

Article

Divergent Adaptation Strategies of Vascular Facultative Epiphytes to Bark and Soil Habitats: Insights from Stoichiometry

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Abstract: Understanding the stoichiometric traits of plants is critical for studying their ecological adaptation strategies. Facultative epiphytes (which can also live on the ground) are an important component of epiphytic flora of montane forest ecosystems. However, a key gap persists in our understanding how facultative epiphytes can adapt different nutritional conditions of ground and canopy habitats? To study adaptive strategies of facultative epiphytes and the characteristics of the content and stoichiometric homeostasis of C, N, and P elements, we conducted a field experiment and a greenhouse N and P additions cultivation experiment. We found that epiphytic individuals of facultative epiphytes showed lower C:N and C:P ratios, higher variation in elemental composition, and more pronounced N limitation than terrestrial individuals. Moreover, facultative epiphytes showed strong control over the elemental composition of leaves, and their stoichiometric homeostasis of leaves and stems were stronger than roots. Furthermore, the homeostasis of facultative epiphytes decreased in the order $N > P$. Our results indicated that epiphytic and terrestrial individuals of facultative epiphytes have difference in nutrient limitation, and they use plastic strategies in different habitats. Epiphytic individuals survive in the intermittent habitat through luxury consumption of nutrient while terrestrial individuals were relatively conservative nutrient users. Furthermore, our results implied that facultative epiphytes maintain stable metabolic leaf activity via variable element concentrations of roots to adapt to highly heterogeneous forest habitats.

Keywords: facultative epiphytes; nutrient use strategy; ecological stoichiometry; stoichiometric homeostasis; carbon; nitrogen; phosphorus



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1. Introduction

As an essential component of the forest canopy, epiphytes are important to the floristic diversity, structure, and function of moist mountainous forest ecosystems, and play a vital role in maintaining ecosystem biodiversity and the circulation of nutrients [1–3]. Facultative epiphytes are an important life history group, being special epiphytes that can grow both on host trees and ground [4–6]. In terrestrial habitats, the primary role of interspecific interaction was competition, while species in harsh epiphytic habitats depend on each other to survive [7]. Furthermore, epiphytic habitats are often characterized by limited water and nutrient storage capacity, sporadic nutrient inputs, low physical stability, variable temperature, and humidity [8–10], while terrestrial habitats are often characterized by relatively constant nutrient and water supply [5,11,12]. Therefore, facultative epiphytes must not only adapt to a harsh canopy environment but also be well adapted to the relatively stable environment under the forest. Recent work shows that the morphological,

anatomical, physiological, and growth traits between terrestrial and epiphytic individuals of facultative epiphytes have undergone significant plasticity changes in adapting to canopy and terrestrial habitats [5,13]. However, whether there are differences in stoichiometric characteristics and nutrient use strategies between epiphytic and terrestrial epiphytes of facultative epiphytes remains little known.

Epiphytes are generally considered to survive in the harsh habitats through luxury consumption of nutrients [14]. Therefore, epiphytes may show higher N and P concentrations, and lower nutrient use than terrestrial plants [12,14]. However, little research compared the difference in nutrient use between epiphytes and terrestrial plants, and many of them investigated different species and result in a potential phylogenetic bias [12]. Facultative epiphytes can live both in epiphytic and terrestrial habitats, and effectively using both canopy and ground resources to maintain their competitiveness in both habitats [15]. Therefore, facultative epiphytes make an excellent system for the better understanding of the adaptation and nutrient trade-offs of plants in the epiphytic and terrestrial habitats [12].

Ecological stoichiometry mainly studies the balance of energy and multiple chemical elements in biological systems [16,17]. It is a fast-emerging tool that is critical for studying the ability of plants to maintain constant elemental composition [18–21], the ecological strategies of plants [22], and their nutrient limitations [23–25] in natural and semi-natural ecosystems. The conservative species generally showed low N and P content and high C:N and C:P ratios, while luxury species showed the opposite traits [14,26,27]. Moreover, the N:P of plants has long been considered to be an indicator of nutrient limitation. Koerselman and Meuleman [28] proposed that $N:P < 14$ indicates plants are N-limited and $N:P > 16$ indicates they are P-limited. Wanek and Zotz [29] argued that $N:P > 12$ indicates P limitation or co-limitation of N and P in epiphytes, $N:P < 12$ indicates N limitation.

Stoichiometric homeostasis (H) refers to the ability of an organism to maintain relatively constant elemental concentrations and ratios despite changes in its habitat [17,30]. The ecological stoichiometric homeostasis of plants mainly affected by plant species, organs or tissues, and element types [17,22]. Stoichiometric homeostasis not only reflects the stability of plants but it also may be used to analyze their environmental adaptation strategies [21]. Plants with a stronger stoichiometric homeostasis are more conservative in their nutrient use than those plants with weaker stability [22,31]. However, the latter are more adaptable to variable environments while the former may be better suited to a stable environment [32,33]. The facultative epiphytes may, therefore, show weak stoichiometric homeostasis to adapt to variable habitats. Furthermore, an element with high content has higher H than an element with low content; for example, H_N is higher than H_P [34–36].

The aboveground parts of vascular plants have stronger stoichiometric homeostasis that is negatively correlated with that of their belowground parts, reflecting the ability of plants to adapt to their environments by adjusting the nutrient distribution of different organs [22,37]. However, since most research has mainly focused on leaves, far less is known about the stoichiometric homeostasis of stems and roots [20,38], which is important for fully understanding the ecological strategies of plant species [22]. Different organs exhibit different stoichiometric characteristics because of their functional differentiation [16]. In terrestrial plants (e.g., tree seedlings and *Arabidopsis thaliana* (L.) Heynh.), as the chief photosynthetic organs, leaves exert stronger control over their elemental composition than do either the stems or roots, whose primary role is nutrient acquisition and storage [16,20,38]. Yet, whether this pattern also generally applies to epiphytes needs further study.

The C, N, and P stoichiometric patterns of terrestrial plants have been extensively studied at regional [39], national [40], and global scales [41]. However, the ecological stoichiometry traits of epiphytes dwelling in the forest canopy remain little known, despite the vital role these plants play in the nutrient and energy cycling of subtropical forest ecosystems [42]. To date, only a few studies focused the stoichiometric traits of epiphytes [29,43], no studies have reported the stoichiometric homeostasis of facultative epiphytes. Moreover, according to Zotz [12], epiphytes are luxury consumption plants that have high nutrient concentrations but low rates of photosynthesis, which general feature

a low nutrient use efficiency [14]. However, whether epiphytic individuals of facultative epiphytes (which occur both epiphytically and terrestrially) are more efficient in nutrient use than terrestrial individuals remain an open question. In this research, to study the ecological stoichiometric characteristics and homeostasis of C, N, and P in three common vascular facultative epiphytes in the montane moist evergreen broad-leaved forest of Ailao Mountain National Nature Reserve, we conducted a field experiment and a greenhouse cultivation experiment. We proposed the following hypotheses: (1) There are significant differences in adaptation strategy between the epiphytic and terrestrial individuals of facultative epiphytes which reflect in their stoichiometry pattern. (2) Facultative epiphytes exhibit weak stoichiometric homeostasis to adapt to variable habitats, (3) and they show stronger control on the elemental composition of leaves than that of roots.

2. Materials and Methods

2.1. Study Area and Species

This study was conducted in subtropical montane moist evergreen broad-leaved forest in Xujiaba, the core area of the Ailao Mountain National Natural Reserve, Southwest China (23°36′–24°56′ N; 100°44′–101°30′ E). The Ailao Mountain have the largest, most intact mountain moist evergreen broad-leaved forest in China, forming an important portion of this country's subtropical forest ecosystem [44]. In this montane moist evergreen broad-leaved forest, the canopy and trunk are rich in epiphytic plant communities [43], providing a natural and ideal place to study the stoichiometric characteristics of epiphytes. The Ailao Mountain are located in a climate transition area in the central and northern parts of Yunnan's subtropical zone, characterized by dry and rainy seasons due to the influence of the southwest monsoon. According to long-term monitoring data from the Ailao Mountain Ecological Station of the Chinese Academy of Sciences, the annual precipitation in this area is 1947 mm, with an annual evaporation of 1192 mm, and the dry season (November–April) and rainy season (May–October) are distinct. The precipitation during the rainy season accounts for ca. 85% of the annual precipitation at the site, where the relative humidity is 85%, annual average temperature is 11.3 °C, monthly average maximum temperature is 15.7 °C, and monthly average minimum temperature is 5.6 °C [45].

Xujiaba area is rich in epiphytes, there are nearly 600 species, including lichens (183), bryophytes (176), ferns (117) and spermatophytes (113) [8,43]. The dominant facultative epiphytic spermatophytes are *Cautleya gracilis* (Smith) Dandy (an annual erect herb, 0.25–0.8 m in height), *Elatostema monandrum* (D. Don) Hara (a small annual herb, 0.05–0.2 m in height), and *Briggsia longifolia* var. *multiflora* (a perennial herb without stem) [43]. In this area, according to our survey, epiphytic individuals of facultative epiphytes are usually found on tree trunks with moss mat or thicker humus soil, while terrestrial individuals are usually distributed in the forest floor under canopy gap (Figure 1). Most individuals of *C. gracilis* grow on the forest floor, while *E. monandrum* and *B. longifolia* show the inverse pattern. The distribution of facultative epiphytes may be affected by the seed supply and microclimatic conditions [46].



Figure 1. The pictures of investigated species. (A,B) epiphytic and terrestrial individuals of *Cautleya gracilis*, (C,D) epiphytic and terrestrial individuals of *Elatostema monandrum*, (E,F) epiphytic and terrestrial individuals of *Briggsia longifolia*, respectively.

2.2. Field Sampling and Greenhouse Culture

In the field sampling experiment, we used the natural nutrient gradients of the forest canopy and ground soil stands to carry out nutrient additions. Many factors, such as light, substrate water and nutrient content, jointly affect the content of chemical elements in plants in the field [32,34], so the relationship between a plant's elemental content and its growth substrate cannot be accurately estimated by field sampling alone. Therefore, to accurately evaluate the stoichiometric stability of facultative epiphytes, we also performed a greenhouse cultivation experiment in addition to the field experiment.

Field sampling was done during the rainy season (August 2018). Four collection line transects were set along four evenly divided directions in the core area of montane moist evergreen broad-leaved forest in the Ailao Mountains, and 3–5 sampling points were selected per line transect. We defined individuals that grow on the trunk as epiphytic individuals, and individuals that grow on the ground as terrestrial individuals. The healthy mature terrestrial and epiphytic individuals of three dominant facultative epiphytes (*C. gracilis*, *E. monandrum*, and *B. longifolia*) were separately collected from each sampling

point, for which terrestrial and epiphytic individuals were collected from the forests soil and c. 1.5 m of their host trees, respectively. In total, 34 samples (16 samples from epiphytic individuals and 18 samples from terrestrial individuals) were collected for *C. gracilis*, 30 samples (18 samples from epiphytic individuals and 12 samples from terrestrial individuals) for *E. monandrum*, and 38 samples (20 samples from epiphytic individuals and 18 samples from terrestrial individuals) for *B. longifolia*. We collected whole plant individuals, whose roots, stems, and leaves were then separated and stored, as well the soil at their growth positions of the target species for use a growing substrate for these plants. These plant samples were first washed with tap water, then washed with distilled water and placed into envelopes and oven-dried to a constant weight (48 h) at 65 °C, then the dried samples were ground to powder. The soil samples were dried, ground, and passed through a 60-mesh sieve before their analysis.

The cultivation experiment was carried out in a greenhouse from April to August 2018. In this experiment, the N and P fertilizers used were respectively NH_4NO_3 and NaH_2PO_4 ; their fertilization gradients are shown in Table 1, which consisted of nine treatments in total, with three replicates per treatment. There were five N levels (0.5, 1, 2, 4, and 6 mmol L^{-1}) under a moderate P gradient (0.25 mmol L^{-1}) and five P gradients (0.0625, 0.125, 0.25, 0.5, and 0.75 mmol L^{-1}) under a moderate N gradient (2 mmol L^{-1}). It is difficult to collect and cultivate seedlings of *C. gracilis*, thus only the other two species were used for the cultivation experiment. Healthy epiphytic seedlings (*E. monandrum* and *B. longifolia*) were collected from the montane moist evergreen broad-leaved forest in the Ailao Mountains. These seedlings were pre-incubated in tap water for two weeks; hence, the nutrient content of different individuals was made relatively equal. Sterilized vermiculite was used as growth substrate, with an equal volume of vermiculite (100 mL) poured into each cultivated pot, three seedlings per pot. Fertilizer was added in the form of nutrient solutions, 10-mL nutrient solutions were added to the culture pots every two days. In August 2018, the leaf, stem, and root of each individual were collected separately and first washed with tap water, then washed with distilled water and placed into envelopes and oven-dried to a constant weight (48 h) at 65 °C. These dried samples were placed in a mortar containing liquid nitrogen and powdered using a pestle; each powder sample was placed in a small Ziplock bag. Because both stems and roots did not reach the minimum mass required for element analysis, only the element concentrations in leaf were measured.

Table 1. The N and P concentrations and ratios in nutrient solutions used in treatments of greenhouse cultivation experiment.

| Treatment | N (mmol L^{-1}) | P (mmol L^{-1}) | N: P |
|-----------|----------------------------|----------------------------|------|
| N1P3 | 0.5 | 0.25 | 2 |
| N2P3 | 1 | 0.25 | 4 |
| N3P3 | 2 | 0.25 | 8 |
| N4P3 | 4 | 0.25 | 16 |
| N5P3 | 6 | 0.25 | 24 |
| P1N3 | 2 | 0.0625 | 3.2 |
| P2N3 | 2 | 0.125 | 16 |
| P4N3 | 2 | 0.5 | 4 |
| P5N3 | 2 | 0.75 | 2.7 |

Five N levels under moderate P level (P3), five P levels under moderate N level (N3).

2.3. Laboratory Analysis

The total C and N concentrations of all plant samples in the cultivation and field experiments and soil samples in the field experiment were measured with a carbon and nitrogen element analyzer (Vario MAX CN, Elemental Analyzer, Elementar, Langensfeld, Germany), about 0.1 g dried powder of each plant and soil sample was used for the measurement of C and N concentrations. The P concentration of plant and soil samples were measured by an inductively coupled plasma atomic emission spectrometer (iCAP6300, Thermo Fisher Scientific, Waltham, MA, USA) after digested with $\text{HNO}_3\text{-HClO}_4$. For the

determination of P concentrations of plant and soil samples, 0.48–0.52 g and 0.1–0.12 g dried powder was needed, respectively. Total C, N, and P concentrations of both plant and humus soil samples were calculated on per dry weight basis.

2.4. Data Analysis and Statistics

The stoichiometric homeostasis index (H) of different organs of each plant species was calculated according to the ecological stoichiometric homeostasis model [17]:

$$y = cx^{1/H}, \quad (1)$$

where x refers to the N or P content or the ratio of N:P in the growing substrate; y refers to the content of N or P, or the N:P ratio in a given plant organ; c is a constant. In this model, a value of $H > 1$ may be interpreted to mean that the plant has the ability to regulate elemental composition [17]. Persson et al. [33] classified organisms into four types according to the range of their H values as follows: $H > 4$, strict homeostasis; $2 < H < 4$, weakly homeostasis; $3/4 < H < 2$, weakly plastic; $H < 3/4$, plastic.

In the field experiment, the differences in the C, N, and P elements and their stoichiometric ratios of facultative epiphytes between epiphytic and terrestrial habitats were analyzed by independent t -test and two-way ANOVA. The H for N, P, and N:P of leaves, stems, and roots of three species were estimated through regression analysis. Variation of H across different species, organs, and elements in the field experiment was analyzed by one-way ANOVA and two-way ANOVA, for which statistical significance was set at $p = 0.05$. Data normality and homogeneity were checked through Shapiro-Wilk and Levene tests, for the data not met the assumptions, Kruskal-Wallis tests were used.

In the cultivation experiment, the H for N, P, and N:P of leaves were estimated through regression analysis. Variation of N, P, and N:P in leaves of two species across different fertilization levels were analyzed by two-way ANOVA, for which statistical significance was set at $p = 0.05$. All statistical analyses were done using IBM SPSS Statistics 19.0 (SPSS, Inc., Chicago, IL, USA).

3. Results

3.1. Stoichiometric Patterns of C, N, P Concentrations and Their Ratios in Different Organs in Two Habitats in the Field

The C concentration and C:N were only affected by species, the N and P concentrations and the C:P and N:P ratios in leaves were significantly affected by species and habitat, while the C:P was also affected by the interaction between species (Table 2). The C and N concentration and the C:N, C:P, N:P ratios in stems were significantly affected by species, while C and C:N were also affected by habitat, the P concentration was only affected by habitat. For roots, the C and N concentration were significantly affected by habitat and species, the C:N and N:P ratios were significantly affected by species and the interaction between habitat and species, the P and C:P was only affected by species.

Table 2. Effects of species, habitats, and their interactions on stoichiometric traits of C, N, and P in different organs of facultative epiphytes in field experiment.

| Organ | Variable | Habitat | | Species | | Habitat × Species | |
|-------|----------|----------|----------|-----------|-----------|-------------------|-------|
| | | F | df | F | df | F | df |
| Leaf | C | 3.67 | 1, 93 | 634.20 ** | 2, 93 | 1.54 | 2, 93 |
| | N | 4.56 * | 1, 93 | 91.22 ** | 2, 93 | 1.29 | 2, 93 |
| | P | 10.83 ** | 1, 89 | 43.99 ** | 2, 89 | 3.01 | 2, 89 |
| | C:N | 0.56 | 1, 93 | 170.12 ** | 2, 93 | 1.10 | 2, 93 |
| | C:P | 7.73 ** | 1, 89 | 94.48 ** | 2, 89 | 3.70 * | 2, 89 |
| | N:P | 3.99 * | 1, 89 | 4.53 * | 2, 89 | 0.89 | 2, 89 |
| | Stem | C | 7.06 * | 1, 57 | 206.77 ** | 1, 57 | 2.03 |
| N | | 1.43 | 1, 57 | 93.92 ** | 1, 57 | 0.70 | 1, 57 |
| P | | 11.38 ** | 1, 44 | 2.84 | 1, 44 | 1.07 | 1, 44 |
| C:N | | 4.40 * | 1, 57 | 84.56 ** | 1, 57 | 0.82 | 1, 57 |
| C:P | | 3.74 | 1, 44 | 8.92 ** | 1, 44 | 0.02 | 1, 44 |
| N:P | | 3.24 | 1, 44 | 10.39 ** | 1, 44 | 2.25 | 1, 44 |
| Root | | C | 23.39 ** | 1, 90 | 21.88 ** | 2, 90 | 1.93 |
| | N | 4.69 * | 1, 90 | 34.30 ** | 2, 90 | 0.75 | 2, 90 |
| | P | 3.38 | 1, 65 | 13.60 ** | 2, 65 | 0.81 | 2, 65 |
| | C:N | 0.09 | 1, 90 | 62.97 ** | 2, 90 | 3.73 * | 2, 90 |
| | C:P | 0.10 | 1, 65 | 9.03 ** | 2, 65 | 0.72 | 2, 65 |
| | N:P | 0.00 | 1, 65 | 4.34 * | 2, 65 | 3.20 * | 2, 65 |

* $p < 0.05$, ** $p < 0.01$. F indicates F value, df denotes degree of freedom.

For *C. gracilis*, the difference in the leaf N concentration and P concentration of stem and root between the two habitats was significant ($p < 0.05$), the P concentrations of leaf and the root's C and N concentrations in the epiphytic habitat significantly exceeded those in terrestrial habitat ($p < 0.01$), while the C:N and C:P in leaf between the two habitats showed a reverse trend (Table S1). For *E. monandrum*, the C and P concentration in leaf and the C and N concentration and the C:N ratio in root in the epiphytic habitat were higher than those in terrestrial habitat (Table S2). For *B. longifolia*, the C, N, and P concentrations in leaf and root in the epiphytic habitat were higher than those in terrestrial habitat, but vice versa for the C:N and C:P in leaf (Table S3). At the species level, the plasticity of element composition in epiphytic individuals of the three species were relatively higher than that of terrestrial individuals expect C in root and P in stem of *C. gracilis*, C and N in leaf and root of *E. monandrum*, and C and N in leaf and root, C:N in leaf of *B. longifolia* (Tables S1–S3).

3.2. Variation of Stoichiometric Homeostasis among Different Species, Organs, and Elements in the Field

For leaves, the H_N of *C. gracilis* was weaker than either that of *E. monandrum* or *B. longifolia*, while the latter was characterized by the strongest N homeostasis (Figure 2, Table S4). The H_P of species was ranked in the order of *E. monandrum* > *C. gracilis* > *B. longifolia*. In terms of $H_{N:P}$, it was strongest in *C. gracilis*, followed by *E. monandrum*, being weakest in *B. longifolia*. For stems, with the exception of N:P, *E. monandrum* had H values for N and P that were each stronger than those characterizing *C. gracilis*. For roots, except for H_N , the H values for P and N:P descended among species in the order of *B. longifolia* > *C. gracilis* > *E. monandrum*. Whereas the corresponding order for H_N was *B. longifolia* > *E. monandrum* > *C. gracilis*. For the mean values of H , the difference of leaves and roots among three species and stems between two species were all not significant (Figure S1).

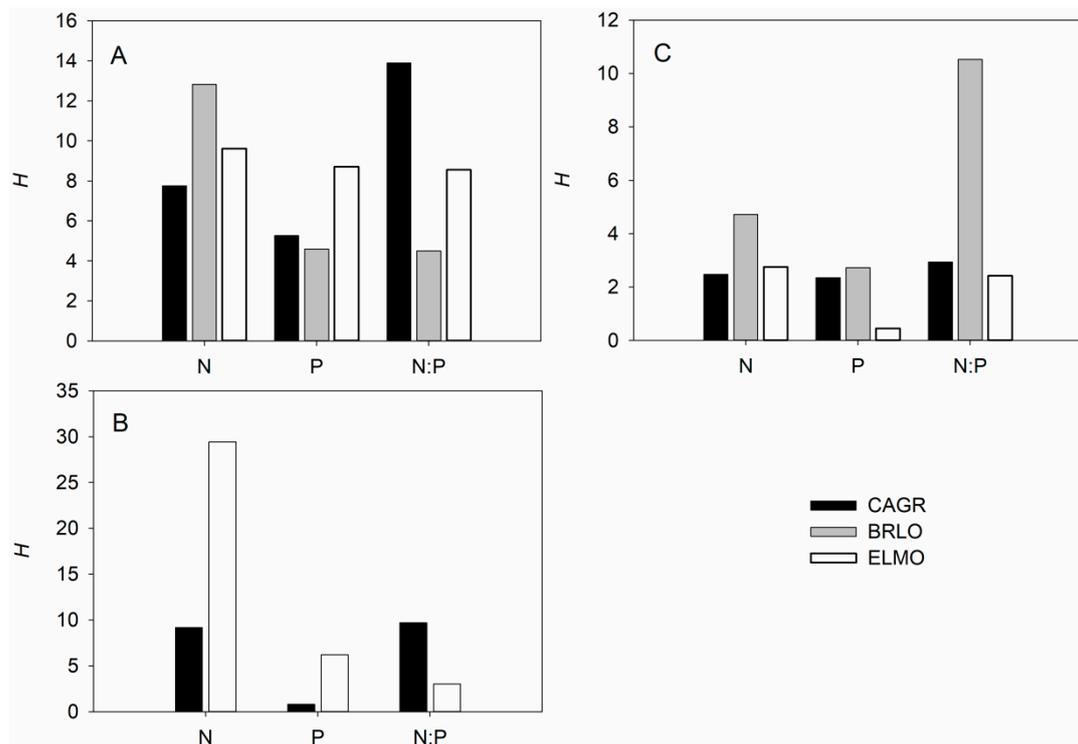


Figure 2. The stoichiometric homeostasis (H) values for N and P elements and their element ratios in the (A) leaf, (B) stem, and (C) root parts of different species. CAGR: *Cautleya gracilis*, BRLO: *Briggsia longifolia*, ELMO: *Elatostema monandrum*. *B. longifolia* has no stem and thus only stems of *C. gracilis* and *E. monandrum* were analyzed.

The mean value of H for N and P elements in leaves and stems of three species all stronger than their roots, while $H_{N:P}$ decreased in the order of leaf > root > stem (Figure 3).

Although the differences between H_N and H_P were insignificant, for leaves, stems, and roots, the mean values for H_N and H_P of the three species were all decreased in the order of $H_N > H_P$ (Figure 3). In leaves, $H_{N:P}$ exceeded either H_N or H_P . In stems, the homeostasis for N:P was stronger than the P element but weaker than the N element. In roots, the rank order of H_N , H_P and $H_{N:P}$ was consistent with that for leaves (i.e., $H_{N:P} > H_N > H_P$).

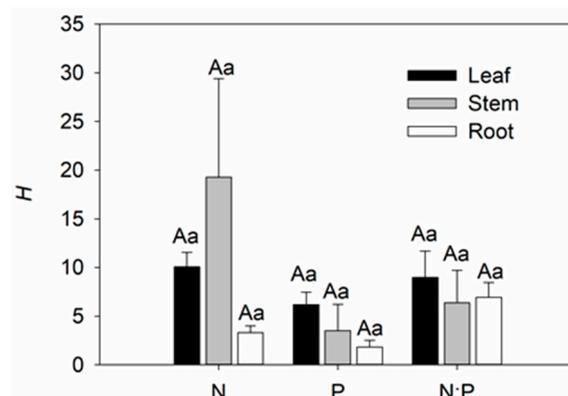


Figure 3. The mean stoichiometric homeostasis (H) values for the N and P elements and their ratios in leaves, stems, and roots of three species. Bars are the mean values with standard error. Capital and lowercase letters indicate significant differences among organs and element types, respectively.

3.3. Stoichiometric Homeostasis of Leaf N, P, and N:P in Greenhouse Cultivation Experiment

In the cultivation experiment, the concentration of N and P in leaves were significantly affected by species and treatment levels; N:P was significantly affected by the treatment level,

while the interaction between species and treatment level had no significant effects on the N and P concentration and their elemental ratio (Table 3). The N and P concentrations of leaves were both increased as higher N and P concentrations were applied in solution. For the stoichiometric homeostasis values of different elements of leaves in the two species, all values were greater than 4 ($p = 0.002$), which indicated a state of strict homeostasis, for which the N element was under stronger homeostasis than the P element ($p = 0.461$) (Figure 4).

Table 3. Results of two-way ANOVA of the effects of the species and treatment level and their interaction on N and P concentrations and N:P ratios in leaves of two species in the cultivation experiment.

| Variable | Species | | | Treatment | | | Species \times Level | | |
|----------|---------|----|------|-----------|----|------|------------------------|----|------|
| | F | df | p | F | df | p | F | df | p |
| N | 226.11 | 1 | 0.00 | 4.17 | 8 | 0.03 | 1.32 | 8 | 0.22 |
| P | 241.34 | 1 | 0.00 | 4.94 | 8 | 0.02 | 1.97 | 8 | 0.18 |
| N:P | 8.95 | 1 | 0.02 | 0.73 | 8 | 0.67 | 0.20 | 8 | 0.98 |

The numerator df are given in the table, the denominator df is 8.

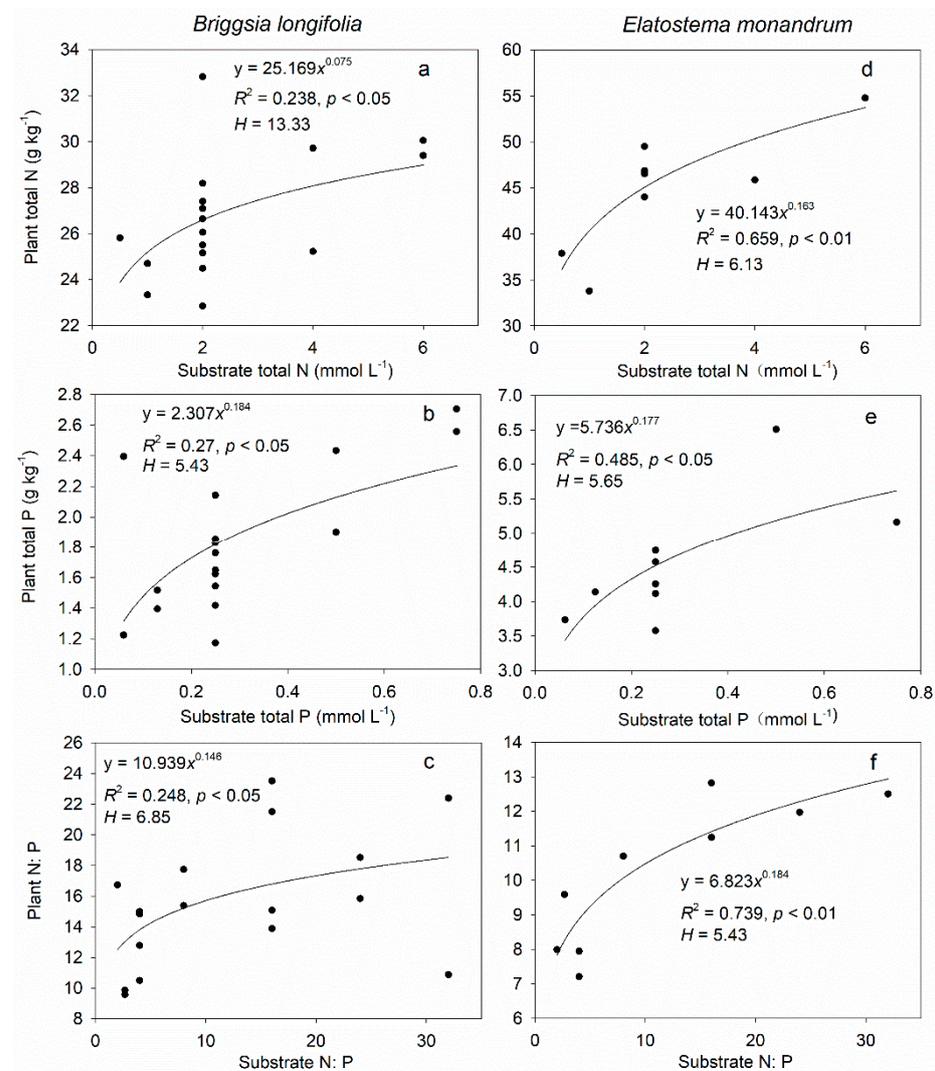


Figure 4. The statistics of homeostasis model and stoichiometric homeostasis (H) values for leaf N, P, and N:P in the greenhouse cultivation experiment. (a–c) H values for leaf N, P, and N:P of *Briggsia longifolia*, (d–f) H values for leaf N, P, and N:P of *Elatostema monandrum*, respectively.

4. Discussion

4.1. Differences in Nutrient Use Strategy between Epiphytic and Terrestrial Individuals of Facultative Epiphytes

In our field experiment, the concentrations of N, and P in epiphytic individuals of three species in the natural forest were higher than those in terrestrial individuals, but C:N, C:P, and N:P ratios in the former were lower than the latter (Tables S1–S3). This agreed with the results from fern in our study area and bromeliads in humid montane forest and lowland forests elsewhere [13,47,48]. C:N and C:P ratios reflect the carbon fixation per unit nutrient, the higher N and P concentration and lower C:N and C:P values are associated with luxury consumption of plants [16,49,50]. Accordingly, in our study, the use of N and P by epiphytic individuals were more luxurious than terrestrial individuals, which agrees with the result that terrestrial individuals of fern are more efficient in nutrient use than epiphytic individuals [13]. The plasticity in nutrient use strategy of facultative epiphytes is considered to be an adaptive mechanism to different environmental conditions in order to exploit the available resources efficiently [12,13]. Our results indicated that facultative epiphytes had more flexible plasticity in nutrient use strategies to adapt habitat shifts.

Winkler and Zotz [51] found that epiphytes possessed lower nutrient use efficiency than that of terrestrial plants. Epiphytes are generally considered to survive in the nutrient intermittent epiphytic habitats through luxurious consumption of nutrients [12]. They usually absorb large amounts of nutrients and store them in vacuoles when the nutrient is abundant [14,29,49]. Accordingly, the lower N and P use of epiphytic individuals may be related to the luxury uptake of N and P in epiphytic habitats. Furthermore, we found that variation in the elemental composition of epiphytic individuals exceeded that of terrestrial individuals, most likely because epiphytic habitats are more heterogeneous [5,52] and the elemental composition of plants is influenced by other environmental factors (e.g., water availability, light intensity) besides soil alone [38,49].

4.2. Effects of Nutrient Limitation on the Distribution of Three Facultative Epiphytes

The foliar N:P ratio can be used as an indicator of the type of nutrient limitation on plant growth, the lower N:P ratios indicate the plants were limited by N [24,49,53], whereas the higher N:P ratios indicates P limitations were present [29,54]. Epiphytes are usually restricted by P [55], but in our research, nutrient restriction types differ among the three species. The N:P ratio of terrestrial and epiphytic individuals of *E. monandrum* and epiphytic individuals of *B. longifolia* was lower than 12 (p -values = 0.214, 0.526, 0.225, respectively) (Tables S2 and S3), suggesting the growth of which was restricted by N availability [29]. Since the N:P ratio in terrestrial and epiphytic individuals of *C. gracilis* and terrestrial individuals of *B. longifolia* was higher than 12 (p -values = 0.004, 0.227, 0.009, respectively) yet still lower than 16 (p -values = 0.005, 0, 0.006, respectively) (Tables S1 and S3), we interpreted this to mean that the growth of which were limited by N or co-limited by N and P [28]. Our results were consistent with the finding that facultative epiphytes on date palms (*Phoenix dactylifera*) in southeastern Spain were subject to N-limited conditions [14]. Furthermore, in our research, the lower N:P ratio in epiphytic than terrestrial individuals implied that N-restriction in the epiphytic habitat was more pronounced. The higher P concentration in epiphytic individuals probably increases the demands for N, thus making them more pronounced. Furthermore, the higher P concentration in plants can alleviate the damage caused by drought stress [49]. In this study, the higher P concentration in epiphytic individuals may reflect their adaptation to epiphytic habitats where water is intermittent.

The factors that drive the distribution of facultative epiphytes are not clear, but previous results suggested that environmental factors can affect the distribution of epiphytes [14,46]. For the three species in our research, most individuals of *E. monandrum* and *B. longifolia* grow on the bark with mass mat or thick humus, while the majority of *C. gracilis* grow on the forest floor. For *E. monandrum* and *B. longifolia*, the N-restriction in epiphytic habitats was stronger than terrestrial habitats, therefore, they may gradually shift to forest floor to alleviate N limitation. For *C. gracilis*, the type of nutrient limitation in terrestrial and

epiphytic habitats was same, this indicated that the nutrient status in epiphytic habitats can satisfy its requirement. Previous research indicated that the interspecific competition in terrestrial habitats was more intense than that in epiphytic habitats [7]. Therefore, *C. gracilis* may shift to epiphytic habitats to escape interspecific competition.

4.3. Differences in Stoichiometric Homeostasis among Species, Organs, and Elements of Facultative Epiphytes

Traditional theory predicts that the stoichiometric homeostasis of autotroph was relatively weak [17,56]. However, mounting data suggest that plants have a strong regulatory capacity for their element composition [20,22,37]. Our results of the field and greenhouse cultivation experiment indicated that the values of H_N , H_P , and $H_{N:P}$ of leaves were all >4 ($p = 0.002$, 0.004 , respectively) (Figure 4; Table S4), both showed strong homeostasis, which did not support our second hypothesis that the homeostasis of facultative epiphytes is weak. These results for facultative epiphytes in our study are also at odds with previous research concluded that a weak homeostasis of plants implied higher ecological adaptability and better suitability to a more variable environment [33]. This discrepancy may be because that conclusion about relationship between stoichiometric homeostasis and ecological adaptability of plants was almost based on studies of plant leaves [33,49]. The elemental composition of leaves is insensitive to nutrient changes in the soil; instead, roots are more valid indicators of nutrient change in the environment [20,38,57–59]. Therefore, a leaf's stoichiometric homeostasis cannot accurately reflect the ecological adaptability of plants [38,60]. In our work here, although leaves did have strong stoichiometric homeostasis, it was rather weak for roots (Table S4). The main function of roots is to absorb mineral nutrients and water from the soil [33], their plastic nutrient absorption is helpful for facultative epiphytes to efficiently exploit the available resources in different habitats. This result indicated that facultative epiphytes could adapt to variable environment by changing the elemental composition of their roots.

Moreover, the difference in stoichiometric homeostasis among the three species in our field study was not significant, and the stoichiometric homeostasis mainly affected by organs (Table S5), likely because all three share a similar species richness in the sampling area, and their ecological strategy and adaptability to the environment were comparable [22]. This was also confirmed by the consistent response of the two species to nutrient addition in the greenhouse cultivation experiments in our study (Table 3).

Different organs of the same species exhibit disparate stoichiometric characteristics to better adapt to the environment [16,20,33]. We found that stoichiometric homeostasis was stronger in aboveground than belowground of the three facultative epiphytes. Roots were more sensitive to changes of elements concentrations in environmental resources, which agrees with findings reported for terrestrial grass and woody plants [21,22,31,38]. However, unlike the related studies on terrestrial woody plants [38], the stems of *C. gracilis* and *E. monandrum* show strong stoichiometric homeostasis (Table S4). This may be related to the insensitivity of some key elements in stems of facultative epiphyte to changes in soil nutrient concentrations. The stems of woody and herbaceous plants take different functions, the stems of woody plants mainly play transportation and supporting role, while the stems of herbaceous plants have less structural C than woody plants, yet bear the functions of photosynthesis, transportation, and the supporting action [20]. Therefore, the stems of herbaceous plants need relatively stable supply of elements to maintain their physiological functions.

The strength of homeostasis is also related to the elemental concentration [61]. Previous research for terrestrial plants indicated that the homeostasis of macro-elements was higher than trace elements [34,61]. In our study, the value of stoichiometric homeostasis of N and P in the three facultative epiphyte species showed the order of $H_N > H_P$. This is consistent with results from vertebrates, and trees with greater control over high-demand elements [34–36]. Therefore, the facultative epiphytic plants may also have greater control over macro-elements highly demanded for physiology functioning. However, our research only focused on the stoichiometric homeostasis of N and P elements in facultative

epiphytes, the stoichiometric homeostasis of trace elements remains unknown. Therefore, whether the stoichiometric homeostasis of macro-elements in facultative epiphytes is higher than trace elements still requires further testing and verification.

Due to the synergistic changes of N and P within plant tissues, in that the accumulation of N within a given plant tissue is usually accompanied by an increase in its P content, the homeostasis of N:P is stronger than N and P elements [17,62]. However, in our study, the stoichiometric homeostasis value of N:P in leaf and root were all higher than that of P but lower than that of N (Figure 3). Based on the theory that limiting elements should have strong homeostasis [31,34,63], we speculate that facultative epiphytes may be restricted by N availability. These plants, therefore, would take strong regulation of N to cope with the unpredictable fluctuations of N elements in their habitat.

5. Conclusions

This study systematically elucidates the nutrient use and ecological adaptation strategies of facultative epiphytes from the perspective of stoichiometry using field investigation and greenhouse cultivation experiments. Our study showed that epiphytic individuals of facultative epiphytes survive intermittent habitat via luxury consumption of nutrients, while terrestrial individuals use more conservative nutrients (Figure 5). The nutrient use strategies of facultative epiphytes were flexible, which enabled facultative epiphytes to exploit bark and soil interchangeably. Facultative epiphytes had strong control over N and P concentrations and N:P ratio of leaves and stems, while roots had weaker stoichiometric stability. These findings suggested that to adapt to the variable habitats in montane forest ecosystem, facultative epiphytes maintain stable metabolic activities of leaves by regulating the absorption and composition of elements in roots.

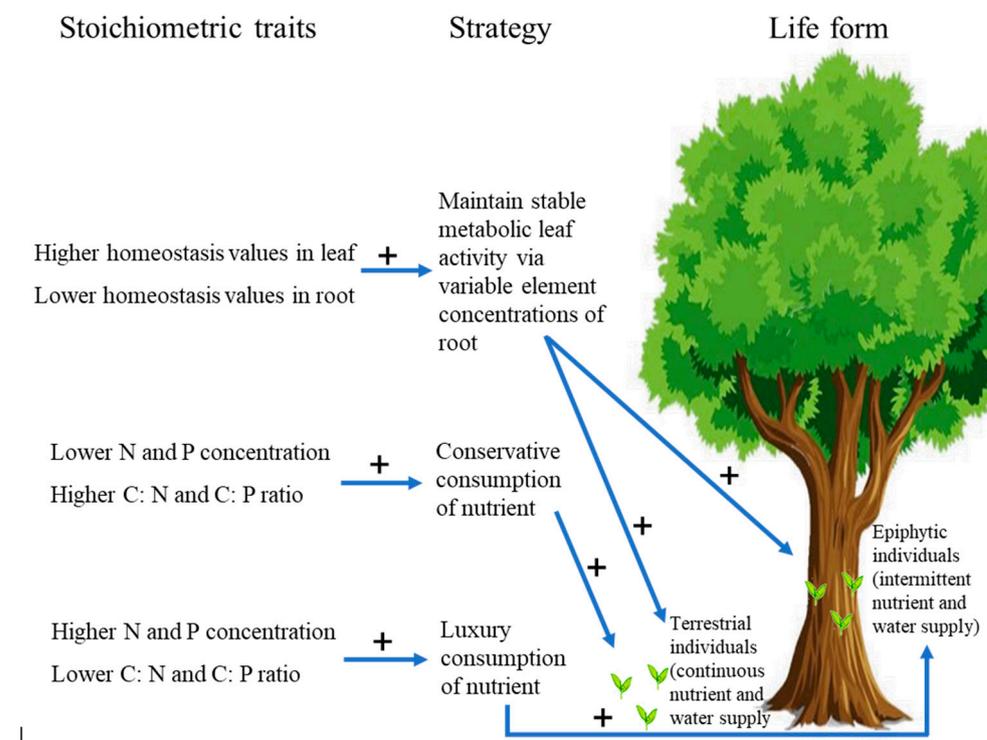


Figure 5. Summary of links between nutrient composition and nutrient use strategy of epiphytic and terrestrial individuals of facultative epiphytes. The (+) denotes that effects are positive.

Supplementary Materials: Supplementary materials can be found at <https://www.mdpi.com/1999-4907/12/1/16/s1>. Figure S1: The mean stoichiometric homeostasis (H) values for N, and P elements and their element ratios in leaf, stem, and root of different species. Table S1: The difference of stoichiometric traits of C, N, and P concentrations and their element ratios in different organs of C.

gracilis between epiphytic and terrestrial habitats. Table S2: The difference of stoichiometric traits of C, N, and P concentrations and their element ratios in different organs of *E. monandrum* between epiphytic and terrestrial habitats. Table S3: The difference of stoichiometric traits of C, N, and P concentrations and their element ratios in different organs of *B. longifolia* between epiphytic and terrestrial habitats. Table S4: The stoichiometric homeostasis values for different elements, organs, and species in the field experiment. Table S5: Comparison of stoichiometric homeostasis values (mean \pm SE) for different organs, and species in the field study and the effects of organ, species and their interactions on stoichiometry homeostasis.

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