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Leaf Nutrient Resorption of Vascular Epiphytes Is Regulated by Stoichiometry and Nutrient Limitation Control Strategies

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ABSTRACT

Nitrogen (N) and phosphorus (P) resorption are assumed to be crucial for epiphyte growth in nutrient-poor canopies, yet remain poorly understood due to unique habitats and limited access. We examined the N, P and ^{15}N natural abundance in mature and senesced leaves of 10 vascular epiphyte species in southwest subtropical China, integrating data from a previous study in tropical lowland forest. We found that subtropical epiphytes experienced N-limitation, likely because of the high P availability, making N relatively scarce. The mean N and P resorption efficiencies per leaf unit were 63.1% and 67.7%, with 14.7% and 12% higher than those on leaf mass, and 3.9% and 3.8% higher than those on leaf area. The combination of strategy analysis, generalized linear models and variance decomposition revealed that the N and P resorption in tropical epiphytes were combinedly regulated by stoichiometry and nutrient limitation control strategies, while subtropical epiphytes employed either the combined strategies or stoichiometry strategy alone. Notably, functional group type strongly influenced N resorption. Leaf δ^{15}N reflected nutrient resorption with species-specific variation, driven by functional traits. Epiphytes and terrestrial plants exhibit similar nutrient resorption patterns, which help alleviate the N and P deficiencies and support high biodiversity in forest canopies.

1 | Introduction

Nutrient resorption (NuR) is the process of nutrient transfer from senescing leaves to other plant tissues before abscission (Xu et al. 2021). This process can extend the retention time of nutrients within the plant, enhance nutrient use efficiency and reduce the dependence on external nutrient sources (Aerts and Chapin 1999). The resorption of nitrogen (N) and phosphorus (P), the two primary growth-limiting nutrients (Chapin 1980), is crucial for conserving nutrients in plants (Aerts and Chapin 1999; Killingbeck 1996; Kobe et al. 2005). Compared to terrestrial plants, epiphytes are more severely limited by the N and P (Zotz 2016), and have 45% lower leaf N concentration but equivalent leaf P concentration (Hietz et al. 2022). This limitation arises because epiphytes typically grow in extremely nutrient-poor canopies (Zotz 2016) and lack direct contact with ground soil (Lesica and Antibus 1990). However, epiphytes are highly diverse, with over 31 000 vascular species alone, comprising 10% of global vascular plants (Zotz et al. 2021). Therefore, the NuR is assumed to alleviate the N and P deficiencies in epiphytes, playing a key role in maintaining their high biodiversity (Aerts 1996; Zotz 2004; Suriyagoda et al. 2018). Nevertheless, virtually no scholarly attention has focused on the NuR in epiphytes.

Studies of terrestrial plants may still provide foundational insights into epiphyte leaf NuR. The NuR can be expressed as either resorption proficiency (RP, the nutrient concentration [mg/g] in senesced leaves) or resorption efficiency (RE, the proportion of nutrients resorbed from senesced leaves) (Killingbeck 1996; van Heerwaarden et al. 2003). A lower nutrient concentration of senesced leaves corresponds to a higher RP (Killingbeck 1996; van Heerwaarden et al. 2003). The RE can be calculated from the nutrient concentration expressed on per leaf unit basis (RE_{leaf}, mg/leaf) (P. Lin and Wang 2001), per unit leaf mass (RE_{mass}, mg/g, dw) (Chapin and Kedrowski 1983) or per unit leaf area (RE_{area}, mg/cm^2) (Killingbeck 1985; Pugnaire and Chapin 1993). For example, the mean leaf NRE_{mass} and PRE_{mass} are known to be 50% (12.75%−72.94%) and 52% (29.66%−97.62%) in global terrestrial plants (Vergutz et al. 2012), and 56.93% (4.36%−78.8%) and 62.17% (18.42%−86.27%) in some epiphytes (W. Zhang et al. 2022; Zotz 2004).

Globally, leaf N and P resorption in terrestrial plants are primarily influenced by foliar N and P nutrient levels and their stoichiometry, either independently or in combination, which have been categorized into three basic control strategies (Sun et al. 2023). The nutrient concentration control strategy assumes that plants resorb nutrients from senesced leaves depending on the absolute concentration of nutrients in mature leaves. If a nutrient is abundant in mature leaves, the RE is low; if scarce, its RE is high (Richardson et al. 2005). The nutrient limitation control strategy predicts that the NuR depends on the nutrient limitation status of plants (Güsewell 2005). N- or P-limited plants will resorb more of the respective nutrients from senesced leaves. Finally, the stoichiometry control strategy suggests that NuR from senesced leaves is dependent upon the nutrient stoichiometry of mature leaves (Güsewell 2005; Han et al. 2013).

Besides the mature leaf N, P and N:P ratio, N and P resorption efficiencies (NRE and PRE) and proficiencies (NRP and PRP) vary across plant functional groups (Estiarte et al. 2023; He et al. 2020; Xu et al. 2021). On average, herbs exhibit significantly higher NRE and PRE, as well as NRP and PRP (Killingbeck 1996), than woody plants (He et al. 2020). Compared to evergreen species, deciduous species have higher NRE but significantly lower PRE (He et al. 2020). Species identity also plays a crucial role in regulating the RE and RP (He et al. 2020; Zhi et al. 2023). Estiarte et al. (2023) argued that the leaf NuR exhibits significant interspecies variability, which is genetically determined.

Moreover, variation of ^{15}N natural abundance (δ^{15}N) can potentially reveal the biochemical processes involved in the N resorption from senescing leaves (Kolb and Evans 2002). As amino acids are the primary form of N transport, variations in their composition may influence the N isotope ratios (C. Li et al. 2019). Processes such as chlorophyll degradation, protein hydrolysis and ammonia volatilization during leaf N resorption cause significant isotope fractionation, resulting in δ^{15}N enrichment in senesced leaves (Kolb and Evans 2002; Yue et al. 2013). However, if no N isotope fractionation occurs, this may indicate that plants resorb ^{14}N and ^{15}N in the same proportion, leaving the underlying biochemical processes unclear (Garten et al. 2011; Templer et al. 2007). Furthermore, changes in leaf δ^{15}N during senescence can indicate nutrient limitation status. N-limited plants exhibit no significant N isotope fractionation, whereas P-limited plants show notable fractionation (Wanek and Zotz 2011). Despite many studies have examined leaf N resorption, few have utilized isotope analysis to investigate N isotope fractionation during this process, particularly in epiphytes (Enta et al. 2020; Kolb and Evans 2002).

Epiphytes are particularly crucial components of forest ecosystems in southwest China (Hu et al. 2023; Su et al. 2023). Due to their unique habitats and difficulties in access, little is known about their leaf NuR, especially in Asia (Wu et al. 2016). To our knowledge, only three studies have reported on the NRE and PRE of epiphytes (W. Zhang et al. 2022; Zotz 2004; Suriyagoda et al. 2018). To test whether their resorption mechanism aligns with that of terrestrial plants globally, we collected mature and senesced leaves from 10 common vascular epiphytes with varying characteristics in subtropical forests in southwest China. We also integrated relevant data from a previous study in a tropical lowland forest (Zotz 2004) to explore control strategies on N and P resorption of epiphytes. Our main objectives were: (1) to identify a reliable index for assessing the NuR; (2) to determine the leaf resorption strategies of epiphytes; (3) to evaluate the impact of factors on resorption; and (4) to assess the variation of δ^{15}N during the resorption process. We hypothesize that: (1) the RE_{leaf} will be more reliable than the RE_{mass} or RE_{area} due to mass and area loss during senescence (P. Lin and Wang 2001); (2) the resorption of epiphytes will follow all three strategies, with stoichiometry control strategy coexisting with nutrient limitation control strategy, according to those of terrestrial plants (Chen et al. 2021; Sun et al. 2023) and previous research in this region (J. B. Huang et al. 2019; W. Zhang et al. 2022); and (3) resorption and (4) ^{15}N fractionation of epiphytes will be group- and species-specific based on previous research regarding N and P limitations in epiphytes in this area (J. B. Huang et al. 2019).

2 | Materials and Methods

2.1 | Sampling Sites

The study was conducted in the Xujiaba region of the Ailao Mountains National Nature Reserve (23°35′−24°44′ N, 100°54′−101°30′ E) in central Yunnan Province, southwest China. The area is at an altitude of 2400−2750 m. The mean annual precipitation is 1947 mm, the mean annual relative humidity is 85%, and the mean annual temperature is 11.3°C (S. Li et al. 2013). The predominant vegetation is montane moist evergreen broad-leaved forest, including the dominant tree species *Lithocarpus xylocarpus*, *Castanopsis wattii* and

Lithocarpus hancei (Qiu and Xie 1998). The primary forest contains a highly diverse epiphyte community comprising lichens (217), bryophytes (176), ferns (117) and spermatophytes (113) (J. B. Huang et al. 2019; S. Li et al. 2013). The dominant vascular epiphytes include *Polygonatum punctatum*, *Cautleya gracilis* and *Aeschynanthus buxifolius* (J. B. Huang et al. 2019).

2.2 | Sampling and Measurement

We selected 10 common vascular epiphytes with different characteristics for analysis, including evergreen versus deciduous, herb versus woody and ferns versus monocots versus dicots (Supporting Information S1: Figure S1; Table 1). As most epiphyte individuals are relatively small, individual N storage would change significantly if a certain number of mature leaves were collected, thereby significantly influencing their NuR. We thus adopted an alternative method of collecting mature and senesced leaves from different individuals. In late August and September 2023, undamaged and fully expanded mature leaves were collected from the target vascular epiphytes, situated from 1 m above the ground (without contact with the ground) to the lower canopy using free-climbing and pole pruners. Senesced leaves were collected in late November and December 2023. To minimize sampling error at the individual level, each sample per species was taken from several healthy individuals growing on different trees, with more than 50 m between replicates. Each target species comprised 3–5 replicates.

All samples were immediately taken to the laboratory and the leaf area was measured using a flatbed scanner (Epson Perfection V700, Seiko Epson Corporation, Nagano, Japan) and the software WinRHIZO Pro 2009b (Regent Instruments, Quebec, Canada).

The samples were then washed with distilled water, dried at 60°C for at least 48 h, ground in a mill, sieved (60-mesh), and stored for chemical analyses. The P concentration was determined using an inductively coupled plasma atomic-emission spectrometer (iCAP6300, Thermo Fisher Scientific, USA) after digestion in HNO_3-$HClO_4$ and HCl, while N and $\delta^{15}N$ were measured using a continuous flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, USA) coupled with an elemental analyser (Flash 2000, Thermo Fisher Scientific, USA). The $\delta^{15}N$ values are expressed as ‰ deviation, relative to atmospheric N_2 ($\delta^{15}N = 0‰$):

$$\delta^{15}N \quad (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000 \qquad (1)$$

where R_{sample} and $R_{standard}$ are the isotope ratios ($^{15}N/^{14}N$) of the sample and standard substance, respectively. Analytical errors are less than 0.2‰ for $\delta^{15}N$.

Additionally, we attempted to explore the leaf NuR of epiphytes by integrating data from previous studies (W. Zhang et al. 2022; Zotz 2004; Suriyagoda et al. 2018). However, when data of cultivated *Pleione aurita* in W. Zhang et al. (2022) were excluded, and species-level data of epiphytes were unavailable in Suriyagoda et al. (2018), the available data were obtained only from Zotz (2004). This data set included N and P data from 34 individuals representing 20 vascular epiphyte species naturally growing in a moist tropical lowland forest in Panama (Supporting Information S1: Table S1).

2.3 | Parameter Calculations

The RE was calculated according to the following equations (P. Lin and Wang 2001):

$$RE_{leaf} = (1 - A_2/A_1) \times 100\% \qquad (2)$$

$$RE_{mass} = [1 - (A_2/A_1 \times W_1/W_2)] \times 100\% \qquad (3)$$

$$RE_{area} = [1 - (A_2/A_1 \times S_1/S_2)] \times 100\% \qquad (4)$$

where the RE_{leaf}, RE_{mass} and RE_{area} are the REs based on leaf unit basis (mg/leaf), per unit leaf mass (mg/g) and per unit leaf area (mg/cm^2), respectively (Table 2). The A_1 and A_2, W_1 and W_2 and S_1 and S_2 are the mean nutrient content (mg), mass (g) and area (cm^2) per mature and senesced leaf, respectively.

The variation of $\delta^{15}N$ ($\Delta^{15}N$; Table 2) was calculated as follows (Yue et al. 2013):

TABLE 1 | The 10 target vascular epiphyte species in the Xujiaba region of the Ailao Mountains.

Species	Leaf habit	Growth form	Phylogenetic group
Aeschynanthus buxifolius	Evergreen	Woody	Dicot
Briggsia longifolia	Evergreen	Herb	Dicot
Haplopteris flexuosa	Evergreen	Herb	Fern
Lepisorus loriformis	Evergreen	Herb	Fern
Polygonatum punctatum	Evergreen	Herb	Monocot
Begonia yui	Deciduous	Herb	Dicot
Cautleya gracilis	Deciduous	Herb	Monocot
Lepisorus scolopendrium	Deciduous	Herb	Fern
Pleione hookeriana	Deciduous	Herb	Monocot
Sorbus rhamnoides	Deciduous	Woody	Dicot

TABLE 2 | List of common abbreviations.

Key terms	Abbreviation (unit)
Nutrient resorption	NuR
N or P concentration of mature leaves	N_m; P_m (mg/g)
N or P concentration of senesced leaves	N_s; P_s (mg/g)
Resorption proficiency	RP (mg/g)
N or P resorption proficiency	NRP; PRP (mg/g)
Resorption efficiency	RE (%)
Resorption efficiency per leaf unit basis, per unit leaf mass or per unit leaf area	RE_{leaf}; RE_{mass}; RE_{area} (%)
N or P resorption efficiency	NRE; PRE (%)
N resorption efficiency per leaf unit basis, per unit leaf mass or per unit leaf area	NRE_{leaf}; NRE_{mass}; NRE_{area} (%)
P resorption proficiency per leaf unit basis, per unit leaf mass or per unit leaf area	PRE_{leaf}; PRE_{mass}; PRE_{area} (%)
Leaf N isotope natural abundance	$\delta^{15}N$ (‰)
The percental variation of $\delta^{15}N$ during leaf senescence	$\Delta^{15}N$ (%)

$$\Delta^{15}N = (\delta^{15}N_s - \delta^{15}N_m)/|\,\delta^{15}N_m\,| \times 100\% \qquad (5)$$

where the $\delta^{15}N_m$ and $\delta^{15}N_s$ are the $\delta^{15}N$ of mature and senesced leaves, and the |##| denotes the absolute value.

The resorbed N:P ratio was calculated as follows (Chen et al. 2021; Sohrt et al. 2018):

$$\text{Resorbed N:P} = (N_m - N_s)/(P_m - P_s) \qquad (6)$$

where the N_m and N_s and P_m and P_s are the N and P concentrations (mg/g) of mature and senesced leaves (Table 2), and the $(N_m - N_s)$ and $(P_m - P_s)$ denote absolute N and P resorption, respectively.

2.4 | Criteria and Assessment of Nutrient Limitation and Control Strategy

Three parameters were measured to assess the potential nutrient limitation status of epiphytes. First, if the mature leaf N:P ratio is < 10, the plant is likely N-limited; if the N:P ratio > 12, it indicates P-limited. If the N:P ratio is between 10 and 12, the plant may be co-limited by both N and P, or it may not be limited by either nutrient (Wanek and Zotz 2011). However, plants are rarely free from nutrient limitation under natural conditions (Wanek and Zotz 2011). Second, a leaf NRE:PRE ratio of < 1 or > 1 implies P- or N-limited, respectively (Du et al. 2020). Finally, N-limited plants exhibit no significant ^{15}N fractionation during leaf senescence, whereas P-limited plants show significant ^{15}N fractionation (Wanek and Zotz 2011).

According to Killingbeck (1996), certain thresholds in leaf N_s or P_s are used to determine whether the resorption is complete or not. A leaf $N_s < 7$ mg/g indicates biochemically complete resorption, while $N_s > 10$ mg/g indicates incomplete resorption (Figure 1A). In evergreen species, a leaf $P_s < 0.4$ mg/g or > 0.5 mg/g denote complete or incomplete P resorption, respectively. In deciduous species, a leaf $P_s < 0.5$ mg/g or > 0.8 mg/g indicates complete or incomplete P resorption, respectively (Figure 1B). Complete resorption is synonymous with high RP, while incomplete resorption is synonymous with low RP (Killingbeck 1996).

The control strategies on leaf NuR of N and P were determined as follows (Supporting Information S1: Figure S2): For plants with the nutrient concentration control strategy, the RE would decrease significantly as mature leaf concentrations increase (Kobe et al. 2005), accompanied by a significantly positive correlation between the nutrient concentrations of mature leaves and those of senesced leaves (Chen et al. 2021). For plants with the stoichiometry control strategy, a significantly positive correlation between leaf NRE and PRE is a fundamental premise (Aerts 1996; Chen et al. 2021). If plants adopt this strategy alone, the leaf NRE:PRE ratio (or resorbed N:P) should be significantly and positively related to the leaf N_m:P_m ratio and all data should adhere to a 1:1 line (Chen et al. 2021; Güsewell 2005). If plants adopt the nutrient limitation control strategy alone, the NRE should significantly decrease and PRE significantly increase as the N_m:P_m increases (Güsewell 2005; Sorrell et al. 2011), and simultaneously the NRE:PRE should be negatively related to the N_m: P_m (Han et al. 2013).

2.5 | Statistical Analysis

Before comparing nutrient indices between mature and senesced leaves within and across species and functional groups, all data were tested for normality using a Shapiro–Wilk test and for homogeneity of variance using Bartlett's test. The data that met these assumptions were analysed with one-way ANOVA and Tukey's HSD test for multiple pairwise comparisons, while the data that did not meet the assumptions were analysed with a nonparametric Kruskal–Wallis test and Dunn's test.

Simple linear regression analyses were employed to examine the relationships between the resorption variables. Generalized Linear Models were used to identify the predictors of the NRE, PRE and $\Delta^{15}N$. All predictors were standardized before analysis using *Z*-scores to interpret parameter estimates on a comparable scale and were checked for collinearity using Pearson's correlation analysis. When the pairwise correlation coefficient was

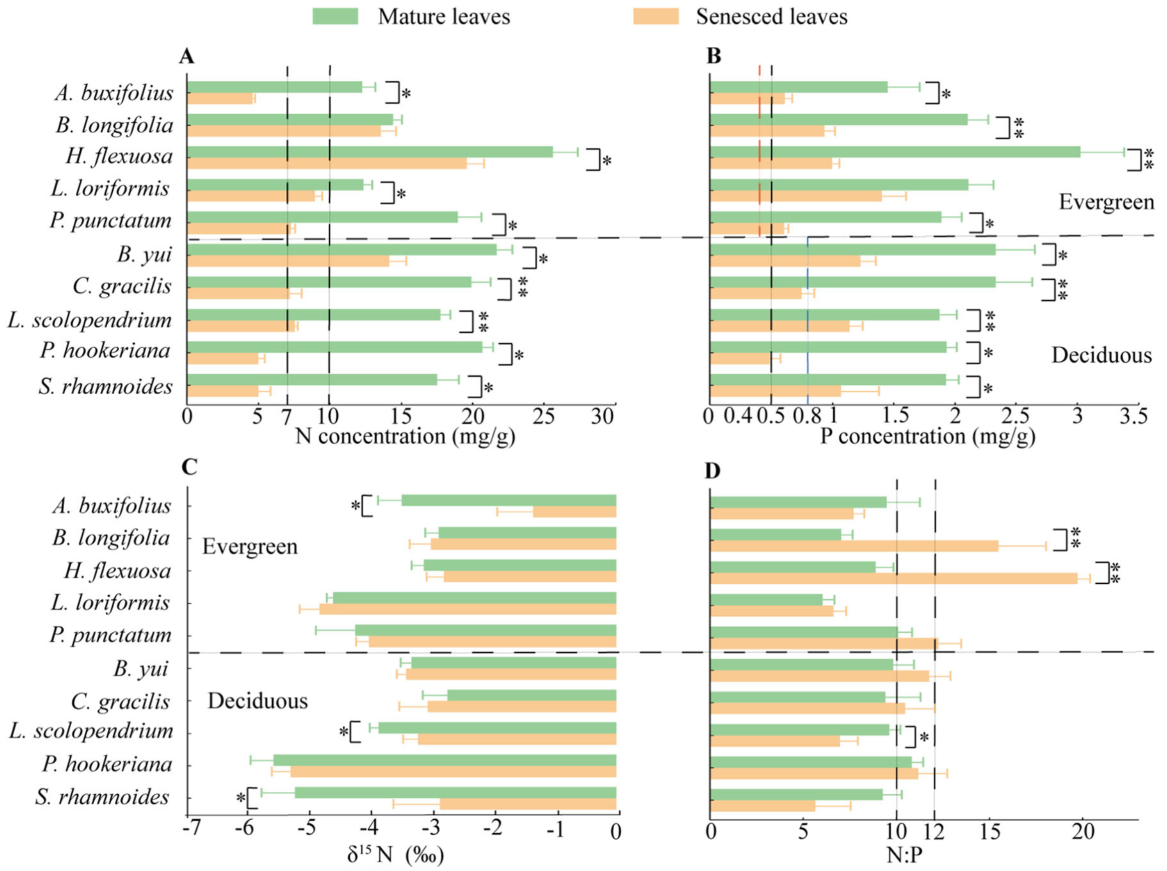

FIGURE 1 | The values of leaf N concentrations (A), leaf P concentrations (B), δ^{15}N (C) and the N:P ratios (D) (mean ± standard error) of 10 epiphyte species ($*p < 0.05$; $**p < 0.01$; no asterisks denote nonsignificance). In each panel, evergreen species are above the horizontal dashed line, while deciduous species are below. (A and D), Vertical line values for senesced and mature leaves serve as thresholds for N resorption completeness and nutrient limitation status, respectively (Killingbeck 1996; Wanek and Zotz 2011). (B) Red and black lines indicate P resorption completeness thresholds of senesced leaves in evergreen species (Killingbeck 1996), while black and blue lines represent thresholds for deciduous species. (C) The asterisks signifie significant ^{15}N fractionation during leaf senescence.

high ($|r| \geq 0.7$), one of the variables was removed, followed by the one with the highest generalized variance inflation factor (GVIF) among the remaining variables, and the model was refitted. This process was repeated until all continuous variables exhibited GVIF < 10 and categorical variables exhibited $\text{GVIF}^{(1/2\times\text{df})} < \sqrt{10}$ (mentioned as the full models). To identify the best predictors, model selection was further conducted using the dredge function in the R package MuMIn based on the corrected Akaike's information criterion (AICc; $\Delta\text{AICc} < 2$) (mentioned as the optimal model) (Barton 2023). Additionally, to estimate the individual fixed effects of the predictors, variance decomposition analysis for both the full and optimal models was conducted using the glmm.hp package (Lai et al. 2022).

All data analyses were conducted in R 4.2.1 (R Core Team 2022).

3 | Results

3.1 | Leaf N, P and δ^{15}N Values in Vascular Epiphytes

The mean N and P concentrations were significantly higher in mature leaves ($N_m = 18.12 \pm 1.34$ mg/g, $P_m = 2.10 \pm 0.13$ mg/g) than in senesced leaves ($N_s = 9.29 \pm 1.56$ mg/g, $P_s = 0.92 \pm 0.10$ mg/g) for most epiphyte species (Figure 1A,B), indicating that the NuR had occurred in them.

The mean leaf N_m:P_m ratio was 9 (Figure 1D), suggesting that most studied epiphytes were primarily N-limited, while *P. punctatum* and *Pleione hookeriana* (with the N_m:P_m ratios ranging from 10 to 12) appeared to be co-limited by both N and P.

N isotopic fractionation was found to be species-specific during leaf N resorption, with significant fractionation observed only in *A. buxifolius, Lepisorus scolopendrium* and *Sorbus rhamnoides* (Figure 1C). Together, these results implied once again that epiphytes were primarily N-limited, although some species may also be P-limited.

3.2 | Resorption Characteristics of Leaf N, P and δ^{15}N in Vascular Epiphytes

For senesced leaf N (Figure 1A), *A. buxifolius*, *P. hookeriana* and *S. rhamnoides* had high RPs ($N_s < 7$ mg/g), whereas *Briggsia longifolia*, *Haplopteris flexuosa* and *Begonia yui* exhibited low RPs ($N_s > 10$ mg/g). For senesced leaf P (Figure 1B), most species exhibited low RPs, suggesting that the studied species may not be P-limited.

Significant interspecies differences in leaf NRE and PRE were observed (Table 3). The mean NRE_{leaf} was 14.70% (0%–57.60%) and 3.90% (0.10%–12.70%) higher than the mean NRE_{mass} and NRE_{area} (Supporting Information S1: Table S2), respectively, corresponding to a 25.72% (0%–61.20%) loss in mass and an 8.64% (0.78%–23.30%) loss in area during leaf senescence (Supporting Information S1: Table S3). Similar patterns were observed for the PRE, with underestimations of 12% (0%–33.60%) for the mean PRE_{mass} and 3.80% (0.20%–11.60%) for the mean PRE_{area} compared to the mean PRE_{leaf} (Supporting Information S1: Table S2). Furthermore, variation in the three PREs was generally more pronounced than variation in the three NREs (standard error: 1.44–18.90 vs. 0.63–7.46 for the PREs and NREs) (Table 3). The mean NRE:PRE ratios across all three contexts were > 1, indicating once again that our study species were likely N-limited at the community level, though some species may be P-limited (that of five epiphyte species < 1, Table 3).

In all three bases, both NREs and PREs tended to exhibit consistent patterns across functional groups (Figure 2; Supporting Information S1: Figure S3), although some differences were not statistically significant. Deciduous epiphytes had significantly higher NREs than evergreen ones (Figure 2A; Supporting Information S1: Figure S3A,B). Woody epiphytes had significantly higher NRE_{mass} than herbs (Figure 2B). Monocots had significantly higher NRE_{mass} and PRE_{mass} than ferns and dicots (Figure 2C,F), and significantly higher NRE_{leaf} than ferns (Supporting Information S1: Figure S3K). No significant differences were observed in the remaining comparisons. Regarding leaf $\Delta^{15}\text{N}$, only woody epiphytes had a significantly higher $\Delta^{15}\text{N}$ than herbs (Figure 2H).

3.3 | NuR Strategies of Vascular Epiphytes

Three basic control strategies were evaluated using three epiphyte data sets (Figure 3). First, all data sets showed that both leaf N_{s} and P_{s} (Figure 3D,I), as well as NRE_{mass} and PRE_{mass} (Figure 3A,F), increased with the leaf N_{m} and P_{m}, respectively, which did not fully meet the criteria for the nutrient concentration control strategy. Second, in both Zotz's and the full data sets, the NRE_{mass} and PRE_{mass} were significantly positively correlated (Figure 3C), as were the resorbed N:P and N_{m}:P_{m} ratios, although they did not adhere to a 1:1 line (Figure 4). However, a similar relationship was not statistically significant in our data set. Furthermore, no significant correlations were observed between the NRE_{mass}:PRE_{mass} and N_{m}:P_{m} in any of the data sets (Figure 3H). These results suggested that epiphytes favoured the stoichiometry control strategy, albeit accompanied by other strategies (i.e., nutrient limitation control strategy). Third, the NRE_{mass} did not significantly decrease, and the PRE_{mass} did not significantly increase with increased N_{m}:P_{m} in any data set (Figure 3B,G), suggesting that epiphytes did not utilize nutrient limitation control strategy independently. Finally, Zotz's data set indicated that the studied epiphytes were P-limited ($\text{N}_{\text{m}}:\text{P}_{\text{m}} = 16.06$ and $\text{NRE}_{\text{mass}}:\text{PRE}_{\text{mass}} < 1$), and their PREs were higher than NREs (Figure 4; Supporting Information S1: Table S1), confirming that the NuR of tropical Panamanian epiphytes employed nutrient limitation control strategy. In contrast, our data revealed that one epiphyte subgroup (*A. buxifolius*, *L. scolopendrium*, *P. hookeriana* and *S. rhamnoides*) had higher NREs than PREs, while the other species exhibited the opposite trend under N-limited conditions, implying that only the former employed nutrient limitation control strategy. Overall, it appeared that the NuR of epiphytes was governed by the combined stoichiometry and nutrient limitation control strategies in tropical Panamanian, while our epiphytes employed either the combined strategies or the stoichiometry control strategy alone.

Additionally, leaf $\Delta^{15}\text{N}$ was positively (but not significantly) correlated ($r^2 = 0.18$, $p = 0.22$) with leaf NRE_{mass} (Figure 3E), and negatively (but not significantly) correlated ($r^2 = 0.10$, $p = 0.37$) with leaf N_{m} at the species level (Figure 3J). Interestingly enough, the $\Delta^{15}\text{N}$ was negatively and marginally significantly correlated with the P_{m} ($r = -0.53$, $p = 0.11$) at the species level (Supporting Information S1: Figure S4A), and significantly negatively correlated with the P_{m} ($r = -0.38$, $p = 0.01$) for all the samples (Supporting Information S1: Figure S4B; Table S4). Structural equation models were also generated, but the path coefficient between $\Delta^{15}\text{N}$ and P_{m} was too high (absolute value > 1) to be displayed.

3.4 | Variations and Drivers of the NuR in Vascular Epiphytes

Our data showed that the full models explained high proportions of variance in the three NREs ($R^2 = 0.86$–0.88) for epiphytes, with three categorical variables and two interaction terms representing the functional group types, explaining 63.71%–79.61% of R^2 (Table 4). The optimal models further highlighted the interaction between leaf habit and the phylogenetic group as the predominant factor influencing leaf NRE_{leaf} (40.85% of R^2) and NRE_{area} (46.10% of R^2), whereas leaf NRE_{mass} was only affected by their additive effects (Supporting Information S1: Table S5).

Apart from the functional group, the interaction between leaf N_{m} and P_{m} ($\text{N}_{\text{m}}\times\text{P}_{\text{m}}$) and N_{m}:P_{m}, but not N_{m} or P_{m} alone, had greater impacts on three NREs (3.85%–24.40% and 11.90%–16.55% of R^2, respectively) (Table 4). Similar patterns were observed for the three leaf PREs, albeit with moderate proportions of variance ($R^2 = 0.53$–0.63) (Table 4). The optimal models again corroborated these results (Supporting Information S1: Table S5). These findings further suggested that epiphytes adopted stoichiometry and nutrient limitation control strategies (Figures 3 and 4).

For leaf $\Delta^{15}\text{N}$ (Table 4), the full models explained moderate proportions of variance ($R^2 = 0.49$). Overall, $\Delta^{15}\text{N}$ was primarily influenced by the functional group types (88.57% of R^2), as well as by the leaf $\text{N}_{\text{m}}\times\text{P}_{\text{m}}$ and N_{m}:P_{m} (3.21% and 8.22% of R^2, respectively).

Moreover, in Zotz's data set, the full models had very low explanatory power for leaf NRE and PRE, likely due to the homogeneous nature of the functional groups (Table 4). In the full data set, the full models further reinforced the general importance of functional group in leaf NuR.

TABLE 3 | The leaf NRE, PRE and their ratios of 10 epiphyte species (mean ± standard error).

Species	NRE_{leaf} (%)	NRE_{mass} (%)	NRE_{area} (%)	PRE_{leaf} (%)	PRE_{mass} (%)	PRE_{area} (%)	NRE_{leaf}: PRE_{leaf}	NRE_{mass}: PRE_{mass}	NRE_{area}: PRE_{area}
A. buxifolius	72.8 ± 1.14 bA	62.6 ± 1.57 bcB	72.2 ± 1.17 bA	69.6 ± 3.27 bcdA	58.1 ± 4.50 abcA	68.9 ± 3.35 bcdA	1.05 ± 0.04 abA	1.09 ± 0.07 abA	1.05 ± 0.04 abcA
B. longifolia	63.5 ± 2.89 cdA	5.9 ± 7.46 eB	61.4 ± 3.06 cA	82.9 ± 1.66 aA	55.8 ± 4.28 bcB	81.9 ± 1.76 aA	0.77 ± 0.04 cdA	0.11 ± 0.14 eB	0.75 ± 0.04 deA
H. flexuosa	24.1 ± 4.76 eA	23.6 ± 4.79 deA	19.2 ± 5.06 dA	67.3 ± 2.01 cdeA	67.1 ± 2.02 abA	65.2 ± 2.14 cdeA	0.35 ± 0.06 dA	0.35 ± 0.06 deA	0.29 ± 0.07 eA
L. loriformis	39.3 ± 3.85 eA	27.4 ± 4.60 deA	26.6 ± 4.65 dA	44.3 ± 7.87 eA	33.4 ± 9.41 dA	32.7 ± 9.51 eA	1.01 ± 0.24 bcA	1.56 ± 0.90 bcA	1.76 ± 1.10 cdA
P. punctatum	72.8 ± 1.28 bA	61.7 ± 1.81 bcB	64.5 ± 1.67 bcB	77.4 ± 1.44 abcA	68.2 ± 2.02 abB	70.6 ± 1.87 abcdB	0.94 ± 0.03 abcA	0.91 ± 0.05 abcA	0.92 ± 0.04 bcdA
B. yui	59.1 ± 3.57 dA	34.7 ± 5.70 dB	58.5 ± 3.63 cA	67.1 ± 3.46 cdeA	47.5 ± 5.52 cdB	66.6 ± 3.51 cdeA	0.88 ± 0.06 bcA	0.75 ± 0.13 cdA	0.88 ± 0.06 cdA
C. gracilis	63.9 ± 4.2 bcdA	63.9 ± 4.20 bA	61.9 ± 4.43 cA	68.1 ± 4.72 cdA	68.1 ± 4.72 abA	66.3 ± 4.98 cdA	0.96 ± 0.10 bcA	0.96 ± 0.10 bcA	0.95 ± 0.11 cdA
L. scolopendrium	81.0 ± 0.63 aA	57.4 ± 1.41 cB	80.9 ± 0.63 aA	72.9 ± 2.61 bcdA	39.3 ± 5.87 dB	72.7 ± 2.64 abcA	1.12 ± 0.04 aA	1.60 ± 0.25 aA	1.12 ± 0.04 abA
P. hookeriana	82.5 ± 1.58 aA	75.7 ± 2.19 aA	81.1 ± 1.71 aA	81.9 ± 3.45 abA	74.9 ± 4.79 aA	80.4 ± 3.74 abA	1.01 ± 0.03 abA	1.02 ± 0.05 abcA	1.01 ± 0.03 abcA
S. rhamnoides	71.8 ± 4.77 bcA	71.3 ± 4.86 abA	66.1 ± 5.75 bcA	45.2 ± 15.7 deA	44.2 ± 16.0 cdA	34.0 ± 18.9 deA	1.98 ± 0.58 aA	2.07 ± 0.64 aA	5.13 ± 3.34 aA
Total	63.1 ± 3.24 A	48.4 ± 4.31 B	59.2 ± 3.61 A	67.7 ± 6.16 A	55.7 ± 7.07 B	63.9 ± 7.26 A	1.01 ± 0.20 A	1.04 ± 0.37 A	1.39 ± 1.11 A

Note: Different lowercase letters indicate significant differences among species in the same column, while different uppercase letters indicate significant differences in the NRE, PRE or their ratios across the three bases within the same species ($p < 0.05$). Term abbreviations follow Table 2.

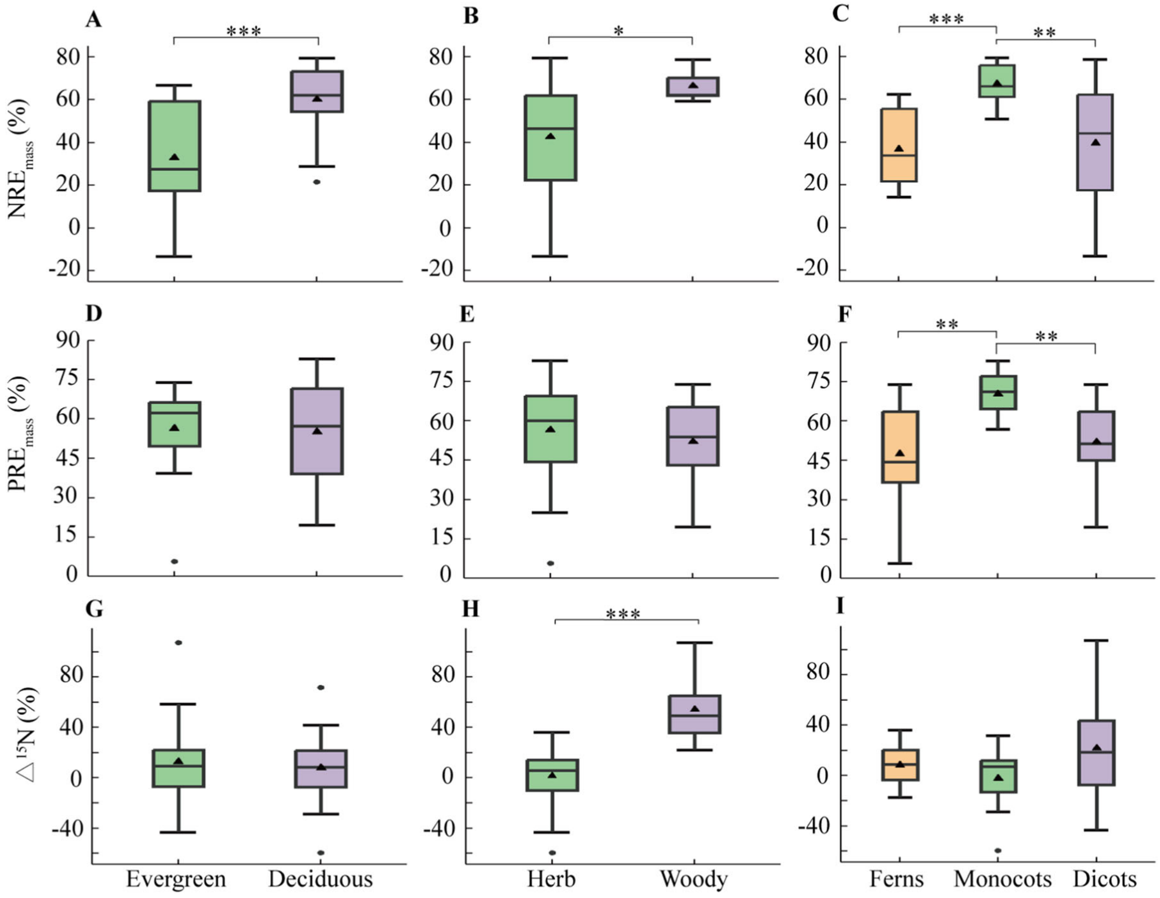

FIGURE 2 | Comparisons of leaf NRE_{mass} (A–C), PRE_{mass} (D–F) and $\Delta^{15}N$ (G–I) among various functional groups of epiphytes (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; no asterisks denote non-significance, $p > 0.05$). Term abbreviations follow Table 2. [Color figure can be viewed at wileyonlinelibrary.com]

4 | Discussion

4.1 | N and P Limitation of Epiphytes

Despite general interest in canopy epiphytes, it remains an open debate whether they are globally N or P-limited. At the global scale, Hietz et al. (2022) analyse 2882 species of vascular epiphytes, representing 40 families and spanning five continents, and find that the mean leaf N_m is 12.9 mg/g and that the leaf N_m:P_m ratios for 61% of species are < 10, strongly supporting the notion that epiphytes are predominantly N-limited. Here, we found that the mean leaf N_m (18.12 ± 1.34 mg/g) of our epiphytes was significantly higher than that of epiphytes in Panama (13.75 mg/g) (Zotz 2004) and the global mean of epiphytes (Hietz et al. 2022), slightly higher than that of epiphytes in tropical forests of Sri Lanka (17.27 mg/g) (Suriyagoda et al. 2018), but slightly lower than the global mean of terrestrial plants (18.74 mg/g) (Han et al. 2005; Tian et al. 2021). These results were in good agreement with previous studies in our study area (J. B. Huang et al. 2019). Based on the three parameters of assessing nutrient status, however, we further concluded that epiphytes should still be primarily N-limited at the community level in the subtropical Ailao Mountains.

In contrast, the mean leaf P_m (2.10 ± 0.13 mg/g) of epiphytes in our study, in accordance with earlier studies in the same area (J. B. Huang et al. 2019), was considerably higher than the values reported by Zotz (2004) (1.04 mg/g) and Suriyagoda et al. (2018) (0.88 mg/g), as well as the global mean of 1.21 mg/g for terrestrial plants (Han et al. 2005; Tian et al. 2021). Soil nutrient sources can directly or indirectly influence epiphyte diversity and productivity (Benner and Vitousek 2007; Suriyagoda et al. 2018; Su et al. 2023). Therefore, the observed higher leaf P_m of our epiphytes may be attributed to the elevated P levels in the canopy (total P = 1.24 mg/g and available P = 85.55 mg/kg) (Z. X. Li. 2012) and floor soil (total P = 1.17 mg/g and available P = 2.39 mg/kg) (Z. Y. Lu et al. 2017) of the study forest, compared to other subtropical forest floor soil in China (total P = 0.20 mg/g and available P = 1.75 mg/kg) (W. Huang et al. 2013; X. Zhang et al. 2018). Nevertheless, previous studies have concluded that epiphytes are generally P-limited rather than N-limited, or co-limited by both N and P (Wanek and Zotz 2011; Zotz and Asshoff 2010), as is the case in moist tropical lowland forests in Panama (Zotz 2004). Unlike tropical epiphytes (Wanek and Zotz 2011; Zotz and Asshoff 2010; Suriyagoda et al. 2018), epiphytes were primarily N-limited in the subtropical Ailao Mountains, though some species might be P-limited or N and P co-limited. Furthermore, the significant negative correlation between leaf $\Delta^{15}N$ and P_m (Supporting Information S1: Figure S4B; Table S4) indicated that N-limitation experienced by our epiphytes was likely a response to the higher available P in the local environment, leading to a greater relative demand for N.

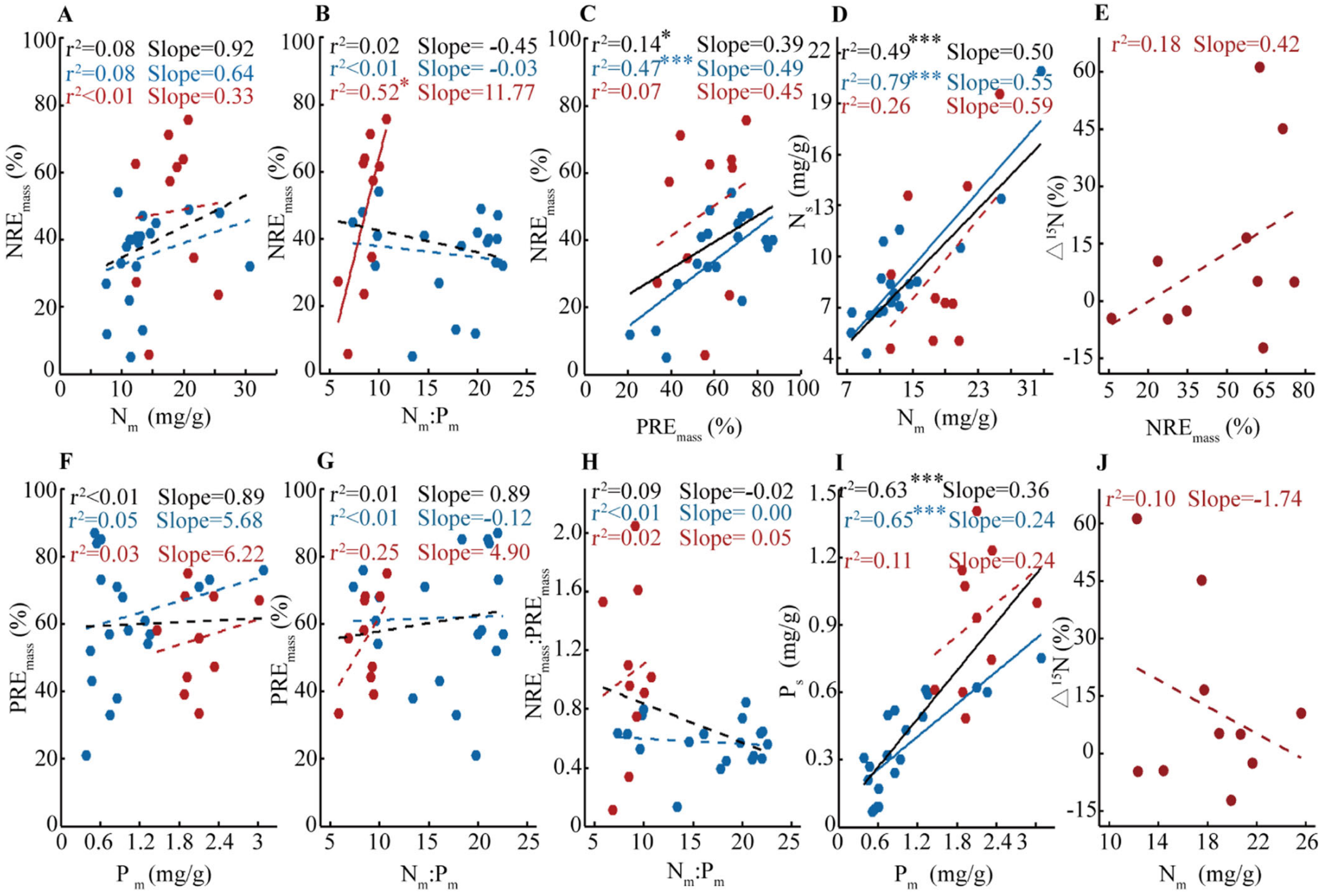

FIGURE 3 | Correlations between N_m and NRE_{mass} (A), N_m:P_m and NRE_{mass} (B), PRE_{mass} and NRE_{mass} (C), N_m and N_s (D), NRE_{mass} and $\vartriangle^{15}N$ (E), P_m and PRE_{mass} (F), N_m:P_m and PRE_{mass} (G), N_m:P_m and NRE_{mass}:PRE_{mass} (H), P_m and P_s (I), N_m and $\vartriangle^{15}N$ (J) of epiphytes. Term abbraviations follow Table 2. In each panel, red, blue and black points and lines represent our dataset, Zotz's dataset, and full dataset, respectively. Solid and dashed lines indicate significant and nonsignificant effects between variables, respectively (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; unmarked data were not significant, $p > 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

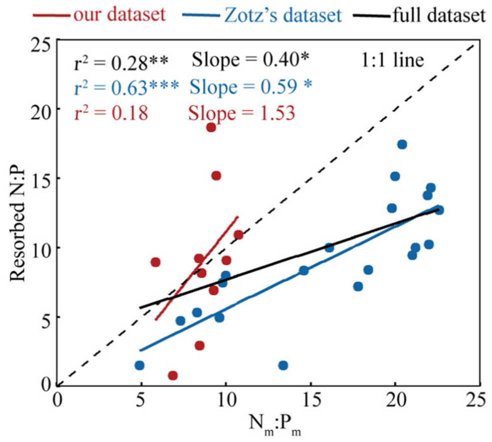

FIGURE 4 | Linear regressions of the resorbed N:P and N_m:P_m ratios. A dashed line representing a 1:1 ratio is included in the panel for reference. A slope significantly greater than 1 indicates higher N resorption, while a slope significantly less than 1 indicates higher P resorption (Chen et al. 2021) (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; unmarked data were not significant, $p > 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

4.2 | Ecological Implications of RE Calculated on Different Bases

When considering the effects of leaf senescence, the RE_{leaf}, RE_{area} and RE_{mass} will be identical if leaf mass ($W_1 = W_2$) or area ($S_1 = S_2$) is not reduced. In reality, however, reductions in soluble carbon and other elements result in decreased leaf mass, while tissue water loss and resulting shrinkage lead to decreased leaf area (P. Lin and Wang 2001; J. Y. Lu et al. 2018). Nonetheless, studies based on leaf mass or area often fail to take these senescence-associated changes into account (Chapin and Kedrowski 1983; Killingbeck 1985; Pugnaire and Chapin 1993; van Heerwaarden et al. 2003), thereby underestimated the true RE (Pugnaire and Chapin 1993). Here, we found that the $RE_{mass} < RE_{area} < RE_{leaf}$, supporting the first hypothesis that the RE_{leaf} of epiphytes is more reliable than the RE_{mass} or RE_{area}. This is consistent with the findings in terrestrial plants (Y. M. Lin and Lobo Sternberg 2007). In addition, the RE_{leaf} and RE_{area} were significantly correlated ($r = 0.99$, Supporting Information S1: Table S4), suggesting that the RE_{area} can serve as a proxy for the RE_{leaf}.

TABLE 4 | Results of full linear models and variance decomposition analysis for the NREs and PREs across the three data sets and $\Delta^{15}N$ in our data set.

Predict factor	$\Delta^{15}N$	NRE_{leaf}	NRE_{mass}	NRE_{area}	PRE_{leaf}	PRE_{mass}	PRE_{area}	NRE_{zotz}	PRE_{zotz}	NRE_{full}	PRE_{full}
R^2	0.49	0.88	0.86	0.88	0.59	0.53	0.63	0.07	0.10	0.55	0.23
Relative contribution to R^2(%)											
Phylogenetic group (dicots)	7.14	7.47	15.12	7.56	8.37	25.24	6.82	—	—	29.19	76.46
Leaf habit (deciduous)	0.71	6.99	8.59	7.97	0.99	1.80	0.60	—	—	18.24	—
Growth form (herb)	36.24	1.63	11.84	1.33	8.39	0.34	7.66	—	—	16.86	2.03
Leaf habit×growth form	36.11	10.50	22.34	12.61	16.71	3.20	19.99	—	—	30.86	6.14
Leaf habit×phylogenetic group	8.37	37.12	21.72	40.78	44.93	37.44	44.23	—	—	—	—
N_m	—	—	—	—	—	—	—	81.35 (+)	—	—	—
P_m	—	—	—	—	—	—	—	—	67.08 (+)	—	—
$N_m \times P_m$	3.21 (−)	24.40 (−)	3.85 (−)	16.96 (−)	4.08 (+)	17.54 (+)	5.8 (+)	18.65 (+)	22.56 (−)	3.75 (+)	12.33 (+)
N_m:P_m	8.22 (+)	11.90 (+)	16.55 (+)	12.79 (+)	16.52 (+)	14.44 (+)	14.91 (+)	—	10.36 (+)	1.1 (−)	3.03 (+)

Note: R^2 represents the total proportion explained by all effects. "—" indicates that this factor is not included in the selected model. "×" indicates variable interactions. The symbols "+" and "−" in parentheses represent positive and negative coefficients for the continuous variables, respectively. The categorical variables and their interactions indicate the functional group types. Term abbreviations follow Table 2.

In the absence of comparable studies on senescence-associated changes in leaf mass and area in epiphytes, we compared our results with those from terrestrial plants. In terrestrial plants, senescence resulted in a 21% loss in leaf mass and an 11% loss in leaf area, leading to 10% and 6% underestimations of leaf RE, respectively (Aerts 1996; van Heerwaarden et al. 2003). Interestingly, mass loss was generally greater than area loss in both epiphytes and terrestrial plants, with the exceptions of *C. gracilis*, *S. rhamnoides*, *H. flexuosa* and *Lepisorus loriformis* in our study, as well as *Lyonia lucida* in the Delucia and Schlesinger (1995) study. In addition, the greater mass loss and smaller area loss in epiphytes, compared to terrestrial plants, may be attributed to the fact that epiphytic habitats are more stressful. In response, epiphytes have evolved remarkable morphological and physiological adaptations to resource limitations (Hietz et al. 2022). Faced with severe nutrient constraints, epiphytes may undergo more thorough leaf decomposition and element resorption to reduce their dependence on external nutrient sources (Zotz 2016), resulting in increased mass loss during senescence. Similarly, maintaining a larger leaf area enabled epiphytes to capture more light and rainwater in resource-limited canopies, thereby extending the duration of photosynthesis and enhancing NuR efficiency (Hietz et al. 2022; Oliwa et al. 2023; van Heerwaarden et al. 2003). These attributes may therefore lead to decreased area loss during senescence.

4.3 | N and P NuR Strategies of Epiphytes

We observed that limited environmental N and P promoted more effective NuR in epiphytes, and thereby, NuR played a significant role in alleviating these nutrient limitations (Aerts 1996). Oursecond hypothesis was also partially supported, as strategy analysis showed that epiphytes appeared to employ a combination of stoichiometry and nutrient limitation control strategies, and occasionally relied solely on stoichiometry strategy. First, the RE and RP played distinct roles in exploring leaf NuR patterns and mechanisms (Chen et al. 2021; Killingbeck 1996), reflecting complementary and fundamental aspects of the same process (Killingbeck 1996; Y. Y. Zhang et al. 2021). However, our analysis produced contradictory results. Second, we found that the stoichiometry control strategy was more ubiquitous than the nutrient limitation control strategy in our epiphyte community, consistent with findings in terrestrial plants (Chen et al. 2021; Sun et al. 2023). This may be because the stoichiometry control strategy is essential for maintaining stoichiometric homoeostasis in plants. This strategy likely requires relatively less energy than the nutrient limitation control strategy, which entails the selective transport of elements exceeding their budgets (Chapin and Kedrowski 1983). Finally, while the nutrient limitation control strategy is common across terrestrial plants adapting to the infertile environments (Chen et al. 2021; Estiarte et al. 2023; Güsewell 2005; Rejmánková 2005; Sorrell et al. 2011), however, it appears to be species-specific in epiphytes, coexisting with the stoichiometry control strategy.

Notably, the results of variance decomposition analysis further confirmed the above conclusion. Compared to N_m or P_m alone, the $N_m \times P_m$ and N_m:P_m explained 11.43%–36.30% of the variation (Table 4). The N_m:P_m highlighted the importance of stoichiometry. Negative coefficients for the $N_m \times P_m$ in NRE models suggested that the NREs decreased as the N_m and P_m increased together, while their positive coefficients in PRE models suggested that the PREs increased. These findings aligned with one of the definitions of the nutrient limitation control strategy (Güsewell 2005; Sorrell et al. 2011), supporting the existence of the nutrient limitation control strategy, whereas potentially negating the nutrient concentration control strategy.

All in all, we proposed that utilization of diverse strategies likely aids the adaptation of epiphytes to the highly variable N and P availability in the canopies, and promotes resource niche differentiation to minimize competition.

4.4 | Functional Group Type Driving NuR

In our study, the mean leaf NRE_{mass} and PRE_{mass} of 10 epiphyte species were 48.4% (5.9%–75.7%) and 55.7% (33.4%–74.9%), respectively. These values were closely aligned with global terrestrial plant averages of 50% (12.75%–72.94%) for the NREs and 52% (29.66%–97.62%) for the PREs (Vergutz et al. 2012) and fell within the range typical of N-limited environments in terrestrial plants (Peng et al. 2023). Moreover, we had lower means but similar ranges compared to those of reported epiphytes (NRE_{mass} 4.36%–78.8%; PRE_{mass} 18.42%–86.27%) (Suriyagoda et al. 2018; W. Zhang et al. 2022; Zotz 2004). Thus, we proposed that epiphytes adopted similar NuR strategies to those of terrestrial plants to cope with environmental nutrient stress. Moreover, the three leaf PREs were generally higher than three NREs, likely due to the fact that some N fractions are immobile, while most P is hydrolysable and can therefore be resorbed (Ågren 2008; Han et al. 2013). Consistent with findings in terrestrial plants (Aerts and Chapin 1999; Han et al. 2013), leaf PRE exhibited considerable variability (i.e., high SE). This may reflect a more sensitive response of plant P to environmental variability, as well as high variability in environmental P availability (rock origin) compared to N (biological origin) (Han et al. 2013). Furthermore, the variance decomposition analysis manifested that N resorption of epiphytes was primarily influenced by plant functional traits (Table 4 and Supporting Information S1: Table S2), while P resorption may be mainly influenced by environmental factors (such as climate and soil nutrient availability) rather than plant traits (Table 4 and Supporting Information S1: Table S2) (Tang et al. 2013).

The NuR mode of epiphytes was found to be both group- and species-specific, supporting the third hypothesis. At the species level, research suggested that leaf RE is genetically determined, albeit with significant interspecies variability (Estiarte et al. 2023). At the functional group level, a combination of ANOVA or nonparametric analysis, regression models, and variance decomposition analysis indicated that functional traits significantly influenced leaf RE in epiphytes. First, as observed in terrestrial plants (He et al. 2020), deciduous epiphytes exhibited a higher NRE than evergreen group (Figure 2A). This could be due to the inherently higher photosynthetic rates of deciduous plants Wright et al. 2004), which likely drive them to resorb more N from senescent leaves. Second, leaf NRE and PRE were highest in monocots, followed by dicots, and lowest in ferns, consistent with findings in terrestrial plants (Thompson et al. 1997; Xiong et al. 2020). Previous research attributed this pattern to the nutrient concentration control strategy (Sun et al. 2023), as both leaf N_m and P_m follow the same trend: monocots < dicots < ferns (Tian et al. 2018). For the studied epiphytes, however, we observed that leaf N_m followed the order ferns < dicots < monocots, whereas that of leaf P_m was dicots < monocots < ferns. These discrepancies may have arisen from the limited number of species in our analysis, as well as uneven sample sizes within these functional groups. More importantly, the interaction between leaf habits and phylogenetic groups was the primary factor influencing both leaf NRE and PRE. Finally, we found that woody epiphytes exhibited complete resorption and higher NRE compared to herbaceous epiphytes, which contradicts previous studies in terrestrial plants (Vergutz et al. 2012). Again, this discrepancy may be due to the relatively small sample size of woody epiphytes in our study, which reduced the statistical power of our analysis. In contrast, herbaceous epiphytes had slightly higher PRE than woody epiphytes, consistent with observations in terrestrial plants (He et al. 2020). Herbs are generally smaller and have limited nutrient sink pools and cycling, and therefore, must resorb more P from senescent leaves to meet their nutrient demands (Han et al. 2013; He et al. 2020).

4.5 | Implications of ^{15}N Variation and Its Physiological Mechanisms

We found that changes in $\delta^{15}N$ during leaf resorption of epiphytes were species-specific (Figure 1C), supporting the fourth hypothesis and aligning with previous findings on terrestrial plants (Kitayama and Iwamoto 2001; Kolb and Evans 2002). Variations in amino acids, the primary form of N transport, among species may influence the N isotope ratio, resulting in isotopic fractionation in some species but not in others (C. Li et al. 2019). As outlined in Table 4, we speculated that different functional groups of epiphytes exerted distinct changes in $\delta^{15}N$ during leaf resorption, a process not yet well studied in plants.

We also found a positive correlation between leaf $\Delta^{15}N$ and NRE_{mass} in epiphytes (Figure 3E), while the relationship between leaf $\Delta^{15}N$ and N_m was negative (Figure 3J), contrasting with the findings of Yue et al. (2013). However, the significant negative correlation between the $\Delta^{15}N$ and P_m (Supporting Information S1: Figure S3B) indicated that the low N isotope fractionation in our epiphytes was driven by higher leaf P_m inducing a relative N deficiency (McKee et al. 2002). Despite limited research on this parameter, it is a key piece of the resorption puzzle and warrants further study to explore underlying patterns and mechanisms.

5 | Conclusion

This study provided valuable insights into the leaf NuR characteristics of vascular epiphytes. Despite greater mass loss and smaller area reduction during senescence, the RE_{leaf} was more reliable, and epiphyte NRE and PRE were similar to those of terrestrial plants. The functional group type of plants was the primary factor influencing N resorption. Leaf $\delta^{15}N$ was indicative of the NuR of epiphytes, and its change was species-specific. However, the NuR strategies of epiphytes varied across regions. Tropical and subtropical epiphytes were respectively limited by P and N, with the former's resorption jointly regulated by stoichiometry and nutrient limitation control strategies, while the latter was controlled by either a combination of both strategies or stoichiometry control strategy alone. These results enhance our understanding of how epiphytes adapt to nutrient-poor canopies, though limited sample sizes may affect the generalizability of the conclusion. Despite the challenges of canopy access and obtaining sufficient representative samples, future studies should explore the NuR of epiphytes on a larger scale to expand on this work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.