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# Stoichiometric and isotopic flexibility: facultative epiphytes exploit rock and bark interchangeably

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ABSTRACT

Understanding the stoichiometric characteristics of plants to a substrate shift is a key step in the use of a stoichiometric framework to predict ecosystem responses to environmental change. However, the response and mechanism of stoichiometry to a substrate shift in facultative epiphytes remains unknown.

The foliar stoichiometric (N, P, K, Ca, Mg, S, Mn, Na, and Fe concentrations) and isotopic characteristics ($\delta^{13}C$ and $\delta^{15}N$) of nine facultative epiphyte species in Xishuangbanna karst forest in southwest China were determined. The stoichiometry and isotopy were compared between the epiphytic and lithophytic individuals in the facultative epiphytes, and the possible causes of changes in elemental concentrations to substrate shifts were studied.

We found that the lithophytes were enriched in $\delta^{15}N$ and Ca, but depleted in elements such as Fe, K, and Mn compared with the epiphytes. The $\delta^{15}N$ was positively correlated with P, N, S, and K, while the $\delta^{13}C$ was negatively correlated with $\delta^{15}N$, P, N, S, and Fe. Following a principal component analysis (PCA), the first axis loaded organically bound elements (P, N, and S), while the second axis loaded non-organically bound elements (Fe, Mn, and K). The variances of non-organically bound elements were mostly affected by the substrate-related factors than organically bound elements.

These results revealed that the substrate factor has a strong partitioning effect on elements such as K, Ca, Fe, Mn, and $\delta^{15}N$. The differences of element concentration and isotopy between the two ecotypes suggested stoichiometric and isotopic flexibility, which enabled facultative epiphytes to exploit rock and bark interchangeably.

## 1. Introduction

Ecological stoichiometry, i.e., the ratio and concentration of elements within biological organisms in relation to the structure and function of the ecosystem, can display both stoichiometric homeostasis and stoichiometric flexibility in response to environmental change (Elser et al., 2000; Sterner and Elser., 2002). Stoichiometric homeostasis means that the elemental ratios within organisms are relatively stable (Elser et al., 2010), while stoichiometric flexibility refers to the ability of organisms to adjust their elemental balance to environmental changes (Sterner and Elser., 2002; Sistla and Schimel., 2012). Changes in the resource availability of substrates will directly affect plant nutrient assimilation and change their stoichiometry (Reich and Oleksyn., 2004; Han et al., 2011; Yuan and Chen., 2015; Tian et al., 2019). The understanding of the stoichiometric flexibility of plants on different substrates is a key step in using a stoichiometric framework to predict the ecosystem response to disturbances (Sistla and Schimel., 2012). However, few studies were conducted on the effect of substrate shifts on plant stoichiometry (Sistla et al., 2015).

Stable isotope approach is an important ecological recorder. Analyses of isotope abundances variation have provided new insights into how organisms respond to ecological processes (West et al., 2006). The use of $\delta^{15}N$ to trace sources and pathways of nitrogen and $\delta^{13}C$ to estimate whole-plant water use efficiency for epiphytes have become important tools for ecological research (Querejeta et al., 2018). In general, factors such as life form (Watkins et al., 2007, Watkins and Cardelús., 2012) and taxa (Cardelús and Mack., 2010, Mardegan et al., 2011) would cause the differences in leaf N concentration and the depletion of $\delta^{15}N$ from epiphytes to their terrestrial counterpart. Furthermore, the nutritional microsites of the substrate can also cause the

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isotopy variation (Hietz et al., 2002, Wania et al., 2002), indicating the changes of the ratio between N demand and supply (Querejeta et al., 2018). On the other hand, $\delta^{13}C$ was not significantly changed along with epiphytic, transitional and terrestrial growth phases of *Ficus tinctoria* (Liu et al., 2014), but did deplete with increasing plant size in some epiphytic bromeliads (Hietz and Wanek., 2003). However, much less is known about the foliar elemental concentrations and isotopy respond to substrate shifts (Benzing, 1990; Watkins et al., 2007; Burns, 2010; Zotz, 2016).

Facultative epiphytes can use different substrates simultaneously, such as trees, rocks, or soil (Moffett, 2000; Nadkarni et al., 2001; Benzing 2012; Zotz, 2013a; Lu et al., 2015; Chen et al., 2019). They are ecotypes of the same species present on different substrates. Their use in studies avoids phylogenetic biases, enabling them to become ideal experimental materials for studying the relationship between stoichiometry and substrate shifts (Zotz, 2013a, b; 2016). It is unquestionable that water is abundantly supplied for terrestrial individuals compare with the epiphytes (Putz and Holbrook., 1989; Putz et al., 1995; Feild and Dawson., 1998; Liu et al., 2014). However, the stoichiometry and isotopy of epiphytic individuals does not always have a similar pattern to that of water (Zotz and Hietz., 2001; Zotz, 2016). For example, the foliar N concentration and $\delta^{15}N$ in an epiphytic individual of *Clusia* spp. was lower than that in a terrestrial individual (Wanek et al., 2002), but the opposite pattern was reported in *Ficus* spp. (Putz and Holbrook., 1989). In addition, no difference was reported in the foliar N concentration for facultative epiphytes such as *Aechmea lingulata* (Ball et al., 1991), *Tillandsia capillaris* (Abril and Bucher., 2009), and *Blechnum mochaenum* (Guzman-Marin and Saldana., 2017). These studies imply that epiphytic individuals of facultative epiphytes were generally not more nutrient limited than their terrestrial counterparts (Feild et al., 1996; Hao et al., 2016). Furthermore, epiphytes on thin branches without canopy soil or the upper canopy zones had lower N foliar concentrations and $\delta^{15}N$ than plants rooted on thick branches or the lower canopy zones, suggesting the variations in $\delta^{15}N$ were not simply caused by different N sources, but by different $\delta^{15}N$ discrimination (Hietz et al., 2002, Wania et al., 2002).

The diversity of facultative epiphytes usually peaks in habitats where the forest canopy converges with the forest floor (Benzing, 2004; Burns, 2010). In harsh arid habitats, for example, where the canopy and floor are not distinct, the number of hosts is limited and the competition among terrestrial species is reduced, with epiphytes usually growing on rock outcrops (Johansson, 1974; Zotz, 2005; Melo and Waechter., 2018). Rock and bark substrates are relatively harsh habitats compared with the soil (Benzing, 1990), in which water and humus have accumulated. These hard substrates are also difficult to penetrate and anchor on. The stability, penetrability, nutrient availability, and range of temperature fluctuation of lithophytic substrates (Freiberg, 2001) is generally higher than for epiphytic substrates (Zotz, 2016). The population structure (Bennett, 1991), population density (Gomez et al., 2006), and mycorrhizal fungal diversity (Xing et al., 2015) have been compared between epiphytes and lithophytes. However, the mechanism determining the preference for a substrate shift is largely unknown (Testo and Sundue., 2014; Zotz, 2016).

Plant stoichiometry is not only affected by substrate nutrients, but also by nutrient requirements that maintain their multiple functions (Tian et al., 2019). Most studies of the response of epiphyte stoichiometry to substrate shifts concentrated on N and P (Wanek and Zotz., 2011), while other elements and isotopy have rarely been studied (Querejeta et al., 2018). The chemical elements needed by plants can be divided into three categories: (1) organically bound elements (N, P, and S), (2) ionic elements (K, Ca, and Mg), and (3) trace elements (Fe, Mn, and Na), (Medina et al., 2017; Tian et al., 2019). These elements maintain the plant's ability to perform specific functions and are essential for growth. Elements such as N and P are essential nutrition, but are often limited in the natural environment. The concentration of these elements and their response to environmental changes are relatively stable in plants due to the constraints of physiology and nutrient balance (i.e., the stability of limiting elements hypothesis) (Han et al., 2011). Although Benzing (2004) proposed the environmental conditions convergence hypothesis to explain the occurrence of facultative epiphytes (Burns, 2010), the stoichiometric and isotopic characteristics of plants on both rock and trunk substrates has not yet been studied. The direction and scale of the response of the stoichiometry and isotopy to substrate shifts are still unknown (Tian et al., 2019).

The objective of the study was to determine how the stoichiometry and isotopy of facultative epiphytes respond to a substrate shift between rock and bark. We hypothesized the non-organically bound element contents and isotope abundance would be different between the lithophytes and epiphytes. To test this hypothesis, the foliar stoichiometric (N, P, K, Ca, Mg, S, Mn, Na, and Fe concentrations) and isotopic characteristics ($\delta^{13}C$ and $\delta^{15}N$) of both the epiphytes and lithophytes of nine facultative epiphyte species were measured and compared in a karst forest in Xishuangbanna, southwest China.

## 2. Materials and Methods

### 2.1. Study sites and sampling

Five circular plots with a radius of 50 m were established. They were centered on the summits of five hilly dwarf limestone forests in Xishuangbanna National Nature Reserve, southwest China. The climate and forest community characteristics were reported by Wu et al. (2018). According to field surveys and the regional literature regarding the epiphyte flora (Zhu et al., 1998; Wu et al., 2016), nine species of facultative epiphytes with the highest abundance were selected as experimental materials (Table 1). Ten replicates per species, including five epiphytic and five lithophytic individuals were sampled.

The sampling height was in the range of 0–2 m from the ground to the host trunk and rock outcrops, i.e., the distance that a straight arm can reach (Song et al., 2011). We assumed that the coexisting lithophytes and epiphytes of the same species were exposed to homogeneous microclimatic conditions, and ignored the effects of the spatial heterogeneity of microclimate.

### 2.2. Chemical element and isotope measurement

Similarly to Medina et al. (2017), the sampling of the substrate humus of facultative epiphytes to assess the nutrient availability was not a practical approach due to the extremely rare accumulation of humus on the barks and rock outcrops in the plots. Therefore, our study did not measure the chemical elements in the different substrates directly, the foliar stoichiometry and isotopy of the facultative epiphytes on different substrates was measured (Watkins et al., 2007).

**Table 1**

Sampled species of facultative epiphytes.

| Family | Genera | Species | Abbreviation |
|---|---|---|---|
| Meteoriaceae | *Meteorium* | *M. miquelianum* (Müll. Hal.) M. Fleisch. | *Memi* |
| Antrophyaceae | *Antrophyum* | *A. callifolium* Blume | *Anca* |
| Orchidaceae | *Bulbophyllum* | *B. ambrosia* (Hance) Schltr. | *Buam* |
| Orchidaceae | *Bulbophyllum* | *B. andersonii* (Hook.f.) J.J.Sm. | *Buan* |
| Orchidaceae | *Bulbophyllum* | *B. odoratissimum* (Sm.) Lindl. ex Wall. | *Buod* |
| Orchidaceae | *Coelogyne* | *C. viscosa* Rchb.f. | *Covi* |
| Orchidaceae | *Pelatantheria* | *P. rivesii* (Guillaumin) Tang & F.T.Wang | *Peri* |
| Asclepiadaceae | *Hoya* | *H. pottsii* Traill | *Hopo* |
| Araceae | *Rhaphidophora* | *R. hongkongensis* Schott | *Rhho* |

### 2.3. Determination of elemental concentrations

The sun leaves, but not new or senescent leaves, of facultative epiphytes were collected and the petioles were removed. The leaf surfaces were cleaned with a damp cloth, dried at 80 °C for 48 h to a constant mass weight, and then ground into a powder using a ball mill. The samples were prepared after passing through a 100 mesh sieve, and then stored in a sealed plastic bag. A total of nine elements (i.e., N, P, K, Ca, Mg, S, Mn, Fe, and Na) were measured in the Central Laboratory of Xishuangbanna Tropical Botanical Garden. The N concentration per unit weight was determined by an automatic analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany). The other eight elements were measured by inductively coupled plasma atomic emission spectroscopy (ICP-AES: Thermo Jarrell Ash Corporation, USA) after samples were digested in $HNO_3$-$HClO_4$ and HCl.

### 2.4. Determination of the natural abundance of $\delta^{13}C$ and $\delta^{15}N$

The natural abundance of foliar $\delta^{13}$C and $\delta^{15}$N were determined by a stable isotope mass spectrometer (IsoPrime100, Isoprime, UK). About 2–5 mg of the samples were sealed in a vacuum combustion tube, gasified at 850 °C under the action of a catalyst and an oxidizing agent, and the $CO_2$ and $N_2$ crystals produced by the combustion were purified, and then the $\delta^{13}$C and $\delta^{15}$N abundances were determined. Leaf $\delta^{13}$C and $\delta^{15}$N abundances were expressed in delta notation (‰) relative to their reference standards, Vienna Pee Dee Belemnite (V-PDB) and atmospheric $N_2$ respectively.

The natural abundance formula for $\delta^{13}$C and $\delta^{15}$N were:

$$\delta^{13}C\ [‰\ \text{versus V-PDB}] = (R_{sample}/R_{standard} - 1) \times 1000 \tag{1}$$

$$\delta^{15}N\ [‰\ \text{versus at-air}] = (R_{sample}/R_{standard} - 1) \times 1000 \tag{2}$$

where $\delta^{13}$C and $\delta^{15}$N are the C and N isotope values of the corresponding sample, and $R_{sample}$ and $R_{standard}$ are the ratios of the heavy isotope abundances of the elements in the sample and their reference standards ($^{13}C/^{12}C$ and $^{15}N/^{14}N$), respectively. The precision ( ± SE) of the isotope measurements was less than 0.5‰.

### 2.5. Data Analysis

#### 2.5.1. The stoichiometric and isotopic differences between the epiphytes and lithophytes

Taking the substrate as a fixed factor and the species as a random factor, linear mixed-effects models that determined by restricted maximum likelihood t-tests in the "lme4" package (Bates et al., 2015) were fitted to determine the stoichiometric differences between the epiphytes and lithophytes among the facultative epiphytes on different substrates. Then, an independent sample t-test was used to compare the differences between the two ecotypes in the same species.

All statistical analyses were performed using R software (version 3.5.1) (R Development Core Team, 2018), with significance levels indicated as "*" for $p < 0.05$, "**" for $p < 0.01$, and "***" for $p < 0.001$. The results were visualized using the "ggline" function of the "ggpubr" package (Kassambara, 2018).

#### 2.5.2. Correlation and principal component analysis (PCA) of stoichiometry and isotopy in facultative epiphytes

The "psych" package (Revelle, 2018) was used to calculate the Pearson correlation coefficients among nine chemical elements, $\delta^{13}$C, and $\delta^{15}$N, and the significance level was indicated as "*" for $p < 0.05$. The correlation coefficient matrix and significance were visualized using the "corrplot" package (Wei and Simko., 2017).

The above 11 variables were subjected to a PCA using the "FactoMineR" package (Le et al., 2008) and the results were visualized using the "factoextra" package (Kassambara and Mundt., 2017), to assess how the stoichiometric characteristics affected the distribution of facultative epiphytes on different substrates.

#### 2.5.3. Variance partitioning of stoichiometry and isotopy in facultative epiphytes

The "varpart" function in the "vegan" package (Oksanen et al., 2018) was used to calculate each variable's variance for three factors (i.e., substrate, interspecific, and intraspecific), and determine which of them played a critical role in stoichiometry. The natural abundances of two isotopes ($\delta^{13}$C and $\delta^{15}$N), nine elemental concentrations (N, P, K, Ca, Mg, S, Fe, Na, and Mn), and the N/P ratio were used as response variables, and three categorical variables were used as predictive variables. The variance partitioning was a partial regression, because the response variable was a single vector. The three predictive variables produced seven interpretive parts, i.e., three independent effects of the substrate, interspecific, and intraspecific factors, as well as the interaction of the "substrate–intraspecific," "substrate–interspecific," and "interspecific–intraspecific" factors, and the interactions among the three factors.

## 3. Results

### 3.1. Stoichiometry and isotopy differences between the epiphytes and lithophytes

According to the results of the linear mixed-effects model (Fig. 1, the blue and orange boxplot), significant differences ($p < 0.05$) were found in elemental concentrations (Ca, K, Fe, and Mn) and isotope natural abundances ($\delta^{15}$N) between the epiphytic and lithophytic leaves. The $\delta^{15}$N abundance and Ca concentration in the lithophytes were higher than in the epiphytes ($p < 0.05$), while the K, Fe, and Mn concentrations in the lithophytes were lower than in the epiphytes ($p < 0.05$).

Specifically, the $\delta^{15}$N of *P. rivesii* on rocks was found to be enriched compared with the abundances in the same species on trunks following an independent sample t-test ($p < 0.001$). The Ca concentration of the five species (*M. miquelianum, Bulbophyllum odoratissimum*, *Coelogyne viscosa, P. rivesii*, and *H. pottsii*) in lithophytic habitats were higher than that in epiphytic habitats ($p < 0.05$). However, the K concentration in lithophytes was significantly lower than in the epiphytes for *C. viscosa* and *H. pottsii* ($p < 0.05$). The Fe concentration of *B. ambrosia* and *R. hongkongensis* on rocks was also lower than that on trunks (Fig. 1, the red asterisks) ($p < 0.05$).

There were no significant differences ($p > 0.05$) in $\delta^{13}$C abundance, N, P, S, Mg, and Na concentrations, and the N/P ratio (Fig. 1, the black and gray boxplot) in plants growing on different substrates according to the linear mixed-effects model. However, significant intraspecific differences were found following an independent sample t-test ($p < 0.05$), with the differences being species-dependent (Fig. 1, the red asterisks).

### 3.2. Correlation of stoichiometry and isotopy in facultative epiphytes

The $\delta^{15}$N was positively correlated with P, N, S, and K ($p < 0.05$) for both the lithophytes and the epiphytes (Fig. 2, the blue squares with white asterisks). The $\delta^{13}$C was negatively correlated with $\delta^{15}$N, P, N, S, and Fe ($p < 0.05$) (Fig. 2, the red squares with white asterisks), and positively correlated with Ca ($p < 0.05$). The Ca had a negative correlation ($p < 0.05$) with N, S, and Fe, and a positive correlation ($p < 0.05$) with Mg.

Different correlations in foliar element were found between the lithophytes and epiphytes. In lithophytes, significant negative correlations were obtained for Ca with P, K, and Na, between $\delta^{15}$N and Fe, and for K with Ca and $\delta^{13}$C ($p < 0.05$), and significant positive correlations were obtained for Mg with $\delta^{13}$C and Mn ($p < 0.05$). These correlations were not significant in epiphytes ($p > 0.05$).

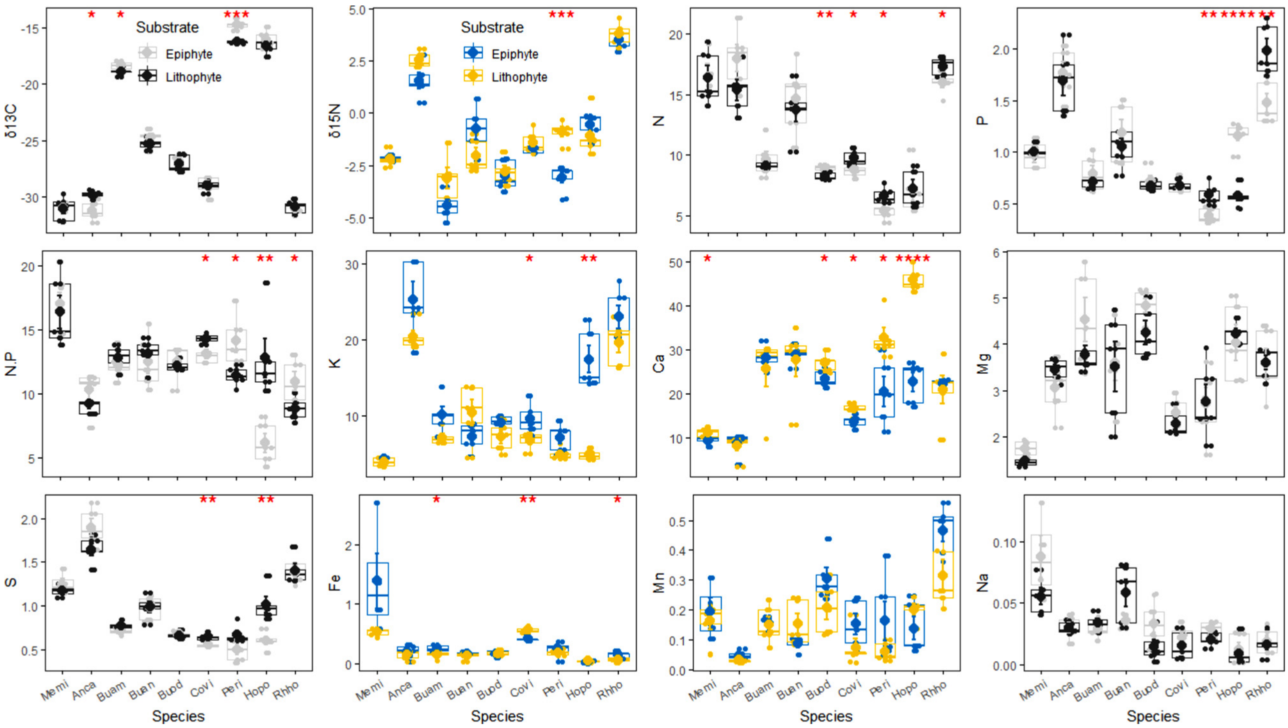


**Fig. 1.** The differences in foliar stoichiometry and isotopy between the epiphytes and the lithophytes among facultative epiphytes in a karst forest in southwest China. The 12 boxplots indicate the $\delta^{13}C$ and $\delta^{15}N$ abundances, the concentrations of nine mineral elements (Ca, N, K, Mg, P, S, Fe, Mn, and Na), and the N/P ratio, respectively. Each boxplot shows the range of elemental concentrations (minimum, lower quartile, median, mean, upper quartile, maximum, and outliers). The horizontal axis gives the abbreviated names of nine species (Table 1). The five blue (epiphyte) and orange (lithophyte) boxplots show the $\delta^{15}N$ abundance and K, Ca, Fe, and Mn concentrations, indicating that the differences were significant (restricted maximum likelihood t-tests, $p < 0.05$). The other seven gray (epiphyte) and black (lithophyte) boxplots show the $\delta^{13}C$ abundance and N, P, N, Mg, S, and Na concentrations, and N/P ratio indicating that the differences were not significant ($p > 0.05$). The red asterisk * above each boxplot indicates a difference in those variables between the lithophytes and epiphytes of each species (t-tests, * indicates $p < 0.05$, ** indicates $< 0.01$, *** indicates $< 0.001$).

### 3.3. PCA of stoichiometry and isotopy in facultative epiphytes

The total variation explained by the first axis (44.2%) and the second axis (25.0%) of the lithophytes was higher than that of the epiphytes (41.1% and 24.6%, respectively) (Fig. 3). The positive direction of the first axis of the PCA was mainly loaded with organically bound elements, such as P, N, and S, and $\delta^{15}N$ for both the epiphytes and lithophytes. The negative direction was loaded with $\delta^{13}C$ and Ca.

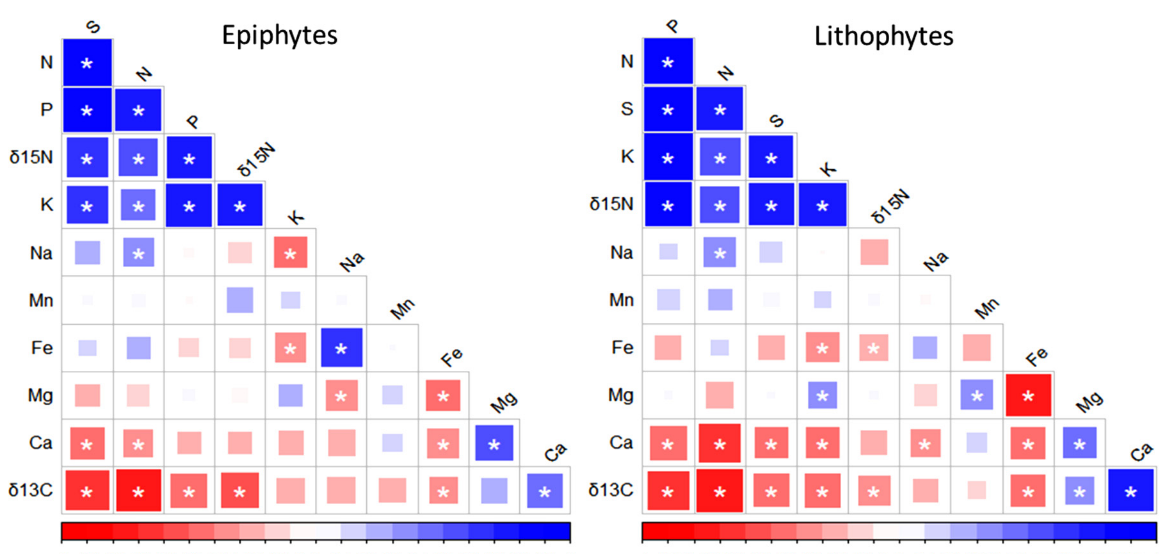


**Fig. 2.** Pearson correlation coefficients among foliar elemental concentrations (Ca, N, K, Mg, P, S, Fe, Mn, Na) and $\delta^{13}C$ and $\delta^{15}N$ abundances in facultative epiphytes in a karst forest in southwest China. The left and right plots stand for the epiphytes and lithophytes, respectively. The size of the square area indicates the magnitude of the correlation coefficient and the color depth indicates the p value. The blue squares in the lower right and upper left indicate where the two variables were positively correlated, while the red squares in the lower left indicate where the two variables were negatively correlated. The white * indicated that the correlation coefficients were significant after testing ($p < 0.05$).

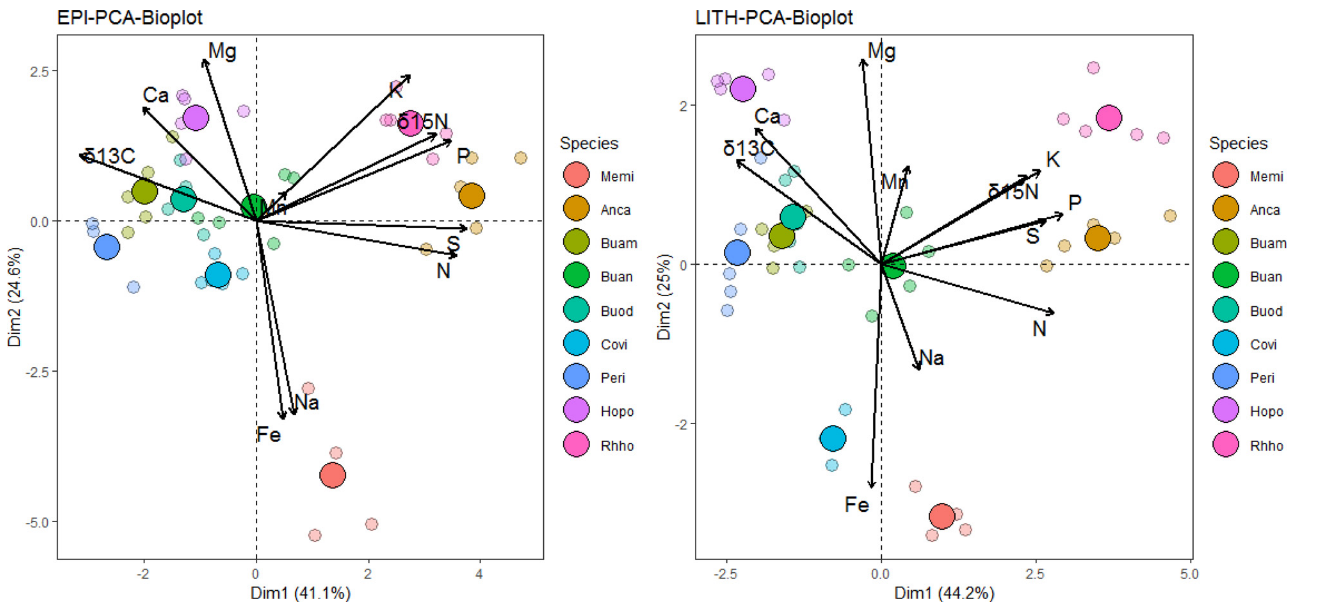


**Fig. 3.** The first two axes of the principal component analysis (PCA) for 11 variables (Ca, N, K, Mg, P, S, Fe, Mn, and Na concentrations and $\delta^{13}$C and $\delta^{15}$N abundances) and nine species of facultative epiphytes in a karst forest in southwest China. The left and right plots show epiphytes and lithophytes, respectively. See Table 1 for the abbreviated species names used in the legend. The larger dots represented the species mean points, and the smaller represented each individual in the legend.

However, on the second axis the positive direction was mainly loaded with Mn, Mg, and K, and the negative direction was loaded with Fe and Na (Fig. 3). Interestingly, Fe was positively correlated with the first axis and S was negatively correlated with the second axis in the epiphytes, while the opposite pattern was observed in the lithophytes.

The epiphytes and lithophytes, *R. hongkongensis*, *A. callifolium*, and *M. miquelianum* were clustered together and distributed in the positive direction of the first axis (Fig. 3). Five orchid species and *H. pottsii* were distributed in the negative direction of the first axis. On the second axis, *M. miquelianum* and *C. viscosa* were distributed in the negative direction, and the other species were mostly distributed in the positive direction. The epiphyte *P. rivesii* was distributed in the negative direction, while the opposite pattern was observed for the lithophytes on the second axis.

### 3.4. *Variation partitioning of stoichiometry and isotopy in facultative epiphytes*

Substrate (Fig. 4, red circle), interspecific (Fig. 4, green circle), and intraspecific (Fig. 4, purple circle) factors and their interactions explained the variance of the 12 variables, ranging from 62% for Na to 99% for $\delta^{13}$C. The three factors had a high interpretation rate for N, P, K, and S concentrations (87% to 92%). In contrast, the interpretation rate for the Mn, Na, Fe, and Mg concentrations was low (62%~64%).

Substrate and interspecific, the “substrate–interspecific” interaction, and the interactions among the three factors could not explain any of the variance. However, the interaction of “substrate–intraspecific”, “interspecific–intraspecific,” and intraspecific factors explained most of the variance. The “interspecific–intraspecific” interaction explained more than 50% of each variable’s variance, especially the interpretation of the N, P, K, and S concentrations, which accounted for more than 75% of the overall variance. The interpretation rate for the Mn, Na, Fe, and Mg concentrations was between 50% and 60%. Interestingly, the “substrate–intraspecific” interaction had a certain proportion of interpretation for $\delta^{15}$N, K, Fe, Ca, and Mn (Fig. 4).

## 4. Discussion

### 4.1. *Effects of a substrate shift on element concentration in facultative epiphytes*

There were no significant differences in the concentrations of organically bound elements (P, N, and S) between the epiphytes and the lithophytes, which supports “the stability of limiting elements hypothesis” (Han et al., 2011). However, the lithophytes were enriched in Ca than epiphytes. This was due to the dissolution and release of Ca from the rock substrate. In addition, low solubility of trace elements such as Mn and Fe in the karst forest soil with high pH, caused low Fe and Mn concentrations in lithophytes (Hou, 1982; Medina et al., 2017; Tian et al., 2019). In contrast, the host bark was usually acidic (Song et al., 2011), and the organic acids secreted by the rhizosphere of the epiphytes can act as chelating agents to facilitate the absorption of Fe and Mn (Medina et al., 2017).

The atmospheric deposition of K originated from natural processes and anthropogenic activities were the main sources of K for terrestrial ecosystems (Sardans and Penuelas., 2015). In southwest China, biomass accumulation in the context of rock outcrops had depleted soil K stocks and caused the reduction of K concentrations (Shen et al., 2020). On the other hand, the concentration of K in fog water collected in the dry season was significantly greater than that of in the rainy season around the study sites, which can be attributed to the ions deposition and emissions by biomass burning in this region (Liu et al., 2005). Moreover, the fog droplets were not deposited on the forest floor but were rather intercepted by the forest canopy (Liu et al., 2008). Therefore, we speculated epiphytes would efficiently absorb and accumulate more K from their canopy habitat with relatively higher K concentration given that K showed greater foliar leaching due to its high solubility (Winkler and Zotz., 2010; Zhang et al., 2012; Querejeta et al., 2018; Tian et al., 2019).

The 11 variables had different contributions to the principal components in the PCA ordination between the epiphytes and lithophytes. This suggested a difference in foliar stoichiometry on different substrates. The first axis loaded organically bound elements (P, N, and S) and a macroelement (Ca), representing a “nucleic acid-protein set,” while the second axis loaded non-organically bound elements (Fe, Mn,

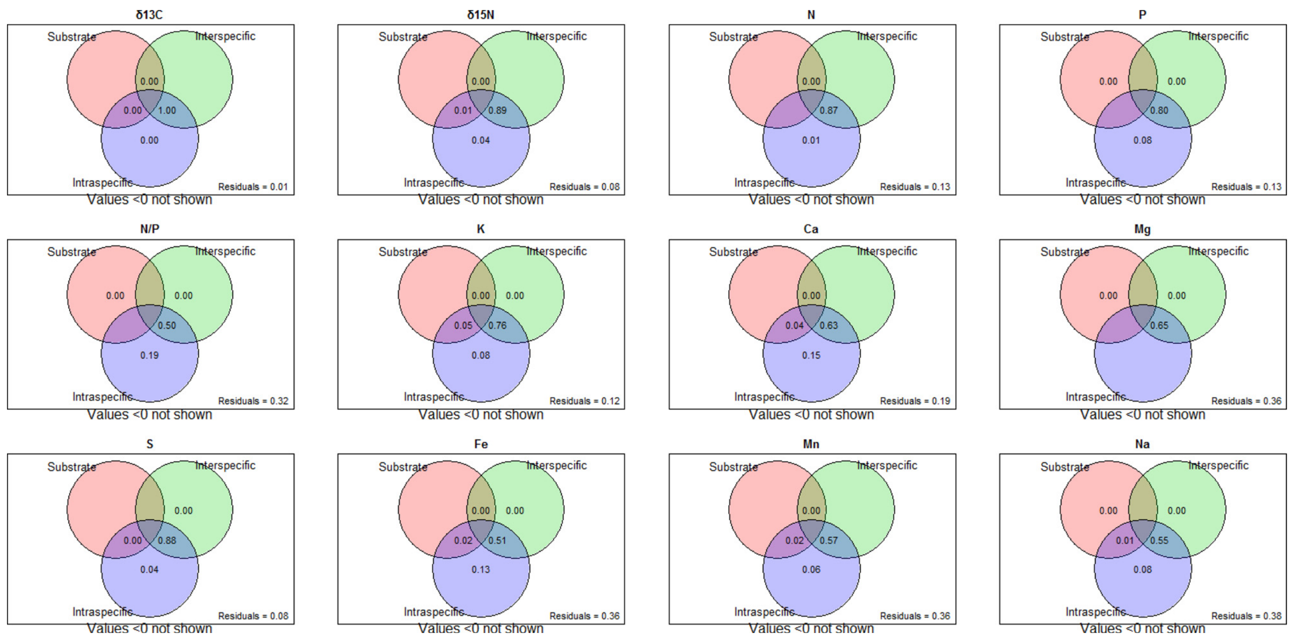


**Fig. 4.** Variance partitioning of foliar stoichiometry and isotopy for different environmental variables in facultative epiphytes in a karst forest in southwest China. The 12 plots shows the $\delta^{13}C$ and $\delta^{15}N$ abundance, the concentrations of nine mineral elements (Ca, N, K, Mg, P, S, Fe, Mn, and Na), and the N/P ratio, respectively. The red, green, and blue circles indicate the variables of substrate, interspecific, and intraspecific factors, respectively. Correspondingly, the overlap of the "substrate–intraspecific," "substrate–interspecific," and "interspecific–intraspecific" interactions, and the overlap among the three factors indicate the interactions of those factors. The part that cannot be explained by the three factors is a residual, and a value less than 0 is not displayed. All values in the circles represent the variance explained by each variable or the interactions of two or three variables.

and K), representing a "photosynthesis–enzyme activity collection" (Wright et al., 2005; Zhang et al., 2012). The opposite relationship between Fe and S was observed on the different substrates on different ordination axes in the PCA, which indicated a difference in microhabitat and substrate mineral nutrients after a substrate shift. For example, the epiphytic individuals of *P. rivesii* were loaded in the negative direction of the second axis, while the lithophytes displayed the opposite pattern. Similarly, the lithophytic individuals of *H. pottsii* were loaded closer to the Ca on the first axis than the epiphytes, suggesting the Ca concentration of the former was higher than that of the latter. Therefore, a substrate shift led to foliar stoichiometry differences in facultative epiphytes.

In general, three factors (i.e., substrate, interspecific, and intraspecific) had a strong influence on the stoichiometry. The "interspecific–intraspecific" interaction played a critical role, and its influence on the organically bound elements (N, P, and S) was stronger than that of the non-organically bound elements (Mn, Na, Fe, and Mg). Intraspecific factors and the "substrate–intraspecific" interaction could explain a certain proportion of the variance of the K, Fe, Ca, and Mn concentrations. The intraspecific factors and the "substrate–intraspecific" interaction were related to the substrate, suggesting that the variance of the non-organically bound elements were more affected by the substrate-related factors. This was consistent with the results of the linear mixed-effects model.

### 4.2. *Effects of a substrate shift on $\delta^{13}C$ and $\delta^{15}N$ abundances in facultative epiphytes*

The $\delta^{13}C$ abundance was related to the water use efficiency (WUE) of the plants, with an efficient water use resulting in an enriched $\delta^{13}C$ (Watkins et al., 2007). Therefore, the water conditions between the epiphytic and lithophytic substrates can possibly converge. The facultative epiphytes accounted for 52% (23/44 species) of all epiphyte species in the 3,500 $m^2$ karst forest plots during the field survey (Wu et al., unpublished data). This was consistent with the habitat convergence hypothesis, which states that the diversity of facultative epiphytes peaks where the within and below canopy environments converge, which is either exceptionally wet or dry (Benzing, 1990, 2004; Burns, 2010).

Foliar $\delta^{15}N$ was determined by the isotope composition of plant N sources and isotope fractionation during absorption (Robinson, 2001), with the latter affected by the plant rhizosphere N supply and demand (Querejeta et al., 2018). There are three main N sources for epiphytes: (1) allochthonous N sources (atmospheric dry and wet deposition), (2) autochthonous N sources (canopy humus and leaching), and (3) biological N fixation (Stewart et al., 1995; Bergstrom and Tweedie., 1998; Hietz et al., 2002; Wania et al., 2002: Watkins et al., 2007: Petter et al., 2016). Here, the N supply from atmospheric deposition was similar in all locations because the facultative epiphytes occurred in a relatively homogeneous habitat, suggesting that a substrate shift was the main cause of the differences in $\delta^{15}N$.

Our results indicated that the lithophytes were able to obtain additional N sources from rock outcrops, originated from rock weathering for ecosystems (Houlton et al., 2018). The older rock humus $\delta^{15}N$ would be more enriched than the canopy humus (Vitousek et al., 1989), because of the slow loss of $\delta^{14}N$ in soil development. Our results showed that substrate shifts play an important role in determining the N isotope composition. The substrate differences in $\delta^{15}N$ abundance were analogous to the "nutritional microsites" at different canopy positions, i.e., the humus epiphytes were enriched in $\delta^{15}N$ compared with the twig epiphytes (Hietz et al., 2002; Wania et al., 2002).

### 4.3. *Correlation between stoichiometry and isotopy in facultative epiphytes*

At global, regional, and landscape scales, the $\delta^{15}N$ of terrestrial plants is positively correlated with the N concentration (Craine et al., 2009). Our findings were consistent with previous studies (Stewart et al., 1995; Hietz et al., 1999; Valiela et al., 2018), confirming that $\delta^{15}N$ and N were positively correlated within both terrestrial and epiphytic plants. Hence, this relationship is not dependent on the substrate, but is mainly regulated by changes in the N supply and demand balance (Querejeta et al., 2018).

In addition, $\delta^{13}C$ was negatively correlated with $\delta^{15}N$, P, N, and S. This was consistent with the results of Hietz et al. (2002), Wania et al. (2002), and Petter et al. (2016). Because $\delta^{13}C$ is positively correlated with WUE, the more the $\delta^{13}C$ is depleted, the less water stress that plants are subjected to, and the P, N, S, and Fe concentrations will increase. This suggests that facultative epiphytes will maximize water and nutrient uptake and photosynthetic activity during the narrow windows of intermittent supply following irregular rainfall pulses when resources become available (Querejeta et al., 2018).

Substrate shifts alter the correlations of elements between different substrates. Our results showed that the correlations among different elements in lithophytes were more significant than those of epiphytes. Thus, we expected the foliar stoichiometry and isotopy of the epiphytes or lithophytes to indirectly reflect their adaptation to environmental stresses, although the substrate shift occurred at a fine scale (Han et al., 2011). These differences suggested that the absorption mechanism and nutrient sources would differ for plants growing on different substrates (Cardelús and Mack., 2010).

### 4.4. Stoichiometric and isotopic flexibility and physiological plasticity

Different growth substrates in the karst forest could affect the stoichiometric and isotopic characteristics of the two ecotypes. Here, epiphytes and lithophytes have shifted their elemental balance to cope with substrate and habitat shifts, confirmed stoichiometric flexibility (Sterner and Elser., 2002). At the individual level, stoichiometric flexibility can occur through changes in nutrient allocation to tissue or synthesis of subcellular components of different element ratios (Sistla et al., 2015).

Stoichiometric flexibility was regulated by physiological plasticity (Sistla et al., 2015), which can be manifested by an adjustment in growth form (Sistla and Schimel., 2012). Facultative epiphytes can change its growth form to adapt the substrate shifts (Zotz, 2016). High physiological plasticity in facultative epiphytes is considered as an adaptive mechanism to exploit different environmental conditions in order to exploit the available resources efficiently (Chen et al., 2019; Grassein et al., 2010). Shifting resource availability appears to be a primary constraint on the expression of stoichiometric flexibility at the individual level (Sistla and Schimel., 2012). In our study, enriched $\delta^{15}N$ in lithophytes suggested lithophytic ecotype is able to obtain additional N sources from rock outcrops. Moreover, Ca is a key element in cell structure and cell division, enabling plants to withstand drought stress (White and Broadley., 2003). Similarly, K is also believed to alleviate the inhibition of water stress on growth and plays an important role in osmotic adjustment (Sardans and Penuelas., 2015). It is possible that K function in water economy for epiphytes, while Ca function in drought stress for lithophytes. Both the epiphytic and lithophytic habitats have low water availability, which can cause plants to increase either $K^{+}$ or $Ca^{2+}$ uptake to improve plant drought resistance (Tian et al., 2019). On the other hand, both Fe and Mn are critical for enzyme formation and the catalysis of plant growth processes (He et al., 2016), representing photosynthesis–enzyme activity collection. Thus, epiphytes enriched in Fe and Mn, which would imply that epiphytic ecotype facilitates a higher light capturing/harvesting and photosynthetic capacity compared with the lithophytes (Chen et al., 2019).

Lithophytes and epiphytes exploited rock and bark simultaneously in Xishuangbanna karst forest, which exhibited remarkably stoichiometric flexibility and high physiological plasticity under harsh habitat (Querejeta et al., 2018). Therefore, the greater physiological plasticity found in facultative epiphytes may play a role in the survival both on rocks or host barks. Our results have confirmed that stoichiometric flexibility in response to changes in the availability of substrate resources in plants.

## 5. Conclusions

In conclusion, our results found that the substrate shifts has a strong partitioning effect on the concentration of elements such as K, Fe, Ca, and Mn and $\delta^{15}N$ abundance. The flexibility of non-organically bound elements for environmental changes was detected by comparing the stoichiometry and isotopy of facultative epiphytes on different substrates, which enabled facultative epiphytes to exploit the nutrients of rock outcrops and host barks flexibly.

## Author Statement

None.

## Declaration of Competing Interest

None.

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## Declaration of Competing Interest

The authors report no declarations of interest.

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