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RESEARCH ARTICLE

Developing together: The elementome and biogeochemical niche of the mutualistic occupants of a fig microcosm

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Abstract

1. In brood-site pollination mutualisms, where flowers provide nutrition and shelter to pollinator offspring in exchange for pollination, resource allocation to inflorescences is directly related to plant and pollinator fitness.
2. We determine resource allocation to components of an enclosed monoecious *Ficus* inflorescence or syconium that, besides seeds, also houses and provides nutrition to pollinator wasp offspring, each developing within individual uniovulate galled flowers. Besides biomass, we determine elemental concentrations as parameters of resource allocation. For the first time, we apply the biogeochemical niche (BN) concept to a mutualism and construct the BN of syconial occupants using the elementomes and stoichiometric ratios of plant, seed and pollinator tissue. We predicted that BNs of seeds and galls containing wasps should differ due to differences in tissue type, facilitating their co-development. We also measure trophic stoichiometric ratios (TSRs) for various elements to determine resource mismatch between consumers and resources.
3. We found that the syconium wall, which insulates and protects developing seeds and wasps, constituted 58% of syconial biomass. Individual pollinators and their galls were significantly heavier than seeds indicating that their development is resource-intensive. As predicted, seeds and adult female pollinators had significantly different BNs, highlighting differences in nutritional needs of these mutualistic occupants within a shared nutrient-providing resource. Pollinators had significantly lower C:N and C:P ratios than the syconial wall indicating limitation of N and P within host resources. The BN of pollinator wasps was distinguished by significantly higher concentrations of nitrogen, phosphorus, zinc and sulphur compared to the syconium wall or seeds. TSRs of >4 for nitrogen and sulphur highlight the heightened resource mismatch that pollinators likely face for these elements during their development. We found no overlap in the BNs of male and female pollinator wasps, likely due to their starkly different anatomical and functional traits.

4. Overall, our study demonstrates how BNs and TSRs can reveal trading of resources within mutualisms highlighting non-overlapping requirements for elements and the potential limitations they can pose for resource providers and consumers. These parameters can serve as common currencies for comparisons across mutualistic interactions.

KEYWORDS
biogeochemical niche, elementome, fig syconium, microcosm, mutualism, resource allocation, trophic stoichiometric ratios

1 | INTRODUCTION

Plants partition resources between different functions, namely, growth, defence, maintenance and reproduction at any given time (Bazzaz et al., 2000). Plants are a metapopulation of organs where source–sink and sink–sink competition also occur (Sadras & Denison, 2009; White, 1979). While optimal partitioning theory focuses on partitioning between roots, stems, leaves and associated trade-offs (McCarthy & Enquist, 2007), allocation at lower levels has been scarcely examined (Obeso, 2004). In many angiosperms, flowers occur in inflorescences with complex architecture (Kirchoff & Claßen-Bockhoff, 2013; Tucker & Grimes, 1999). Inflorescences are pollination units (Torices & Méndez, 2014) or are also dispersed as fruit units serving to attract fruit and seed dispersers (Fleming & Kress, 2011). Understanding allocation of resources to and within these reproductive units constitutes the basis for understanding comprehensive fitness allocation strategies in individual plants and yet has received limited attention (Chen & Pannell, 2023; Torices & Méndez, 2014).

Inflorescences are allocated resources throughout their development including resources to reward pollinators. Some inflorescences can also photosynthesise and fix carbon, offsetting some of their resource demand (Aschan & Pfanz, 2003; Bazzaz et al., 1979; Brazel & Ó'Maoiléidigh, 2019). In brood-site pollination mutualisms, the host plant provides resources for pollinator offspring development as a reward for pollination (Sakai, 2002). In such mutualisms, there is overlap in the developmental time of seeds and pollinator offspring that share the same inflorescence, increasing potential competition between mutualists for the same resources. It is, therefore, important to study resource allocation patterns in such inflorescences by the plant, particularly comparative allocation to seeds versus pollinator offspring.

Resource allocation currency has often been debated. While biomass may be used as a surrogate for final investment (Charlesworth & Morgan, 1991), allocation patterns vary with currency and using multiple currencies is recommended (Brock et al., 2017; Pérez-Martínez & Méndez, 2021), especially in studies pertaining to plant associations with other taxa. A species-specific elemental composition provides a common resource currency generalizable across kingdoms (Elser et al., 2000; González et al., 2017). Ecological stoichiometry usually focuses on relative elemental composition, mainly of carbon, nitrogen and phosphorus (Fernández-Martínez, 2022; Hessen et al., 2013; Sardans et al., 2021). However, many other elements, some of which are also limiting, are important (Kaspari, 2021). The elementome, which refers to the concentrations of most, if not all, elements present in an organism, is increasingly being employed (Arriola et al., 2024; Bartrons et al., 2018; González et al., 2017; Peñuelas et al., 2008) and can be expressed as a multidimensional biogeochemical niche (BN) wherein each species occupies a unique position in multivariate space formed by the axes of element concentrations (Peñuelas et al., 2008). The BN is comparable to Hutchinson's *n*-dimensional niche with elemental concentrations comprising phenotypic traits (González et al., 2017). According to BN theory, which is an extension of niche theory, BN separations of different species can be characterized by (i) taxonomic distance: greater distance provides greater separation; (ii) co-existence: coexisting species have non-overlapping BNs; and (iii) trade-off between homeostasis and plasticity (Peñuelas et al., 2019). The concept of BNs is relatively recent and was first described for plants (Peñuelas et al., 2008), animals (González et al., 2017) and plants and animals together to compare trophic levels (Bartrons et al., 2018). Mutualisms, which are consumer–resource interactions (Holland et al., 2005), can be understood by the application of the BN concept, which to the best of our knowledge has not been attempted. Another parameter of interest for consumer–resource interactions is the trophic stoichiometric ratio (TSR), which is a measure of stoichiometric mismatch between resources and consumers (Filipiak & Weiner, 2017). Together, BNs and TSRs are vital to understand relative patterns of resource allocation and trade between interacting partners in physiologically integrated brood-site pollination mutualisms (Kulkarni & Borges, 2026).

The interaction between fig trees and their species-specific pollinator wasps is an important brood-site pollination mutualism in which seeds and developing pollinators compete for resources. A closed inflorescence, that is, the syconium, acts as a platform for the interaction (Janzen, 1979). In monoecious fig species, female pollinator wasps enter the syconium via an opening (ostiole) and pollinate some female flowers, while laying eggs in others (Janzen, 1979). Pollinated uniovulate flowers that receive pollinator eggs develop into galls, with each galled flower supporting a single fig wasp larva. Hence, host resources are usurped by pollinators in exchange for pollinated flowers that yield seeds. A fig syconium has been aptly termed a microcosm (Borges et al., 2019;

Jackson, 2004), obtaining resources from the plant as a physiological unit (Jandér & Herre, 2016) via a narrow stalk or peduncle serving as a conduit for plant resources (Figure 1A). Stoichiometric ratios of limiting nitrogen and phosphorus (N:P) have been reported before in *Ficus racemosa* with a focus on comparing pollinators with syconial tissue (Zhang & Han, 2010). However, co-limitation of various elements and the elemental niche have not been examined for any mutualism. Non-overlapping trophic niches were observed in symbiotic marine invertebrates sharing a habitat (Guibert et al., 2024); such nutrient niche partitioning is commonly seen across systems where organisms share resources (Salas-López et al., 2022). Furthermore, dietary niche partitioning can enhance sexual dimorphism in arthropods (Bauld et al., 2022). In a monoecious fig syconium, where fig seeds, male and female pollinators and non-pollinators share space and resources, it is important to examine overlap in nutritional requirements of seeds and wasps and to determine if these are different from the composition of available resources. Theories such as the unbeatable seed hypothesis, insufficient number of eggs, interference between pollinators and host sanctions can explain the coexistence of seeds and pollinators, resulting in mutualism stability (Jandér & Herre, 2010; Nefdt & Compton, 1996; Wang et al., 2009; West & Herre, 1994). Determining differences in nutrient composition and BN of these occupants will provide a perspective of coexistence at the elemental level. The quality of resources the host tree supplies to the developing pollinator galls can limit their numbers and further contribute to mutualism stability.

Here, we comprehensively determine resource partitioning to syconium components, beginning with biomass. We examine number–mass trade-off for seeds and pollinator offspring. We

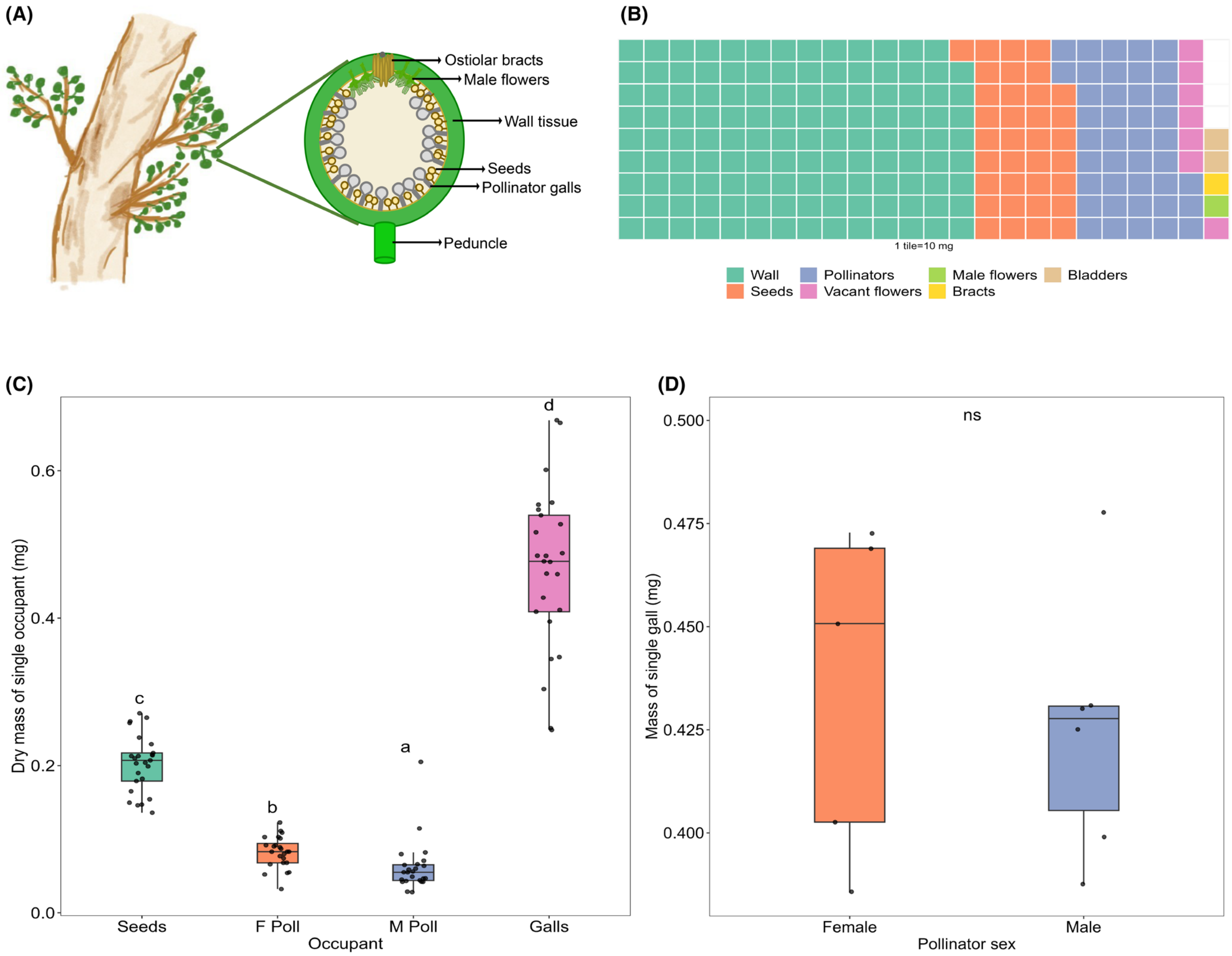

FIGURE 1 (A) Cauliflorous arrangement of syconia and a syconium dissected through the ostiole–peduncle axis. (B) Distribution of biomass to different syconium components. Pollinators include wasps and their galls, averaged for males and females. Bladders are undeveloped galls. $n=24$ syconia from two trees. (C) Boxplots representing mass of single occupants. Letters above error bars indicate significance; bars with common letters are not significantly different. $n=24$ syconia from two trees. (D) Boxplots representing dry mass of empty galls: Single male ($n=300$ galls from 6 syconia) and female pollinator ($n=250$ galls from 5 syconia). ns = not significant. In (C) and (D), horizontal thick lines indicate median values; lower line of the box indicates first quartile and upper, the third quartile; whiskers indicate minimum and maximum values. F Poll, Female pollinators; M Poll, Male pollinators.

determine BNs occupied by seeds, pollinator offspring and syconial wall tissue (as proxy for host plant nutrition available to developing seeds and pollinators), for some of the important micro- and macro-elements—carbon (C), nitrogen (N), phosphorus (P), sulphur (S), potassium (K), magnesium (Mg), calcium (Ca) and zinc (Zn). We compare the C:N:P ratios of these tissues within the syconium to determine if stoichiometric ratios correlate with BN results. By considering the elemental composition of syconium wall tissue as the resource source containing resources immediately accessible to pollinator galls, we also estimate trophic stoichiometric ratio (TSR) mismatch that seeds and pollinators encounter, separately for each element (see Section 2). We expect that seeds and pollinators have distinct, non-overlapping BNs that facilitate their co-development. We also expect pollinators to have different elemental compositions compared to syconial wall tissue, owing to fundamental differences in tissue types and function. We predict different BNs for male and female pollinator offspring owing to their extreme sexual dimorphism in size and functionality (Janzen, 1979), with the neotenic wingless males usually never leaving the syconium while only the winged females serving as pollen vectors. We thus treat the syconium as a microcosm within which resources are partitioned. Through our study, we hope to establish the utility of the BN in understanding the dynamics of resource sharing and trading in mutualisms at the elemental level, which can be further used in other mutualistic systems. Furthermore, the only other study on elemental composition (N:P) has been conducted on the same species (Zhang & Han, 2010), allowing us to compare with and expand on earlier work.

2 | MATERIALS AND METHODS

2.1 | Study site and system

The study was conducted on trees of the monoecious *Ficus racemosa* Linn. (Section: *Sycomorus*), located in and around the Indian Institute of Science campus, Bengaluru (12°58′ N, 77°35′ E), Karnataka, India. No permits were required for the field experiments. *Ficus racemosa* is pollinated by the agaonid wasp *Ceratosolen fusciceps*. Syconia with their single ostiolar opening have an internal lumen linked by numerous protogynous female flowers; a small number of male flowers develop later around the ostiole. Flowers are protected by a thick syconial wall (Figure 1A). Syconium development occurs in five distinct phases (A–E) (Galil & Eisikowitch, 1968). A-phase: small syconia with female flowers developing. B-phase: female pollinator wasps (foundresses) enter through the ostiole, pollinate and oviposit in flowers. C-phase: seeds and pollinator offspring develop. D-phase: wingless male pollinators exit galls, mate with females, which are released from the syconium through exit holes excavated by males. Being monoecious, each syconium of *F. racemosa* hosts both seeds and pollinator offspring resulting in potential conflict while sharing common resources, thus serving as an appropriate and experimentally tractable system for the comparative study of elemental composition.

2.2 | Pollination and sample collection

2.2.1 | Biomass allocation within syconium

All experiments were performed in bagged (muslin-covered) syconia to control extraneous effects. In *F. racemosa*, syconium-bearing bunches are borne on the main tree trunk. Five bunches of syconia in each of two trees were bagged during A-phase, and when syconia reached B-phase, five pollinator wasps (foundresses) were introduced into each syconium. Foundress wasps were obtained from D-phase syconia collected from other trees. The next morning, foundresses were introduced into syconia by placing them near the ostiole using a paint brush and inducing them to enter. Syconia were allowed to develop till D-phase and collected before wasps emerged from them. Syconia were opened along the ostiole–peduncle axis (Figure 1A), and all wasps (males and females) were collected. Post-wasp collection, each syconium was cut into eight equal portions, and seeds and gall remnants were removed from four alternate pieces. Any wasps that failed to emerge were removed from the galls while dissecting. All components were dried at 75°C for 48 h and their dry mass recorded.

2.2.2 | Comparative allocation to seeds and pollinator wasps

In order to compare between male and female galls, naturally available and unmanipulated syconia were collected at the end of C-phase before wasp eclosion. Syconia were divided into eight portions as before and 50 galls each containing male or female pollinator wasps were collected from two randomly selected pieces from each syconium. These galls were dissected to remove the wasps. Similarly, around 200 seeds were also removed from the syconia. The wet mass of seeds, wasps and galls were recorded before drying at 75°C for 48 h to obtain dry mass.

2.2.3 | Elemental analysis

Three sets of syconia were used to obtain adequate samples, two generated by experimental manipulations (Set 1: Tree 1, $n = 43$; Tree 2, $n = 11$; Tree 3, $n = 15$; Tree 4, $n = 21$; and Set 2: Tree 1, $n = 19$; Tree 2, $n = 4$; Tree 3, $n = 24$) and one set of naturally developed and unmanipulated syconia (Set 3: Tree 1, $n = 14$; Tree 2, $n = 21$; Tree 3, $n = 6$; Tree 4, $n = 38$; Tree 5, $n = 3$; Tree 6, $n = 3$; Tree 7, $n = 3$). Experimental manipulations consisted of controlled pollination by introducing pollinators as before. Seeds, wasps and wall tissue of each syconium were separated, dried and used for elemental analysis.

2.3 | Pooling of samples from different syconia

Syconial components were all separately pulverized. To obtain sufficient sample quantity, each syconium component (seeds, wall tissue and wasps) generated from different syconia was appropriately mixed to make up each sample. While pooling, samples from different sets of syconia used (generated from experimental manipulations or naturally developed) were kept separate for elemental analysis, but samples from different trees could not be kept separate due to limited sample biomass. We determined whether statistical pooling of these samples affected the results (see Section 2.7 for more details). Concentrations of elements were unaffected by the type of experimental set, after seeds from one experimental set were excluded (Table S1). This was due to the difference in the method of extracting seeds from the syconium. In two sets of syconia, seeds were extracted by scooping out contents into distilled water and separating them with a soft brush and sieve, effectively removing the achene tissue or seed cover surrounding the seeds. In the remaining set, seeds were extracted under the microscope along with the surrounding achene tissue. When the seed samples with seed covers were excluded from the statistical analysis, the results were unaffected by the type of experimental set (Table S1).

2.4 | Quantification of elements

2.4.1 | Carbon, nitrogen and sulphur

Carbon, nitrogen and sulphur were quantified using a Vario EL cube CHNS analyser (Elementar, Langenselbold, Germany). Powdered samples (5 mg each) were sealed in tin foil and subjected to combustion at 1800°C. The resulting CO_2 and NO_2 were trapped and sequentially analysed using a thermal conductivity detector. Some samples were randomly selected for replicates. Blanks (only tin foil) and standards were also included for comparison. The results obtained are expressed in percentages.

2.4.2 | Other elements

Phosphorus, potassium, magnesium, calcium and zinc were estimated using Inductively Coupled Plasma-Mass Spectrometry (ICP-MS). Up to 200 mg of homogenized samples was mixed with 8 mL of 70% nitric acid and subjected to acid digestion in a microwave digestion system. Digested samples were cooled to room temperature, and the volume was made up to 50 mL with MiliQ water and further diluted (1:9) with 2% nitric acid. Samples were analysed using an Agilent-7800 ICP-MS using appropriate standards.

2.5 | Estimation of trophic stoichiometric ratios (TSRs)

TSRs were estimated for each element using the equation (Filipiak et al., 2024; Filipiak & Weiner, 2017)

$$TSR_X = (C:X)_{\text{syconial wall}} / (C:X)_{\text{seeds or pollinators}}$$

where C is the concentration of carbon, X is concentration of any other element X. Syconial wall is the proxy for plant nutrients accessible to syconial occupants. Elemental ratios were calculated as atomic ratios. A median TSR value was calculated for each element, since sample pooling resulted in different sample numbers for syconial wall, seeds and pollinators. The assimilation efficiency for all elements is assumed to be 100%, except for carbon where respiration results in loss of about 75% as CO_2 (Filipiak & Weiner, 2017). A TSR of >4 (1/0.25), estimated conservatively using assimilation efficiencies as ratio of gross growth efficiency (GGE) of element X compared to carbon, indicates a mismatch between the source and the consumer (Filipiak & Weiner, 2017).

2.6 | Replication statement

	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Biomass allocation	Syconium	Syconium (*n* = 25 syconia from two trees)	25
Comparative allocation to seeds and wasps	Syconium (*n* = 15 syconia from two trees)	Pooled seeds, wasps and galls	Seeds = 8 Galls: Male = 6; Female = 5 Wasps: Male = 6; Female = 5
Elemental analysis	Syconium (naturally pollinated: *n* = 88 syconia from seven trees; two sets experimentally pollinated: *n* = 90 and *n* = 43 syconia from four trees each)	Pooled seeds, wasps and syconial wall tissue	Seeds = 16 Wasps: Male = 3; Female = 8 Wall tissue = 15

2.7 | Statistical analysis

The number and mass of seeds, galls, wasps, empty flowers and bladders (galls that failed to develop) were extrapolated for the entire syconium from the examined sections. Statistical analyses were conducted using R software version 4.1.3 (R Core Team, Vienna, Austria). Mass of single syconial occupants was compared using generalized linear mixed models (GLMMs), considering tree identity (tree ID) as a random factor, with gamma distributions and log link using the *lme4* package (Bates et al., 2015), followed by pairwise Tukey HSD tests using the *emmeans* package (Lenth, 2021). A compact letter display (CLD) was used for the pairwise comparison results using the *multicomp* package (Hothorn et al., 2016). For all number–mass trade-off relationships, Kendall's tau tests were conducted and expressed on semi-log plots.

Concentrations of all elements were converted to mg/g. We used GLMs to determine the effects of type of syconia set used (generated from experimental manipulations or naturally developed) on element concentrations. GLMs with and without the type of syconial set were compared using ANOVAs. Carbon, nitrogen, phosphorus, potassium and magnesium concentrations for different syconial components were compared using one-way ANOVA, followed by Tukey HSD tests for pairwise comparisons with adjustments for multiple testing, using the *emmeans* package. Values of zinc, calcium, sulphur and molar ratios of C:N, C:P and N:P were compared using non-parametric Kruskal–Wallis tests, followed by Dunn's test for pairwise comparisons with the Benjamini–Hochberg correction for multiple comparisons. Scaled values of all element quantities were used for correlation-based principal component analysis (PCA) using the *factoMineR* package (version 2.11) (Lê et al., 2008). To compare BNs, PCA scores from the first two principal components for all syconial components were extracted and compared using PERMANOVA (package *vegan*) (Oksanen et al., 2013) and pairwise PERMANOVA (package *pairwiseAdonis*) (Arbizu, 2020). Variable loadings and PCA scores of the first two principal components were then plotted using the *factoextra* package (Kassambara & Mundt, 2017).

3 | RESULTS

3.1 | Biomass distribution within the syconium

Most syconium biomass was constituted by the wall (58.79%) (Figure 1); seeds and pollinators (gall tissue + wasps) made up 16.47% and 19.18% of the biomass, respectively. Vacant flowers made up 3.35% and bladders (undeveloped galls) formed around 1% of total biomass. Male flowers and ostiolar bracts constituted the least total biomass (0.7% and 0.51%, respectively). Female pollinators made up 2.05%, male pollinators about 0.68% and galls about 16.54% of total syconium mass.

3.2 | Relative allocation of biomass to seeds and pollinator galls

Tree ID significantly affected the biomass of individual seeds and pollinators (Table S2). A single empty gall had significantly higher dry biomass compared to seeds or pollinators (Figure 1C, Table S3). Biomass of male and female empty galls did not differ (Figure 1D); however, male pollinators were significantly lighter than females (Figure 1C, Table S3). Individual seed dry masses were significantly greater than for individual female pollinators (Figure 1C, Table S3). The wet mass of the occupants showed similar patterns (Figure S1a,b).

3.3 | Trade-off between number and mass of single occupants

The number of seeds/galls and mass of single seed or pollinator clustered separately for the two trees used in the experiment (Figure 2a,b); hence, correlations were conducted separately for each tree. The number and individual mass of seeds, male and female pollinators were not related (Figure 2a,b) in either tree. The relationship remained the same on removing the influential outliers.

3.4 | The elementome: Concentrations of different elements

There was a significant effect of component identity (plant tissue: seed, syconium wall; animal tissue: female or male pollinators) on the concentrations of all measured elements (Tables S4 and S5). Female pollinators had significantly higher levels of carbon, followed by seeds and male pollinators (Figure 3, Table S6). Other elemental concentrations showed more or less clear distinction between plant and animal tissues. Male and female pollinators had significantly higher concentrations of nitrogen, phosphorus, sulphur and zinc, with males further showing significantly higher values of nitrogen compared to females (Figure 3). The syconial wall had significantly higher levels of potassium, followed by seeds (Figure 3). Both seeds and wall tissue had higher concentrations of magnesium and calcium compared to pollinators (Figure 3).

3.5 | Stoichiometry: C:N:P ratios

There were significant differences between syconium components in their C:N (Table S5), C:P (Table S5) and N:P ratios (Table S5). Wall tissue had the highest ratios of C:N and C:P, followed by seeds and pollinators (Figure 4, Table S6). The trend changed for N:P where pollinators had significantly higher ratios compared to wall or seeds (Figure 4). Male and female pollinators did not differ in any ratios (Figure 4). The results were similar when ratios for different syconial components were compared without considering seeds with achene seed covers (Figure S2).

3.6 | Syconial biogeochemical niche

The magnitude of the variable loadings in the PCA analysis indicated that all elements contributed nearly equally to the first two principal components, albeit in different ways (Figure 5A). While carbon, phosphorus, nitrogen, sulphur and zinc contributed positively to

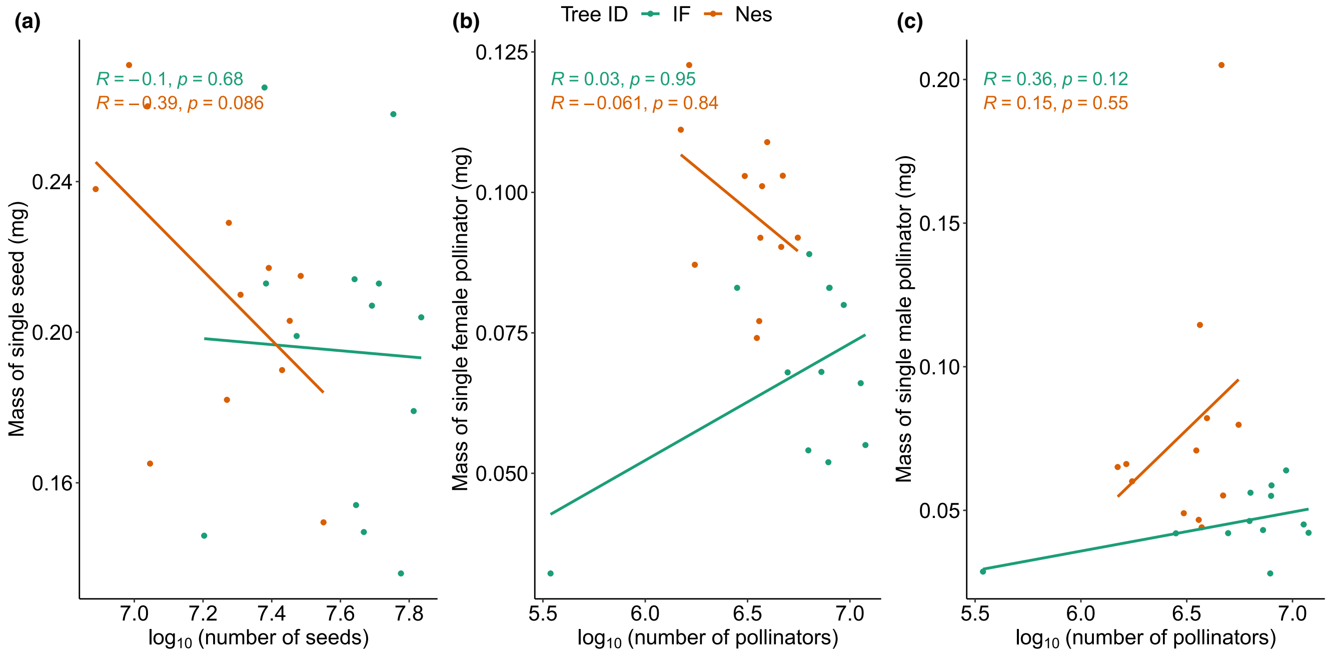

FIGURE 2 Scatter plots showing relationship between $\log_{10}$-transformed number of seeds or pollinators and average mass of single occupants. (a) Seeds, (b) female pollinators and (c) male pollinators. In (b) and (c), pollinator number is the sum of male and females. Each dot represents a single syconium. $n = 24$ syconia for all plots. Nes and IF are Tree ID codes.

PC1, magnesium, calcium and potassium contributed negatively (Figure 5A). Magnesium, calcium, carbon and phosphorus contributed to PC2 by their higher concentrations, and potassium, nitrogen, sulphur and zinc contributed to PC2 by their lower concentrations (Figure 5A). PCA scores, obtained from the PCA of scaled elemental concentrations, showed that PC1 explained 73.96% of variance (eigen value = 5.91) and PC2 explained 18.15% (eigen value = 1.45), together explaining 92.1% of the variance (Figure 5B).

There was an overall significant niche separation of the syconium components on both PC1 (PERMANOVA: $R^2 = 0.97$; $F = 385.13$; $p < 0.001$) and PC2 axes ($R^2 = 0.8$; $F = 50.61$; $p < 0.001$). Pairwise PERMANOVA showed that niche separation on PC1 was driven mainly by higher concentrations of nitrogen, sulphur and zinc in pollinators, higher carbon and phosphorus in seeds and lower concentrations of potassium in seeds and pollinators (Figure 5A, Table S7). On PC2, higher concentrations of magnesium, calcium, carbon and phosphorus in seeds likely caused significant separation of seeds from other components (Figure 5A, Table S7). Analysis without considering the seeds with their seed cover showed similar results except for increased distance between wall tissue and seeds (Figure S3). Squared Mahalanobis distance values indicated that distances were highest between syconial wall and pollinators (male followed by female pollinators) (Figure 5C), followed by distance between seeds and male and female pollinators (Figure 5C).

3.7 | Trophic stoichiometric ratios

As expected, seeds did not show any mismatch between their nutrition source (i.e. syconial wall) and their resource demands for any elements (Figure 6), although sulphur values come closer to the threshold of possible mismatch. In male and female pollinators, TSR values were >4 for nitrogen and sulphur, indicating mismatch between the source and consumers for these elements (Figure 6). TSR values, especially in males, were near the threshold of 4 for phosphorus, potentially causing resource mismatch.

4 | DISCUSSION

Our study provides a snapshot of resource allocation to different parts of a monoecious fig syconium during a phase when wasp and seed development are complete. More than half the syconium biomass is constituted by the syconium wall (Figure 1), which is a complex structure made of 30–40 layers of cells (Fan et al., 2019; Verkerke, 1989). The wall primarily serves as a barrier between developing seeds and galls and the outside environment and provides a homeostatic internal environment (Mukundan and Borges, unpublished data). Wall thickness also controls the number and type (gallers or parasitoids) of parasitic non-pollinators ovipositing into the syconium from the outside by making some resources unreachable for the ovipositor, thus regulating the internal community of non-pollinators and stabilizing the mutualism (Tzeng et al., 2014). A thicker wall is likely of more advantage to pollinators than to seeds, at least till wasps disperse.

Our study has expanded the utility of the elementome by representing acquired resources in multidimensional BN plots. Our results were as predicted by BN theory and reflect fundamental differences between seeds (plant) and pollinator (animal) tissues (Peñuelas et al., 2019). Our results agree with the only other study that

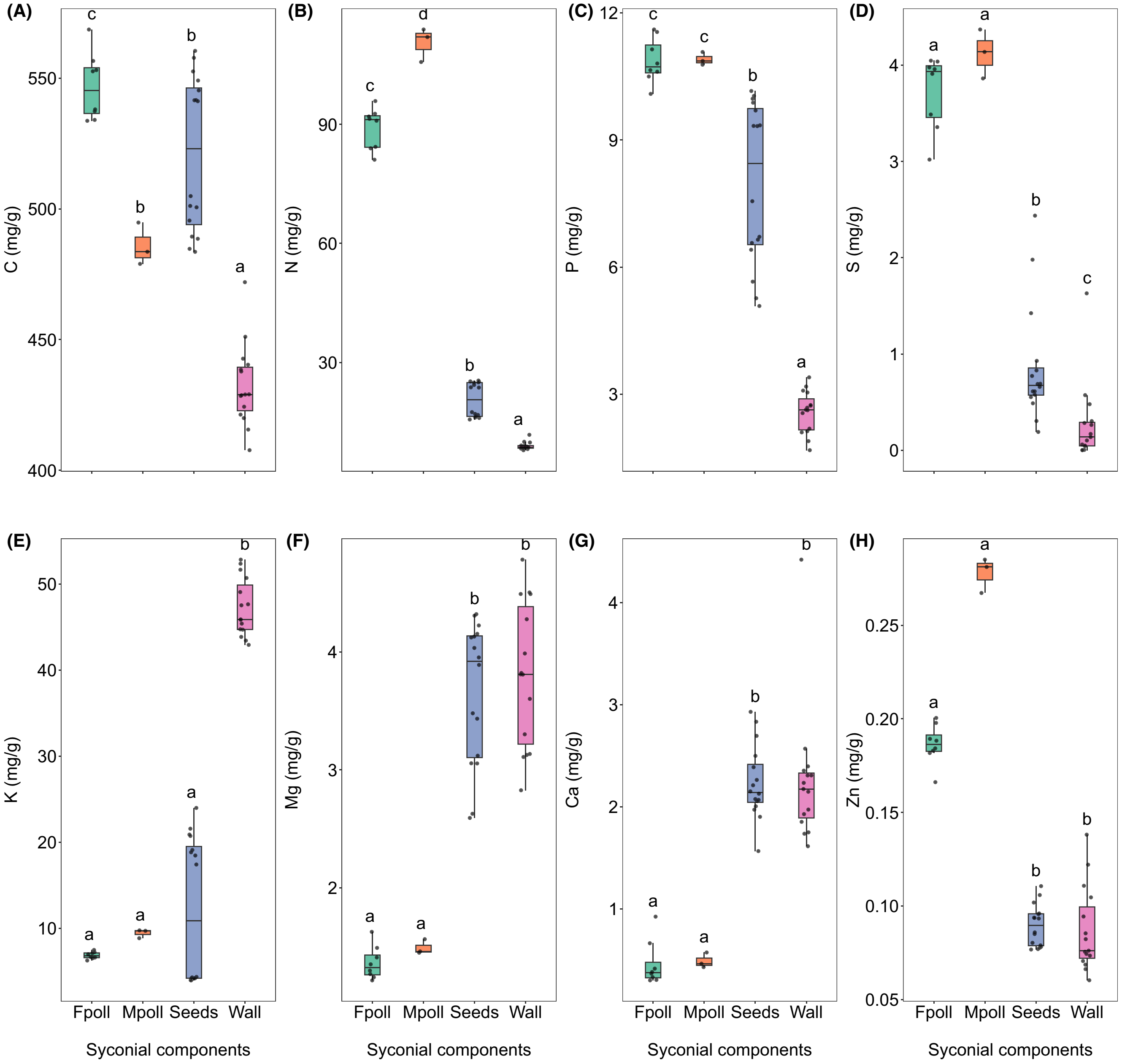

FIGURE 3 Element concentrations for all syconium components. Horizontal thick lines in boxplots indicate median values; lower line indicates first quartile and upper, the third quartile; whiskers indicate minimum and maximum values. (A) Carbon, (B) nitrogen, (C) phosphorus, (D) sulphur, (E) potassium, (F) magnesium, (G) calcium and (H) zinc. (Fpoll, Female pollinators; Mpoll, Male pollinators). Letters above error bars indicate significance; bars with common letters are not significantly different (ANOVA, followed by pairwise Tukey HSD tests for C, N, P, K and Mg; Kruskal–Wallis tests followed by Dunn's pairwise test for S, Ca and Zn).

simultaneously reports the BN of both plants and animals (Bartrons et al., 2018) with non-overlapping BNs for different trophic levels. The distinctive niche of pollinators and seeds reduces competitive pressure and facilitates their co-development and co-existence within the closed syconium microcosm (Peñuelas et al., 2019). BNs reflect species-specific requirements of various elements (Peñuelas et al., 2019). In a consumer–resource relationship, consumers are relatively more homeostatic in elemental composition (Sterner & Elser, 2002). Lack of trade-off between number and mass of pollinator offspring and a distinct and tight BNs observed in our study support these arguments. Our study, for the first time, demonstrates the successful and meaningful application of BN theory to a mutualistic system. Mutualism functions when each participant provides services or resources that the other lacks. Distinctive BNs of mutualists likely allow such favourable transactions.

In monoecious *Ficus*, a single female flower harbours either a seed, a pollinator or a non-pollinator wasp. Single seeds and single female pollinators differed in biomass. Element concentrations for all measured elements were different for pollinators compared to seeds and the syconium wall, highlighting the differential costs of

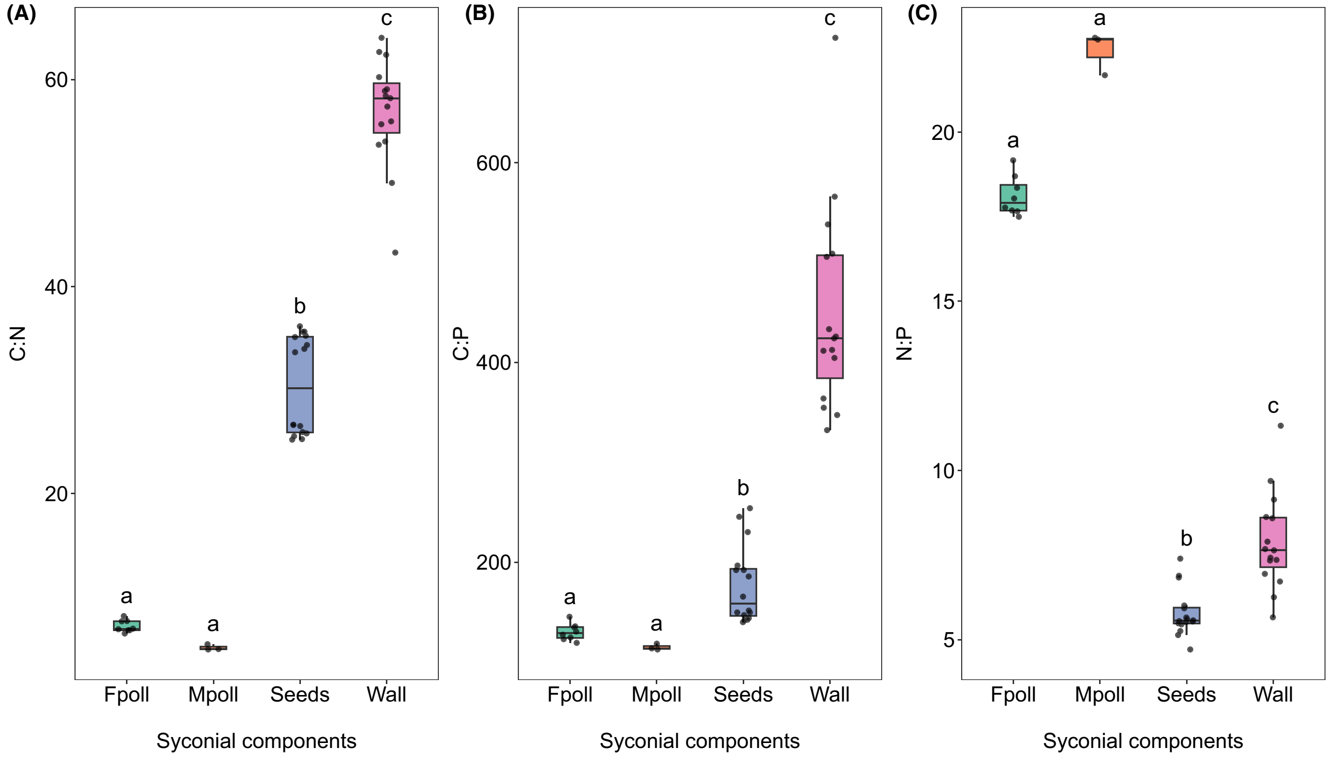

FIGURE 4 Ratios of (A) C:N, (B) C:P and (C) N:P. Horizontal thick lines of boxplots indicate median values; lower line indicates first quartile and upper, the third quartile; whiskers indicate minimum and maximum values. Letters above error bars indicate significance; bars with common letters are not significantly different (Kruskal–Wallis tests followed by Dunn's test for pairwise comparisons). (Fpoll, Female pollinators; Mpoll, Male pollinators).

supporting seeds versus pollinator wasps for the host tree. Nitrogen, phosphorous, sulphur and zinc concentrations were higher in pollinators compared to wall tissue or seeds. Male and female pollinators had significantly lower C:N and C:P ratios than the seeds and the syconial wall. This relationship reversed for N:P ratios, for which pollinators had significantly higher values. The stoichiometric ratios are similar to those obtained in Zhang and Han (2010), where increasing concentrations of N in fig syconia increased N in pollinators, indicating the possibility of N-limitation. Fig tree leaves have lower C:N compared to C-phase syconia (whole syconia; Figure S4; $n=15$ for syconia and $n=9$ for leaves), suggesting no enrichment of nutrients to syconia compared to nearby leaves, and indicating that pollinators must garner N actively. Mismatch between plant resources (here, syconial wall tissue) and consumers as highlighted by C:N:P values is a common concern for herbivores (Filipiak & Weiner, 2017). High C:N and C:P ratios indicate low quality of resources (Bui & Henderson, 2013) and, while nitrogen and phosphorus are limiting in many ecosystems (Wright, 2019), high N:P in pollinators compared to syconial wall tissue indicates that nitrogen may be more limiting than phosphorus (Hillebrand et al., 2009). Many insect herbivores associate with mutualistic bacteria that can either fix nitrogen (Bar-Shmuel et al., 2020; Hansen & Moran, 2014) or convert plant resources into proteins via amino acid synthesis (Hansen et al., 2020). Whether fig wasp pollinators are associated with such symbiotic bacteria is currently unknown. In the absence of any other known mechanism of acquiring nitrogen, the galler herbivores would have to consume more plant resources for nitrogen enrichment, resulting in significant increase in mass of fig syconia in the presence of pollinator galls (Kulkarni et al., 2024), which can hijack plant machinery for their own growth (Kulkarni et al., 2025).

Sulphur also shows consumer–resource mismatch with TSR >4. Although sulphur is an important element in many amino acids in animals (Wiesenborn, 2012), it is inadequately studied. However, it can influence insect herbivore community composition (Joern et al., 2012) and sulphate utilization is also assisted by symbiotic association with bacteria in aphids (Douglas, 1988). With a very high TSR value, sulphur acquisition can pose a challenge to pollinator development and how pollinators overcome this limitation remains an important question. Higher concentrations of zinc, as in the pollinators, are present along with nitrogen and iron when proteins levels are high (Mwangi et al., 2018). Zinc is present at the active sites of various enzymes, but is also a limiting nutrient (Nadeem et al., 2024). Limited availability of nitrogen, sulphur, zinc and to some extent phosphorus, that is, a lower quality of resources, can limit the support the host tree can provide to pollinators, regulating their populations and thus regulating the stability of the mutualism. Concentrations of potassium and calcium were significantly higher in syconial wall tissues. Potassium in plant tissues indicates host quality from a galler's perspective and accumulation of potassium facilitates the movement of photosynthates into those tissues from the phloem (Arriola et al., 2024). Calcium ions perform functions similar to that of potassium and can sometimes act synergistically

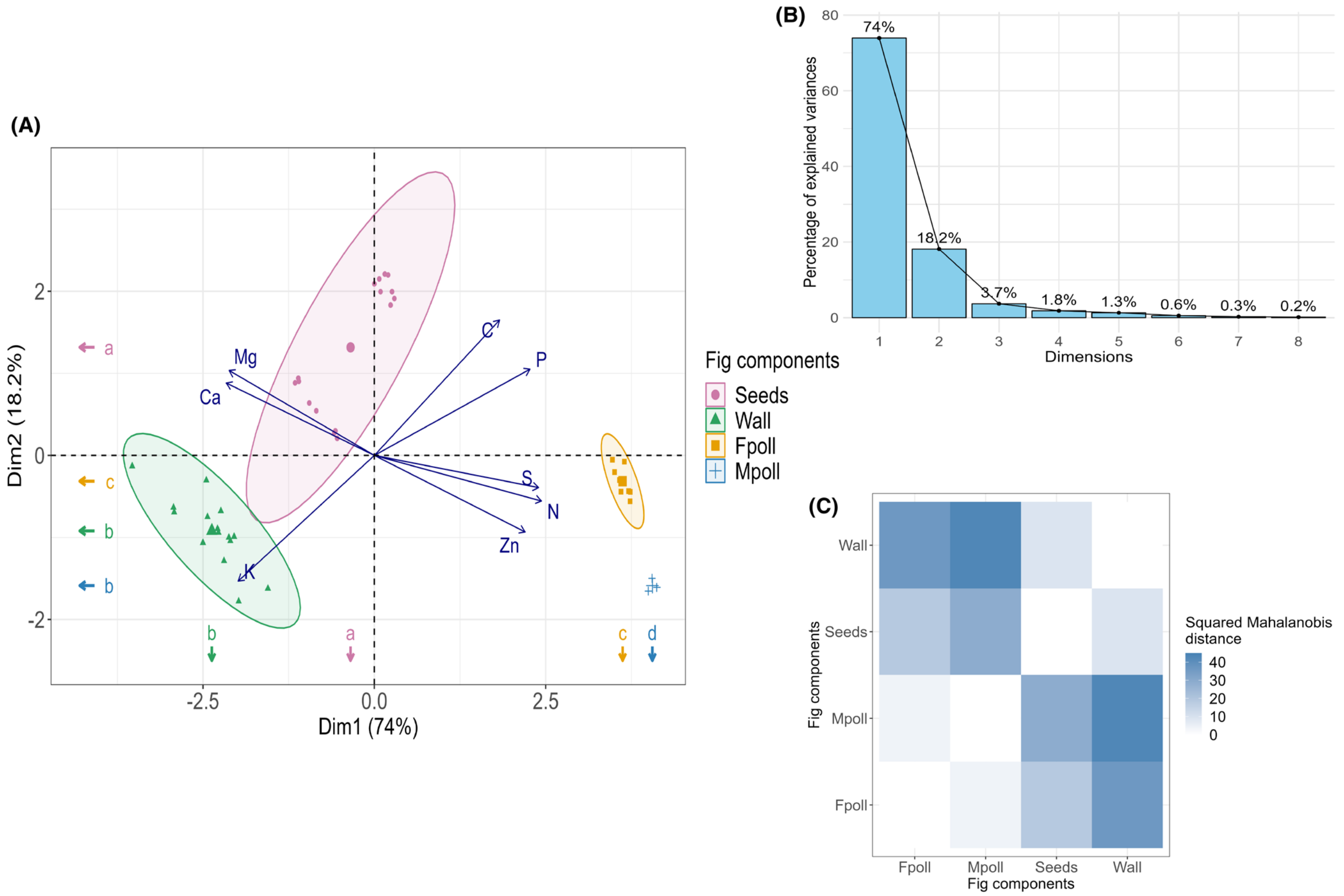

FIGURE 5 (A) PC1 and PC2 scores of principal component analysis indicating stoichiometric niche of syconial components. Letters near axes indicate significant differences between syconial components on those principal axes (pairwise PERMANOVA; $p < 0.05$). Colours of the significance letter as indicated in the legend. Arrows indicate loadings of the original variables (i.e. elements) on first two principal components. Lower angles between arrows indicate positive correlation between variables. Ellipses indicate 95% CI values of the centroid for each syconial component (Fpoll, Female pollinators; Mpoll, Male pollinators). (B) Scree plot with percentage variances explained by the principal components indicated over the bars. (C) Heat map showing squared Mahalanobis distance between stoichiometric niche ellipses as shown in (A). Darker shade of colour indicates greater distance between the niches (Fpoll, Female pollinators; Mpoll, Male pollinators).

(Arriola et al., 2024). Together, potassium and calcium indicate the direction of flow of nutrients, from syconium wall tissues to the pollinator wasps and seeds.

Our results also show BN separation of male and female pollinators. Male pollinators have significantly higher nitrogen and zinc content than females, whereas females have significantly higher concentrations of carbon. Carbon and nitrogen values are consistent with those of Zhang and Han (2010). TSR values reveal that male pollinators are likely more prone to resource mismatch with respect to phosphorus and zinc, given their values being closer to the threshold than females. Females are winged and eventually leave their natal syconium in search of new syconia for oviposition (Janzen, 1979) and sufficient resources are required to fuel this transportation (Venkateswaran et al., 2017). Males are smaller, wingless and besides mating, function primarily in releasing females from galls and the syconium. There is also a female-biased sex ratio in fig wasps determined by local mate competition (Raja et al., 2008). Higher nitrogen cost of producing a single male wasp can be a contributing factor in host trees supporting fewer male compared to female wasps (Li et al., 2016), as also evidenced by the lower total biomass allocated to male pollinators in our study.

5 | CONCLUSIONS

Overall, our study describes resource partitioning in terms of biomass and elemental composition to different components of a syconium which harbours the products of the mutualism between the fig tree and its pollinating wasps. We demonstrate the utility of the elementome and BN to understand the intricacies of trading in mutualisms. A fig syconium also harbours various non-pollinator species which harness resources from the syconium. While our study focuses only on the primary products of mutualism, seeds and pollinator offspring, a comprehensive mapping of BNs of all the occupants of syconium would provide a complete estimate of resource sharing in a microcosm with multiple trophic levels. Further studies in dioecious *Ficus* species, where seeds and pollinator offspring develop in different trees, will help identify any trade-offs that exist

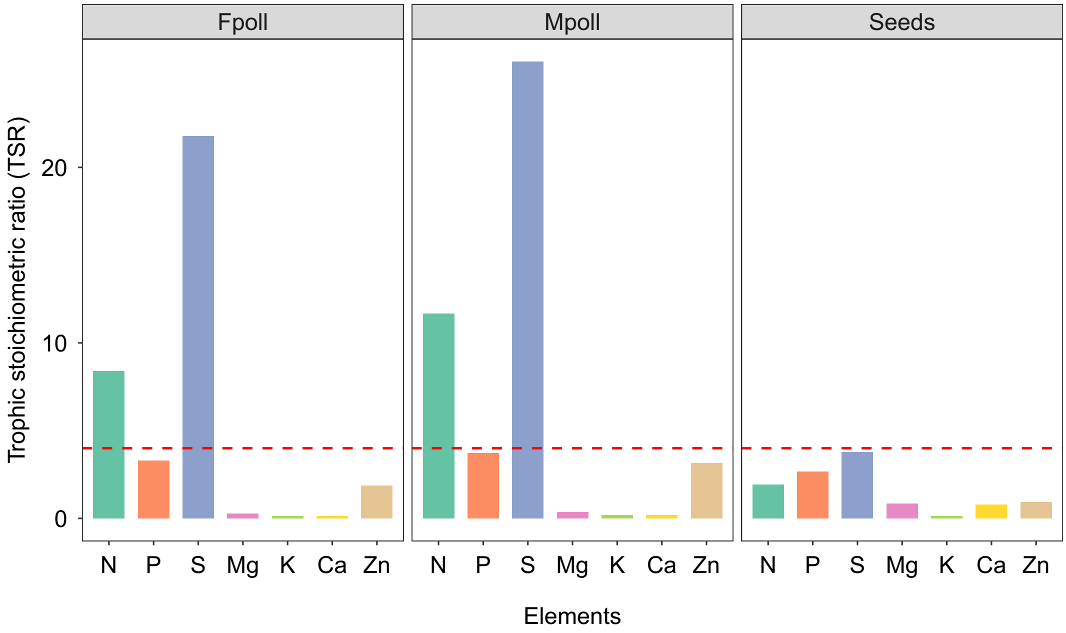

FIGURE 6 Trophic stoichiometric ratios (TSRs) of different elements estimated as the ratio of median values of elemental ratios of syconial wall tissue and occupants (see Materials and Methods). Occupants depicted are Fpoll, Female pollinators and Mpoll, Male pollinators. Horizontal line at 4 indicates the limit, values beyond which denote mismatch between resource and consumer.

due to sharing of a microcosm by seeds and pollinators. We propose that the BN concept can be applied to various mutualistic interactions to understand the exchange of service and rewards at the level of elementome, which reflects the building blocks of all biological structures and functions.

AUTHOR CONTRIBUTIONS

Manasa Kulkarni and Renee M. Borges conceived the idea and designed the experiments. Manasa Kulkarni and Nehal Vijay Naik collected the data; Manasa Kulkarni and Jyothilakshmi Vadassery conducted the elemental analysis. Manasa Kulkarni analysed the data; Manasa Kulkarni and Renee M. Borges led the writing of the manuscript. All authors contributed critically to the manuscript and approved the final draft.

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CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data was available from Dryad Digital Repository: https://doi.org/10.5061/dryad.3xsj3txt9 (Kulkarni et al., 2026).

STATEMENT OF INCLUSION

All authors belong to the country where the study was carried out. The authors list includes both early career and senior scientists. All authors were included early on in the research to ensure diverse perspectives on the study. Wherever relevant, studies published by scientists from the region were cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Results of ANOVA comparing linear models to examine the effect of experimental set type on elemental concentrations. Res. Df = Residual degrees of freedom, RSS = Residual sum of squares, Df = degrees of freedom.

Table S2. Results of GLMMs to compare biomass of individual seeds and pollinator galls.

Table S3. Coefficients for the relative biomass of seeds and pollinator galls.

Table S4. Results of one-way ANOVA on concentrations of elements in different plant and pollinator tissues. FPoll, Female pollinator; MPoll, Male pollinator.

Table S5. Results of Kruskal–Wallis test on concentrations of elements and ratios (molar mass). FPoll, Female pollinator; MPoll, Male pollinator.

Table S6. Coefficients of linear model comparing elemental concentrations of different syconial contents. Mpoll, Male pollinators.

Table S7. Results of pairwise PERMANOVA comparing principal component scores of different contents of a syconium. Df, degrees of freedom; Fpoll, Female pollinators; Mpoll, Male pollinators; Sums of Sqs, Sums of squares.

Figure S1. (a) Boxplot representing wet mass of single occupants. Letters above error bars indicate significance; bars with common letters are not significant. (b) Boxplot representing wet mass of empty galls single male ($n = 300$ galls from 6 syconia) and female pollinator ($n = 250$ galls from 5 syconia). ns = not significant. In both (a) and (b), horizontal thick lines indicate median values; lower line of the box indicates first quartile and upper, the third quartile; whiskers indicate minimum and maximum values. $n = 24$ syconia from two trees.

Figure S2. Molar ratios of (a) carbon to nitrogen (C:N), (b) carbon to phosphorus (C:P) and (c) nitrogen to phosphorus (N:P). Error bars are standard errors. Letters beside error bars indicate significance; bars with common letters are not significantly different (ANOVA, followed by pairwise Tuckey HSD tests on $\log_{10}$-transformed values of molar ratios). (Fpoll, Female pollinators; Mpoll, Male pollinators).

Figure S3. Scores of first two components (PC1 and PC2) of principal component analysis indicating stoichiometric niche of the syconial components (without considering seeds with seed coating). Letters near axes indicate significant differences between the syconial components on those principal axes (pairwise PERMANOVA; $p < 0.05$). Colours of the significance letter match the colour of syconial components as indicated in the legend. Ellipses indicate 95% CI values of the centroid for each syconial component. (Fpoll, Female pollinators; Mpoll, Male pollinators).

Figure S4. Molar ratios of carbon to nitrogen (C:N) of leaves and whole syconia at C-phase. Horizontal thick lines of boxplots indicate median values; lower line indicates first quartile and upper, the third quartile; whiskers indicate minimum and maximum values. Asterisks indicate significance (ANOVA; $F = 126.4$, p-value<0.0001).

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