, 2025) and phosphorus cycles (Allen *et al.*, 2020; Braghiere *et al.*, 2022) into terrestrial biosphere models.

*Plant responses to nitrogen and phosphorus addition are mostly additive*

Supporting our second hypothesis, responses to nitrogen+phosphorus addition were additive for all traits except for leaf N:P and aboveground biomass. Additivity indicates that nitrogen+ phosphorus effects did not differ from the sum of the single-nutrient effects, consistent with prior evidence that plant responses to multiple environmental changes are often additive (Yue *et al.*, 2017; Fang *et al.*, 2024; Ding *et al.*, 2025). In the context of nitrogen and phosphorus enrichment, additivity is expected if each nutrient contributes to a distinct and largely independent process. For example, nitrogen supports the construction and maintenance of photosynthetic enzymes (e.g., Rubisco) while phosphorus supports energy transfer reactions and RuBP regeneration in the Calvin-Benson cycle, implying that additive responses may be expected for traits related to leaf-level photosynthesis. Indeed, most leaf nutrient and photosynthetic traits exhibited additive response to nitrogen+phosphorus addition. However, it is difficult to distinguish whether these additive responses were driven by nutrient treatments or if this additivity reflects climate-related demand for photosynthetic enzymes given the largely null effects of nutrient addition on photosynthetic traits. Regardless, additive leaf-level responses imply that nitrogen+phosphorus addition does not further modify leaf nutrient-photosynthesis relationships beyond single-nutrient effects, indicating an important constraint for models that integrate nitrogen and phosphorus controls on photosynthetic capacity.

Leaf N:P demonstrated a synergistic negative response to nitrogen+phosphorus addition, where leaf N:P decreased more strongly in response to nitrogen+phosphorus addition than the sum of the single-nutrient effects. This synergistic response was likely due to an additive response of *N*mass coupled with a slight antagonistic response of *P*mass, where weaker-than-expected increases in *P*mass due to nitrogen+phosphorus addition created a stronger-than-expected decline in leaf N:P. Given that leaf N:P is often used to indicate whether ecosystems are nitrogen- or phosphorus-limited (Koerselman & Meuleman, 1996; Tessier & Raynal, 2003; Güsewell, 2004; Braghiere *et al.*, 2022; Wang *et al.*, 2025), it is important that models capture these synergistic responses to maintain model realism and avoid misdiagnosing the nutrient limiting ecosystem primary productivity. Moreover, these patterns highlight the benefit of incorporating flexible leaf stoichiometry in models, as models with fixed leaf stoichiometry would not capture the responses observed here (Sistla & Schimel, 2012; Zhu et al., 2020; Hauser et al., 2023).

Aboveground biomass also exhibited a positive synergistic response to nitrogen+ phosphorus addition, demonstrating stronger effect of nitrogen+phosphorus addition than predicted through the sum of the individual nitrogen and phosphorus effects. This pattern contrasts our second hypothesis but supports previous syntheses demonstrating strong nitrogen-phosphorus colimitation of shoot production (Elser *et al.*, 2007; Harpole *et al.*, 2011; Fay *et al.*, 2015; Cleland *et al.*, 2019; Keller *et al.*, 2023; Fang *et al.*, 2024). By contrast, belowground biomass responded additively to nitrogen+phosphorus addition, suggesting that the synergistic aboveground biomass response was likely achieved through an increase in plant nutrient uptake that stemmed either from an increase in per-root nutrient uptake or investment in less costly nutrient uptake strategies that enhanced nutrient uptake efficiency (Rastetter *et al.*, 2001; Perkowski *et al.*, 2025a). Stronger than expected aboveground biomass responses to nitrogen+phosphorus addition coupled with null nutrient addition effects on belowground biomass should logically lead to synergistic root mass fraction and root:shoot ratio responses. However, biomass partitioning traits responded additively to nitrogen+phosphorus addition. This could be due to a lower number of observations for biomass partitioning traits (n = 37, 40 observations for root mass fraction and root:shoot ratio, respectively) as aboveground biomass (n = 125 observations) and belowground biomass (n = 60 observations) or could be due to observations coming from different experiments as those for aboveground and belowground biomass. Future work should consider revisiting these patterns by collecting biomass and biomass partitioning observations from the same subset of experiments.

*Plant responses to nutrient additions are mediated through climatic demand*

Supporting our third hypothesis, leaf nutrient responses to nutrient addition were strongest where climatic demand for soil resources was the greatest. Positive *N*mass, *N*area, and leaf N:P responses to nitrogen addition strengthened as the growing season temperature and moisture index decreased. Similarly, positive *P*mass and *P*area responses and negative leaf N:P responses to phosphorus addition strengthened as the growing season temperature and moisture index decreased. Theory predicts that plants growing in dry environments increase nutrient investment to photosynthetic capacity in dry environments as a strategy for maintaining net carbon assimilation at reduced stomatal conductance, increasing leaf nutrient allocation to support increasing leaf-level demand for to build and maintain photosynthetic enzymes (Wright *et al.*, 2003; Prentice *et al.*, 2014). Similarly, slower enzyme kinetics in colder environments require additional photosynthetic enzymes to sustain a given photosynthesis rate, increasing leaf nutrient allocation to support increased leaf-level demand to build and maintain photosynthetic enzymes (Ali *et al.*, 2015; Scafaro *et al.*, 2017; Peng *et al.*, 2021). In environments where demand to build and maintain photosynthetic enzymes is increased (e.g., colder, drier environments), it is expected that an increase in soil nutrient availability should yield a stronger positive effect on photosynthetic traits, leading to stronger leaf nutrient content responses. Indeed, previous work demonstrates stronger leaf nitrogen responses to nitrogen addition in cold, dry environments (Cheaib *et al.*, 2025b), but this pattern has not been explicitly evaluated for leaf phosphorus responses to phosphorus addition. Complementary leaf nutrient content responses indicate that nitrogen and phosphorus investment in photosynthesis is driven by climate-related demand to build and maintain photosynthetic enzymes, a pattern that has not been previously shown.

Climate significantly modified the two traits that demonstrated a synergistic response to nitrogen+phosphorus addition. In both cases, synergistic leaf N:P and aboveground biomass responses were strongest in regions with greater demand for soil resources. Specifically, the synergistic response of leaf N:P to nitrogen+phosphorus addition was strongest in colder, lighter environments, while the synergistic response of aboveground biomass was strongest in colder, drier environments. These patterns indicate that the environment can dictate the magnitude of interactions between nitrogen and phosphorus addition, highlighting the potential for stronger nitrogen-phosphorus colimitation if environmental conditions support greater leaf and whole-plant demand for soil resources. Stronger nitrogen-phosphorus interactions in regions with greater demand for soil resources have important implications for modeling, as failure to account for these dynamics could lead to underestimated gross primary productivity and land carbon sink projections.

Importantly, most full-factorial experiments that quantified leaf photosynthetic traits were conducted through either greenhouse or growth chamber conditions. This meant that we could not diagnose the role of climate in

*Plant responses to nutrient additions are mediated through species identity traits*

Species identity traits also modified plant trait responses to nitrogen and phosphorus addition. Supporting our fourth hypothesis, plants with the ability to associate with N2-fixing bacteria exhibited dampened responses to nitrogen addition than plants without this ability. These findings support previous work noting stronger plant responses to soil nitrogen availability in non-fixing species compared to N2-fixing species (Adams *et al.*, 2016; Dong *et al.*, 2017; Bytnerowicz *et al.*, 2023; Cheaib *et al.*, 2025b; Perkowski *et al.*, 2025a). C4 species often exhibited stronger responses to nutrient addition than C3 species, perhaps due to greater demand associated with needing to construct additional photosynthetic enzymes such as PEP carboxylase (Valeria & Santiago, 2011). Finally, plants which associated with mycorrhizal fungi that adopt scavenging strategies exhibited stronger trait responses to nutrient addition compared to those that associated with mining strategies, also supporting previous work (Cheaib *et al.*, 2025a). Altogether, these findings indicate that plants who rely more strongly on soil-derived plant-available nutrients and have greater background demand to build and maintain photosynthetic enzymes often exhibit stronger trait responses to nutrient additions.

*Modeling implications*

Recent work has emphasized the role of eco-evolutionary optimality theory for driving photosynthetic trait variation across spatiotemporal scales. The theory calls the use of leaf nutrient-photosynthetic relationships into question, instead positing that photosynthetic investment is the product of demand to build and maintain photosynthetic enzymes as driven by climate and the supply of resources available to satisfy this demand. Our work supports this premise, . However, field experiments that quantify photosynthetic trait responses to full-factorial nitrogen and phosphorus addition combinations are needed to verify this statement. Regardless, studies highlight

*Future research needs and directions*

Unfortunately, we could not investigate the role of climate in modulating photosynthetic responses to nitrogen and phosphorus addition. This constraint was due to the limited number of full-factorial nitrogen and phosphorus experiments that are conducted in the field and measured photosynthetic traits relevant to this study. The paucity of such experiments represents a clear area of needed research and key knowledge gap that remains in our understanding of how photosynthetic processes respond to nutrient additions. Previous work has shown that climatic factors which influence demand play a predictable and key role in determining leaf nitrogen allocation responses to nitrogen and phosphorus addition (Cheaib *et al.*, 2025b). Our work supports these findings by showing that leaf nutrient allocation responses to nitrogen and phosphorus addition are dependent on climate and associated demands for soil resources. However, similar field analyses that scale these patterns to photosynthetic traits have not been conducted. Quantifying these responses is particularly important, as recent work has highlighted that the fraction of leaf nutrients (nitrogen in this case) allocated to photosynthetic tissues decrease in response to increasing nitrogen availability and are dependent on climate-related demand for soil resources

(Waring et al., 2023; Cheaib et al., 2025; Perkowski et al., 2025). Without field experiments that quantify leaf photosynthetic responses to nutrient treatments, we unable to comment on whether these responses scale with leaf nutrient allocation responses in ways that are predicted through eco-evolutionary optimality.

*Conclusions*

Our findings are consistent with previous work showing limited impacts of nutrient addition on leaf-level photosynthesis (Liang *et al.*, 2020; Waring *et al.*, 2023; Stocker *et al.*, 2025), stronger plant responses in regions with high climatic demand for soil resources (Cheaib *et al.*, 2025b) and responses to nutrient addition that are context dependent on photosynthetic pathway (Liang *et al.*, 2020) and acquisition strategy (Perkowski *et al.*, 2021, 2025a; Cheaib *et al.*, 2025a). These results build on previous work by identifying traits that demonstrate synergistic responses to nitrogen and phosphorus addition and show that interactions between nitrogen and phosphorus addition are modified by climatic demand and species identity. Collectively, these findings provide the groundwork for mechanistic frameworks that could be used to incorporate more realistic C-N-P cycle interactions in terrestrial biosphere models.

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