Trethowan, Liam A., Blonder, Benjamin Wong, Kintamani, Endang, Girmansyah, Deden, Utteridge, Timothy M. A. and Brearley, Francis Q. (2025) Clades That Frequently Accumulate Metals Do Not Have Low Abundance in the Tropical Forests of Sulawesi, Indonesia. Biotropica, 57 (4). e70053 ISSN 0006-3606

**DOI:** https://doi.org/10.1111/btp.70053

**Publisher:** Wiley

**Version:** Published Version

**Data Access Statement:** Soil and leaf element data and species composition data available here https://figshare.com/projects/Sulawesi_stoichiometry/97660. The Rmarkdown file to reproduce the manuscript available here https://doi.org/10.6084/m9.figshare.24746811.v5.

*Biotropica*

ORIGINAL ARTICLE OPEN ACCESS

# Clades That Frequently Accumulate Metals Do Not Have Low Abundance in the Tropical Forests of Sulawesi, Indonesia

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**Received:** 14 November 2024 | **Revised:** 15 May 2025 | **Accepted:** 17 May 2025

**Associate Editor:** Jayashree Ratnam | **Handling Editor:** Alvaro Duque

**Funding:** LAT's funding was provided by the Bentham Moxon Trust, Coalbourn Trust, Botanical Research Fund, a Manchester Metropolitan University postgraduate studentship, Emily Holmes awards and NERC/Newton fund grant NE/S007059/1.

**Keywords:** Celastrales | functional distinctiveness | Malpighiales | Oxalidales | serpentine soil | stoichiometric distinctiveness | tropical trees | ultramafic soil | Wallacea

## ABSTRACT

In diverse tropical communities, individuals with more distinct traits typically have lower abundance. In many tropical communities, the most distinct plants with regard to their stoichiometry are metal hyperaccumulators. The Celastrales, Oxalidales, and Malpighiales (COM) clades feature more than 50% of known nickel hyperaccumulators. Metal hyperaccumulation likely incurs high energy costs for physiological processes, potentially reducing competitive ability in nutrient-limited environments. We therefore test if COM species that are increasingly stoichiometrically distinct are also rare, and if these effects depend on soil metal concentrations. We measured leaf element concentration for 283 tree species from ten 0.25 ha plots over ultramafic (metal-rich) and non-ultramafic soils in Sulawesi, Indonesia. We fit a phylogenetic mixed-effects model of abundance with calculated leaf stoichiometric distinctiveness, soil metal concentrations, macronutrient concentrations, pH, and whether species belong to COM clades as further predictors. At all soil metal concentrations, species with more distinct leaf stoichiometry are rare, except for COM species. In tropical forests of Sulawesi, metal accumulation does not have a negative relationship with the abundance of COM species but does with other clades. Metal accumulation reflects a niche axis that impacts the structures of communities across ultramafic and non-ultramafic soils.

## 1 | Introduction

The typical species abundance relationship observed in tropical tree communities is of many rare and few common species (Matthews et al. 2017; Umaña, Mi, et al. 2017; Ibanez et al. 2020). Trait distinctiveness, often tied to tissue stoichiometry, influences abundance through niche specialization and resource allocation (Sterner and Elser 2002; Umaña et al. 2015; Umaña, Zhang, et al. 2017, González et al. 2017; Leal et al. 2017; Violle et al. 2017; Peñuelas et al. 2019; Hofmann et al. 2021; Fernández-Martínez 2022). However, the distinctiveness versus abundance relationship for leaf stoichiometry remains incompletely understood. Here we examine how the distinctiveness of tropical tree species' leaf stoichiometry impacts their abundance in communities over soils with differing element concentrations.

Assessing species in extreme metal-rich ultramafic soils could offer insights into what determines the impact of stoichiometric distinctiveness upon abundance. Ultramafic soils are derived from rocks formed during mantle exposure at subduction zones and spreading centers (Moores 2011). They are richer in metals, such as nickel, cobalt, and chromium, than most other soil types (van der Ent, Baker, van Balgooy, et al. 2013). The extreme soil stoichiometry is thought to be stressful for some species but offers niches to others (Rahbek et al. 2019). Niches on ultramafic soils sustain phenotypes not found elsewhere (Rajakaruna and Bohm 1999; Rajakaruna et al. 2003; Garnica-Díaz et al. 2023). A key example is the ability of plant species to accumulate metal in leaf tissues which, at extreme concentrations, is termed hyperaccumulation (van der Ent, Baker, Reeves, et al. 2013). Hyperaccumulation can drive high levels of leaf stoichiometric distinctiveness in species over ultramafic soils. Stoichiometric distinctiveness is used here as a multi-element proxy of metal accumulation in plants. Here, we use this metric alongside other relevant parameters to identify the dependencies of the distinctiveness to abundance relationship.

How abundance is affected by stoichiometric distinctiveness may be dependent upon whether species occupy ultramafic or non-ultramafic soils (Gonneau et al. 2014; Delhaye et al. 2020; Trethowan et al. 2021). For instance, on metal-rich soils, acquisition of high leaf metal concentrations in leaf vacuoles presumably requires less energetic costs due to increased soil-to-tissue metal ratios (Verbruggen et al. 2009; Lange et al. 2017; Mohiley et al. 2020). The trade-off is therefore lessened, and the protection from herbivory and pathogens of metal-rich tissue could boost abundance, as could the metal-enriched leaf litter that is detrimental to competitors (Boyd 2004; Mohiley et al. 2020). Metal-rich leaf litter-driven allelopathy mirrors negative effects of root chemical exudate (Guerrieri and Rasmann 2024). Also underground, species with conservative root architecture strategies should aid abundance in stressful conditions (Lequeux et al. 2010). In stressful ultramafic conditions, conservative trait strategies are often selected for. Greater distinctiveness due to leaf metals is therefore a possibility in an otherwise limited niche space (Fernandez-Going et al. 2013; Aiba et al. 2015; Peñuelas et al. 2019; Samojedny Jr et al. 2022). Phenotypic distinctiveness could provide a competitive advantage, akin to water-use efficient species on limestone karsts or salt tolerant species in mangroves (Geekiyanage et al. 2019; Whitman et al. 2021; Perri et al. 2023; Delhaye et al. 2024). Increasing environmental stress also causes shifts in species interactions (Hart and Marshall 2013; Chamberlain et al. 2014; Germain et al. 2018; Lekberg et al. 2018). Therefore, negative interactions via metal-rich litter could also be outweighed by benefits for climatic stress tolerance, for example, via increased shading (Nemer et al. 2023; Randé et al. 2024). However, in the wet tropical lowlands, we expect greater effects to be caused by facilitation due to toleration and exploitation of ultramafic habitats. Stoichiometric distinctiveness caused by metal accumulation should be key to exploitation of metal-rich soils.

The relationship of stoichiometric distinctiveness with abundance may be influenced by clade. For instance, in experimental studies on the ultramafic soils of California, the Asteraceae, Lamiaceae, and Plantaginaceae clade had greater fitness than other species (Godoy et al. 2014). In tropical ecosystems with large expanses of ultramafic soil, there tends to be greater species richness of the Celastrales, Oxalidales, and Malpighiales (COM) clades (Pillon et al. 2010, 2019). COM clades feature c. 8% of the globe's species but more than 50% of the c. 700 species that hyperaccumulate metals, including the genera *Rinorea* and *Phyllanthus* that have multiple species exhibiting extremely high tissue Ni and Co content (Reeves et al. 2018; Paul et al. 2020; Brearley 2024). COM clades may better harness the benefits of metals for defense and localized spikes in soil metal caused by metal-rich leaf litter. Whether metal accumulation has driven their increased diversity is unclear. Greater diversification can also be expected for smaller populations due to the increased impact of genetic drift (Gavrilets and Losos 2009). However, greater abundance at local scales may reduce extinction risk, leading to greater opportunity for speciation and increased clade diversity (Tietje et al. 2022). We therefore expect negative effects of high tissue metal content upon abundance to be limited in COM species. Although adaptations restricted to COM species have yet to be identified, their success in tropical ultramafic landscapes suggests this is likely (Pillon et al. 2019). Here we test whether COM species advantages are associated with metal accumulation.

Here, we use a series of forest plots across both ultramafic and non-ultramafic soils in Sulawesi, Indonesia, to test three predictions at local scales. (1) COM species have greater leaf stoichiometric distinctiveness than other clades within a given community. (2) COM species abundance and leaf stoichiometric distinctiveness are not negatively correlated. (3) Abundance and leaf stoichiometric distinctiveness are positively correlated only for ultramafic soils and COM species.

## 2 | Methods

### 2.1 | Sample Collection and Analysis

In 2016, ten 50 ×50 m permanent primary forest plots were established across Sulawesi's two eastern peninsulas around Mount Tompotika (4 plots), Morowali Nature Reserve (2 plots) and Wawonii Island (4 plots) (Trethowan et al. 2020). Each area was roughly 300 km apart (Figure 1). Each plot consisted of 25 10 ×10 m subplots. Four plots were located on ultramafic soils, two on mafic (basalt) soils, two on limestone and two on sand. In general, all soils contained metals expected to be found within the proximity of the tropics' largest ultramafic outcrop (van der Ent, Baker, van Balgooy, et al. 2013). Soils directly over ultramafic rocks had greatest concentrations of Cr, Ni etc. Limestone plots had greatest Ca (Table S1).

We collected shade leaves from trees ≥ 10 cm diameter at breast height (1.3 m) to determine their foliar elemental concentrations. Shade leaves were sampled to standardize leaf type across species, as sun and shade leaves can differ significantly in their stoichiometry (Keenan and Niinemets 2016). Generally, each species was sampled once from each plot it occurred within, totaling 283

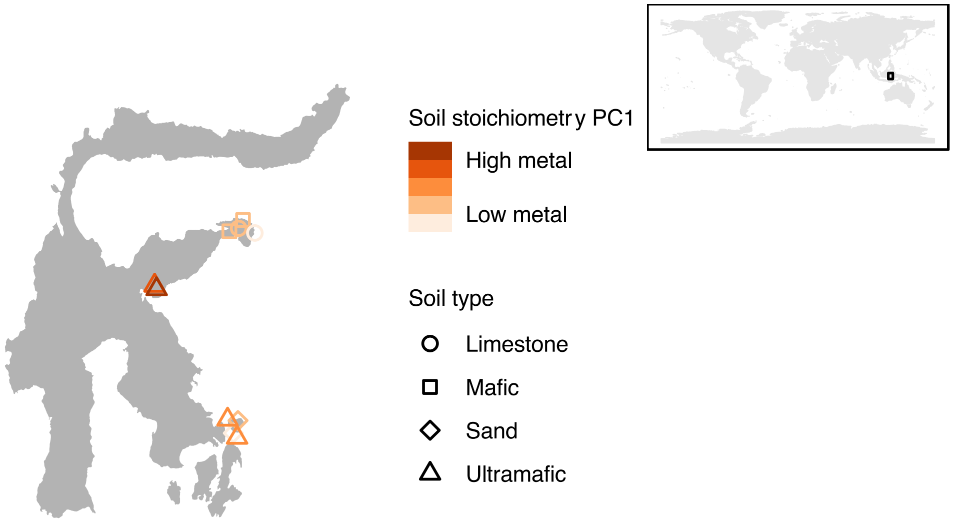

**FIGURE 1** | Ten lowland (c. 300 m asl) 0.25 ha plots across the Indonesian island of Sulawesi where tree species were sampled for this study. Shape represents soil type. Color shows the first soil principal component (PC) value for each plot. This PC axis represents variation from low to high soil metal, particularly those that are not considered macronutrients. Inset shows Sulawesi's global position.

species. Occasionally, species were sampled more than once per plot, in which case the mean concentration of each element for that species within the plot was used. In total, 723 leaf samples (c. 100 mg) were analyzed for Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P, and Zn concentrations using microwave-assisted nitric acid digestion and inductively coupled plasma optical emission spectrometry (details available in Trethowan et al. 2021). This meant we accounted for many of the elements potentially tied to plant niche space (Kaspari and Powers 2016; Ågren and Weih 2020).

Soil samples were taken from the upper 10 cm of topsoil at the center of all 10 × 10 m subplots; all samples from each plot were then pooled for further analysis—giving us a total of 10 soil samples for analysis. Total soil Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Ni, P, and Zn were quantified via digestion in $HNO_3$ and $HClO_4$ and microwave plasma atomic emission (Co, Cr and Ni) or atomic absorption spectrometry (all other elements) (Table S1 and further details available in Trethowan et al. 2021). Soil pH was measured with a pH meter in a 1:5 ratio in 1 M KCl after equilibration for 30 min.

## 2.2 | Phylogenetic Tree

A time calibrated phylogeny was constructed using V. Phylomaker2 software based on the extended GBOTB megaphylogeny (Zanne et al. 2014; Figure 2, Figure S1, Smith and Brown 2018; Jin and Qian 2019, 2022). When genera were present in the backbone phylogeny, species were added as a polytomy at the root node (i.e., most recent common ancestor) of the genus. When a genus was not present in the backbone phylogeny, the tip for the genus was bound to the halfway point between the family root node and basal node, unless the family branch length was longer than two-thirds from the family root node to the tip; here, the tip of a new genus was bound to the upper third of the whole family branch length (Qian and Jin 2016). Random placements were employed due to incomplete species-level phylogenetic data.

## 2.3 | Data Analyses

All analyses were carried out in R version 4.0.2. Leaf stoichiometric distinctiveness was calculated as the mean distance of a species to all others present in a plot in a multivariate space, the axes of which were scaled (*z*-score) leaf element concentration (Grenié et al. 2017; Violle et al. 2017). Species found in multiple plots had their distinctiveness value calculated separately for each plot. This allowed us to account for a degree of intraspecific variation amongst populations but did not risk pseudoreplication given use of phylogenetic random effects (Hulshof and Swenson 2010; Ives 2018; Delhaye et al. 2024). This resulted in a total of 454 'species' across plots which ensured models below did not show residual dispersion values indicative of overfitting (Table S2, Figures S2 and S3). We did not reduce leaf stoichiometry axes down to a set of principal components (PC) for distinctiveness calculation because there was little covariation between elements (9 PC axes were required to explain 90% of the variation in the data).

To test Prediction 1, we examined if leaf stoichiometric distinctiveness differed between COM and non-COM species. We produced a phylogenetic mixed effects model (Equation 1) of $i$ observations in $m$ forest plots of species stoichiometric distinctiveness $\log(\text{distinctiveness}_i)$ as a function of whether species belong to COM clades $\beta$ and soil element concentration principal component axes $\gamma$ $\delta$.

$$\begin{aligned}\log(\text{distinctiveness}_i) = \alpha + \beta\gamma + \beta\delta + \gamma\delta + a_{\text{spp}[i]} \\ + b_{\text{spp}[i]} + c_i + d_i + e_i\end{aligned} \tag{1}$$

$$a \sim \text{Gaussian}\left(0, \sigma_a^2 I_{\text{distinctiveness}}\right)$$

$$b \sim \text{Gaussian}\left(0, \sigma_b^2 \Sigma_{\text{spp}}\right)$$

$$c \sim \text{Gaussian}\left(0, \text{kron}\left(I_\gamma, \sigma_c^2 \Sigma_{\text{spp}}\right)\right)$$

$$d \sim \text{Gaussian}\left(0, \text{kron}\left(I_\gamma, \sigma_d^2 \Sigma_{\text{spp}}\right)\right)$$

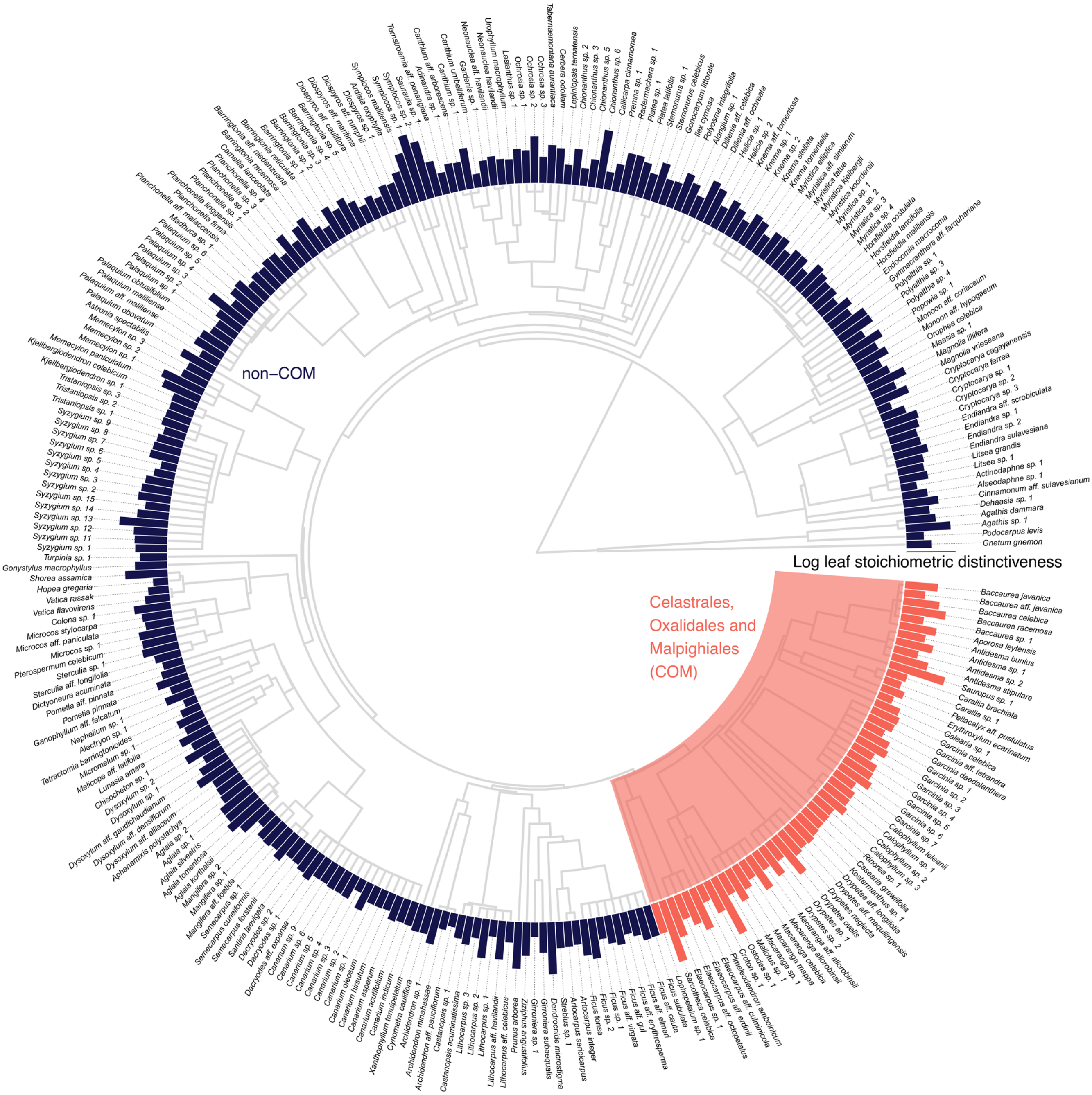

**FIGURE 2** | The distribution of stoichiometric distinctiveness across the phylogeny of tree species found in ten 0.25 ha plots across Sulawesi, Indonesia. Bar colors refer to whether species belong to Celastrales, Oxalidales, and Malpighiales clades or not.

$$e \sim \text{Gaussian}\left(0, \text{kron}\left(I_m, \sigma_e^2 I_{\text{spp}}\right)\right)$$

Here Greek letters refer to fixed effects and Latin to mixed effects (Gelman and Hill 2006; Li et al. 2017). The intercept $\alpha$ estimates species mean log stoichiometric distinctiveness. The first two soil PC axes represented 69% of the variability in the data and are primarily axes of variation in (PC1) metals $\gamma$ that are not defined as macronutrients (following Kaspari 2021), and (PC2) pH and macronutrients $\delta$ (Figure 1, Figure S4). Herein, we refer to the two PC axes simply as metals and pH/macronutrients, to aid clarity in the text and figures. To contrast the effects of soil with clade effects, we included interaction terms between all predictors. We included a random effect $a_{\text{spp}[i]}$ of species and another $b_{\text{spp}[i]}$ where the correlation structure was defined by phylogenetic distance $\sigma_b^2 \Sigma_{\text{spp}}$ (Hurlbert 1984; Li and Ives 2017; Swenson 2019). spp[$i$] connects observations [$i$] to the relevant species. $\Sigma_{\text{spp}}$ represents the matrix resulting from the phylogenetic distance between species. We accounted for unmeasured effects of the edaphic environment by using random effects of species response to soil metals $c_i$ and macronutrients/pH $d_i$ (with the Kronecker product, kron) and a correlation structure defined by phylogenetic distance between species $\sigma^2 \Sigma_{\text{spp}}$. Unmeasured impacts of the local environment and variation in species responses $e_i$ were accounted for by the addition of a species random effect nested within plots. This random effect had a

Gaussian distribution with mean 0 and variance kron$\left(I_m, \sigma_e^2 I_{\text{spp}}\right)$. Non-phylogenetic and non-nested random effects had Gaussian distribution with mean 0 and variance $\sigma^2$.

Predictions 2 and 3 were tested using a phylogenetic generalized mixed effects model (Equation 2) of observations $i$ of log species abundance in forest plots $m$ (Li et al. 2020). We used a Poisson probability distribution rather than Gaussian as this better met model assumptions (Hartig 2021) (Table S2; Figure S2). The predictors were log leaf stoichiometric distinctiveness, belonging to COM clades, $\beta$ (both components of Prediction 2), soil metals, $\delta$ (Hypothesis 3); and pH/macronutrients, $\gamma$.

$$\begin{aligned} \log\left(\text{abundance}_i\right) &\sim \alpha + \log(\text{distinctiveness})\beta \\ &+ \log(\text{distinctiveness})\delta + \beta\delta + \gamma + a_{\text{spp}[i]} + b_{\text{spp}[i]} + c_i + d_i + e_i \end{aligned} \tag{2}$$

The intercept, $\alpha$, estimated average log abundance of species across plots. We included interaction terms relevant to our predictions that COM species, $\beta$, are less negatively affected by leaf stoichiometric distinctiveness and that this relationship is exacerbated on metal-rich soils, $\delta$. As in the model of stoichiometric distinctiveness, we included a random effect of species, $a_{\text{spp}[i]}$, and a random effect of species with the correlation structure defined by phylogenetic distance between species, $b_{\text{spp}[i]}$, and random effects of species response to metals, $c_i$, and pH/macronutrients, $d_i$, with correlation structure in those effects defined by phylogenetic distance between species. For both models of stoichiometric distinctiveness and species abundance, Wald tests were used to identify significance of fixed effects (Ives 2018; Li et al. 2020). We log-transformed stoichiometric distinctiveness and abundance for all analyses to improve residual distributions (Figures S2 and S3) and to be consistent with previous trait distinctiveness-abundance studies (Umaña et al. 2015). Abundance data were counts of the number of individuals of species per plot. Given that plots in closer proximity are more likely to have similar species with greater abundance, we re-ran the model with a random effect of site plus a random effect of site where covariation is determined by scaled exponential spatial distances between plots (Dray et al. 2012; French 2018).

To assess whether our method of building the phylogeny influenced the results, we re-ran models, each time drawing upon a new phylogeny with a different random placement of species within genera and families. We iterated this process 100 times and, because of computational limits, used Bayesian Gaussian models (Held et al. 2010; Martins et al. 2013; Li et al. 2020; Trethowan et al. 2023).

## 3 | Results

Despite expectations, COM species did not exhibit greater stoichiometric distinctiveness than non-COM species, suggesting other factors mediate their niche differentiation. Instead, stoichiometric distinctiveness in the tropical trees in our study had a clear relationship with soil stoichiometry (both metals (effect = 0.11 and standard error [SE] = 0.037) and macronutrients/pH (effect = $-0.14$, SE = 0.068) and their interaction (effect = $-0.098$, SE = 0.0086) all $p < 0.05$, Figure 3a,b, Table S3). There was no clear relationship between leaf stoichiometric distinctiveness and belonging to COM clades (effect = $-0.095$, SE = 0.11, $p > 0.05$, Figure 3a) and there was no interaction with soil stoichiometry PC axes (interactions with both soil metals (effect = $-0.03$, SE = 0.023) and macronutrients/pH (0.014, SE = 0.037), both $p > 0.05$, Figure 3b).

We did, however, find support for Prediction 2 that belonging to COM clades limits the negative effects of leaf stoichiometric distinctiveness upon abundance. Although stoichiometric distinctiveness was negatively correlated with abundance for non-COM species, species within COM clades showed no such trend, indicating possible ecological advantages (effect = $-0.83$, SE = 0.42, Figure 3c,d, Table S4). This represented no decline in abundance in COM clades for species that accumulate metals at high concentrations.

There was no support for Prediction 3 that the influence of being a COM species and leaf stoichiometric distinctiveness upon abundance becomes clearer in metal-rich ultramafic soils. We found no significant interactions between soil metals and leaf stoichiometric distinctiveness (effect = $-0.055$, SE = 0.083) or belonging to COM clades (effect = $-0.83$, SE = 0.42, both $p > 0.05$, Figure 3c, Table S4).

Spatially explicit model results did not differ from results presented above (Figure S5). Replications using 100 different community phylogenies yielded similar results to the models presented above and did not alter our conclusions (Figures S6 and S7).

## 4 | Discussion

COM species did not show greater stoichiometric distinctiveness compared to other species in the tropical forests of Sulawesi. However, more distinct COM species were not rare, whereas non-COM species were. This pattern was consistent across soil types and was not exacerbated on metal-rich ultramafic soils. Together, this study shows that the local abundance of COM species is not limited by occupying distinct elemental niche space, irrespective of soil metal content.

Distinctiveness can be caused by local micro-adaptations or occupying the edges of the possible niche space (Munoz et al. 2023). Both are relevant for ultramafic and other unique ecosystems where species phenotypes can match the extremities of the environment. In these systems, it appears that atypical abundance relationships are observed where functionally distinct species are not necessarily rare (Umaña et al. 2015; Umaña, Zhang, et al. 2017; Delhaye et al. 2024). Our results support this and also suggest that deep-time evolutionary history could also be important in determining abundance in local communities.

Evidence is lacking for the precise cause of COM species abundance being independent of their position along the leaf stoichiometric distinctiveness continuum. COM species may mitigate costs of stoichiometric distinctiveness through traits such as efficient nutrient cycling, enhanced pathogen resistance, herbivore defense, and competitive ability seen previously (Mohiley et al. 2020; Paul et al. 2021, 2022). However, limited surveys of tropical ultramafic forests preclude immediate resolution of this

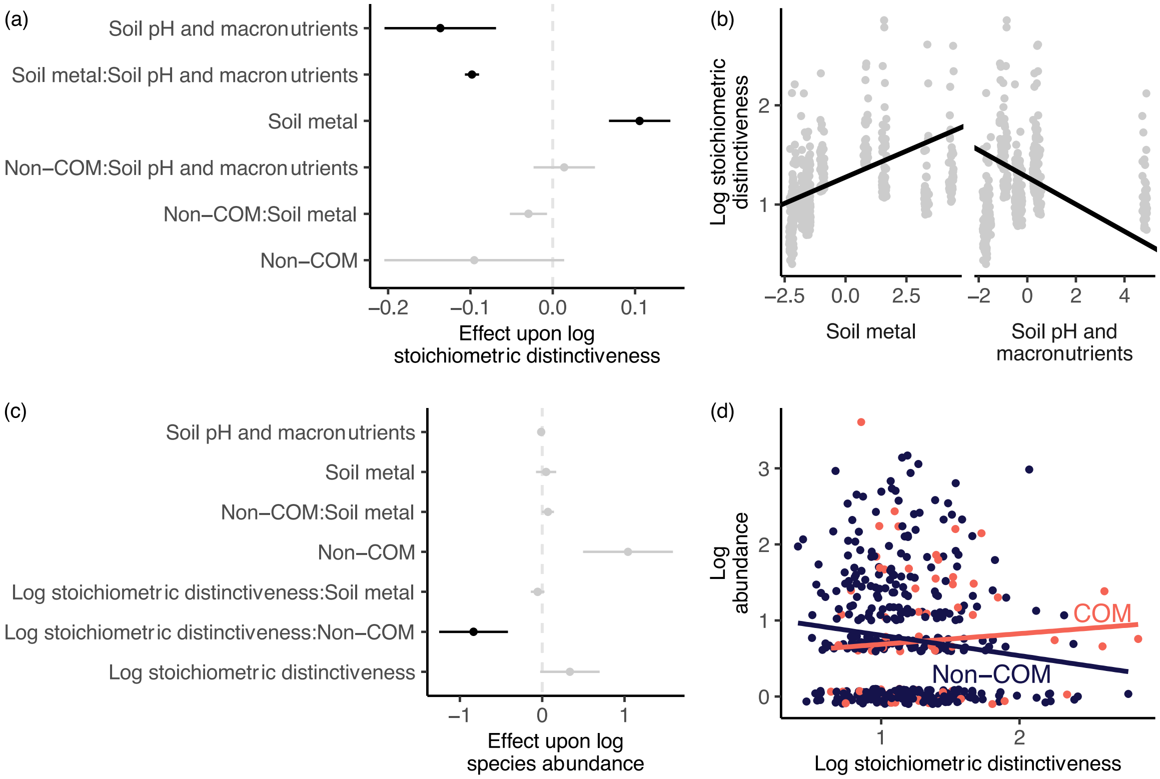

**FIGURE 3** | (a) The effects (points) of soil, not belonging to COM clades, and their interaction upon leaf stoichiometric distinctiveness for tropical tree species in plots across Sulawesi, Indonesia. Standard errors (horizontal lines) and significant effects (black points) are also shown. (b) Log-transformed leaf stoichiometric distinctiveness' relationship with soil metals and pH and macronutrients as determined by phylogenetic mixed-effect models. Points represent each tree species in each plot. (c) Effects of stoichiometric distinctiveness, not belonging to COM clades, soils and their interactions upon tree species abundance in forest plots in Sulawesi, Indonesia. Standard errors (horizontal lines) and significant effects (black points) are also shown. (d) The relationship between stoichiometric distinctiveness and abundance for non-COM and COM tree species.

question. Normally, abundance is limited by increased herbivory and disease when species and their close relatives become common (Parker et al. 2015). For COM species to avoid these limitations, it would mean that many pathogens and herbivores are unable to tolerate high plant metal content and fail to damage conspecifics and closely related species when they are abundant (Boyd et al. 1994; Salazar and Marquis 2012; Parker et al. 2015). COM metal accumulation and high stoichiometric distinctiveness could complement physical and chemical defenses that may be sufficient to limit pathogen/herbivore driven reductions in abundance (Agrawal 2007, 2011; Salazar et al. 2018; Volf et al. 2018; Coley et al. 2019; Blonder et al. 2020; Waterman et al. 2021). COM species may also benefit from facilitative microbial communities that reduce the energetic cost of metal uptake (Kushwaha et al. 2022). Additionally, metal-rich leaf litter that can cause localized spikes in soil metal concentrations may be best exploited by accumulator COM species (Kazemi-Dinan et al. 2014; Mohiley et al. 2020). More fine-scale soil stoichiometry data would be needed to examine this. Lack of fine-scale soil stoichiometry data also may be why we found no evidence for soil context-dependence upon the links between distinctiveness and abundance. Future studies should include spatially explicit soil sampling to capture microhabitat variability influencing plant–soil interactions. Why non-COM species are less abundant when they accumulate metal is also unclear. If metal accumulation has costs, their fitness may also decrease (Clark et al. 1998; Sollins 1998; Delhaye et al. 2020; Mohiley et al. 2021; Rubio and Swenson 2022). This could be caused by limitations due to root architecture differences or perhaps an inability to benefit from microbial communities (Lequeux et al. 2010; Kushwaha et al. 2022). Measurement of growth rates and reproductive success in tropical forests are required to determine this (e.g., Umaña et al. 2023). Whether metal accumulating species are less affected by herbivory in tropical forests also requires assessment. Measuring tissue metal content with X-ray fluorescence in the field could help speed up such in-depth study (Purwadi et al. 2024). Overall, there are great possibilities for new insights into these unique habitats by compiling datasets that span trophic levels.

New work could fill the drawbacks of this study. For instance, we were limited to measurements of single leaves per tree. We therefore have limited knowledge of comprehensive metal uptake from root to crown. A study in the wet tropics replicating the advances in tree sampling from New Caledonia would be worthwhile (Paul et al. 2022). We also have sampled fewer species in COM clades than non-COM; further work is required to build a larger, more balanced dataset. Another knowledge gap left unfilled here is how tropical rainfall seasonality affects these patterns; for instance, does available soil metal flux with monsoon onset cause similar distinctiveness pulses with consequences for species interactions (Zhang et al. 2018)? The seasonally dry/ultramafic-rich island of Luzon (Philippines) would be an ideal study system for such questions (Trethowan 2021). Such work would give greater depth to our understanding of community ecology in ultramafic systems.

There are further extreme tropical habitats that require study. Two of the non-ultramafic plots used in this study are found on limestone. These systems often have high endemism and distinct phenotypes (Geekiyanage et al. 2019). We have shown previously that their high soil Ca drives greater leaf Ca (Trethowan et al. 2021). Whether distinct trait suites on limestone are observed more broadly across Indonesia and the wider tropics needs further study (Trethowan et al. 2024). Likewise, how trait distinctiveness relates to species dominance in these landscapes more broadly remains to be seen (Matas-Granados et al. 2024). We still require unifying rules and expectations for community ecology in extreme tropical habitats.

Greater knowledge of how evolutionary dynamics build ultramafic floras is needed. In the tropics, ultramafic-rich regions are often more diverse than elsewhere (Rahbek et al. 2019; Struebig et al. 2022). Stoichiometric distinctiveness is likely important for diversification in these regions. In general, the occupation of novel niche space that underpins speciation events and adaptive radiations is influenced by increasing distance from optimum niche space (Parker and Smith 1990; Gavrilets and Losos 2009; Bouchenak-Khelladi et al. 2015). Metal accumulation effects upon speciation and diversification in the COM clades and others such as the Symplocaceae and Rubiaceae that frequently hyperaccumulate warrant further study (Metali et al. 2012; Schmitt et al. 2016; Turner et al. 2021). It remains to be seen if the greater variation in stoichiometry/accumulation of metals in landscapes of contrasting ultramafic and non-ultramafic soils offers novel niche space, which underpins why ultramafic-rich regions are some of the most diverse on earth (Paun et al. 2016; Rahbek et al. 2019; Brambach et al. 2020). Similarly, it is not clear whether the COM clades have convergent molecular mechanisms for metal accumulation (Broadley et al. 2001). Understanding whether these mechanisms are distinct from metallophyte families more frequently found in temperate regions such as the Brassicaceae would clarify evolutionary history-driven establishment of floras and communities across biomes. Overall, there are many opportunities for advances in eco-evo understanding across metal-rich landscapes.

This work across the ultramafic mosaic tropical forests of Sulawesi has shown that COM species successfully cope with metal accumulation and maintain high abundance, and that the opposite is true for non-COM species. Thus, there is substantial variation in ecological strategy with respect to leaf metals across soil metal gradients. Metal stoichiometry is, therefore, an important dimension of variation for community assembly.

## Author Contributions

L.A.T. carried out analysis supported by B.W.B. and F.Q.B., L.A.T., E.K., D.G., and T.M.A.U. gathered data. L.A.T. wrote the first draft. All authors contributed to the final manuscript.

## Acknowledgments

We thank the Indonesian Ministry of Research and Technology for permission (88/SIP/FRP/E5/Dit.KI/11/2016) to perform fieldwork and Herbarium Bogoriense for the Memorandum of Understanding and Material Transfer Agreement to support this permission. We thank Indonesian forestry departments and staff at Aliansi Konservasi Tompotika for support in the field. Fieldwork was only possible due to the help of guides: Aga, Yes, Amin, Muksin, Sumardin, Dado, Hanya, Ete, Asrion, Lendo, Manto, and Peno. We thank David McKendry for help with leaf analysis and the Indonesian Agricultural Research Agency (Badan Litbang Kementerian Pertanian) for conducting soil analysis. We thank Jennifer Rowntree and Tim Baker for comments that much improved an early version of the manuscript. We thank an anonymous reviewer and Claudia Garnica-Diaz for contributions that benefited the manuscript.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

Soil and leaf element data and species composition data available here https://figshare.com/projects/Sulawesi_stoichiometry/97660. The Rmarkdown file to reproduce the manuscript available here https://doi.org/10.6084/m9.figshare.24746811.v5.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.