

[Comment 1]: The abstract could be refined to highlight more clearly the quantitative outcomes of the synthesis (e.g., mean global leaf C, N, P values and N:P ratios across life forms).

[Response]: Thanks for the suggestions. In this version, we have revised the abstract accordingly as follows: “**Abstract:** Ecological stoichiometry examines the balance and ratios of multiple elements in ecological processes. In shrubs, characterized by their adaptability to extreme environments such as alpine and arid regions, stoichiometric traits likely differ from those in trees and grasses, reflecting unique ecological strategies. However, this hypothesis remains insufficiently explored. Here we review the current state of shrub stoichiometry and then identify research hotspots of shrub stoichiometry. Then, we summarize the effects of climate, soil properties, phylogeny, ontogeny, and human activities on stoichiometry of shrub leaves. In addition, we compared the stoichiometry of shrublands with that of forests and grasslands. The development of shrub stoichiometry research can be broadly divided into three stages: the initial stage, the rapid development stage, and the high-quality development stage. Notably, existing studies have primarily focused on leaf stoichiometry. Mean values of C, N, P, C:N, and N:P in shrub leaves globally were 454.66 mg g<sup>-1</sup>, 18.93 mg g<sup>-1</sup>, 1.20 mg g<sup>-1</sup>, 23.4, and 16.1, respectively. Shrub leaf N and P content were higher than those of trees (16.58 mg g<sup>-1</sup>, 1.18 mg g<sup>-1</sup>, respectively) and lower than herbs (21.72 mg g<sup>-1</sup>, 1.64 mg g<sup>-1</sup>, respectively). In contrast, C content and C:N ratio showed opposite trends, being lower than trees (502.31 mg g<sup>-1</sup>, 30.1) but higher than herbs (414.22 mg g<sup>-1</sup>, 17.9). Importantly, the N:P ratio in shrub leaves exceeded that of both trees (15.4) and herbs (13.3), suggesting stronger P limitation in shrubs. Leaf N and P content correlated positively with soil nutrients and precipitation, and negatively with temperature. Functional types also influenced stoichiometry, with deciduous and leguminous shrub species showing higher N and P content than evergreen and non-leguminous shrubs. Future studies should integrate above- and below-ground stoichiometry, consider phylogenetic influences, and standardized sampling and analytical protocols to better understand shrubland adaptation and

formation mechanisms under global change.”

**[Comment 2]:** The section discussing phylogenetic influences is quite dense; a table summarizing key findings from major studies could improve accessibility.

**[Response]:** We have revised this section and added Table 1 accordingly. The revised content is presented as follows.

#### **“4.3 Phylogenetic Relationships, Functional Types, and Age Effects**

Apart from environmental factors, an increasing number of studies have revealed a strong correlation between the variation in stoichiometry and phylogenetic relatedness among plant species (He et al., 2006; Kerkhoff et al., 2006), supporting the biogeochemical ecological niche hypothesis. This hypothesis posits that organisms require specific quantities and proportions of essential nutrients to sustain growth. Due to differences in functional traits and life strategies, different species exhibit distinct nutrient requirements and thus occupy varying positions and sizes within the n-dimensional space of multiple elemental content (Peñuelas et al., 2008, 2019). For example, Sardans et al. (2021) analyzed the leaf concentration of N, P, and other elements in 2,3962 trees from 227 species and found that shared ancestry explained 60-94% of the total variation in leaf nutrient concentration and ratios, while current climate, atmospheric nitrogen deposition, and soil types collectively explained 1-7%. Similar findings have been reported at regional scales; however, some studies have yielded contrasting results (Table 1). Therefore, the influence of phylogenetic factors on leaf stoichiometry remains inconclusive. Although few studies have examined the impact of shrubs phylogeny on their ecological stoichiometry, they all agree that phylogeny plays a crucial role in regulating the variation of shrub stoichiometry (Table 1), particularly for N content. Studies on shrub elemental stoichiometry in the southwestern karst region of China (Li et al., 2021;), Gansu Province (Akram et al., 2020), and northern China (Yang et al., 2016) have consistently reported strong phylogenetic signals in leaf N. These findings suggest that species phylogeny should

be carefully considered in future research on shrub stoichiometry, particularly when a large number of species are involved.”

Table 1 Summary of studies on phylogenetic and environmental effects on leaf elements.

Study area	Vegetation type	Species (n)	Elements	Variance explained by phylogeny	Variance explained by environment	Reference
Global	Forests	227	N, P, K, Ca, Mg and S	60–94%	1–7%	Sardans et al. 2021
Global	Forests	2,000	N, P, K	>60%	–	Vallicrosa et al. 2022
China	Grasslands	213	N, C:N	58.8%	<3%	He et al. 2006
China	Grasslands	147	N	36%	38%	He et al. 2010
China	Woody plants	702	N, P	16–38%	42–55%	Zhang et al. 2012
China	Woody plants	3,000	N, P	3.9–23.3%	44.4–65.5%	An et al. 2021
Arid deserts, China	Woody plants	15	C:N:P stoichiometry	1.8–54.2%	3.6–66.3%	Akram et al. 2023
Inner Mongolia, China	Shrubs	55	N,P and N:P ratio	29.6–48%	<11%	Liu et al. 2013
China	Shrubs	11	C:N:P stoichiometry	32.9–40.3%	17.0–19.0%	Yang et al. 2015

[Comment 3]: Consider expanding on methodological challenges (e.g., variation in sampling organs, geographic biases, or digitization uncertainty) that might affect comparability across studies.

[Response]: Thanks for this valuable suggestion. We have integrated this content into the Conclusion and Future Prospects, as shown below.

“6.5 Methodological Considerations for Future Research

Future studies should place greater emphasis on ensuring methodological consistency. Differences in sampling organs, geographic sampling biases, statistical approaches, and uncertainties related to data extraction from published sources can all reduce the comparability of results across studies and affect their accuracy. For example, root elemental concentrations can vary substantially between fine roots, coarse roots, and roots of different diameter classes, making it difficult to compare findings across studies without consistent sampling protocols (You et al., 2023). Similarly, using different analytical methods—such as random forest models versus linear mixed-effects models—may lead to opposite conclusions about the relative importance of

phylogeny and environment in shaping leaf stoichiometry, depending on the data structure and model assumptions (Tian et al., 2024). Therefore, developing standardized protocols for sample collection, spatial representation, and data reporting is essential to improve the reliability, comparability, and overall synthesis of shrub stoichiometry research across regions and species.”