Leaf habit drives leaf nutrient resorption globally alongside nutrient availability and climate

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Abstract

Nutrient resorption from senescing leaves can significantly affect ecosystem nutrient cycling, making it an essential process to better understand long-term plant productivity under environmental change that affects the balance between nutrient availability and demand. Although it is known that nutrient resorption rates vary strongly between different species and across environmental gradients, the underlying driving factors are insufficiently quantified. Here, we present an analysis of globally distributed observations of leaf nutrient resorption to investigate the factors driving resorption efficiencies for nitrogen (NRE) and phosphorus (PRE). Our results show that leaf structure and habit, together with indicators of nutrient availability, are the two most important factors driving spatial variation in NRE. Overall, we found higher NRE in deciduous plants (65.2% ± 12.4%, n=400) than in evergreen plants (57.9% ± 11.4%, n=551), likely associated with a higher share of metabolic N in leaves of deciduous plants. Tropical regions show the lowest resorption for N (NRE: 52.4% ± 12.1%) and tundra ecosystems in polar regions show the highest (NRE: 69.6% ± 12.8%), while the PRE is lowest in temperate regions (57.8% ± 13.6%) and highest in boreal regions (67.3% ± 13.6%). Soil clay content, N and P atmospheric deposition - globally available proxies for soil fertility - and MAP played an important role in this pattern. The statistical relationships developed in this analysis indicate an important role of leaf habit and type for nutrient cycling and guide improved representations of plant-internal nutrient re-cycling and nutrient conservation strategies in vegetation models.

Keywords: Leaf nutrient content; Leaf structure; Nitrogen and phosphorus resorption efficiency; Plant ecophysiology; Plant functional traits; Plant nutrient limitation.

1. Introduction

Nutrient cycling plays an important role in shaping the global distribution of terrestrial primary productivity (Le Bauer et al., 2008; Zaehle, 2013; Du et al., 2020). Nitrogen (N) and phosphorus (P) are the main limiting nutrients for plant growth. N is needed to maintain and produce essential proteins for the biosynthesis; while P is an element of genetic material and plays a major role in the regeneration of the main receptor of carbon (C) assimilation, and in the production of energy that conducts many processes in living cells (Chapin, 1980; Güsewell, 2004). The anthropogenic increase in atmospheric CO_2 since the beginning of industrialization has the potential to enhance the terrestrial carbon sink through increasing plant photosynthetic rates, a process known as CO_2 fertilization (Bazzaz, 1990). A potential limitation to the fertilization effect is progressive nutrient limitation to growth (Luo et al., 2004) and associated plant strategies to deal with such limitations. Thus, understanding the ways in which nutrients circulate in ecosystems and are acquired, lost, and conserved by plants, is essential for simulating plant response to global changes.

Nutrient resorption - defined here as the translocation of nutrients from senescing leaves to temporary storage tissues - is a plant strategy for nutrient conservation (Killingbeck, 1996; Kobe et al., 2005). It allows plants to directly reuse nutrients, decreasing the dependence on soil nutrient availability and the competition for these nutrients with other plants and microbes, especially in nutrient-limited environments (Aerts, 1996; Aerts and Chapin, 1999). The question that arises is then why do plants not all resorb the entirety of leaf nutrients for being more efficient? The fact that they do not achieve their maximum resorption capacity implies the existence of costs and limitations to resorption. A quantitative understanding of nutrient resorption can yield insights into plant strategies to cope with nutrient limitation (Aerts and Chapin, 1999; Chapin et al., 2011). This is because the resorption process influences most other ecosystem processes that determine plant growth, as it directly affects litter quality and therefore soil organic matter decomposition and has indirect consequences for plant nutrient uptake, carbon cycling and finally plant competition (Killingbeck, 1996; Berg and McClaugherty, 2008). The average fraction of leaf nutrients resorbed before abscission is estimated to be ~62% for N and ~65% for P (Vergutz et al., 2013). Cleveland et al. (2013)

70 estimated that this corresponds to 31% of a plant's annual demand for N and 40% of the annual

71 demand for P, but with large geographical and species variations.

72 However, despite advances in recent years, the drivers behind nutrient resorption and its

73 variation are still unclear: First, soil fertility has long been assumed to be a key driver for

74 variations in nutrient resorption, with increased resorption in infertile soils as the plant's main

75 strategy for nutrient conservation (Aerts and Chapin, 1999). This interpretation has also

76 provided a basis for modeling dynamic resorption efficiency by accounting for nutrient

77 availability in global vegetation models (Fisher et al., 2010; Lawrence et al., 2019).

78 Nonetheless, there is diverging evidence established at different geographic scales, showing

79 positive correlations (Aerts and Chapin, 1999), negative correlations (Yuan and Chen, 2015;

80 Xu et al., 2021), and even a lack of correlation between soil fertility and resorption efficiency

81 (Vergutz et al., 2013). Second, climate factors are also considered to be important drivers for

82 resorption, but the evidence is equally conflicting: On the one hand, Yuan and Chen (2009)

83 and Yan et al. (2017) suggested NRE is decreasing with mean annual temperature (MAT) and

84 precipitation (MAP), with the opposite trend for PRE, arguing that colder regions tend to be

85 more N-limited, while P-limitation is observed more commonly in warmer environments. From

86 low to high latitudes globally, the role of N in limiting productivity tends to increase as the

87 availability of N is mainly determined by temperature-limited processes such as biological N

88 fixation and mineralization of soil organic matter (Cleveland et al., 2013; Fay et al., 2015; Deng

89 et al., 2018), but the presence of N fixers in tropical forests introduces complexity to the pattern

90 of nutrient limitation between tropical and temperate zones (Hedin et al., 2009). Nevertheless,

91 the limited availability of P in the tropics due to highly weathered soils distinguishes low- to

92 mid-latitude environments (Elser et al., 2007). On the other hand, Vergutz et al. (2013) and Xu

93 et al., 2021 showed that NRE and PRE are both increasing with decreasing MAT and MAP

94 toward higher latitudes.

95 A third set of studies suggests plant functional types, leaf stoichiometry and plant nutrient

96 demand as drivers for nutrient resorption (Reed et al., 2012; Han et al., 2013; Tang et al., 2013;

97 Brant and Chen, 2015; Du et al., 2020; Chen et al., 2021a; Sun et al., 2023). When found greater

98 nutrient resorption in evergreen species, it is assumed to be a conservation strategy given their

99 comparatively low leaf nutrient content and slow growth rate and predominant occurrence in

100 nutrient-limited biomes (Killingbeck, 1996; Yan et al., 2017; Xu et al., 2021). The same

101 argument has been used for interpreting differences between broad-leaves and needle-leaves,

102 in which nutrient resorption is generally observed to be higher in needles as a strategy to
103 acclimatize and survive in resource-limited environments (Aerts and Chapin, 1999; Yuan et
104 al., 2005; Yan et al., 2017; Xu et al., 2021). Previous studies have suggested that shrub species
105 generally display higher nutrient resorption rates compared to trees, due to their smaller leaves
106 with shorter life cycles and for the need to optimize nutrient use in resource-limited
107 environments (Killingbeck, 1996; Yuan and Chen, 2009; Yan et al., 2017; Xu et al., 2021).
108 However, Brant and Chen (2015) suggest that deciduous plants are more dependent on nutrient
109 resorption as their investment in green leaf nutrients is higher to maintain their fast growth
110 through high physiological activity during the growing season. Plants with a slow growth
111 strategy, such as evergreens and needle-leaves, have lower photosynthetic nutrient use
112 efficiency due to a higher allocation of C and N to leaf structural rather than metabolic
113 compounds (Reich et al., 2017). Onoda et al. (2017) empirically supports this by showing that
114 a greater allocation of nutrients to structural compounds is associated with decreased specific
115 leaf area (SLA) and increased diffusive limitation to photosynthesis. Thus, variations in leaf
116 traits and construction costs could contribute to differences in resorption between plant
117 functional types (PFTs). Nevertheless, Drenovsky et al. (2010; 2019) suggested that resorption
118 variability is influenced by an interplay of the discussed drivers, that includes soil properties,
119 climatic conditions, and plant characteristics. Estiarte et al. (2023) support that leaf
120 biochemistry of plants determine the first limitation to nutrient resorption, with a secondary
121 regulation in resorption by environmental conditions, while the costs of leaf aging remain
122 consistent.

123 The divergence of observed patterns highlights the need for further investigation into the main
124 drivers of variations in nutrient resorption, distinguishing the influence of plant types, soil and
125 climatic conditions. In this study, we present a meta-analysis that combines the version 5.0 of
126 TRY Plant Trait database (Kattge et al., 2020) with different ancillary datasets for climate and
127 soil factors to investigate global patterns of resorption efficiencies for nitrogen (NRE) and
128 phosphorus (PRE). We aim to extend woody species observations for nutrient resorption and
129 investigate the factors that explain observed patterns along three main axes: climate, soil
130 fertility and leaf properties.

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2. Methods

2.1 Data collection

We assembled the dataset from the TRY Plant Trait database (https://www.try-db.org, Kattge et al., 2020, version 5.0) containing field measurements of paired leaf and litter mass-based tissue N and P concentrations ($N_{mass, leaf}$, $P_{mass, leaf}$, $N_{mass, litter}$, $P_{mass, litter}$) to derive the fractional nutrient resorption (described in Sect. 2.2), and plant functional traits recorded in parallel from the same species and same location to consider as biological predictors variables (Table 1). As additional predictors for nutrient resorption, we combined it with climate and soil input data (Table 2). We processed the data using R statistical software (version 4.0.4), keeping the data at species-level. To manipulate the extracted functional traits, we used the package {rtry} (Lam et al., 2022) developed to support the preprocessing of TRY Database (version 1.0.0), and {tidyverse} package (Wickham et al., 2019) with its dependencies (version 1.3.2). The data processing followed the quality control according to the published protocol of TRY (Kattge et al., 2011; 2020).

Table 1. Traits extracted from TRY database to derive nutrient resorption.

Plant traits	Variable name	Unit
$N_{mass, leaf}$	Leaf nitrogen (N) content per leaf dry mass	mg g
$P_{mass, leaf}$	Leaf phosphorus (P) content per leaf dry mass	mg g
$N_{mass, litter}$	Litter nitrogen (N) content per litter dry mass	mg g
$P_{mass, litter}$	Litter phosphorus (P) content per litter dry mass	mg g
SLA	Leaf area per leaf dry mass: petiole, rhachis and midrib excluded	$mm^2\ mg^{-1}$
SLA	Leaf area per leaf dry mass: petiole excluded	$mm^2\ mg^{-1}$
SLA	Leaf area per leaf dry mass: petiole included	$mm^2\ mg^{-1}$
SLA	Leaf area per leaf dry mass: undefined if petiole is in- or excluded	$mm^2\ mg^{-1}$
	Leaf dry mass	mg
	Leaf senescent dry mass	mg
LML	Leaf Mass Loss	unitless
PFT	Plant functional type / growth form	unitless
KGC	Köppen Climate Classification	unitless

153 As predictors, we used a set of climate variables, N and P deposition, vegetation type-related

154 variables, and soil data (Table 2) with a spatial resolution of 0.5° × 0.5° to match that of the

155 lowest resolution dataset (P deposition). Soil fertility was represented here by N and P

156 deposition and other soil characteristics that globally correlate with nutrient availability, such

157 as total soil P and soil texture. Mean annual temperature (MAT), mean annual precipitation

158 (MAP) and the seasonal temperature amplitude were derived from the global climate database

159 WorldClim (Fick and Hijmans, 2017). We extracted the Köppen climate classification to

160 represent different climate zones from the TRY database and filled data gaps using the {Kgc}

161 R package (Bryant et al., 2017), which provides the Köppen climate classification for each

162 latitude and longitude. We calculated mean annual evapotranspiration (ET) and growing season

163 length (GSL) from FLUXCOM (Jung et al., 2011), in which GSL was based on the seasonal

164 phasing of gross primary productivity (GPP) considering the time period between 20% and

165 80% of maximum GPP in an average year for the period 2002-2015. Total soil P concentrations

166 were derived from Yang et al. 2013; soil clay content and soil pH were extracted from the

167 Harmonized World Soil Database (HWSD; Wieder et al., 2014). We used atmospheric N

168 deposition values from CESM-CMIP6 (Hegglin; Kinnison and Lamarque, 2016) taking the

169 year 2010 as a reference considering that the fields are relatively smooth, summing the

170 emissions and making the annual mean, and P deposition was extracted from Brahney et al.

171 (2015) and Chien et al. (2016). All variables used as predictors of global N and P resorption

172 are described in table 2.

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174 **Table 2.** All possible predictors for nutrient resorption.

	Variable name	Unit	Reference
MAT	Mean Annual Temperature	°C	Fick and Hijmans, 2017
MAP	Mean Annual Precipitation	mm	Fick and Hijmans, 2017
AmplT	Temperature amplitude	°C	Fick and Hijmans, 2017
ET	Evapotranspiration	mm	Jung et al., 2011
N_dep2010	Nitrogen deposition	kgN ha yr	Hegglin; Kinnison and Lamarque, 2016
P_dep	Phosphorus deposition	kgN ha yr	Brahney et al., 2015; Chien et al., 2016
soilP_tot	Total soil P	g P/m^2	Yang et al., 2013
Clay	Top soil clay content	% weight	Wieder et al., 2014
pH	Top soil pH	-log(H+)	Wieder et al., 2014
GSL	Growing season length	days	Jung et al., 2011
SLA	Specific leaf area	$mm^2\ mg^{-1}$	Kattge et al., 2020

LLS	Leaf Longevity	month	Kattge et al., 2020
Leaf habit(phenology)	Deciduous/Evergreen	-	Kattge et al., 2020
Leaf Type	Broadleaves/Needles	-	Kattge et al., 2020

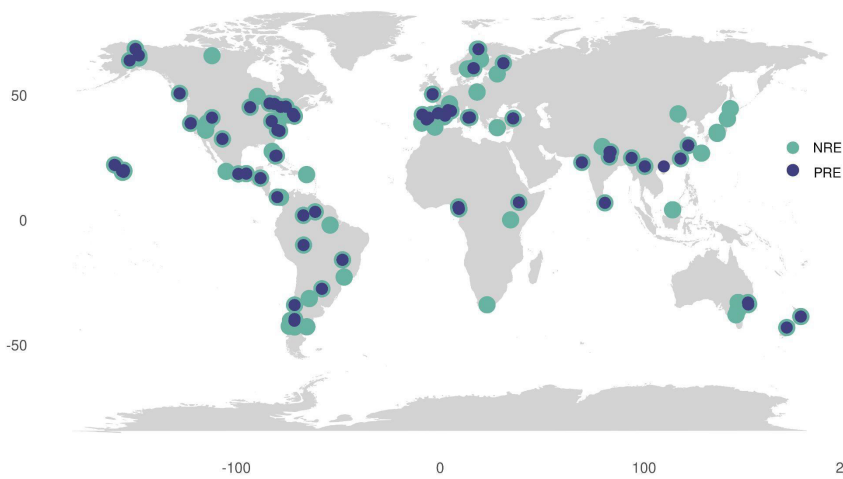
2.2 Data derivation

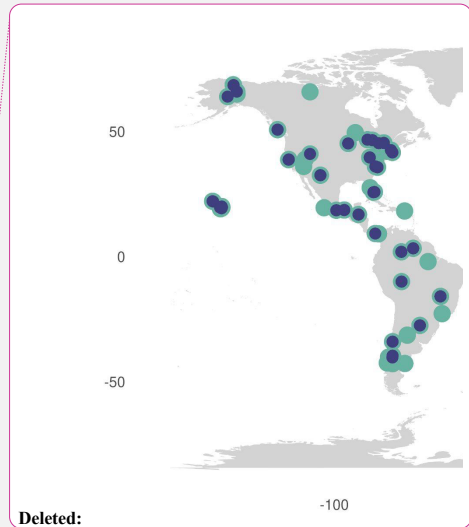
We define nutrient resorption efficiency (NuRE) as the amount of nutrient resorbed during leaf senescence calculated as:

$$NuRE = \left(1 - \frac{Nu_{senesced}}{Nu} MLCF\right) \times 100 \tag{1}$$

where Nu_{green} and $Nu_{senesced}$ are nutrient (N or P) concentrations in dry green and senesced leaves (mg g), respectively; MLCF (unitless) is the mass loss correction factor during senescence to account for the loss of leaf mass when senescence occurs. Omitting MLCF overestimates nutrient concentration in senescent leaves and underestimates resorption values (Zhang et al., 2022). Zhang et al. (2022) showed a significant overall improvement when considering MLCF, where both average of N and P resorption increased by ~9%, particularly for cases with low resorption efficiencies. In the present study, not considering the MLCF also underestimates the actual nutrient resorption efficiency when comparing the fraction of resorption of four sub datasets from the final global dataset (Appendix A).

We calculated MLCF as the ratio between the dry mass of senesced and green leaves (van Heerwaarden et al., 2003a), where it was not directly available as percentage leaf mass loss (LML) in the data. We derived average values of MLCF per plant type from nutrient resorption dataset to fill missing values: 0.712 for deciduous, 0.766 for evergreen, 0.69 for conifers, and 0.75 for woody lianas, respectively. To fill in MLCF values for the remaining leaf nutrient and litter data from TRY, we associated these means of MLCF with leaf habit, leaf type and growth form information available on each species. For that, trees with needle evergreen leaves were associated with conifers MLCF; deciduous trees/shrubs with deciduous woody MLCF, and evergreen trees/shrubs with evergreen woody MLCF, respectively. We grouped climbers and lianas with shrubs. Initially, 107 observations for NRE and 76 observations for PRE were derived from site-level MLCF data. We increased these numbers by 847 for NRE and 378 for PRE when applying the mean MLCF per PFT. In total we extracted data from 131 sites for NRE and 74 for PRE (Fig. 1), with more than one entry per site giving a total of 954 and 454 data points for NRE and PRE species-level, respectively. Temperate biomes were most

205 strongly represented in the dataset (518 entries), followed by tropical (180), boreal (103), polar
206 (102) and dry ecosystems (65).

208 **Figure 1:** Global distribution of data used for nitrogen resorption efficiency (NRE) and phosphorus resorption
209 efficiency (PRE).

212 **2.3 Statistical analysis**
213 As the nutrient resorption data did not conform to a normal distribution (Shapiro–Wilk test),
214 we used the nonparametric Kruskal–Wallis one-way ANOVA test of variance to examine
215 differences of NRE and PRE among different climate zones, and Mann-Whitney Wilcoxon test
216 to evaluate differences between leaf habit, leaf type and growth form (deciduous vs evergreen
217 plants, broad-leaves vs needle-leaves, shrubs vs trees), using the {ggstatsplot} R package (Patil,
218 2021). We applied Pearson correlation and linear regression to analyze the relationship between
219 nutrient resorption and the predictors described in Table 2. For MAP and N deposition, we
220 performed a log transformation prior to conducting the analysis to have the distribution close
221 to the normal. To find the best set of predictors for the variance in NRE and PRE, we used
222 multimodel inference (MMI; Burnham and Anderson, 2002) using the Akaike's information
223 criterion (AIC) and estimated the relative importance of each explanatory variable. Different
224 from setting only a single model based on AIC, multimodel inference accounts for uncertainties
225 in the model performance and in the considered parameters. This approach involves modeling

227   and evaluating all possible combinations of a predetermined set of predictors. The evaluation

228   is typically conducted using a criterion, such as AIC or Bayesian information criterion (BIC),

229   which favors simpler models and allows for a comprehensive examination of all possible

230   models and their respective performances. By synthesizing the estimated coefficients of

231   predictors across these models, MMI enables inference regarding the overall importance of

232   specific predictors. Before applying MMI, we used generalized linear mixed effect models

233   (GLMER) to fit different models after removing drivers described in Table 2 that showed: (1)

234   high collinearity between them (R $\geq$ 0.7; Fig. S5); (2) non-significant correlation with NRE

235   (soil P) and PRE (MAP and SLA) (Fig. S5); (3) a threshold of Variance Inflation Factor (VIF)

236   higher than 10 (James et al. 2013). Specifically, temperature amplitude, GSL and ET were not

237   considered due to their high correlation with MAT and MAP and due to high VIF. Based on

238   ecological interactions, we fitted the model considering interactions between climate variables

239   MAT and MAP, as well as between plant characteristics such as leaf structure, leaf habit and

240   leaf type (SLA:LeafPhenology:LeafType). We are accounting for species identity as a random

241   factor in the mixed effect models to test if intrinsic intra-specific variability plays a role.

242   Environmental and biotic factors have strong shared effects in linear mixed models and

243   therefore are not assessed separately in this study. If the ratio between the sample size and the

244   number of parameters considered was higher than 40, we fitted the model using Restricted

245   Maximum Likelihood REML and AICc (corrected for small sample sizes) to avoid bias. We

246   selected the model with lowest AIC and applied it into the 'dredge' function implemented in

247   the multimodal inference package {MuMIn} (Bartoń K, 2023) which generated a full submodel

248   set. A set of best-performing models for NRE and PRE was selected using a cut-off of ΔAIC

249   < 2, and based on these top models, the best model parameters were generated. Using {MuMIn}

250   package, we also calculated the relative importance of each predictor through the sum of the

251   Akaike weights across all models in which the respective parameter was being considered, with

252   a cut-off of 0.8 to distinguish between important and unimportant predictors (Terrer et al.,

253   2016). The marginal and conditional R^2 values for the fitted mixed models were 0.23 and 0.98

254   for NRE, and 0.29 and 0.48 for PRE respectively, therefore, fixed and random effects explain

255   98% of the variance in NRE and 48% in PRE, with fixed effects alone explaining 23% for NRE

256   and 29% for PRE. We performed all statistical analysis using p-value < 0.05 as statistically

257   significant.

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3. Results

3.1 Global patterns of nutrient resorption between different climate zones

The global median of nutrient resorption for nitrogen (NRE) and phosphorus (PRE) is 60.0% ± 12.3% of standard deviation (n=954) and 61.2% ± 13.6% (n=454), respectively. We find differences for both NRE and PRE between the climate zones (Fig. 2). Tropical regions show the lowest resorption for N (NRE: 52.4% ± 12.1%) and tundra ecosystems in polar regions show the highest (NRE: 69.6% ± 12.8%) (Fig. 2a). PRE in temperate regions shows the lowest values (57.8% ± 13.6%). PRE increases towards the higher latitude with significant difference of P resorption from temperate to boreal regions (67.3% ± 13.6%) (Fig. 2b). In contrast to NRE, the difference of PRE between tropical and other climate zones, as well as polar regions, is not statistically significant (P > 0.05). NRE in dry regions (61.6% ± 9.7%) is statistically different from tropical and polar regions, while for PRE, the difference is not significant between climate zones. However, the sample for this zone is substantially smaller. Details of minimum, maximum, and median values can be found in Table B1.

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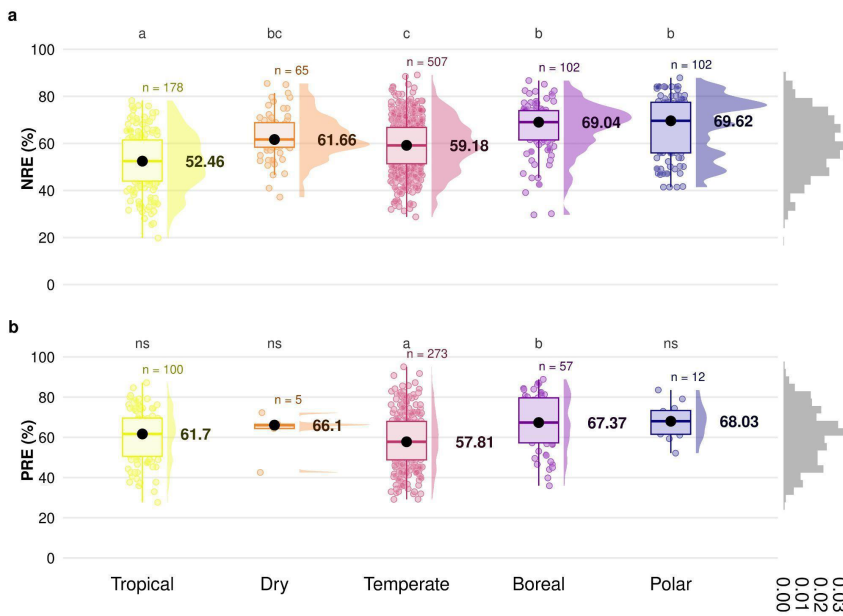
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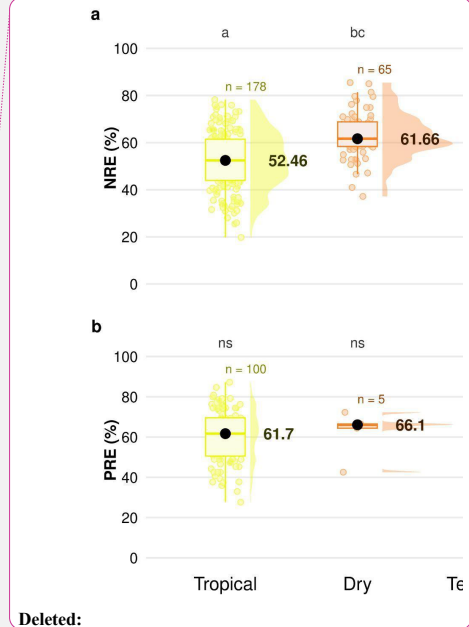
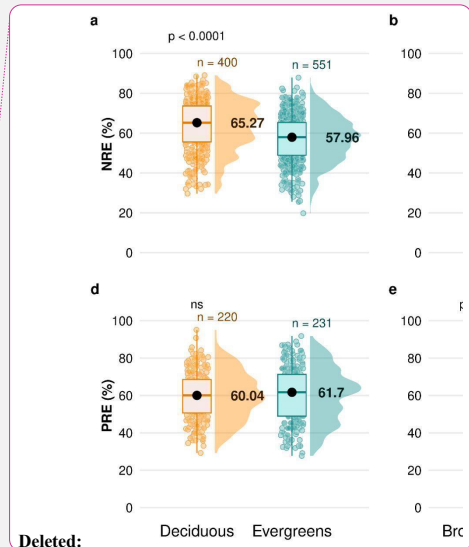
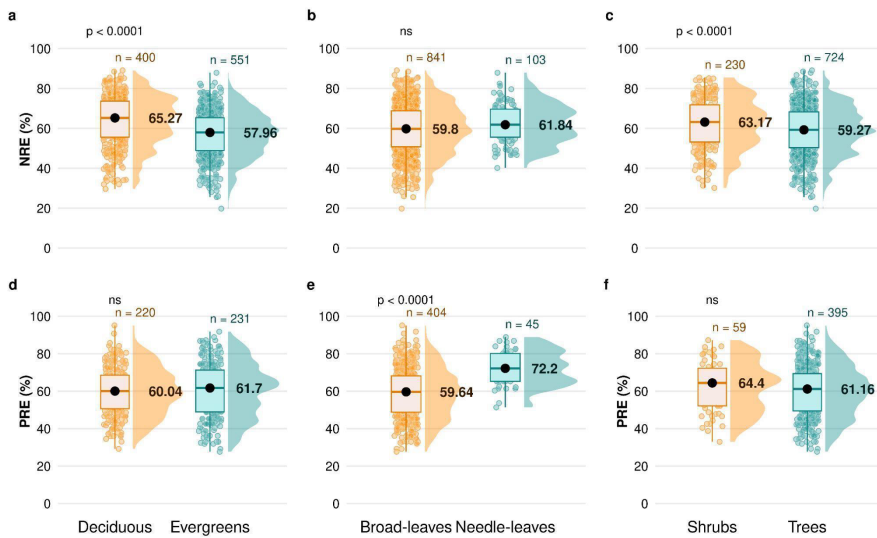


Figure 2: Difference in the resorption efficiency of nitrogen (NRE; a) and phosphorus (PRE; b) between climate zones by Köppen climate classification. Different letters indicate the significant differences in nutrient resorption between the climate zones, 'ns' means non significant, and 'n' represents the number of observations.

3.2 Patterns of nutrient resorption between plant functional types

We explore the variation of nutrient resorption between plant functional groups. Deciduous woody plants have a significantly higher NRE (65.2% ± 12.4%, n=400) than evergreens (57.9% ± 11.4%, n=551) (P < 0.001) (Fig. 3a), and shrubs have a significantly higher NRE (63.1% ± 12.4%, n=230) than trees (59.2% ± 12.1%, n=724) (P < 0.001) (Fig. 3c). Conversely, there is no significant difference in NRE between broad- (59.8% ± 12.5%, n=841) and needle-leaved plants (61.8% ± 9.9%, n=103) (P > 0.05) (Fig. 3b). PRE does neither differ significantly between deciduous (60.0% ± 12.8%, n=220) and evergreen plants (61.7% ± 14.4%, n=231) (P = 0.4) (Fig. 3d) nor between shrubs (64.4% ± 13.5%, n=59) and trees (61.1% ± 13.6%, n=395) (P = 0.2) (Fig. 3f). However, PRE differs significantly between leaf types, with needle-leaved showing higher resorption (72.2% ± 9.2%, n=45) than broad-leaved plants (59.6% ± 13.5%, n=404) (P < 0.001) (Fig. 3e). Details of minimum, maximum and median values can be found in Table B2.

Figure 3: Difference in the nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE) between plant functional types (PFTs) on a global scale, comparing deciduous versus evergreens (a d),

300 broadleaved species versus needle leaves (b e), and shrubs versus trees (c f). 'n' represents the number of
301 observations, and 'p' indicates the significant difference of nutrient resorption between each PFT.
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303 We next explore how climate zones affect NRE and PRE within plant functional groups. NRE

304 tends to increase from tropical to boreal climates (Fig. 4a) – a pattern seen among deciduous

305 and evergreen woody plants, among shrubs and trees, and among broadleaved, but not needle-

306 leaved plants. Also PRE increases from temperate to boreal and polar climates, but declines

307 from the tropics to temperate climates in evergreens (Fig. 4b). Apart from the overall tendency,

308 we observe a few statistical deviations from the general pattern that emerged across all plants

309 pooled: NRE is significantly lower in polar regions compared to boreal forests for evergreens

310 (NRE: 56.0% ± 13.4%; NRE: 70.5% ± 10.8%) and compared to needle leaved plants (NRE:

311 56.0% ± 11.5%; NRE: 51.5% ± 7.3%) (P < 0.001); PRE shows the same pattern deviation

312 between these regions, but the pattern is not statistically significant (P > 0.05). Also, we did

313 not observe lower NRE for tropical regions in needle leaved plants because the only

314 observation of this plant type is in this climate zone. Details of minimum, maximum and

315 median values can be found in Table B3.

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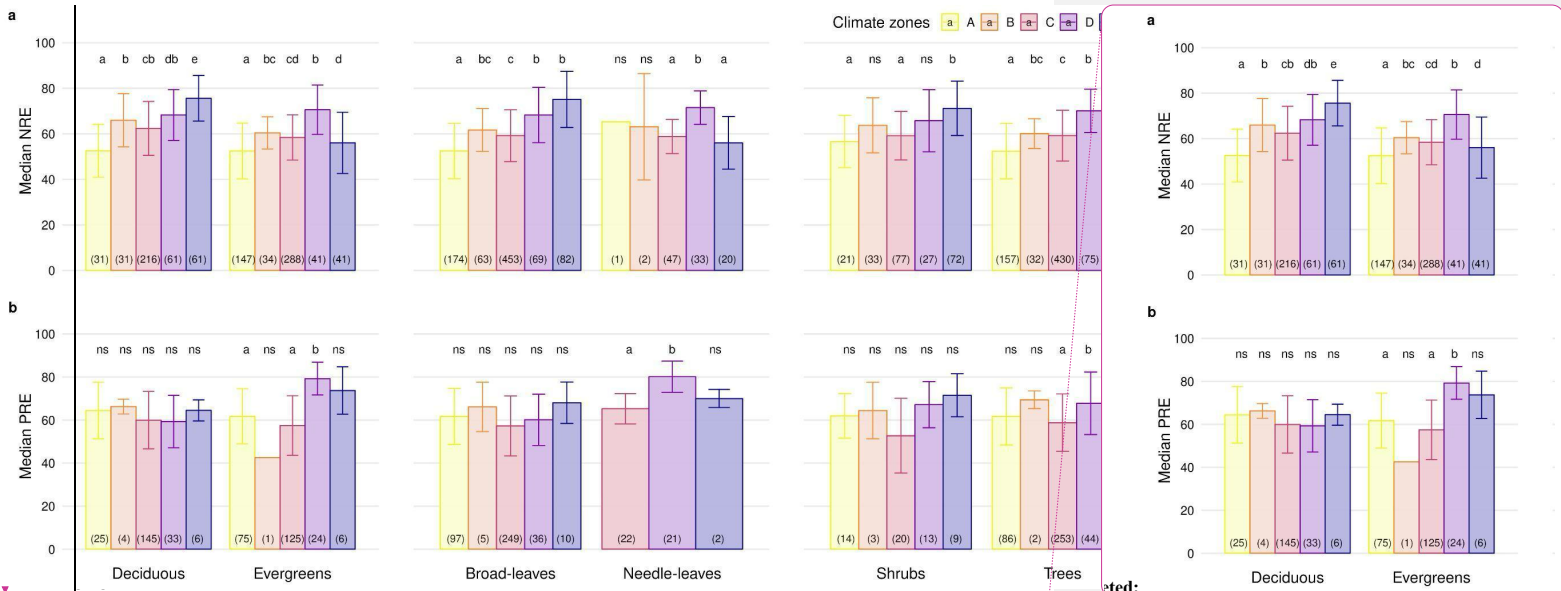
319 **Figure 4:** Median of nitrogen resorption efficiency (NRE; a) and phosphorus resorption efficiency (PRE; b)
320 between deciduous versus evergreens, broad- versus needle-leaves and shrubs versus trees in different climate

zones. Error bars are the standard deviations of the medians. Different letters indicate the significant differences in nutrient resorption between the climate zones. Numbers in parentheses represent the number of observations. Climate zones (A Tropical; B Dry; C Temperate; D Boreal; E Polar).

3.3 Main drivers of nutrient resorption

We investigate the main drivers for variation in nutrient resorption, considering biological, climatic, and soil factors and using data from all PFTs and climate zones pooled. Dredge model averaging based on a set of best-performing models with corrected AIC (see Methods 2.3) shows that the best model for NRE includes soil clay content, N deposition, MAP and growth form (Table 3). The best combination of predictors for the PRE model includes N deposition, leaf type, and MAT (Table 3). Sums of Akaike weights indicate that the order of importance of predictors for NRE is N deposition (RI 0.99), MAP (RI 0.99), leaf habit (RI 0.98), followed by soil clay content (RI 0.97), growth form (RI 0.93) and leaf type (RI 0.87) (Fig. 5a); while for PRE, the order is P deposition (RI 0.99), leaf type (RI 0.99), N deposition (RI 0.94) followed by leaf habit (RI 0.89) (Fig. 5b). The criteria to fit the model selecting and/or excluding predictors and interactions for the multimodel inference can be found in Sect. 2.3. Correlations between all variables, as well as linear relationships with the regression slope between nutrient resorption and all possible predictors can be found in Figs. C1 and C2.

Table 3 | Summarized results of dredge model averaging for nitrogen resorption efficiency (NRE) and phosphorus resorption efficiency (PRE). Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. SE means standard error.

NRE	Estimate	SE	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	63.24	2.86	2.87	21.96	<0.001	***
Clay content	-0.33	0.09	0.09	3.54	<0.001	***
Growth Form	2.57	1.11	1.12	2.30	0.02	*
Leaf habit	2.02	2.32	2.33	0.86	0.38	
Leaf type	0.66	2.51	2.52	0.26	0.79	
MAP	-5.07	1.58	1.58	3.19	0.001	**
N deposition	0.57	0.11	0.11	5.07	<0.001	***
Leaf habit:Leaf type	-0.51	2.69	2.70	0.19	0.84	
PRE	**Estimate**	**SE**	**Adjusted SE**	**z value**	**Pr(>|z|)**	
(Intercept)	78.28	9.45	9.56	8.18	<0.001	***
Clay content	-0.44	0.24	0.24	1.81	0.06	.
Growth Form	-1.35	2.99	3.03	0.44	0.65	
Leaf habit	2.72	1.75	1.77	1.53	0.12	
Leaf type	-10.34	4.29	4.35	2.37	0.01	*
MAT	1.08	0.49	0.49	2.18	0.02	*
N deposition	-1.77	0.54	0.54	3.23	0.001	**
P deposition	-97.13	65.80	66.75	1.45	0.14	
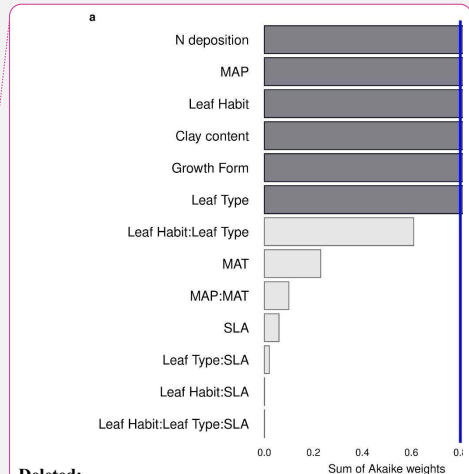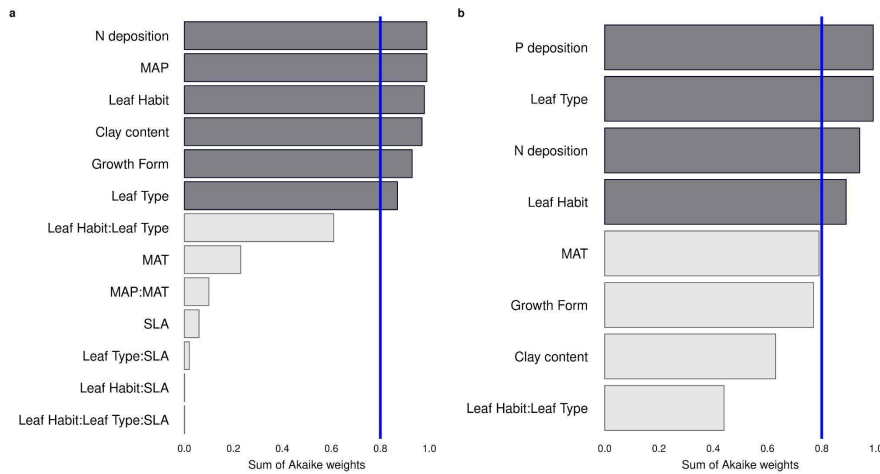
Figure 5: Importance of the abiotic and biotic predictors on nitrogen resorption efficiency (NRE; a) and phosphorus resorption efficiency (PRE; b). The relative importance (RI) of each predictor is calculated through the sum of the Akaike weights derived from multimodal inference selection, using corrected Akaike's information criteria. The blue line distinguishes between important and unimportant predictors. Mean Annual Precipitation (MAP); Mean Annual Temperature (MAT); SLA (Specific Leaf Area). Colon means interaction between predictors. Leaf habit is represented as 'Leaf Phenology'.

4. Discussion

Through an extensive global dataset of leaf nutrient resorption and a multifactorial analysis, we show that leaf habit and type are a strong driver of the spatial variation in nutrient resorption, with thicker, longer-lived leaves having lower resorption efficiencies. Climate, and soil-availability-related factors also emerge as strong drivers, in which we discuss a secondary regulation related to environmental conditions in space and time. Our study covers significantly more woody species observations for nutrient resorption, especially for N, than previous studies (Yuan and Chen, 2009; Yan et al., 2017; Xu et al., 2021). We also account for variations in the mass loss of senescing leaves by deriving the MLCF when leaf mass loss or leaf dry mass were available, and then apply the calculated average MLCF to the missing data, rather than using a single average of MLCF from the literature per PFT (Yan et al., 2017; Xu et al., 2021), which may lead to a more correct estimate of nutrient resorption (see Methods 2.2).

4.1 Nutrient resorption limited by leaf structure

369   The structural properties of leaves limit the efficiency of resorption along geographic and
370   climatic ranges. We find that the global mean for NRE is significantly higher in deciduous than
371   evergreen plants, and is higher in shrubs than trees (discussed at the end of this section) (Fig.
372   3a; 3c). This finding is in contrast to previous global studies that found decreasing nutrient
373   resorption with increasing green leaf nutrient content, implying that deciduous species, which
374   generally have higher leaf N content than evergreen species, have higher resorption (Yan et al.,
375   2017; Xu et al., 2021). Nevertheless, our finding is in agreement with Vergutz et al (2013),
376   who reported that deciduous woody species had higher NRE than evergreen woody species and
377   who found no significant differences for PRE.

378   We find that leaf habit is a strong driver for variation in resorption for both nutrients (Table 3;
379   Fig. 5). Fig. 3a shows that leaf habit is associated with clearly different mean NRE values for
380   evergreen and deciduous species, while the relationship of the average resorption is less clear
381   for PRE (Fig. 3d). This is likely the consequence of a dominance of evergreen species in the
382   tropics in our data set, but we cannot conclude that the lower amount of data for PRE is also a
383   drive of this pattern. The inconsistencies of patterns and significance in P resorption can be
384   related to high biochemical divergence in leaf P fractions compared to N, leading to varied
385   mobilization paths (Estiarte et al., 2023). The breakdown of proteins is the main way N moves
386   around as 75-80% of N is allocated in proteins, while P mobilization involves many different
387   catabolic pathways that lead to wider variety in P dynamics in leaves during leaf development
388   (Estiarte et al., 2023).

389   We observe no statistical difference between leaf types for NRE (Fig. 3). The higher PRE in
390   needle- than broad-leaves (Fig. 3e) is likely a species effect since almost all needle observations
391   for PRE are plants of the same family, *Pinaceae*. Nevertheless, leaf type is also a strong driver
392   for variance in NRE and PRE (Table 3; Fig. 5). This finding goes together with the view of
393   thicker, longer-lived leaves - such as evergreens and needle-leaves - having lower resorption
394   efficiencies. One possible explanation for this global leaf habit and type pattern is that thicker
395   leaves from evergreens plants, i.e. those with low specific leaf area (SLA), have more N
396   allocated to structural leaf compartments, which means it is harder to break down and resorb
397   nutrients back, leading to less resorption. This is different to deciduous plants, in which leaves
398   are characterized by a higher SLA and a larger N investment into metabolic compounds (Onoda
399   et al., 2017). Although SLA was not directly selected in the statistical model, our results

400 implicitly contain the effects of SLA on nutrient resorption through the strong and known
401 relationship between SLA and leaf type and habit (Fig. C4).

402 The leaf economics spectrum (LES) distinguishes "fast" and "slow" economic strategies found
403 globally and existing independent of climate (Wright et al., 2004). A rapid return on
404 investments, or "fast" economic strategy, is typically associated with deciduous plants and
405 achieved through a combination of traits such as shorter leaf longevity, higher nutrient
406 concentrations, and thinner leaves (high specific leaf area SLA), resulting in higher gas
407 exchange rates per unit mass/area (Reich et al., 1992, 1997; Wright et al., 2004). Conversely,
408 a slow return on investments is associated with the opposite set of traits and typically found in
409 evergreen plants (Reich et al., 1992, 1997; Wright et al., 2004). The low SLA of long-lived
410 leaves is associated with low photosynthetic N-use efficiency, but with nutrient investment
411 spread over a longer period. The low photosynthetic N-use efficiency can be attributed to a
412 higher proportion of C and N being allocated to structural rather than metabolic components
413 of the leaf (Reich et al., 2017), which aligns with the theory on leaf carbon optimization
414 proposed by Kikuzawa (1995) and posits that shorter leaf longevity is associated with higher
415 photosynthetic rates or lower costs of leaf construction.

416 Here, we found that plants with a conservative nutrient resorption strategy are located at the
417 non-conservative end of the LES, that is, in the "fast" economic strategy. The discussion that
418 revolves around the LES is determined by a combination of trade-offs between investments in
419 structural and metabolic components, as well as trade-offs over time in the expected returns on
420 those investments (Reich et al., 2017). The non-transferable and possibly transferable nutrients
421 depend on where they are located in the cell and their biochemistry (Estiarte et al., 2023).
422 Metabolic fractions are considered to be fully accessible for resorption while structural
423 fractions have been considered non-degradable (Estiarte et al., 2023). Wang et al. (2023) brings
424 the worldwide pattern of high leaf lifespan (LLS) in plants with low SLA as a natural selection
425 response to maximize carbon gain during leaf development, with variations in SLA in
426 deciduous and evergreen species being determined by microclimate conditions. This pattern
427 scales up from the organ level to a broader perspective that encompasses the trade-off between
428 growth and survival at the plant level (Kikuzawa and Lechowicz, 2011). We found higher NRE
429 in shrubs than trees as observed in previous studies (Yuan and Chen, 2009; Yan et al., 2017;
430 Xu et al., 2021), which is also reflected in the identification of plant growth form as one of the
431 main driving factors for NRE in the multimodel inference analysis (Table 3; Fig. 5a).

432   Compared to trees, shrubs typically have smaller leaves and shorter leaf-lifespans. With that
433   they need to be more resourceful with the nutrients available and prioritize nutrient resorption
434   as a way to optimize nutrient usage for growth.

435   Resorption is an internal plant process that aims to maintain the balance of soil-plant
436   interactions in the acquisition and conservation of nutrients, considering which process is less
437   costly for the plant. The efficiency in nutrient-use by plants is determined mainly by the nutrient
438   residence time in the plant, in which they can access through the leaf longevity maintaining the
439   nutrients or through resorption before leaf abscission (Veneklaas, 2022). Our results support
440   the concept that nutrient resorption is mainly driven by the share of metabolic vs total leaf N
441   (P), which co-varies with SLA (proxy for construction costs).

442   Therefore, higher resorption in deciduous trees may be an important conservation strategy as
443   this process is less energetically costly than new growth. Brant and Chen (2015) discuss the
444   dependence of deciduous trees on nutrient resorption efficiency as their investment in green
445   leaf nutrients is higher to keep fast physiological activity during growing season, or the entire
446   nutrient economy is compromised. With that, we can argue that leaf longevity may be an
447   important strategy for evergreen plants to conserve their lower leaf nutrient content, as the
448   nutrient residence time is higher in evergreens. These plants retain nutrients for as long as
449   possible, because once the nutrients are transferred to the soil through litterfall, they are
450   partially lost from the system.
451

452   **4.2 Effects of climate factors**
453   Our global dataset shows that NRE significantly increases from tropical to polar zones (Fig.
454   2a), while PRE is lowest in temperate zones and significantly increases toward the poles (Fig.
455   2b). This suggests that the resorption of both nutrients is governed to some extent by a
456   comparable dependency on climate, possibly related to slowed soil organic matter
457   decomposition at lower mean annual temperatures, which reduces the net rate of mineralization
458   and in turn, limits the availability of nutrients for plant uptake from the soil (Sharma and Kumar
459   2023). MAT emerges as one of the main drivers for PRE but not for NRE (Table 3). This result
460   may be the outcome of the overall distribution of deciduous and evergreen species across
461   climate zones, suggesting that global variations in N and P resorption along climatic gradients
462   may arise primarily from global patterns in deciduous vs. evergreen and needle-leaved vs.
463   broadleaved plants. This statement is important in the context of projecting nutrient cycling

464 under altered climate and indicates limited responses in resorption to temporal changes in
465 climate at decadal time scales – before the global distribution of leaf habit and type changes as
466 a result of shifts in species composition.

467 MAP emerged as an important driver for NRE (Table 3; Fig. 5). One explanation is that low
468 MAP leads to low soil moisture, constraining nutrient mobility and increasing the carbon cost
469 for plants to take up nutrients (Gill and Penuelas, 2016). Therefore, together with limited N
470 resorption mobility in leaf tissues discussed above (Estiarte and Penuelas, 2015), soil moisture
471 constrains N mobilization during the mineralization process (Thamdrup, 2012). Liu et al.
472 (2016) analyzed the relation between soil N mineralization and temperature sensitivity on a
473 global scale, and showed largest N mineralization rates at tropical latitudes and a general
474 poleward decrease. We can observe a similar pattern of NRE with latitude (Fig. C3). Deng et
475 al. (2018) observed a negative relationship between NRE and mineralisation rate, which
476 suggests a reciprocal causal relationship where systems emerge exhibiting either
477 simultaneously low mineralization and high resorption rates. The strong link found here
478 between NRE and leaf habit and leaf type - traits that are immutable within a given species -
479 indicates that the variations we observe in resorption might be a possible reflection of species
480 composition with direct consequence for N cycling. It suggests that a positive feedback
481 mechanism exists that leads ecosystems to be characterized by high resorption and a slower
482 soil cycling, or vice versa (Phillips et al. (2013). For example, species adapted to low soil N
483 are favored in N-limited environments, but they also produce low-N litter that decreases
484 mineralisation and further favors their competitiveness (Chapin et al., 2011).

485 In addition, we found a negative correlation between resorption and growing season length
486 (Figs. C1). Plant strategies in regions with short growing seasons (e,g. high latitudes or
487 seasonally dry subtropical regions) are focused on nutrient conservation to maximize growth
488 during the favorable period, despite nutrient availability. In very cold and seasonal
489 environments, as seen in grassy tundra vegetation, soil nutrients are often not available
490 concurrently with plant demand (Lacroix et al., 2022), implying that it may be more
491 advantageous for plants to retain their nutrients. While we did not include growing season
492 length in the multimodel inference analysis due to its high collinearity with MAT, this aspect
493 is partially reflected in leaf habit.

494 When we separate the global patterns for different climate zones in plant functional types
495 (PFTs), our results show that the major climatic pattern is consistent across the growth forms

496 and leaf types and leaf habit (Fig. 4), in which NRE and PRE increases towards higher latitudes
497 and PRE shows a minimum at mid-latitudes. Our findings support that maximum NRE and
498 PRE may be firstly constrained by leaf properties, with secondary effects from climate and soil
499 texture (discussed below). Estiarte et al. (2023) suggest that a plant's leaf biochemistry
500 (biochemical and subcellular fractions of N and P) is the primary factor in limiting nutrient
501 resorption, followed by secondary regulation related to environmental conditions in space and
502 time. They present that resorption efficiency declines when soil nutrient availability rises, as
503 plant uptake becomes less costly in more fertile soil. However, the expenses linked to aging
504 leaves remain constant (Estiarte et al., 2023).

505

506 **4.3 Effect of soil nutrient availability**
507 N and P deposition and clay content emerged as important predictors for both PRE and NRE
508 (Table 3; Fig. 5). This likely reflects the influence of soil N and P availability for NRE and
509 PRE. Clay content is an important factor determining the nutrient retention capacity and cation
510 exchange capacity in soils (Chapin et al., 2011). Chronic N deposition has increased soil N
511 availability (Galloway et al., 2004) and leaf nutrient content (Chapin et al., 2011) over the 20th
512 century, and likely affected plant internal recycling and resorption as indicated by our spatial
513 results. In a fertilization experiment, higher P input had a negative effect on both NRE and PRE
514 (Yuan & Chen, 2015), suggesting that increased P deposition may reduce the plant internal
515 recycling and thus resorption. The cycling and accessibility of soil P are influenced by N
516 deposition (Marklein and Houlton, 2012) through various mechanisms, including changes in
517 plant P use strategies (Dalling et al., 2016; Wu et al., 2020a). Higher N deposition tends to
518 reduce total soil P content (Sardans et al., 2016) so plants would need to increase PRE to
519 compensate for the high soil N:P stoichiometry and P limitation. Jonard et al. (2014) suggested
520 that forest ecosystems are becoming less efficient at recycling P due to excessive N input and
521 climatic stress. This observation likely contributes to our finding that N and P deposition
522 emerge as a stronger driver in a negative correlation with PRE (Fig. 5; Table 3; Figs. C1). The
523 lack of effect by total soil P on NRE and PRE may result from the fact that this variable does
524 not represent the actual fraction of P available for plant uptake. Nevertheless, N deposition was
525 found here to have a strong positive effect on NRE (Fig. 5; Table 3) – contrary to expectations
526 (Aerts and Chapin, 1999; Yuan and Chen, 2015; Fisher et al., 2010). This indicates that the
527 influence of N deposition might be via effects on SLA, whereby increasing N deposition

increases the fraction of non-structurally bound N and therefore increases the fraction of N that can be resorbed. This effect, corrected for covariant factors such as leaf type and growth form, overlaps the negative effect of soil clay content on NRE and PRE which suggests that resorption decreases with nutrient availability in clay-rich soils. Our results raise an important point on the correlation of leaf nutrient resorption and nutrient limitation, showing that the relationships are complex and driven by multiple interacting and seemingly opposing factors.

Another soil factor found to be important for nutrient resorption is the clay content (Table 3). Clay minerals are formed during soil weathering and have high surface area that influences the soil's water retention capacity, and a negative charge that enables nutrients retention and exchange with plant roots (Chapin et al., 2011). High-latitude soils that are younger and experience slow rates of chemical weathering usually have low clay content and therefore, less potential for mineral nutrient storage, which may affect their availability for plant uptake (Chapin et al., 2011). As a result, plants in these environments need to invest more in resorption. Thus, together with MAP and MAT, soil clay content is also closely related to soil nutrient supply on a global scale, which is reflected in its role as driving resorption (Table 3; Fig. 5), as well as in the negative correlation between clay content and nutrient resorption (Figs. C1). In the context of an important effect on nutrient resorption found for leaf properties together with climate, soil texture and soil fertility - previously suggested to be important (Aerts and Chapin, 1999; Yuan and Chen, 2015; Xu et al., 2021) - may indicate that biological and environmental factors are not fully independent, as it is also determined by multiple elements such as litter quality, precipitation, parental materials and soil texture. For example, P availability is geologically and pedologically limited in warm environments, which means mainly determined by soil parent materials (Augusto et al., 2017), and therefore, soil texture becomes an important factor for P limitation in tropical regions. Also, the role of P deposition in relation to plant demand is high for tropical forests (Van Langenhove et al., 2020) but low worldwide (Cleveland et al., 2013). PRE in the tropics did not differ statistically from other climate zones although we observe an increase of PRE from mid to low latitudes (Figs. B1b and C3), which could indicate data limitation for PRE. The combination of plant properties with an underlying soil and climate control as driving factors for resorption variation is also supported by Drenovsky et al. (2010; 2019), who suggested a combination of soil properties, climatic factors, and plant morphology to explain changes in nutrient resorption.

4.4 Data uncertainties and implications

Our study contributes to the existing research on nutrient resorption by using a comprehensive approach to derive resorption values from the TRY database. However, we encountered limitations in this derivation due to a lack or limited quality of data. The absence of co-located nutrient measurements in leaf and litter led to a shortage of suitable data pairs, mainly for PRE, in which the robustness of the model selection raised concerns about its reliability. In addition, it is not possible to assess the entire temporal aspect of data collection, which increases intraspecific variability. For NRE, 645 of a total of 954 observations are from the same growing season, as we have collection information for green leaves and litter samples whether they were picked from the plant, recently fallen or from litterfall traps cleared every week. Consequently, for approximately 30% of the data, we cannot confirm that the leaf and litter measurements are from the same growing season and legitimately from the same individual. This is indeed one of the greatest limitations in assessing reliable nutrient resorption values. Nevertheless, it remains the accepted - and only - method for evaluating resorption on a broad scale.

While our approach of accounting for the MLCF improved estimates of resorption (Appendix A), we could not estimate the MLCF for all data pairs, and could not fill all gaps using average functional type characteristics due to lacking trait attributes in the TRY database. These two factors reduced the number of data points available for statistical analysis using multi-model inference. Furthermore, although recognized the importance of leaf lifespan (LLS), it was not possible to analyze the relationship between resorption and LLS due to the few measurements of this functional trait. Nevertheless, applying the available statistical methods to analyze the drivers behind NRE and PRE, we found consistent patterns for the key gradients of climate, soil and plant functional type, that are informative for other studies despite remaining unexplained variance. In addition, we found that even within species of the same family, the distribution of NRE values is nearly as wide as the distribution for PFTs. This coordination in the observed spread likely reflects a substantial contribution from environmental variability, which would be interesting for further analysis if more data is available. In order to improve the depth of resorption investigation, we encourage researchers in field work to perform concurrent measurements of litter nutrient content as well as leaf and litter dry mass.

The statistical analysis of dredge multi-model inference is dependent on the specific factors used in the analysis. We removed highly collinear variables and tested the impact of different combinations of factors. Although such a change in factors affected the exact number of data

595 points used in each multi-model inference, the overall identification of important and less
596 important factors for NRE and PRE was robust, especially for PFTs. However, ensuring that
597 our analysis is as global as possible, the statistical dredge model analysis can consequently be
598 influenced by temperate regions bias, which is an inherent limitation we cannot fully mitigate
599 but one that is present in any global meta-analysis of this kind.
600 By quantifying these trends that we have found, we can delve deeper into ecosystem models
601 by improving model parametrization and developing a dynamic nutrient resorption concept.
602 Studies that utilize data to infer nutrient cycling frequently simplify resorption making general
603 assumptions (Finzi et al., 2007; Cleveland et al., 2013), or simply representing this process as
604 a fixed value of 50% (Vergutz et al., 2013; Zaehle et al. 2014), which may cause inaccuracies
605 in their findings on nutrient cycling. The flow of recycling nutrients in land surface models is
606 a factor that determines how strong the soil nutrient availability controls plant production. N
607 resorption and N uptake in the FUN model (Fisher et al., 2010), for example, is defined by the
608 relative acquisition cost of the two sources. They discuss that the cost of resorption assumes a
609 constant based on global observations, but it may require a clearer connection to leaf
610 physiology. Here, we provide a start for a statistical model that can connect resorption and
611 plant properties and restrict how much plants could actually resorb nutrients, as well as the
612 dataset to test the predictions of a physiological model. In addition, environmental drivers that
613 have been shown to influence the overall patterns, such as soil texture and climate, could be
614 considered to influence the resorption efficiency after primary leaf physiology limitation. Such
615 information is essential when estimating how it can constrain carbon assimilation in face of
616 global changes (Galloway et al., 2008), and therefore, essential to predict future plant growth
617 and the capacity of the forest to act as a carbon sink (Thornton et al., 2007; Arora et al., 2022).
618

619   **5. Conclusions**
620 Our analysis of the global plant trait database indicates that variations of NRE and PRE are
621 driven by the combination of plant properties with an additional soil and climate control.
622 Systematic variations of NRE across leaf habit and type indicate that these traits are linked to
623 plant nutrient use and conservation strategies and that leaf structure plays an important role in
624 determining the proportion of nutrients that can be resorbed. Different metrics of soil fertility
625 and soil-related variables were tested and found to have an influence on NRE and PRE together
626 with climatic variables and leaf structure and habit. Clay content, N and P deposition had strong

influence with a negative relationship - possibly an expression of its role in nutrient retention - as well as MAP. These trends provide a target to benchmark the simulation of nutrient recycling in global nutrient-enabled models. A focus on considering the links between leaf structure and nutrient resorption efficiency should enable a more realistic consideration of ecological and environmental controls on nutrient cycling and limitation than the current state-of-the-art. The importance of intrinsic plant properties raises important questions about the flexibility of leaf resorption under future changes in climate, CO_2 concentrations and atmospheric deposition.

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Author contributions

GS, SC and SZ designed the study. GS performed the analysis. All authors contributed to interpreting the results. GS drafted the manuscripts; all authors contributed to writing and editing the manuscript.

Data Availability Statement

All data used in this study is publicly available through the TRY database https://www.try-db.org/.

Conflict of Interests

SZ is a member of the editorial board of Biogeosciences.

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Appendix A - Sensitivity study of the importance of MLCF

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1031 We assembled the global dataset from the gap-filled version of TRY Plant Trait database
1032 (https://www.try-db.org, Kattge et al., 2020, version 5.0) containing field measurements of
1033 paired leaf and litter mass-based tissue N and P concentrations ($N_{mass, leaf}$, $P_{mass, leaf}$, $N_{mass, litter}$,
1034 $P_{mass, litter}$) to derive the fractional nutrient resorption (described in Methods Sect. 2.1).

1035 In order to understand the importance of considering MLCF in the formula to derive reliable
1036 nutrient resorption values, we compared four sub datasets from the final global dataset:

1037 (a) we derived nutrient resorption from nutrient resorption database, in which MLCF was
1038 calculated directly from leaf dry mass or leaf mass loss measurements;

1039 (b) the second dataset we derived nutrient resorption from nutrient resorption database as well,
1040 but we filled the missing values of MLCF using the mean for each plant functional type: 0.712
1041 for deciduous, 0.766 for evergreen, 0.69 for conifers, and 0.75 for woody lianas, respectively.

1042 (c) the third dataset we derived nutrient resorption using leaf nutrient and litter data from TRY
1043 traits, in which we did not include MLCF in the formula, calculated as:

1044
$$NuRE = \left(1 - \frac{Nu_{senesced}}{Nu}\right) \times 100 \tag{2}$$

1045 (d) the fourth dataset we derived nutrient resorption using leaf nutrient and litter data from
1046 TRY, but here we filled MLCF with the mean per PFT calculated before, in which we
1047 associated these means with leaf phenology, leaf type and growth form information. For that,
1048 trees with needle evergreen leaves received conifers MLCF, deciduous trees/shrubs received
1049 deciduous woody MLCF, and evergreen trees/shrubs received evergreen woody MLCF,
1050 respectively.

1051 Figure A1 shows nitrogen resorption efficiency (NRE) between different climate zones, where
1052 we can see underestimated values of resorption only when we do not consider MLCF in the
1053 formula (Fig. A1c), with values around or lower 50% of N resorption. We can see more reliable

resorption values around 60% when considering MLCF in the formula (Fig. A1a A1b A1d).

When applying the mean of MLCF for the table deriving NRE from TRY traits (Fig. A1d), we

could reproduce a similar pattern compared to the resorption database imported from TRY

(Fig. A1a). Figure A2 shows the distribution of NRE for each subset described before, where

we can see a clear difference in data distribution only when we do not consider MLCF in the

formula (Fig. A2c). For our final dataset, we then considered together the dataset (b) and (d),

in which are the most reliable data for nutrient resorption as it is providing more data points

for resorption, and considers MLCF in the formula.
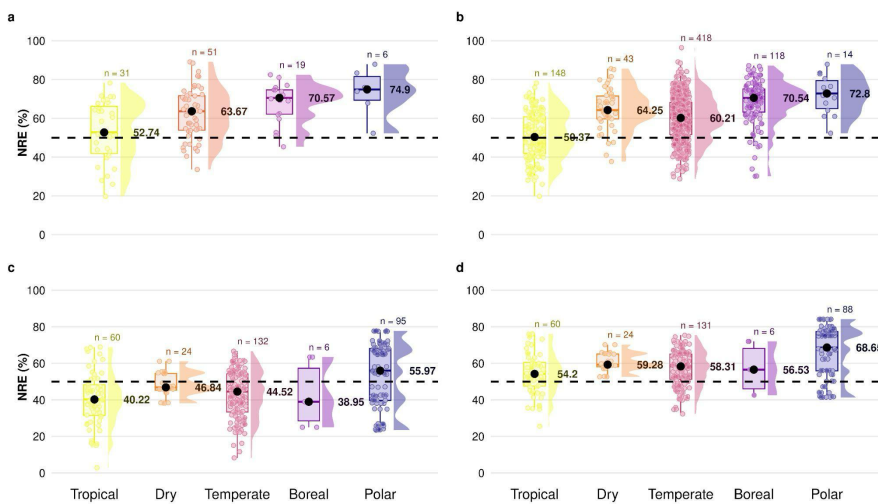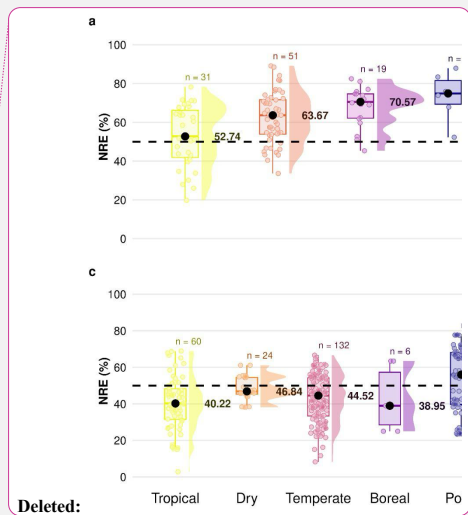
Figure A1: Nitrogen resorption efficiency (NRE %) between climate zones by Köppen climate classification. (a) nutrient resorption values derived directly from nutrient resorption dataset, with MLCF calculated from leaf dry mass or leaf mass loss measurements; (b) nutrient resorption values derived directly from nutrient resorption dataset, but with missing MLCF filled by the mean for each plant functional type; (c) nutrient resorption values derived from TRY traits with no MLCF in the formula; (d) nutrient resorption values derived from TRY traits, but with missing MLCF filled by the mean for each plant functional type.

Figure A2: Distribution of Nitrogen resorption efficiency (NRE %) for all subsets: (a) nutrient resorption values derived directly from nutrient resorption dataset, with MLCF calculated from leaf dry mass or leaf mass loss measurements; (b) nutrient resorption values derived directly from nutrient resorption dataset, but with missing MLCF filled by the mean for each plant functional type; (c) nutrient resorption values derived from TRY traits with no MLCF in the formula; (d) nutrient resorption values derived from TRY traits, but with missing MLCF filled by the mean for each plant functional type.

Appendix B - Global patterns of nutrient resorption efficiency for N and P by PFTs and climate zones

Table B1 | Summary of Nitrogen resorption efficiency (NRE; %) and Phosphorus resorption efficiency (PRE; %) in different climate zones. For each relationship, the number of observations (N), minimum (Min), maximum (Max), median, and standard deviation (SD) were reported. Letters in Significance show the statistical comparison between each climate zone.

Resorption (%)	Climate zone	N	Min	Max	Median	SD	Significance
NRE	Tropical	178	19.77	78.23	52.46	12.15	a
	Dry	65	37.17	85.48	61.66	9.72	bc
	Temperate	507	28.77	89.11	59.18	11.06	c
	Boreal	102	29.64	86.72	69.03	11.0	b
	Polar	102	41.42	87.89	69.62	12.84	b
PRE	Tropical	100	27.65	87.23	61.7	12.84	ns
	Dry	5	42.55	72.31	66.09	11.47	ns
	Temperate	273	29.14	95.11	57.80	13.65	a
	Boreal	57	35.92	88.88	67.36	13.65	b
	Polar	12	52.16	83.58	68.02	8.84	ns

Table B2 | Summary of Nitrogen resorption efficiency (NRE; %) and Phosphorus resorption efficiency (PRE; %) in different plant functional types (PFTs). For each relationship, the number of observations (N), minimum (Min),

1092 maximum (Max), median, p value and standard deviation (SD) were reported. 'p-value' < 0.05 indicates statistical
1093 significance.

Resorption (%)	PFT	N	Min	Max	Median	p value	SD
NRE	Deciduous	400	29.64	89.11	65.27		12.48
	Evergreens	551	19.77	87.89	57.96	**<0.001**	11.45
	Broad-leaves	841	19.77	89.11	59.8		12.53
	Needle-leaves	103	40.19	87.89	61.84	0.05	9.97
	Shrubs	230	30.13	85.48	63.17		12.48
	Trees	724	19.77	89.11	59.27	**<0.001**	12.17
PRE	Deciduous	220	29.22	95.78	60.04		12.86
	Evergreens	231	27.65	91.78	61.7	0.46	14.41
	Broad-leaves	404	27.65	95.11	59.64		13.50
	Needle-leaves	45	51.35	88.88	72.2	**<0.001**	9.23
	Shrubs	59	32.97	87.23	64.4		13.50
	Trees	395	27.65	95.11	61.1	0.89	13.67

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1096 **Table B3** | Summary of Nitrogen resorption efficiency (NRE; %) and Phosphorus resorption efficiency (PRE; %)
1097 in different plant functional types (PFT) separated in different climate zones. For each relationship, the number
1098 of observations (N), minimum (Min), maximum (Max), median, and standard deviation (SD) were reported.
1099 Letters in Significance show the statistical comparison between each climate zone.

NRE

PFT	Climate zones	N	Min	Max	Median	SD	Significance
Deciduous	Tropical	31	31.97	71.80	52.53	11.64	a
	Dry	31	37.17	85.48	65.95	11.68	b
	Temperate	216	31.95	89.11	62.39	11.84	cb
	Boreal	61	29.64	86.72	68.28	11.17	db
	Polar	61	47.15	84.16	75.60	9.99	e
Evergreens	Tropical	147	19.77	78.23	52.43	12.28	a
	Dry	34	40.97	79.57	60.42	7.06	bc
	Temperate	288	28.77	81.56	58.40	9.93	cd
	Boreal	41	30.13	82.44	70.57	10.87	b
	Polar	41	41.42	87.89	56.03	13.44	d
Broad-leaves	Tropical	174	19.77	78.23	52.46	12.15	a
	Dry	63	37.17	85.48	61.66	9.42	bc
	Temperate	453	28.77	89.11	59.18	11.36	c
	Boreal	69	29.64	86.72	68.28	12.13	b
	Polar	82	41.42	84.16	75.10	12.34	b
Needle-leaves	Tropical	1	65.25	65.25	65.25	-	ns

PFT	Climate zones	N	Min	Max	Median	SD	Significance
	Dry	2	46.60	79.65	63.13	23.37	ns
	Temperate	47	40.19	81.56	58.80	7.45	a
	Boreal	33	51.02	82.44	71.52	7.33	b
	Polar	20	46.76	87.89	56.03	11.58	a
Shrubs	Tropical	21	33.81	74.33	59.60	11.45	a
	Dry	33	37.17	85.48	63.72	12.08	ns
	Temperate	77	31.29	80.96	59.16	10.63	a
	Boreal	27	30.13	85.15	65.77	13.66	ns
	Polar	72	41.42	84.16	71.16	11.92	b
Trees	Tropical	157	19.77	78.23	52.35	12.18	a
	Dry	32	47.10	76.26	60.08	6.59	bc
	Temperate	430	28.77	89.11	59.18	11.13	c
	Boreal	75	29.64	86.11	70.05	9.49	b
	Polar	30	46.76	87.89	68.44	14.89	bc

PRE

PFT	Climate zones	N	Min	Max	Median	SD	Significance
Deciduous	Tropical	25	35.92	76.26	64.40	13.14	ns
	Dry	4	64.40	72.31	66.29	3.44	ns
	Temperate	145	29.22	95.11	59.95	13.32	ns
	Boreal	33	35.92	84.33	59.31	12.18	ns
	Polar	6	59.31	71.52	64.51	4.90	ns
Evergreens	Tropical	75	27.65	87.23	61.70	12.81	a
	Dry	1	42.55	42.55	42.55	-	ns
	Temperate	125	29.14	91.78	57.44	13.85	a
	Boreal	24	61.38	88.88	79.26	7.58	b
	Polar	6	52.16	83.58	73.73	11.03	ns
Broad-leaves	Tropical	97	27.65	87.23	61.70	12.98	ns
	Dry	5	42.55	72.31	66.10	11.47	ns
	Temperate	249	29.14	95.11	57.28	13.93	ns
	Boreal	36	35.92	84.33	60.14	11.92	ns
	Polar	10	52.16	83.58	68.03	9.63	ns
Needle-leaves	Temperate	22	51.35	82.62	65.25	7.06	a
	Boreal	21	61.38	88.88	80.14	7.22	b
	Polar	2	67.02	73.00	70.01	4.22	ns
Shrubs	Tropical	14	47.85	79.97	61.95	10.39	ns
	Dry	3	42.55	66.09	64.40	13.13	ns
	Temperate	20	32.97	87.23	52.72	17.36	ns
	Boreal	13	46.60	82.20	67.17	10.70	ns
	Polar	9	52.16	83.58	71.52	10.0	ns
Trees	Tropical	86	27.65	87.23	61.70	13.24	ns
	Dry	2	66.49	72.31	69.40	4.11	ns
	Temperate	253	29.14	95.11	58.78	13.35	a
	Boreal	44	35.92	88.88	67.78	14.48	b

Polar	3	61.11	68.68	67.03	3.97	ns	

Appendix C - Linear regressions of nutrient resorption with environmental and biological factors

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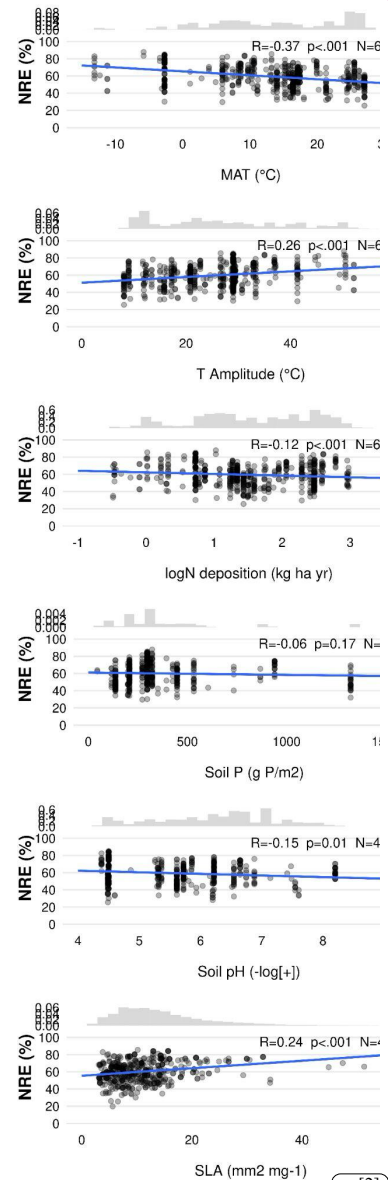
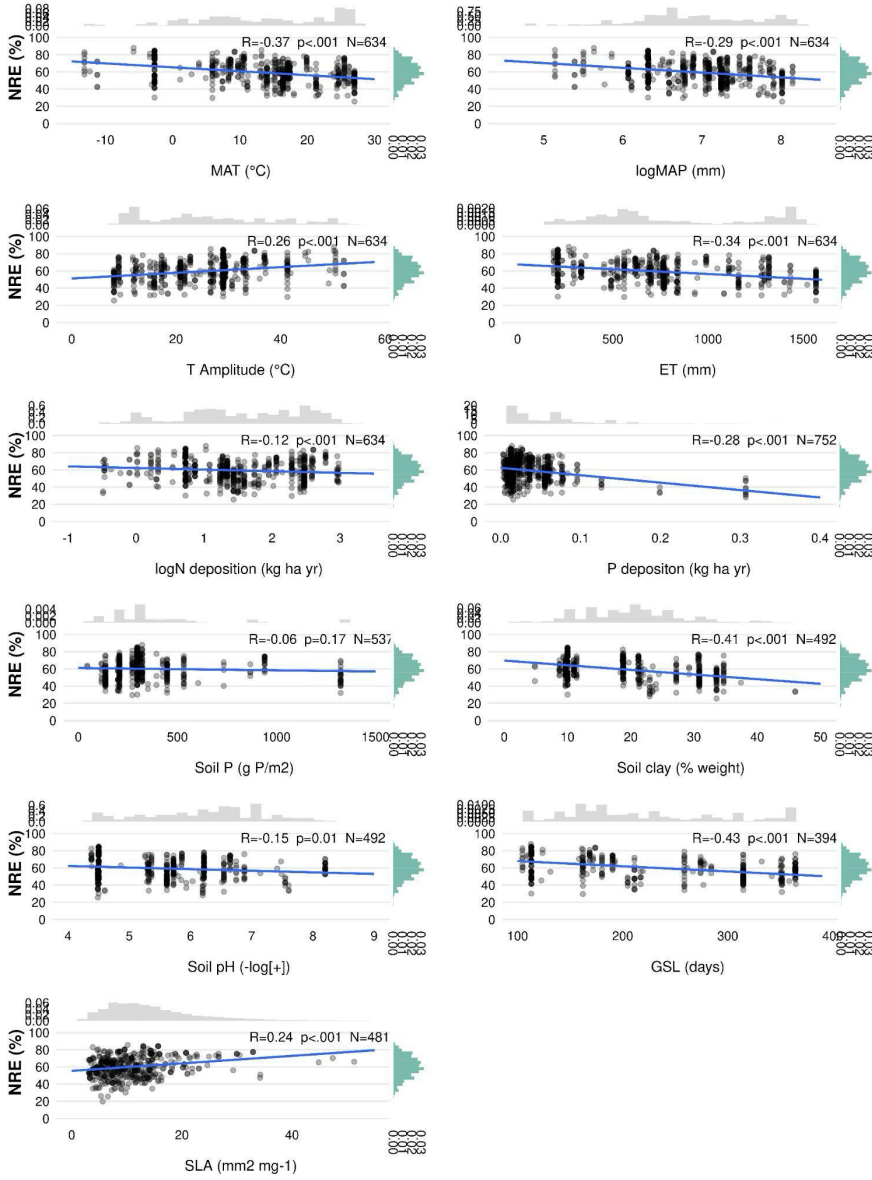
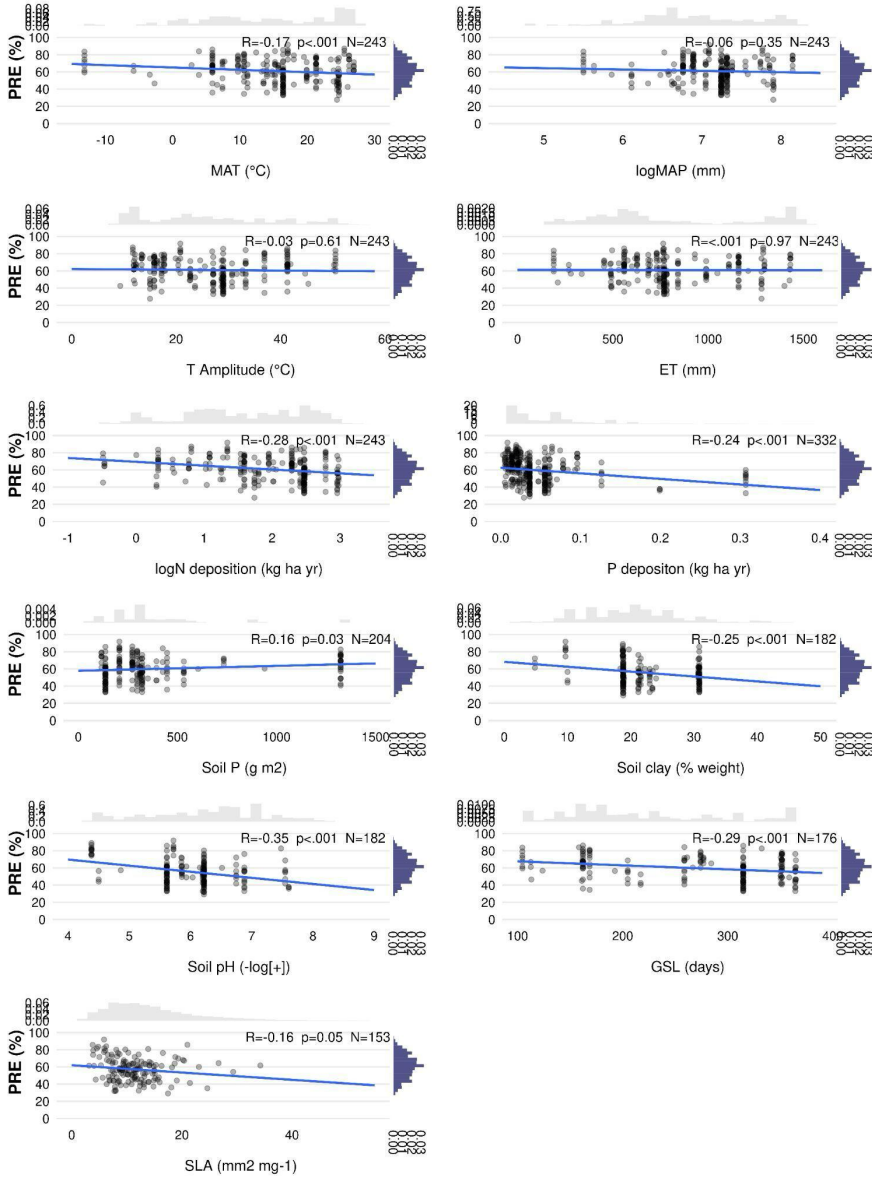


Figura C1. Linear regression of Nitrogen resorption efficiency (NRE; %) and Phosphorus resorption efficiency (PRE; %) with all possible predictor variables. Environmental predictors: Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), Evapotranspiration (ET), Temperature amplitude (T amplitude), Nitrogen deposition (N deposition), Phosphorus deposition (P deposition), total soil P (soil P) soil clay fraction (Soil Clay),

soil pH. Biological predictors: Growing Season Length (GSL), Specific Leaf Area (SLA). R: Pearson correlation; p < 0.05 indicates statistical significance; N: number of observations.

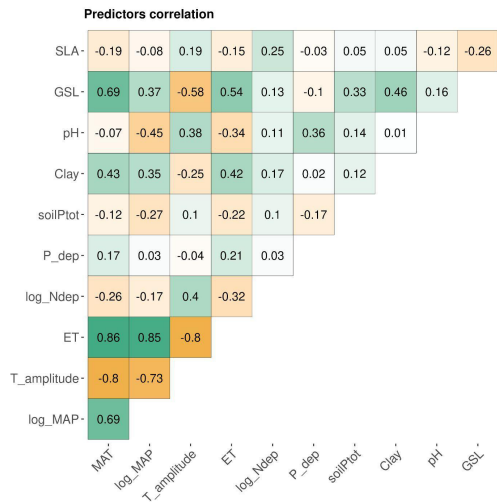



Figure C2: Multiple Pearson correlation between all predictors. Mean Annual Temperature (MAT); Mean Annual Precipitation (MAP); Evapotranspiration (ET); Temperature amplitude (T amplitude); Nitrogen deposition (N deposition); Phosphorus deposition (P deposition); total soil P (soilPtot); soil clay fraction (Clay); soil pH; Growing Season Length (GSL); Specific Leaf Area (SLA).

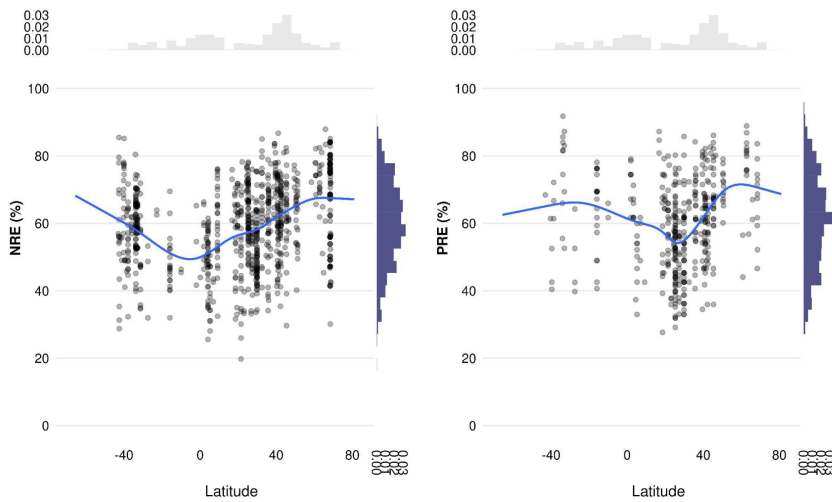
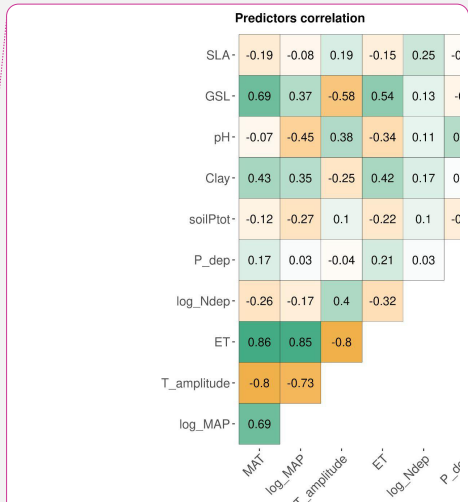
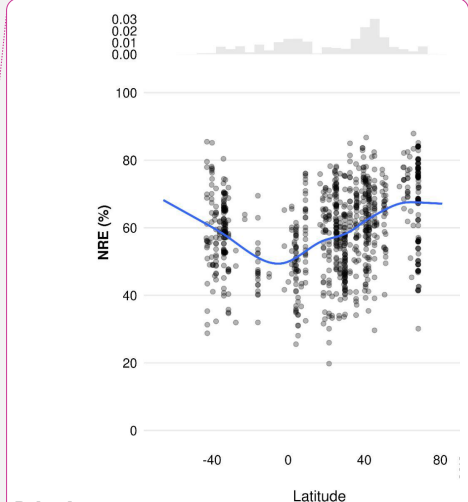
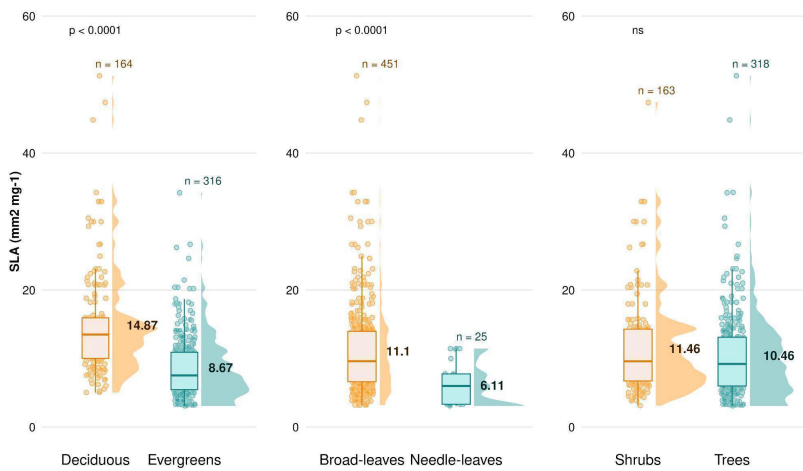



Figure C3: Linear regression of nitrogen and phosphorus resorption efficiency (NRE %; PRE %;) with latitude.

1136 Plant functional type (PFT) does not appear in the correlation matrix shown in Fig. C1 and C2,
1137 as it is a categorical variable. However, we explore the implication of SLA on nutrient
1138 resorption based on the strong and known relationship between SLA and PFTs in our dataset
1139 (Fig. C4), which derives from the leaf economics spectrum (LES) theory.

1140

1141 **Figure C4:** Difference in the specific leaf area (SLA; mm2 mg-1) between plant functional types (PFTs) on a
1142 global scale, comparing deciduous versus evergreens, broadleaved species versus needle leaves, and shrubs versus
1143 trees. 'n' represents the number of observations, and 'p' indicates the significant difference of nutrient resorption
1144 between each PFT.

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