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LETTER

Plant chemical traits define functional and phylogenetic axes of plant biodiversity

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Abstract

To determine which types of plant traits might better explain ecosystem functioning and plant evolutionary histories, we compiled 42 traits for each of 15 perennial species in a biodiversity experiment. We used every possible combination of three traits to cluster species. Across these 11,480 combinations, clusters generated using tissue %Ca, %N and %K best mapped onto phylogeny. Moreover, for the 15 best combinations of three traits, 82% of traits were chemical, 16% morphological and 2% metabolic. The diversity-dependence of ecosystem productivity was better explained by the %Ca, %N and %K clusters: compared to adding a new species at random, adding a species from an absent cluster/clade better-explained gains in productivity. Species number impacted productivity only when all clusters were present. Our results suggest that tissue elemental chemistry might be more phylogenetically conserved and more strongly related to ecosystem functioning than commonly measured morphological and physiological traits, a possibility that merits exploration.

KEYWORDS
biodiversity, Cedar Creek, ecosystem functioning, elementome, functional diversity, functional trait, hypervolume, ionome, phylogenetic signal, productivity

INTRODUCTION

Ecology is in the midst of a search for the plant traits that best explain how and why species composition and biodiversity influence ecosystem functioning (Chacón-Labella et al., 2023; Díaz et al., 2016; Hagan et al., 2023; Loreau, 2010; van der Plas et al., 2020, 2023; Walker et al., 2022). Such traits might be based on important aspects of plant physiology and morphology (Carmona et al., 2021; Reich, 2014), the mechanisms controlling competitive coexistence (Klausmeier et al., 2020; Kraft et al., 2015; Lehman & Tilman, 2000), or the processes that drive fluxes of matter and energy (Furey & Tilman, 2021; Loreau, 2010; Roscher et al., 2004, 2012). Analyses of plant biodiversity experiments have suggested that greater plant functional trait diversity may cause greater primary productivity (Bongers et al., 2021; Clark et al., 2012; Roscher et al., 2012; Tilman et al., 1997; Tilman & Fornara, 2009; Weisser et al., 2017). However, it is not clear which functional traits are most relevant (Chacón-Labella et al., 2023; van der Plas et al., 2020; Walker et al., 2022). Other analyses have suggested that phylogenetic diversity may be a better predictor of ecosystem functioning than plant species richness, perhaps because phylogeny may capture an ecologically relevant suite of as-yet undetermined or difficult-to-measure underlying traits that promote niche complementarity (Cadotte, 2017; Cadotte et al., 2009; Huang et al., 2020). Moreover, a deeper understanding of which traits are phylogenetically conserved (Cadotte, 2017; Cavender-Bares et al., 2009; Davies et al., 2016; Flynn et al., 2011; Srivastava et al., 2012; Steudel et al., 2016) may help clarify why certain suites of competing species coexist locally and why biodiversity has ecological impacts (Tilman et al., 2014).

Because local biodiversity requires multispecies coexistence, empirically determining which plant functional traits are associated with coexistence, evolutionary history and ecosystem functioning could offer significant insights into the traits, and theories, of greatest ecological and evolutionary importance (Klausmeier et al., 2020). For example, coexistence might be explained by seed traits and dispersal abilities (Sullivan et al., 2018; Tilman, 1994), by how height and numerous aspects of leaf physiology and morphology impact light capture and competition (Reich, 2014; Westoby, 1998), or by tradeoffs in plant defences and competitive abilities (Holt & Bonsall, 2017). Other types of traits that reflect chemical stoichiometric differences (Sterner & Elser, 2002) or other plant chemical traits, including plant secondary chemistry (Walker et al., 2022), might also explain coexistence. In particular, all plants require and may compete for essential elements (Kaspari & Powers, 2016; Peñuelas et al., 2019; Salt et al., 2008; Sterner & Elser, 2002; Tilman, 1982; Walker et al., 2022).

It seems plausible that chemical traits might offer insights into both plant competitive coexistence and plant evolutionary history (Broadley et al., 2003; Fernández-Martínez et al., 2021; Neugebauer et al., 2018; Peñuelas et al., 2019; Walker et al., 2022; White et al., 2012). For example, differing requirements for elements such as N, P, K and Ca may allow competing plant species to coexist (Tilman, 1982), and may cause tissue levels of certain elements such as Ca to be phylogenetically conserved within plant families (Bitomský et al., 2023; Broadley et al., 2003; Mládková et al., 2018; Neugebauer et al., 2018; Sardans et al., 2021; White et al., 2012). From an ecosystem perspective, because of plant–soil feedback effects, interspecific differences in plant elemental chemistry could alter the quantities and the stoichiometric ratios of limiting elements in an ecosystem (Ehrenfeld et al., 2005; Furey & Tilman, 2021; Hobbie, 2015; Jobbágy & Jackson, 2001; Reich et al., 2005; Sterner & Elser, 2002; Waring et al., 2015; Wedin & Tilman, 1990; Zinke, 1962). The resultant changes in the supply rates of limiting elements could increase primary productivity, change outcomes of resource competition (Tilman, 1982; Wedin & Tilman, 1990) and shift ecosystem biogeochemistry (Chapin et al., 1986; Kaspari & Powers, 2016; Vitousek & Reiners, 1975). For these reasons, expanding the commonly measured set of functional traits to include tissue chemical traits might provide novel insights (Fernández-Martínez, 2022; Walker et al., 2022).

The ecological importance of chemical elements such as nitrogen (N) and phosphorus (P) is well known (Chapin et al., 1986; Guiz et al., 2016, 2018; Sterner & Elser, 2002; Walker & Syers, 1976), but other elements may also be important (Kaspari & Powers, 2016). For example, boron (B) may be a limiting micronutrient for the tropical rainforest of Barro Colorado Island (Steidinger, 2015; Turner et al., 2017), and is one of the more limiting micronutrients in many agricultural soils (Shorrocks, 1997). Tissue % Ca has been shown to differentiate some plant families, with % Ca being low in grasses (*Poaceae*) relative to other angiosperm families (Bitomský et al., 2023; Broadley et al., 2003; Mládková et al., 2018; Neugebauer et al., 2018). Furthermore tree species within *Acer* have higher % Ca than those within *Pinus* (Reich et al., 2005). Tissue % Ca also discriminated among the herbaceous plant families in the Park Grass Experiment at Rothamsted (White et al., 2012). These findings suggest that the plant tissue levels of less commonly measured elements may capture axes of niche differentiation, may be phylogenetically conserved and may help explain why biodiversity impacts ecosystem functioning (Fernández-Martínez, 2022; Kaspari & Powers, 2016; Peñuelas et al., 2019; Sardans et al., 2021; Schaller et al., 2016; White et al., 2012).

Here we analyse a suite of 42 plant traits, including 21 morphological traits (e.g. specific leaf area, height, seed mass, fine root density), six metabolic traits (e.g. leaf photosynthesis rate, leaf stomatal conductance, leaf delta ^{13}C) and 15 chemical traits (concentrations of leaf N and concentrations of C, N, P, K, S, Ca, Mg, Fe, Mn, Zn, Cu, B, Al and Na in whole aboveground biomass) for each of the 15 perennial grassland plant species that survived in monocultures and coexisted in mixtures in a long-term grassland biodiversity experiment (Table S1). To determine which of these 42 traits were most informative (Table S2), we used these species traits and the independently determined phylogeny of these species to explore the following questions:

1. What are the relative strengths of the phylogenetic signal of chemical traits versus morphological and metabolic traits for each trait on its own?
2. Which suites of three traits, one for each major clade, differentiate these plant species into functional trait clusters, and what is the correspondence between these clusters and the reported phylogeny of these species?
3. Do the clusters based on the set of three traits with highest congruency to the phylogeny have statistical power to explain the effect of biodiversity on ecosystem primary productivity?

MATERIAL AND METHODS

Study site

Our study was conducted in the Biodiversity II experiment at the Cedar Creek Ecosystem Science Reserve in East Bethel. The soil of the site is sandy, low in organic matter, high in P, and low in N and K (Grigal, 1974). The experimental details are published (Tilman et al., 1997). In brief, the fully randomised experimental design consists of 154 plots, with each 9 × 9 m plot seeded in spring 1994 with 1, 2, 4, 8 or 16 perennial grassland herbaceous species, and with 32, 28, 29, 30 and 35 replicates of each diversity level respectively. The plant species composition of each plot is a separate random draw. Each plot is weeded to remove plant species not assigned in 1994.

Collection of trait data

Traits of the 15 plant species that persisted in the one-species treatment (Table S1) were determined using biomass collected in the plots and from data obtained from the TRY trait database (Kattge et al., 2020) including the following studies and databases (Abakumova et al., 2016; Atkin et al., 1997, 2015; Bahn et al., 1999; Belluau & Shipley, 2017, 2018; Bragazza, 2009; Byun et al., 2013; Cadotte, 2017; Campbell et al., 2007; Ciocârlan, 2009; Cornelissen, 1996; Cornwell et al., 2008, 2016; Craine et al., 2005, 2009, 2011, 2012, 2013; Dalke et al., 2018; de Vries & Bardgett, 2016; Díaz et al., 2004; Everwand et al., 2014; Fitter & Peat, 1994; Fry et al., 2014; Garnier et al., 2007; Gos et al., 2016; Green, 2002; Guy et al., 2013; Han et al., 2005; Herz et al., 2017; Hickler, 1999; Iversen et al., 2017; Kattge et al., 2009; Kew, 2014; Kleyer et al., 2008; La Pierre & Smith, 2015; Laughlin et al., 2010; Lhotsky et al., 2016; Lin et al., 2015; Louault et al., 2005; Loveys et al., 2003; Maire et al., 2015; Meziane & Shipley, 1999; Miller et al., 2018; Moles et al., 2004; Onoda et al., 2011, 2017; Ordoñez et al., 2010; Poorter et al., 2009; Prentice et al., 2011; Quested et al., 2003; Reich et al., 2008, 2009; Sandel et al., 2011; Schroeder-Georgi et al., 2016; Schweingruber & Landolt, 2005; Shipley, 2002; Shipley & Vu, 2002; Siefert, 2012; Siefert et al., 2014; Smith & Dukes, 2017; Takkis, 2014; Tucker et al., 2011; Vergutz et al., 2012; Walker, 2014; Wang et al., 2017; Willis et al., 2010; Wright et al., 2004, 2017; Wright & Sutton-Grier, 2012). We queried all possible traits within the TRY 5.0 database and use all numeric traits with at least one measurement, with no trait imputation, for each of the 15 species (Supplemental Information S2).

We additionally used locally measured chemical, leaf and morphological traits. Leaf and morphological traits are described in Cadotte et al. (2009). There was some overlap between the locally measured traits and those pulled from the TRY repository, but the local measurements were used as separate variables in case they explained more variance. We additionally used local aboveground tissue elemental concentrations (Al, B, C, Ca, Cu, Fe, K, Mg, Mn, N, Na, P, S, Zn) measured on samples of each of the 15 species collected from a 0.10 m by 6 m clipped strip of biomass from both 1-species and 16-species plots (further information in Supplemental Information S1). Throughout the manuscript reference to a single element refers to its % abundance by mass in dry aboveground biomass. However, if a chemical trait is prefixed with 'leaf', for example, leaf %N, this represents the % N of dry leaves.

Analyses

All analyses were run using R version 4.2.1 (R core Team 2022). Data processing and figure generation used packages within *tidyverse* (Wickham, 2017). The analyses are reproducible using a *targets* pipeline (Landau, 2021).

Phylogenetic signal

Based on the Leipzig catalogue of vascular plants *lcvplants* (Freiberg et al., 2020), on the Angiosperm Phylogeny Group et al. (2016), and using package *taxize* (Chamberlain & Szöcs, 2013), the studied plant species are in five plant families: *Poaceae* (6 species), *Fabaceae* (4 species), *Asteraceae* (3 species), *Lamiaceae* (1 species) and *Apocynaceae* (1 species) (Table S1). The latter three families are all within a monophyletic clade, the Asterids. The phylogeny therefore consists of three broad clades, with *Poaceae* corresponding to the common grassland functional group of grasses, *Fabaceae* to legumes and *Asterids* to forbs. Analyses were initially run with a phylogenetic tree (Kothari et al., 2018) and then updated using package *V-phylomaker* and found to be qualitatively consistent with *V-Phylomaker* (Jin & Qian, 2019). We used the 42 traits in Table S2, each measured on each of the species in Table S1, to test for a phylogenetic signal using Blomberg's K (Blomberg et al., 2003), with package *picante* (Kembel et al., 2010). P-values were adjusted using the false discovery rate correction (Benjamini & Hochberg, 1995).

Species clustering

Agglomerative hierarchical clustering

For each trait, the distribution of trait values across the 15 species was first normalised to have a multi-species mean of 0 and a standard deviation of 1.0. The resultant trait values were used for clustering. Clustering used three traits to create a distance matrix using function *cluster::daisy* with the Euclidean distance (Maechler, 2021). The distance matrix was then run through an agglomerative hierarchical clustering (AGNES) algorithm (*cluster::agnes*). Ward's method was used to minimise within-cluster variance (Legendre & Legendre, 2012). The clusters were converted to a dendrogram using package *dendextend*.

Comparison of phylogeny with AGNES clustering

We calculated all possible three-way combinations of traits for the 42 traits ($n = 11, 480$). Each combination of three traits was then run through AGNES as previously described. Next, the phylogenetic tree for these same species was converted to a dendrogram object using package *phylogram* (Wilkinson & Davy, 2018). Each trait-based dendrogram was then compared to the phylogenetic tree dendrogram using the cophenetic correlation (*dendextend::cor_cophenetic*). Display of the functional trait dendrogram and the phylogenetic tree was done with *dendextend::tanglegram*.

Species trait volumes, clustering and relation to aboveground productivity

Trait volumes

For the three-way combination of traits with the highest cophenetic correlation of their trait-based cluster to the phylogeny, we used the package *hypervolume* (Blonder et al., 2014) to calculate and visualise the three-dimensional trait volume occupied by the 15 species. Trait data for each species within each of the three trait clusters were used to estimate a volume for each of three groups, specifically a gaussian volume using a Silverman kernel bandwidth estimator. Intersection of the three volumes was tested using 50 bootstrapped volumes each with Sorensen's index reported. Further details are provided in Supplemental Information S3.

Relationship of trait clusters to aboveground biomass

Each plot was assigned a cluster richness value of 1, 2 or 3 based on having been planted in 1994 with species from one, two or three clades based on the experimental design of *Poaceae*, *Fabaceae* or *Asterids*. For example, all monocultures had a cluster richness value of 1. A two-species plot with two-species in the same cluster also received a value of 1 whereas a two species plot with species from different clusters had a cluster richness value of 2. Two C3 grasses, *Elymus canadensis* and *Agropyron smithii* failed to persist in the experiment and were not counted. However, a two-species plot (Plot 234) originally planted with *Elymus canadensis* and *Lupinus perennis* consistently contained other grasses, despite weeding, and was given a cluster richness value of 2.

A linear regression was performed testing the dependance of mean aboveground plot biomass from 2010 to 2018 on a two-way interaction between the natural log of plant species number as a continuous variable and cluster richness as a categorical variable (further details in Supplemental Information S1).

Clustering and principal components

To visualise the variation in the traits of these species and to reduce dimensionality, we conducted two principal component analyses (PCA) using function *rda* in package *vegan* on the scaled mean for each trait (Oksanen et al., 2022): one with the top three traits based on their cophenetic correlation, and one with all traits that had a significant phylogenetic signal.

RESULTS

Testing the phylogenetic signal of 15 species' plant traits

For this set of 15 species, we found that 30 out of 42 individual traits carried no significant phylogenetic signal ($p > 0.05$) (Table S3). Of the 12 traits that carried statistically significant phylogenetic information, eight traits were aboveground tissue chemical traits (%B, %C, %Ca, %N, %K, %Mg, %S) and leaf %N. Three morphological traits were significant (leaf shape (width to length ratio); leaf dry matter content (LDMC); leaf water), as was one metabolic trait, leaf delta ^{13}C, which differentiates C4 versus C3 photosynthetic pathways. Among the 30 traits that did not differ from random variation were specific leaf area, leaf photosynthetic capacity, seed mass, plant height and fine root density (Table S3).

Which traits drive congruence of functional traits and phylogeny?

As the species in this experiment are drawn from three main clades, we sought to determine which combinations of three traits better clustered these species according to their phylogeny. Sets of three traits were chosen to seek a potential low-dimensional tradeoff surface that might also help explain ecological coexistence. We therefore tested the association between a functional trait dendrogram drawn from each set of three traits and the phylogenetic tree using the cophenetic correlation.

Out of the total of 11, 480 possible three-way combinations of these 42 traits, the single best correlation between trait-based clusters and phylogeny occurred for a set of three chemical traits, %Ca, %N and %K (Figure 1). These three chemical traits divided the 15 plant species into clusters and sub-clusters that were strongly congruent to their phylogeny (Figure 1). The three trait-based clusters correspond with the family *Poaceae*, the family *Fabaceae* and the *Asterids* clade.

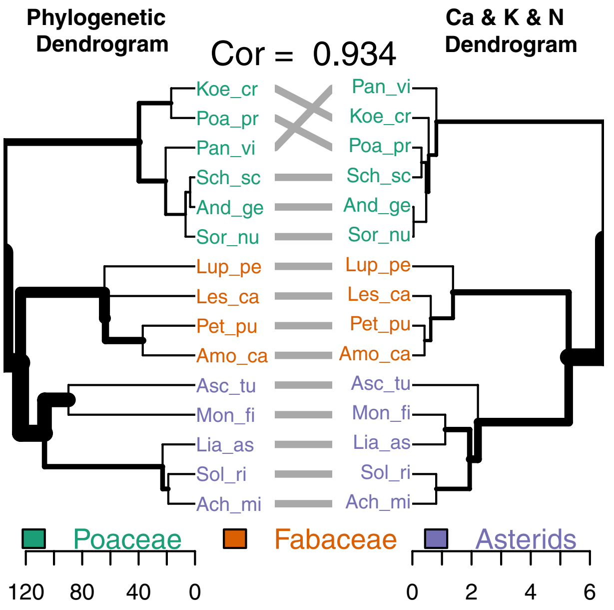

FIGURE 1 Similarity between a dendrogram based on the phylogenetic tree and a dendrogram based on algorithmic clustering with tissue % Ca, K and N. This case shows the best fit out of all 11,480 three-trait combinations tested. The Ca, K and N dendrogram results from Ward's clustering algorithm on the Euclidean distance of standardised mean trait values of % aboveground tissue Ca, K and N for 15 species. 'Cor' represents the cophenetic correlation comparing the two dendrograms. The first three letters of genus and the first two letters of species denote the Latin binomial found in Table S1 for Asterids (purple, $n=5$), Fabaceae (orange, $n=4$) and Poaceae (green, $n=6$).

For the top 15 combinations of three traits based on their cophenetic correlations (ranging from 0.934 to 0.883), 82% of the traits were chemical traits, 16% were morphological and 2% were metabolic (Figure S1). For the top 137 trait combinations, which have cophenetic correlation greater than 0.8, chemical traits occurred 70.3% of the time compared to 24.1% for morphological and 5.6% for metabolic traits. %B, %N, %Ca, %K and then leaf shape occurred most frequently (Figure 2a,b).

The highest mean cophenetic correlation for each possible combination of the three types of traits also suggests that chemical traits are of high importance for the co-existing plants we studied. The top 3-trait combinations for each single type of trait are: for just chemical traits, a cophenetic correlation, r, of 0.93 (%Ca, %N and %K, rank=1); for just morphological traits, $r=0.78$ (LDMC, leaf shape and number of leaflets, rank=196); for just metabolic traits $r=0.35$ (leaf delta 13C, leaf delta 15N and stomata conductance per leaf mass, rank=4229). For the best two-way combinations of types of traits, chemical + morphological traits have $r=0.91$ (%Ca, %K and number of leaflets, rank=3); for chemical + metabolism traits, $r=0.88$ (%N, %K and leaf photosynthesis per leaf mass, rank=15); and for metabolic + morphological traits, $r=0.69$ (fine root tissue density, leaf photosynthesis per leaf area and leaf shape, rank=690). For all three trait types, which is a chemical + a metabolic + a morphological trait, $r=0.84$ (%B, leaf delta 15N and leaf water, rank=55).

%Ca %N and %K best separated the phylogenetic groups, because *Poaceae* had low %Ca whereas *Fabaceae* and *Asterids* had high %Ca (Figure 2c); *Fabaceae* had high %N, but low %K; while *Asterids* had low %N, but high %K (Figure 2c). In addition, *Poaceae* were in general lower in concentration of other essential elements (N, leaf N, K, Ca, Mg, S and B), with narrower leaves with higher LDMC (Figure 2c). Within *Poaceae*, leaf delta ^{13}C distinguished C4 grasses from C3 grasses and other C3 species (Figure S3). Both *Fabaceae* and the *Asterids* had relatively higher %B and %Ca than grasses along with wider leaves (Figure 2c). *Asterids* and *Fabaceae* were differentiated as *Fabaceae* had higher %N and wider leaves and *Asterids* had higher %K and %B (Figure 2c).

Testing the dependance of aboveground biomass on trait-defined clusters

The three tissue-chemistry-based clusters (Figure 3a) each had distinct ecological impacts. Higher aboveground productivity was associated more with adding a species from an absent cluster than randomly adding a new species (Figure 3a). A multiple regression demonstrates a significant two-way interaction ($p=0.016$) between the log of the number of planted species and the number of clusters planted in each plot ($F_{5,148}=46.18$, $R^2=0.61$) (Table S4). The interaction reveals that at low levels of species richness (1–4), increasing the number of distinct clusters explains more variance in aboveground productivity than increasing the number of species when either just one or just two clusters were represented in a plot (Figure 3a). Although there is a well-known main effect of productivity increasing with species richness, this slope did not differ from zero when there was only one cluster present (slope=3.77 95% CI [−53.6, 61.1] (Figure 3a)). Similarly, the slope did not differ from zero when only two clusters were present (slope=−6.23 95% CI [−51.2, 38.7] (Figure 3a)). It was only when all three clusters were present that productivity positively depended on species richness (slope=68.41 95% CI [35.5, 101.3]).

Examination of the trait volumes, which were generated using replicate samples of tissue %N, %K and %Ca (Supplemental Information S3), shows that *Poaceae* were distinct from the other groups with the greatest distance from their centroids (*Poaceae* to *Asterids* 1.39, or *Poaceae* to *Fabaceae* 1.43 vs. *Fabaceae* to *Asterids* 1.14) and with no detectable overlap of their estimated trait volumes (*Poaceae* to *Asterids*: Sorensen 95% CI [0.0, 0.046], $p=0.65$; *Poaceae* to *Fabaceae*: Sorensen 95% CI [0.00, 0.0018], $p=0.83$). *Asterids* and *Fabaceae* were statistically distinct but do overlap (Sorensen 95%

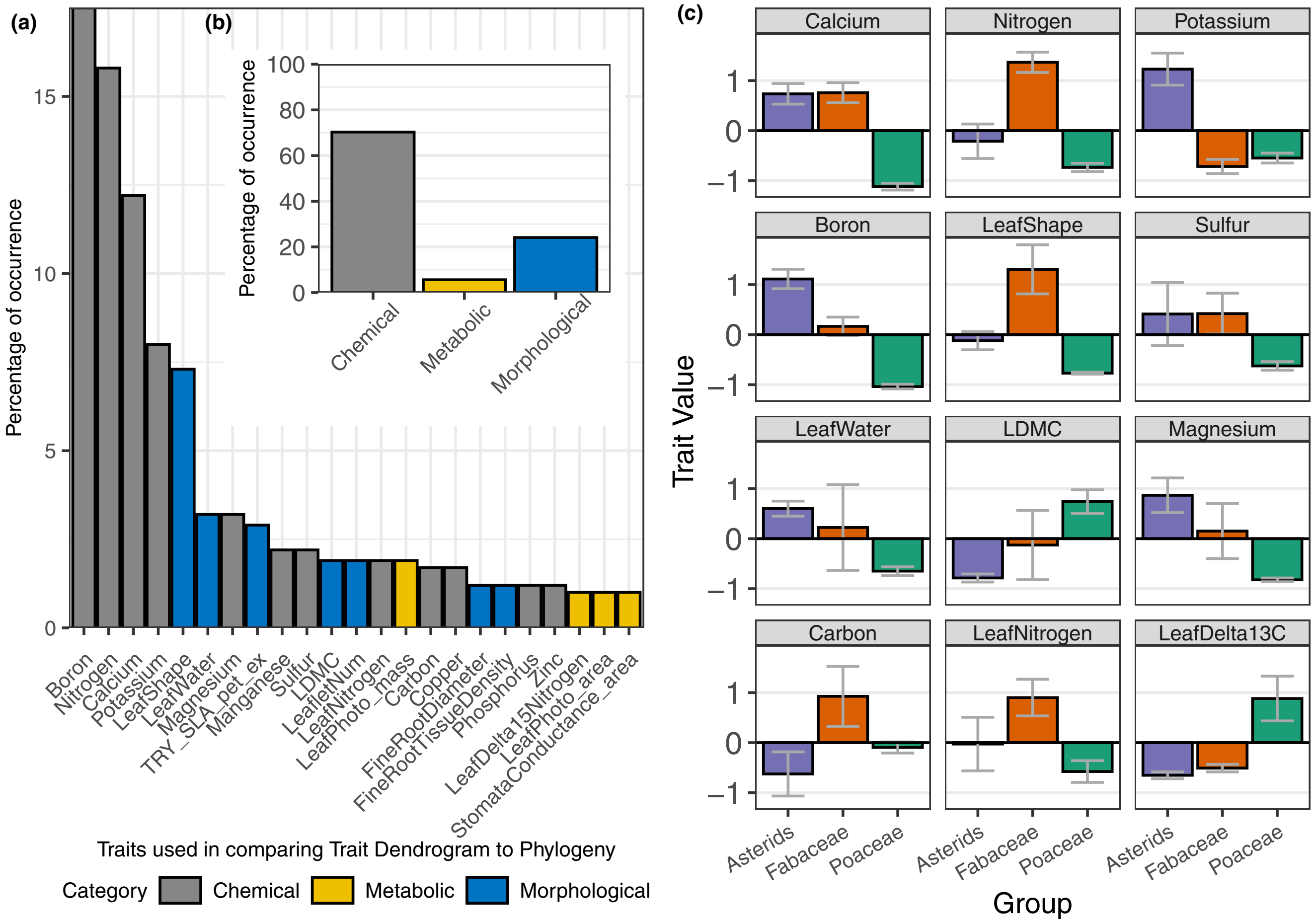

FIGURE 2 (a) Percentage of occurrence for each trait and sub-panel (b) each trait category on average across all functional trait dendrograms with a cophenetic correlation greater than 0.8 ($n = 137$ out of 11, 480 total; top 1% of fits) to the genetic phylogeny for 15 species. Three categories are presented as chemical (grey), metabolic (mustard) and morphological (blue). n.b. traits with a per cent occurrence <1% are not shown to improve readability (c) Mean ± 1 SE for standardised trait values for each of 12 traits. All traits had a significant phylogenetic signal (Table S3). Each mean represents values for Asterids (purple, $n = 5$), Fabaceae (orange, $n = 4$), and Poaceae (green, $n = 6$) for species in Table S1.

CI [0.04, 0.27], $p = 0.59$) because the high %N content of *Asclepias tuberosa* which makes it be closer to the *Fabaceae*. Examining both panels of Figure 3 in tandem, we can see that as the cluster richness of a plot increases from one to two to three clusters present, the traits of the community span a greater volume of the three-dimensional trait space. Note the distinctness of each cluster, and how any single cluster alone occupies a much smaller volume of trait space than when two or three clusters are present (*Poaceae* volume = 0.37, *Fabaceae* volume = 1.9, *Asterids* volume = 4.7; total volume of three clusters = 6.99). Plots with two, three or four species from the same cluster occupy a smaller volume of trait space than when these species are from two or three different clusters. Consistent with this effect, the analysis in Figure 3 shows that productivity increases as a function of cluster richness. Indeed, it is only when all three clusters are present that increases in the number of plant species is associated with higher productivity (Figure 3a).

Within cluster variation and axes of trait coordination

To explore a higher-dimensional trait space that is evident once all three clusters were present (Figure 3a), we use PCA on the mean trait values for the 15 species using all 12 traits that had a phylogenetic signal (Table S3) and compare it to a similar PCA that used just tissue %Ca, %N and %K. The latter PCA reveals a first axis showing *Poaceae* being low in Ca, N and K and *Asterids* and *Fabaceae* relatively higher in those elements (Figure 4a). The second axis separates *Asterids* and *Fabaceae*, with *Asterids* higher in %K and *Fabaceae* higher in %N (Figure 4a). For the 12-trait PCA, which used tissue %B, %Ca, %C, %K, %Mg, %N, LDMC, leaf shape, leaf water, leaf delta ^{13}C, leaf %N, %N and %S (Table S3), the first principal component separated the *Poaceae* from the non-grasses (Figure 4b) based on *Poaceae* being higher in LDMC and leaf delta ^{13}C (C4 grasses) and having

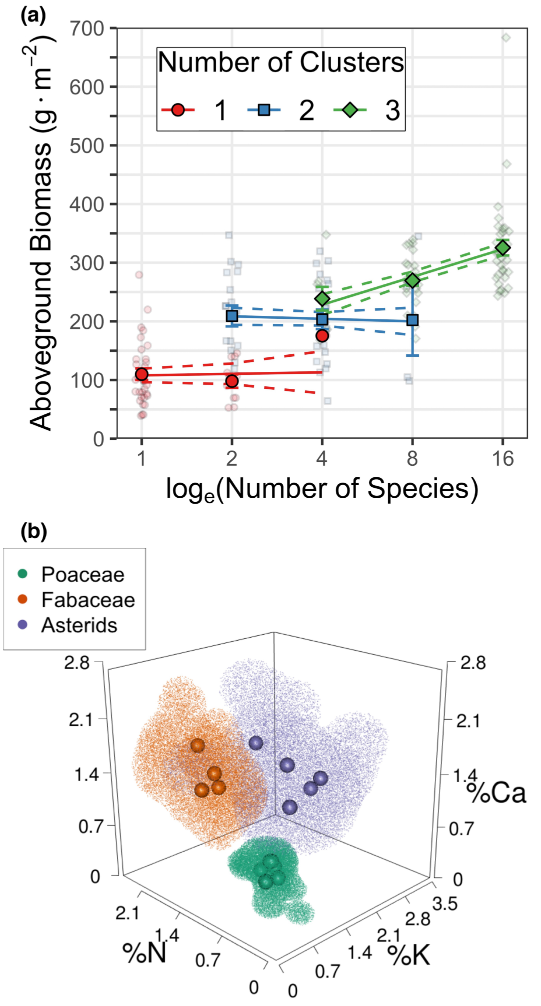

FIGURE 3 (a) Mean aboveground biomass (g m^{-2}) versus the natural log of the number of planted species. Each jittered point represents the mean aboveground biomass of a given plot from 2010 to 2018 (n=154 plots). Each point is coloured based on the number of clusters present in a given plot, with 1 being red circles, 2 being blue squares and 3 being green diamonds. The mean plot biomass ±1 SE for plots with a given value is displayed with a black outline and error bar for each associated value of plant species diversity, that is, the number of species planted in a plot. The solid line ± a dashed line represents fitted values from a two-way interaction in a linear regression between the log$_e$(Number of Species) × cluster richness (p=0.016). (b) The mean % whole aboveground percentage of calcium, nitrogen and potassium for 15 species. Each point is coloured as to whether it is within Poaceae (green), Fabaceae (orange) or the Asterids (purple). The cloud of smaller points surrounding the larger spheres represents an estimated gaussian probability volume using replicated values for all species in each cluster (Poaceae n=43; Asterids n=35; Fabaceae n=30).

narrower leaves (leaf shape), and lower %B, %Ca, %K, leaf water, %Mg, leaf %N, %N and %S (Figure 4b). The second principal component splits the *Fabaceae* and *Asterids* with the *Asterids* being relatively higher in %B, %K, %Mg and leaf water content and lower in LDMC and *Fabaceae* higher in %C, leaf %N, %N and %S (Figure 4b).

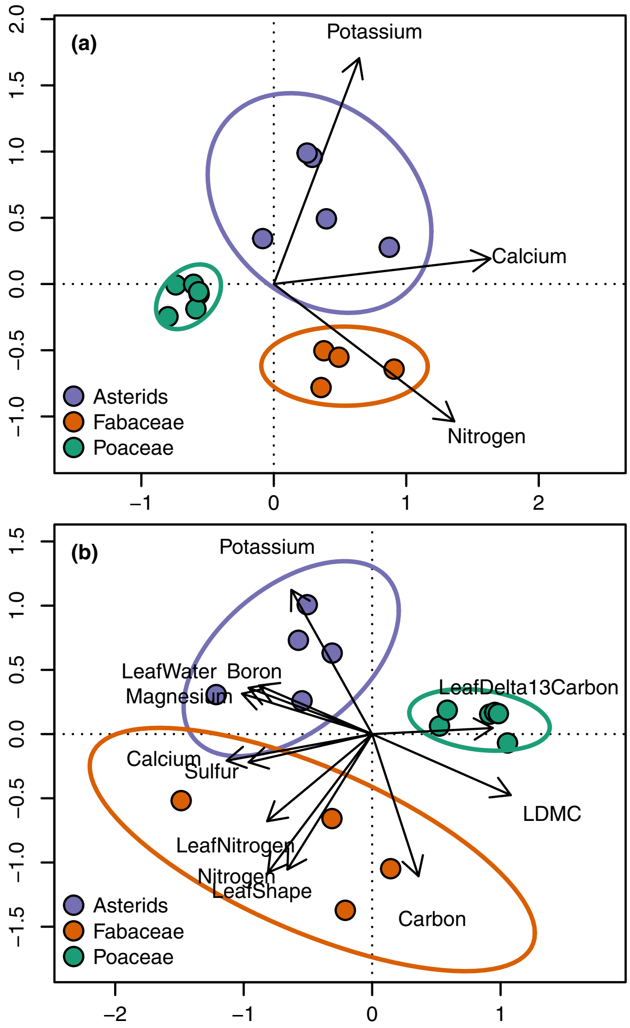

FIGURE 4 Each panel shows results of a principal component analysis (PCA) using standardised mean trait values for the 15 species. Each biplot is scaled symmetrically where each point is the mean value of a species, with a 95% ellipsoid shown for Asterids, Fabaceae and Poaceae. Panel (a) shows a PCA based solely on aboveground tissue %Ca, %N and %K. Panel (b) shows loadings for all 12 significant traits (see Table S3): % aboveground %B, %Ca, %C, %K, %Mg, leaf %N, %N and %S, leaf dry matter content (LDMC), leaf shape, leaf water, leaf delta ^{13}C.

DISCUSSION

Our analyses show that species-specific plant chemical traits, particularly aboveground tissue concentrations of N, Ca, K and B, clustered species into groups highly consistent with their phylogeny. These three functional and phylogenetic clusters were also important determinants of ecosystem productivity in these grasslands. Our comparisons suggest that plant chemical traits were at least as important, and potentially more important, than commonly measured morphological and physiological traits in describing the phylogeny of these species and the productivity of the plot-scale ecosystems that contain various combinations of these species (Fernández-Martínez, 2022;

Kaspari & Powers, 2016; Peñuelas et al., 2019; Sardans et al., 2021; Walker et al., 2022). Our results suggest that chemical trait differences among these grassland species within *Poaceae, Fabaceae*, and the *Asterids* may quantify phylogenetically conserved axes of niche differentiation between these three clades that might structure their local competitive coexistence. If so, we wonder if such tissue chemical differences, and their potential impacts on competitive coexistence, might be a more general feature of these and other plant taxonomic groups and if so, if these chemical trait differences might have persisted during their radiations (Broadley et al., 2004; Neugebauer et al., 2018). Because phylogenetic clusters drawn from chemical traits align with known ecological functional groups, our results help explain the reported ecological effects of phylogenetic diversity (Cadotte, 2017; Cadotte et al., 2009; Cavender-Bares et al., 2021; Davies et al., 2016; Flynn et al., 2011; Schweiger et al., 2018; Srivastava et al., 2012; Steudel et al., 2016).

Cadotte et al. (2009) predicted that phylogenetic distance was an important axis of diversity that could explain ecosystem functioning because it captures traits that might not be measured in a given study, but were still important as latent variables. Here expanding on the common set of functional traits by using a wide-array of chemical, metabolic and morphological traits, we found that it was a combination of chemical traits (Fernández-Martínez, 2022), that best mapped onto phylogenetic distances. For this reason, increasing species richness in this experiment increases both functional and phylogenetic space (Liu et al., 2015).

The three-dimensional trait space defined by the tissue % Ca, % K and % N for the 15 species illuminates plausible multidimensional tradeoffs between the three phylogenetic clusters (Figure 3b), which correspond with traditional grassland functional groups of grasses, legumes and forbs (Tilman, 2001). These trait differences are reminiscent of Hutchinsonian niche hypervolumes (Blonder, 2018; Clark et al., 2018; Holt, 2009; Hutchinson, 1957; Schweiger et al., 2018), with *Poaceae, Fabaceae* and the *Asterids* occupying distinct regions of trait space (Figures 3b and 4a). Perhaps lower tissue concentration of each element in a plant species may be indicative of a lower R* for that nutrient (sensu Tilman, 1982) and thus greater competitive ability for that element (except, of course, for N in *Fabaceae*). If so, chemical trait differences might be a useful proxy to help explain competitive tradeoffs that lead to coexistence (Klausmeier et al., 2020; Kraft et al., 2015; Tilman, 1982).

Because theory suggests that niche differences may explain coexistence and that coexistence can underpin overyielding (Lehman & Tilman, 2000; Vandermeer, 1989), our analyses suggest that increasing species richness with species from distinct functional and phylogenetic clusters may help explain the positive effect of plant biodiversity on productivity (Reich et al., 2012). No single species, or group of functionally similar species, is likely able to drive the full suite of biogeochemical processes that cause an ecosystem to accumulate higher amounts of all the essential elements that underpin soil fertility and primary productivity (Crocker & Major, 1955; Furey & Tilman, 2021; Hobbie, 2015; Jenny, 1958; Tansley, 1935; Vitousek & Reiners, 1975; Zinke, 1962).

A growing body of evidence suggests the ecological importance of interspecific differences in plant chemical traits, including both elemental concentration and secondary metabolites (Aerts & Chapin III, 2000; Bitomský et al., 2023; Fernández-Martínez et al., 2021; Kaspari & Powers, 2016; Mládková et al., 2018; Peñuelas et al., 2019; Reich et al., 2005; Walker et al., 2022; White et al., 2012). The full elemental composition of a plant species has been called its elementome or ionome and is thought to be related to competitive abilities for different nutrients and to function as a biogeochemical niche (Peñuelas et al., 2019; Salt et al., 2008). For example, in the Park Grass Experiment, such chemical differences were associated with plant species abundances and presumed competitive abilities that led to coexistence or displacement in response to different patterns of fertilisation (Lawes et al., 1882; Tilman, 1982; White et al., 2012). In addition, while beyond the scope of our data, the consideration of plant secondary metabolites, for example, the metabolome (Raguso et al., 2015; Walker et al., 2022), may further help to differentiate the trait space elucidating within clade/functional group differences. For example, secondary metabolites within genus *Asclepias* help define both its clade and its functional responses to herbivory (Agrawal et al., 2009). Further studies might benefit from examination of herbivore-relevant chemical elements such as Si (de Tombeur et al., 2023; Schaller et al., 2016) and Na (Borer et al., 2019; Kaspari & Welti, 2023). We believe that our general approach may be insightful in many kinds of ecosystems, but our precise results are of greatest relevance to our experiment, which has low levels of soil N and K, and high levels of soil P (Grigal, 1974), and no large herbivores.

In total, plant chemical traits, specifically tissue elemental concentrations of potentially limiting nutrients, were significantly associated with plant phylogeny and ecosystem productivity in our grassland study. While our small number of species limits any broad evolutionary arguments, we demonstrate that both functional and phylogenetic differences underpinning ecosystem functioning can be described using tissue % Ca, N, K and B (Fernández-Martínez, 2022). These findings lead us to wonder the extent to which plant species in tropical, temperate and boreal forests, deserts and other grasslands might be similarly differentiated (Bitomský et al., 2023; Fernández-Martínez et al., 2021; Kaspari et al., 2021; Mládková et al., 2018; Neugebauer et al., 2020; Sardans et al., 2015, 2021; White et al., 2012). Might plant tissue ratios beyond solely N and P, but including K, Ca and/or B and Si be as insightful in terrestrial ecosystems as have been Redfield (1934) C:N:P ratios in aquatic ecosystems?

If so, it would be interesting to know the ecological consequences of how chemical traits, plant stoichiometry and secondary metabolites covary along known tradeoff axes of leaf and whole plant physiology (e.g. Carmona et al., 2021; Raguso et al., 2015; Reich, 2014; Sterner & Elser, 2002; Walker et al., 2022). More studies will be needed to determine if, in general, plant chemical traits may be more likely to be phylogenetically conserved than other types of traits and if they capture functional clusters important for understanding how biodiversity regulates ecosystem processes. Our results suggest that plant chemical traits merit more attention than they have received to date and may illuminate recent debates in the literature on the merits of functional traits in driving ecosystem functioning (Chacón-Labella et al., 2023; Hagan et al., 2023; van der Plas et al., 2020, 2023).

AUTHOR CONTRIBUTIONS

D.T. designed and managed the experiment and supervised data collection. G.N.F. formulated the research questions and collected additional data. G.N.F. is responsible for data preparation and statistical analyses in R. G.N.F. and D.T. wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The R code to reproduce the analyses, along with all the original and derived summary data, are archived on Zenodo via github (https://doi.org/10.5281/zenodo.7834892). The original data can be found on the Environmental Data Initiative (Furey & Tilman, 2023; Tilman, 2018, 2021) and the TRY plant trait database (Kattge et al., 2020) along with according data use policies of the respective organisations.

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SUPPORTING INFORMATION

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

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