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# Legacy effects control root elemental composition and stoichiometry in subtropical forests: Empirical support for the biogeochemical niche hypothesis

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## Abstract

1. Under biogeochemical niche (BN) theory, plant allocation of elements to organsto maintain fundamental biological processes varies with species, leading to theformation of species-specific BNs. However, empirical support for the BN theoryis largely restricted to plant leaf elemental composition and stoichiometry, with alack of clarity about the contribution of fine root element content.

2. Here, we analysed fine root concentrations and stoichiometry of 9 elements in-cluding carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), mag-nesium (Mg), iron (Fe), aluminium (Al) and manganese (Mn) in 137 tree species ofa subtropical forest to quantify BN and test the theoretical framework of the BNhypothesis.

3. Our study showed phylogenetic signals of fine root elemental composition andstoichiometry. Fine root elemental composition of the 21 most abundant co-existing species tends to be unique and primarily driven by root N content, asindicated by canonical discriminant analysis. Legacy effects (phylogeny and spe-cies) explained 23.3%–70.7% of the variation across the different variables usedto characterize fine root elemental composition, stoichiometry and BNs, whereascombined effects of soil property, mycorrhizal association type and topographyfactors explained 3.9%–17.7%.

4. Synthesis: These results indicate that phylogenetic and taxonomic distance (cal-culated as distance metrics) represent a proxy for species-specific evolution andachievement of optimal function linked to bio-element use. Thus, our study pro-vides new empirical

evidence in support of the BN hypothesis, based on plantfine root elemental composition and stoichiometry, and improves our mechanisticunderstanding of species coexistence dynamics.

KEYWORDS

biogeochemical niche, fine root elemental composition, phylogeny, soil property, stoichiometry, topography, tropical forest

## 1. Introduction

Ecological theory states that stable coexistence among competing species requires occupancy of different ecological niches (Gause 1934); however, the quantification of species niches has long been a challenge in community ecology (Hutchinson 1957, Silvertown 2004). Organisms comprise chemical elements, including carbon (C), nitrogen (N), and phosphorus (P), that are closely linked to life history strategy, such as reproduction and survival (Wright et al. 2004, Sardans et al. 2021, Furey and Tilman 2023). The biogeochemical niche (BN) hypothesis, where BN is defined as the species-specific occupation of an n-dimensional bio-element space (Peñuelas et al. 2008, Peñuelas et al. 2019), has been proposed as an approach to quantify ecological niches and explain community assembly (Zhao et al. 2017, Fernandez-Martinez et al. 2021, Sardans et al. 2021). However, empirical studies of the BN hypothesis have tended to measure leaf chemical element content as a proxy for whole-plant element status, with little regard to other plant organs involved in biological processes, such as root nutrient uptake.

There are contrasts in function of plant organs in the support of fundamental biological processes, such as growth, secondary metabolism, and reproduction, where organs tend to be characterized by unique chemical characteristics under long-term singular evolution (Zhang et al. 2017, Zhao et al. 2019). For example, ratios of C:N and N:P in leaf organs of terrestrial plants have been shown to be lower and higher, respectively, than in roots (Yuan et al. 2011, Zhang et al. 2017, Zhang et al. 2021), while stoichiometric sensitivity to environmental change has been shown to be greater in roots, as indicated by higher levels of phenotypic plasticity, than in leaf organs where stoichiometric homeostasis (element regulation) is greater (Zhang et al. 2017). Although it is possible that definition of species BN may vary when based solely on root or leaf element composition, the quantification of root BN and validity of its inclusion in the theoretical framework of the BN hypothesis remain unclear, despite the importance of roots in nutrient and water uptake.

Given the fundamental basis for the BN hypothesis is that unique species gene pools are the product of long-term specific evolutionary processes (Peñuelas et al. 2019), it follows that species are characterized by specific morphological structures and functionality, from gene expression to physiological and metabolic processes. For example, rates of fundamental biological processes, such as growth, secondary metabolism, reproduction, and storage of bio-elements, vary among species, depending on selection pressure, such as topographic resource heterogeneity (Körner 2007, Wang et al. 2018), leading to species-specific allocation of elements to tissues and organs, and an associated plant element composition and stoichiometry (Zhang et al. 2017, Zhang et al. 2021), where it is possible that individual adaptation to shifts in environmental conditions to maintain biological processes necessitates phenotypic plasticity in function and morphology (Peñuelas et al. 2019).

Studies have demonstrated that foliar element composition and stoichiometry that reflect species BN primarily depend on legacy effects (phylogeny and species) across a range of spatial scales (Sardans and Penuelas 2014, Sardans et al. 2016, Peñuelas et al. 2019, Sardans et al. 2021) and there is evidence that root chemical traits quantify BN in a small number of species at the site scale (Zhao et al. 2017, Hu et al. 2018). However, there is a lack of evidence for the relative contribution of phylogenetic variation to root element composition and stoichiometry, compared with the leaf elementome, the contribution of shared ancestry in subtropical tree species root element composition remains unclear.

Phenotypic plasticity for adaptation to environmental shifts and resource competition is reflected by changes in element composition and stoichiometry (Peñuelas et al. 2019, Sardans et al. 2021) likely derived from prevailing soil physicochemical properties, such as level of pH and content of N, P, and K (Zhang et al. 2017, Wang et al. 2019, Wang et al. 2020, Zhang et al. 2021, Hartemink and Barrow 2023); for example, soil pH and moisture affect soil nutrient availability (Cavagnaro 2016, Hartemink and Barrow 2023), root growth (Haling et al. 2011), and plant nutrient status (Zhao et al. 2017, Wang et al. 2019). Some plants have evolved to recruit beneficial mycorrhizal fungi to uptake key nutrients, such as N and P (Johnson 2009, Phillips et al. 2013, Lu and Hedin 2019, Genre et al. 2020), where species associated with arbuscular mycorrhizal (AM) fungi scavenge inorganic nutrients decomposed by microorganisms, while species symbiotic with ectomycorrhizal (EM) fungi tend to easily mine organic-bound nutrients

(Phillips et al. 2013, Lu and Hedin 2019), likely leading to contrasting nutrient status of AM- and EM-associated plant species. However, there is a lack of integration of phylogenetic differences, environmental factors, and mycorrhizal symbiosis into the BN hypothesis framework, based on root elementomes.

Given the links between leaf and root chemical traits (Reich 2014, Li et al. 2021) and local-scale species coexistence through BN differentiation (Zhao et al. 2017), we quantified fine root element composition and stoichiometry of 137 subtropical forest woody species in Southern China to test the hypotheses that: (1) root element composition and stoichiometry vary with taxonomic group; (2) legacy (phylogenetic) effects drive species-specific element use; and, (3) elementomes and BNs of subtropical tree species are a product of legacy effects, type of mycorrhizal association, and local-scale variability in resources.

# 2. Materials and methods

## 2.1 Study area

The study was conducted across a 50-ha plot located within a subtropical evergreen broadleaf monsoon forest in the Heishiding Provincial Natural Reserve, Guangdong Province, southern China (23°27′N, 111°52′E), on ferrasols developed from granite and where elevation ranges from 430 to 700 m asl, with slopes range from 10 to 70°. Prevailing climate is a typical subtropical monsoon, with mean annual temperature of

19.6 °C and mean annual precipitation of 1740 mm that accumulates predominantly during April to September (Jiang et al. 2020).

The 500 × 1000 m plot was established in 2011 and all living trees with diameter at breast height (DBH) ≥1 cm were identified to species and measured (DBH) in 2016. In total, 213,629 individuals, belonging to 256 species from 138 genera and 61 families were recorded (Fig. S1),with dominant species including *Cryptocarya concinna* (Lauraceae), *Litsea lancilimba* (Lauraceae), *Neolitsea phanerophlebia* (Lauraceae), *Altingia chinensis* (Altingiaceae), *Castanopsis carlesii* (Fagaceae), and *Artocarpus styracifolius* (Moraceae).

### 2.2 Root sampling and analysis

In 2020, we selected at least three replicates of 137 commonly occurring species (Fig. 1), comprising 118 and 19 AM and EM species, respectively, amounting to 708 individuals (Fig. S1). We used a shovel to loosen soil within a 2-m radius around each selected tree stem, from which we traced and removed terminal root branch orders (1–5) that were subsequently washed gently using water to remove soil and other adherent material. Then, fine roots (≤ 2mm) were removed and oven-dried at 65 °C for 48 h to a constant weight prior to analysis.

We determined total C and N content using an elemental analyzer (Vario ELI, Elemental analysis, Germany) and total P content was determined using the sodium hydrogen carbonate solution-Mo-Sb anti-spectrophotometric method (Wang et al. 2024).

Total potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), aluminum (Al), and manganese (Mn) content was determined using the $HNO_3$- $HClO_4$ (5:1) digestion method and inductively coupled plasma atomic emission spectrometry (Hu et al. 2023, Wang et al. 2024).

### 2.3 Soil sampling and physicochemical analysis

In 2016, we collected 625 soil cores (10 cm depth) across the study plot and from which we measured content of total N, P, and K, pH, electrical conductivity, and water content. Using elevation and slope topographical measurements of the study plot collected in 2011, we created Kriging maps to interpolate soil physicochemical properties and topography (He et al. 2018) for locations of the 708 sampled plants.

### 2.4 Data analysis

All analyses were conducted with R 4.3.2 (R Core Team 2023). We used the R package 'Taxonstand' (Cayuela et al. 2012) to match species with accepted name in 'The Plant List' (http://www.theplantlist.org/) and then phylogeny was constructed using the V.PhyloMaker2' package in R (Jin and Qian 2022). As in a previous study (Sardans et al. 2021), we tested phylogenetic signals of fine root element composition and stoichiometry based on Pagel's λ ($P \leq 0.05$), calculated using the 'phytools' package in R (Revell 2012). Pagel's λ indicates phylogenetic dependence of traits, based on the assumption that trait evolution follows the Brownian motion (BM) model (Pagel 1997), and, compared with other methods, it does not vary with increasing number of phylogenetic species and is more suitable for large phylogenies of >50 species (Felsenstein 1985, Sardans et al. 2021). We assumed phylogenetic independence of traits when λ = 0, weak phylogenetic dependence when 0 < λ < 1, and trait dependence when λ = 1.

We quantified BN space size for 137 study species based on a principle component analysis (PCA) of log-transformed fine root element composition and C:N:P stoichiometry as independent variables (Sardans et al. 2016), using the 'FactoMineR' package in R (Lê et al. 2008). We tested for variation in BN size between 21 of the most abundant species (Table S1) using canonical discriminant analysis (CDA) of log-transformed root element content, based on squared Mahalanobis distance of CDA scores between species pairs; CDA derives the optimal inter-group separation by maximizing inter-group variance, while minimizing intra-group variance (Cacoullos 2014).

As in a previous study (Sardans et al. 2023), we tested the importance of species in root element composition and C:N:P stoichiometry performing permutational multivariate analyses of variance (PERMANOVA) using the 'vegan' package in R, based on Euclidean distance (Anderson et al. 2008), with soil physicochemical property, type of mycorrhizal association, topography, and species as independent factors.

The relative contributions of evolutionary history, soil physicochemical property, mycorrhizal association type, and topography to root element composition, stoichiometry, and BN size, as estimated by the PCA, were estimated by Bayesian phylogenetic general linear mixed models (GLMM) using the 'MCMCglmm' package in R (Hadfield 2010), with soil property, mycorrhizal association type, and topography as fixed factors, and phylogeny and species as random factors. The analysis showed that phylogeny accounted for variability in shared ancestry, while species accounted for species-specific traits independent of shared ancestry (Sardans et al. 2021); therefore, phylogeny and species together accounted for variance explained by heritability.

We tested for spatial autocorrelation of fine root element composition, stoichiometry in the 708 individual study trees, and environmental (soil physicochemical and topography) variables at the tree locations using Moran's I correlograms in the sp.correlogram function of the 'spdep' package in R (Bivand and Piras 2015). While there was no evidence of spatial autocorrelation of root elements (Fig. S2), there was strong spatial autocorrelation of the spatially interpolated soil and topography variables (Fig. S3). Therefore, we implemented pairwise Pearson's correlation for the environmental variables to avoid collinearity, excluding pairwise variables with correlation coefficients >0.75 from the analysis (Jiang et al. 2020); as a result, eight environmental factors (Fig. S4) were then included in a phylogenetic generalized least squares (PGLS) regression analysis of effects of soil and topography, and mycorrhizal association type on root element composition and C:N:P stoichiometry. Root element content and stoichiometry were response variables, while the eight environmental factors and mycorrhizal type were explanatory variables.

## 3. Results

### 3.1 Phylogenetic signal and biogeochemical niche size of root element traits

Phylogenetic signals in root element composition and stoichiometry were observed for all measured elements across the 137 tree species and, with the exception of Mn, for AM species; for EM species, there were phylogenetic signals for root content of P and Ca and ratio of C:P (Table 1).

Axes 1 and 2 (PCs 1 and 2) of the PCA accounted for 52.1% of the variation in fine root element composition and stoichiometry in the 137 tree species (Fig. 2), while PCs 1–3 accounted for 66.7% of the variation; therefore, we selected scores along PCs 1–3 to represent the BNs of the study species. There were phylogenetic signals in BN for each PC (Table 1; Fig. S5) and BNs were most similar in closely-related species and by mycorrhizal type (Fig. 1; Fig. S5).

Element composition of the 21 most abundant, co-existing species tended to be unique (Table S2) and as indicated by separation of CDA scores along axes 1 and 2 (Can1 and 2) that jointly explained 61.2% of variation in root element composition, principally driven by root N content (Fig. 3).

### 3.2 Species, phylogeny, mycorrhizal association type, and environmental conditions as drivers of root element composition and stoichiometry

The combined effects of soil physicochemical properties, mycorrhizal association type, and topography accounted for little variation in root element composition and stoichiometry ($R^2 = 0.071$), whereas species accounted for greater proportions when included in the mixed PERMANOVA model ($R^2 = 0.589$) or as a single independent factor ($R^2 = 0.638$) (Table 2).

Bayesian phylogenetic GLMM estimates showed legacy effects of phylogeny and species explained 23.4–70.7% of variation in root element composition and stoichiometry, and BNs, as indicated by PCA scores, while combined effects of soil physicochemical property, mycorrhizal association type, and topography explained 3.9–17.7% of variation (Fig. 4; Table S3). Estimates of the phylogenetic GLMM accounted for similar levels of variation in legacy effects root element composition and stoichiometry (average: 54%) to PERMANOVA estimates (58.9%) (Table 2).

### 3.3 Relationships between root element composition and stoichiometry and abiotic factors.

We found several relationships between root element composition and stoichiometry and environmental factors (Table S5; Fig. 5). Root N content and N:P ratio were positively related to slope steepness, and root content of P and Ca were positively related to soil water content, and there were negative relationships with root C:P ratio (Fig. 5). Root P were negatively related to elevation and ratios of C:P and N:P were positively related with elevation, while root Mg and N:P ratio were positively related to soil K content and soil pH, respectively (Fig. 5). Root Al content was negatively related to soil electrical conductivity (Fig. 5). We found no difference in root element composition and stoichiometry with mycorrhizal association type (Table S5).

# 4. Discussion

We found contrasting BNs between co-occurring species, based on analysis of root element composition and stoichiometry traits, supporting our first hypothesis, where the positive and negative values for *Lauraceae* and *Altingiaceae* spp., respectively, on Can1 of the CDA plot (Fig. 3) indicate contrasting BN position and size in multi-hypervolume niche space. These findings are supported by previous, smaller-scale studies of trees and herbs in subtropical forest and wetland ecosystems that report separation of root traits in coexisting species (Zhao et al. 2017, Hu et al. 2018). A key determinant of the contrasts in BNs of co-existing species was found to be root N content, inferring that phylogenetic variation in chemical traits may drive niche differentiation through differences in plant metabolic and physiological function and reduced nutrient competition, given the essential role of N in plant growth and reproduction (Güsewell 2004). For example, root N content of *Lauraceae* spp. (*C. concinna*, *L. lancilimba*, *N. phanerophlebia, Lindera chunii*) was greater than in phylogenetically distant species of other families (*A. chinensis*, Altingiaceae; *Myrsine seguinii*, Primulaceae; *Schima superba*, Theaceae) that occupy different BNs in the hypervolume (Fig. 3).

Our study showed greater differences in root element composition in phylogenetically distant species, such as *Rhodomyrtus tomentosa* and *Dendropanax dentiger* (Fig. S5), consistent with studies based on leaf element traits that show a positive correlation between phylogenetic distance and species-specific BNs (Sardans et al. 2016, Sardans et al. 2021). Although our results indicated that elementome of plant organs depended to a high degree on species phylogeny, there were contributions from other legacy effect factors. For example, distantly related species that have recently been subject to analogous environmental conditions, such as those caused by orogenic processes, may be subject to convergent evolution (Sardans et al. 2021), whereas evolutionary paths in other species may diverge from those of close relatives under environments with intense inter-specific competition, resulting in accelerated divergent evolution. Thus, we suggest phylogeny did not account for 100% of legacy effect variation in BNs among species, due to ancestry and evolution factors, and we recommend that the inclusion of species as a factor will lead to more robust analyses of BN legacy effects.

Our results indicated that legacy effects directly explained 23.4–70.7% of the variation in root element composition, stoichiometry, and BN, as indicated by PCA scores, supporting our second hypothesis, a previous global meta-analysis that reported evolutionary processes (phylogeny and species) explained 57–94.5% of the variation in foliar nutrient content and stoichiometry (Sardans et al. 2021), and a study of semi-pristine South American lowland wet tropical forest that reported legacy effects accounted for 28.6–75.4% of the variation in leaf element content (Sardans et al. 2023). Thus, our results agree with one of the basic postulates of BN, that coexisting species maintain a degree of divergent evolution to avoid direct competition for resources.

Combined effects of soil property, mycorrhizal association type, and topography explained 3.9–11% of variation in root elementome, as supported by the PERMANOVA analysis (7.1%), where main effects of soil property explained a greater proportion of the variation in root element content (4.6%) than previously reported variation in element content of tree leaves (0.1–2%) (Sardans et al. 2021). These contrasting impacts of soil properties on leaf and root element content may be due to regulation of plant nutrient use strategies, and greater sensitivity of root than leaf chemical traits to environmental change (Zhang et al. 2017). Our finding of positive relations between soil water content and root P and Ca content, and a negative relation with C:P ratio may reflect the greater desorption and dissolution of P and Ca (Dijkstra et al. 2012) and improved the P and Ca uptake (Lambers et al. 2006) under increasing soil moisture.

Plant-mycorrhizal symbiotic associations benefit plants, through greater root uptake of nutrients, such as N, P, K, Al, Zn, Cu, and Mn (Clark and Zeto 2000, Kariman et al. 2012), that then drives plant population and community dynamics, through effects of individual plant competitive ability (Tedersoo and Bahram 2019, Tedersoo et al. 2020). However, our results unexpectedly showed that mycorrhizal association type explained just 1.2% of the variation in root elementome and BNs (PCA scores), possibly due to the small number of EM species included in our study (19 out of 137).

We found that topography explained only 1% of the variation in root elementome, supporting findings from a study that showed topography and geography accounted for

3.7% of variation in tropical tree elementome (Sardans et al. 2023), indicating that topography, being closely associated with soil temperature and resource availability (Körner 2007), may be regarded as a driver of subtropical species diversity (species coexistence) (Medvigy et al. 2019, van Breugel et al. 2019). Our results showed a decrease in root P content and an increase in root C:P and N:P stoichiometry with increasing elevation, supporting a previous study that reports similar elevational decreases in fine root P content and N:P ratios in *Quercus aquifolioides* (Wang et al. 2018), possibly due to low soil P availability at high elevations (Tsui et al. 2004, Wang et al. 2018) caused by reduced microbial activity and associated declines in P mineralization rates under low temperatures (temperature-biogeochemistry hypothesis) (Reich and Oleksyn 2004).

Our GLMM analysis, which considered soil property, mycorrhizal association type, and topography and excluded phylogeny and species as random factors, explained 7.8–25.5% of the variation in root element composition and stoichiometry (Table S4), where inclusion of environmental factors and mycorrhizal association increased explained variation by 1.5–16.2%, indicating that variance explained by differences in environment are partially explained by legacy effects. These results are consistent with those reported by Sardans et al. (2021) for a Bayesian analysis, who found a decrease in variance explained by climatic variables, when legacy effects were added as a random factor. Thus, variation in plant species-specific responses to environmental conditions reflect genetic adaptations in function, physiology, metabolism and morphology and specific use of the contrasting bio-elements.

We found that legacy effects (phylogeny + species) accounted for 65.2, 68.8, and 23.4% of variation in PC1, PC2, and PC3 scores, respectively, whereas combined effects of soil property, mycorrhizal association type, and topography explained only 6.1, 4.1, and 17.7%, respectively, supporting the fundamental basis of the BN hypothesis, that the combination of phylogenetic, abiotic, and biotic factors determine species BNs based on root element composition (Peñuelas et al. 2019). Plants tend to be characterized by an optimal element composition that coincides with their optimal niche function and occupation, representing the homeostatic component of BN (Peñuelas et al. 2019); concurrently, plants require a degree of flexibility in element composition, to meet demands of phenotypic plasticity during adaptation to fluctuating environmental conditions (Han et al. 2011, Sardans and Penuelas 2014, Sardans et al. 2016, Sardans et al. 2017, Sardans et al. 2021). However, species display varying capacities to tolerate competition and stressors that leads to the occupation of distinct BN positions within the n-dimensional space around their associated homeostatic component. Positioning of multiple individuals of a species occurs within a given volume, due to inherent intra-specific variation in BN, that then facilitates community level responses to fluctuating environmental conditions. For example, species growing in environments with low levels of competitive pressure and high abundance of resources exhibit higher levels of BN plasticity than those growing in environments with high levels of competitive pressure and poor resource availability, and are characterized by greater homeostatic life histories and lower capacities to respond to environmental time-space fluctuations in resource-rich environments (Yu et al. 2011, Peñuelas et al. 2019). The position of species in the hyper-dimensional volume may shift with time and changing environmental conditions, depending on the degree of species-specific stoichiometric plasticity; however, there should be a maintenance (homeostasis) of relative species BN (Peñuelas et al. 2019). Thus, our results demonstrate that species BN is the result of a trade-off between stoichiometric homeostasis and plasticity (Peñuelas et al. 2019) under the control of evolutionary changes and environmental shifts (Peñuelas et al. 2019, Sardans et al. 2021).

## 5. Conclusion

Our study provides empirical evidence for the quantification of local-scale species BN using root element composition and stoichiometry, in support of the BN hypothesis. We found phylogenetic signals in root element composition and BN of the 137 coexisting subtropical tree species, largely driven by legacy (phylogeny + species) effects, with smaller contributions from soil property, mycorrhizal association type, and topography factors. While quantification of species BN based on root chemical traits improves understanding of species coexistence, it remains unclear whether root chemical traits better represent and account for BN than other plant organs with contrasting function and associated element composition. Nevertheless, this study shows similar levels of support for the BN hypothesis using plant root element composition as previous studies based on leaf elements. We suggest further studies of whole-plant chemical traits to quantify species BN to improve understand community assembly dynamics.

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