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RESEARCH ARTICLE

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Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants

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Abstract

1. Correlations among plant traits often reflect important trade-offs or allometric relationships in biological functions like carbon gain, support, water uptake, and reproduction that are associated with different plant organs. Whether trait correlations can be aggregated to "spectra" or "leading dimensions," whether these dimensions are consistent across plant organs, spatial scale, and growth forms are still open questions.
2. To illustrate the current state of knowledge, we constructed a network of published trait correlations associated with the "leaf economics spectrum," "biomass allocation dimension," "seed dimension," and carbon and nitrogen concentrations. This literature-based network was compared to a network based on a dataset of 23 traits from 2,530 individuals of 126 plant species from 381 plots in Northwest Europe.
3. The observed network comprised more significant correlations than the literature-based network. Network centrality measures showed that size traits such as the mass of leaf, stem, below-ground, and reproductive tissues and plant height were the most central traits in the network, confirming the importance of allometric relationships in herbaceous plants. Stem mass and stem-specific length were "hub" traits correlated with most traits. Environmental selection of hub traits may affect the whole phenotype. In contrast to the literature-based network, SLA and leaf N were of minor importance. Based on cluster analysis and subsequent PCAs of the resulting trait clusters, we found a "size" module, a "seed" module, two modules representing C and N concentrations in plant organs, and a "partitioning" module representing organ mass fractions. A module representing the plant economics spectrum did not emerge.
4. *Synthesis*. Although we found support for several trait dimensions, the observed trait network deviated significantly from current knowledge, suggesting that

previous studies have overlooked trait coordination at the whole-plant level. Furthermore, network analysis suggests that stem traits have a stronger regulatory role in herbaceous plants than leaf traits.

KEYWORDS
allometry, biomass allocation, leaf economics spectrum, network centrality, plant development and life-history traits, stoichiometry, trait dimensions

1 | INTRODUCTION

Plant organs perform different functions: roots take up resources from the soil and anchor the plants, rhizomes ensure resource storage and vegetative regeneration, stems provide support and hydraulic pathways, leaves gain carbon via photosynthesis, and seeds provide generative reproduction. Plants adjust allocation of carbon and nutrients between their organs so that these functions ensure the persistence of the species in their particular habitat (Luo et al., 2017; Minden & Kleyer, 2014). Plant traits such as organ mass, form, density, surface area, volume, and chemical composition, among others, may reflect this coordinated allocation (Kleyer & Minden, 2015; Kramer-Walter & Laughlin, 2017). Coordination among traits is often expressed by positive and negative correlations, representing trade-offs and allometries based on biomechanical and physiological requirements in response to environmental conditions (Freschet, Kichenin, & Wardle, 2015; Stearns, 1989).

With increasing numbers of traits published (see try-db.org), ecologists have striven to reduce the linkages among multiple traits to a few axes of variation, "spectra," or "leading dimensions," reflecting major ecological strategies of plant life (Diaz et al., 2004; Grime et al., 1997; Laughlin, 2014; Westoby, Falster, Moles, Vesk, & Wright, 2002). It is a long-standing research agenda to elucidate whether leading trait dimensions are themselves coupled or decoupled (Laughlin, 2014). For instance, Westoby (1998) proposed that SLA, plant height, and seed size represent independent axes of plant specialization in different environments. Since then, knowledge concerning correlations among traits and their functional significance has greatly advanced (e.g., Reich et al., 2003; Shipley et al., 2016). However, several aspects remain understudied. First, many studies are restricted to the trait relationships within a leading dimension, not across dimensions (see below). Second, many studies cover traits of only one or two plant organs, such as leaves and stems or seeds, thus preventing a whole plant perspective on functional ecology (Kleyer & Minden, 2015). Third, it is not clear whether dimensions or spectra found on a global scale are reproducible at smaller scales or in specific growth forms (Messier, Lechowicz, McGill, Violle, & Enquist, 2017; Poorter, Lambers, & Evans, 2014). A better understanding of trait correlations and the interplay between leading dimensions is fundamental to predict plant responses to environmental change.

In this study, we examine the correlation patterns of leaf, stem, root, and seed traits of herbaceous plants occurring in temperate Northwest Europe, asking whether well-known leading dimensions can be found in this growth form and at this scale. We consider the plant economics spectrum (PES), the biomass allocation dimension, the seed dimension, and the distribution of carbon and nitrogen in plant organs. Trait correlations leading to each of these dimensions have received considerable attention, but few studies addressed the overlap between these dimensions.

1.1 | Leaf economics spectrum

The leaf economics spectrum (LES) describes a positive relationship between leaf nitrogen concentration, maximum photosynthetic capacity, and SLA, which are all negatively related to leaf life span (Shipley, Lechowicz, Wright, & Reich, 2006; Wright et al., 2004). Short leaf life span requires rapid growth of new leaves and acquisition of resources, whereas persisting leaves allow slower growth and conservation of resources. There is some evidence for a corresponding root economics spectrum (RES) in non-woody species. Roumet et al. (2016) found that specific root length (SRL, the length of a root divided by its dry mass) was positively correlated to both root nitrogen concentration and root respiration, considered as acquisitive traits, and negatively correlated to root C:N and to root dry matter content, considered as conservative traits. Freschet, Cornelissen, van Logtestijn, and Aerts (2010) and Reich (2014) proposed that the LES might be expanded to a whole PES.

1.2 | Biomass allocation dimension

The capacity for light pre-emption and soil resource acquisition depends on the allocation of biomass to leaves, stems, roots, and rhizomes (Grime, 1979; Moles et al., 2009; Westoby et al., 2002). Allometric scaling suggests that biomasses of leaves, stems, and roots increase proportionally from small to large plants, but the existence of a fixed allometric exponent is contentious (Poorter et al., 2015). Nevertheless, strong positive correlations between the biomass of leaves, stems, and roots were often found (e.g., Minden & Kleyer, 2011) and plant biomass is associated with other size traits such as plant canopy height and leaf area (Garnier, Navas, & Grigulis, 2016).

The "partitioning" perspective on biomass allocation among organs emphasizes size-independent ratios such as mass fractions, that is, the biomass of a single organ divided by the biomass of the total plant (Poorter & Sack, 2012). With increasing plant height or total biomass, plants increase stem mass fraction (SMF) at the expense of

leaf mass fraction (LMF) and, to a lesser extent, root mass fraction (RMF; Poorter et al., 2012). This suggests a positive relationship of plant height with SMF, a negative one with LMF, and almost no relationship with RMF.

1.3 | Element concentrations

Due to their specific functions, leaves, roots, stems, and seeds exhibit different element concentrations and ratios (Agren, 2008). Supportive stems display higher C:N ratios than "metabolic" organs such as leaves (Kerkhoff, Fagan, Elser, & Enquist, 2006). Global datasets display strong interspecific differences in nutrient concentrations of leaves, depending on growth rate, size, and life span (Kattge et al., 2011; Niklas, Owens, Reich, & Cobb, 2005; Wright et al., 2004). On the other hand, carbon content is seen as highly conserved across many plant taxa (Knecht & Göransson, 2004). Some studies revealed positive correlations between element concentrations of leaves, stems, and roots (Kerkhoff et al., 2006; Minden & Kleyer, 2014). A study in a subarctic flora showed that carbon content strongly correlates among leaves, stems, and roots, whereas their nitrogen concentrations are only moderately correlated (Freschet et al., 2010). Other studies found a negative relationship between leaf- and root nitrogen content (Li & Bao, 2015).

1.4 | Seed dimension

A given amount of resources may either be allocated to many small or few large seeds, resulting in a trade-off between seed size and number (Thompson, Bakker, Bekker, & Hodgson, 1998). Large seeds facilitate seedling growth in shade (Leishman & Westoby, 1994), whereas small seeds facilitate the formation of soil seed banks (Thompson, Bakker, & Bekker, 1997). A higher seed number may increase the chance of colonization even if the dispersal range is limited (Grashof-Bokdam & Geertsema, 1998).

1.5 | Trait covariation across leading dimensions

By definition, trait correlations within leading dimensions should be stronger than between leading dimensions (Klingenberg, 2008). Thus, relationships between biological functions such as growth, maintenance, dispersal, and regeneration may be weaker than within these functions (Murren, 2002). Relationships between LES traits and size traits may be weaker than between traits of the biomass-allocation dimension or between organ element concentrations (Poorter et al., 2012). On the other hand, traits may not be completely uncoupled from each other, because functions associated with one dimension may be intricately linked to the functions of other dimensions. For instance, the relationship between height, a size trait, and stem density, a plant economics trait, should be indirectly determined by critical buckling height, canopy weight and avoidance of cavitation (Niklas, 1994). Empirical studies investigating covariation among traits from two or more of the dimensions mentioned above had mixed results. For instance, Baraloto et al. (2010) found that traits associated with the leaf economics spectrum were uncoupled from those associated with a stem economics spectrum. Price et al. (2014) found almost no relation between plant height and leaf traits, apart from leaf area. On the other hand, Reich (2014) gathered much evidence supporting phenotypic integration of leaf, stem, and root traits associated with nutrient and carbon acquisition. Díaz et al. (2016) showed that size traits (plant height, diaspore mass, leaf area) and PES traits (leaf mass per area, leaf nitrogen content, stem specific density) are correlated on a global scale, thereby constraining the potential trait space towards a relatively small set of successful trait combinations.

1.6 | Correlation networks

The notion of complex networks, that is, sets of nodes that are connected by edges, plays an increasing role in ecology (Cohen & Havlin, 2010; Proulx, Promislow, & Phillips, 2005). Correlations among multiple traits can be represented as a trait network, where the traits correspond to the network nodes and highly correlated traits correspond to edges, the connections of the network. Because edges are based on correlations, not effects, they are undirected, and can be weighted according to correlation strength. Given a trait network, the relevance of specific traits can be identified by their topological position in the network and be described by centrality measures such as the number of connections leading to a trait (the degree; Figure 1a) and the position of a trait between several subnetworks (the betweenness centrality; Figure 1b; Proulx et al., 2005). Hub traits with a large number of connections to other traits have strong effects on the plant phenotype as a whole. Trait subnetworks or "modules" with

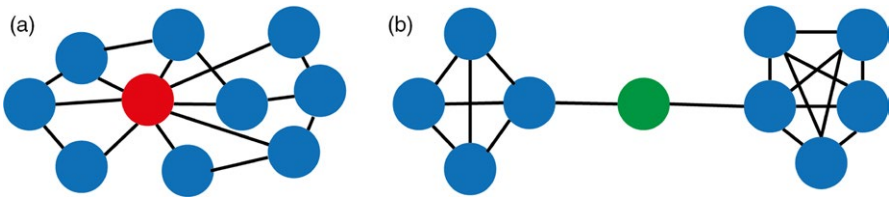

FIGURE 1 Network concepts applied to examine correlations among multiple traits. Here, the circles represent nodes in hypothetical networks and correspond to plant traits. The edges depict connections between correlated traits. (a) "Hub" traits (red circle) interact with many other traits, have a high degree, and likely play central regulatory roles that affect the whole phenotype. (b) Traits with high betweenness (green circle) likely coordinate several subnetworks. [Colour figure can be viewed at wileyonlinelibrary.com]

a high number of intragroup connections and very few connections to other traits in the network may indicate the formation of independent dimensions (Cohen & Havlin, 2010). Correlation networks are increasingly being used in biology and social sciences to capture large, high-dimensional datasets (Mantegna, 1999; Villa-Vialaneix et al., 2013; Zhang & Horvath, 2005), but despite the elegance of this approach, we know of only a few studies that applied network theory to trait correlations (de la Riva, Olmo, Poorter, Ubera, & Villar, 2016; Mason & Donovan, 2015; Messier et al., 2017; Poorter et al., 2014; Poorter, Anten, & Marcelis, 2013).

To illustrate the available knowledge, we started our analysis by assembling published trait correlations into a network, focusing on traits of herbaceous plants. The traits encompass those highlighted in the leaf economics spectrum, the biomass allocation, and seed dimension, as well as the elemental composition of all relevant plant organs. This literature-based trait correlation network was then compared with a correlation network based on observed values of herbaceous plants. The observed network consists of a large trait dataset of plants collected from diverse habitats in northwest Europe. Most traits were measured on the same individual, which we consider a prerequisite to interpret their correlations in terms of trade-offs or allometries.

Using the literature-based network as a baseline, we asked whether (a) the observed network differs from the literature-based network; (b) the dimensions could be reproduced in herbaceous species; (c) if so, whether dimensions are consistent across leaves, stems, and below-ground organs although the functions of these organs are different; and (d) which traits are hub traits. To compare our results with the dimensions described above, we decomposed the network into trait modules, each comprising highly correlated traits. Modules are conceptually similar to leading dimensions but based exclusively on observed correlations.

2 | MATERIALS AND METHODS

2.1 | The literature-based network

We compiled a matrix of trait–trait relationships reported in the literature, focusing on the number of known relationships. To cover all possible combinations of the 21 traits considered (see below), we searched the Web of Science and own libraries using the traits as key-words. Studies dealing exclusively with single species, mature woody species or cultivated plants were omitted. The search yielded 45 bivariate relationships reported in one or more studies. Because it was a presence-only matrix, we selected one or two exemplary studies as references for a reported relationship, resulting in 27 studies altogether (Supporting Information Table S2.1). When several studies reported similar relationships between two traits, we selected one of the earliest or most comprehensive studies in terms of spatial scale and number of species. Most of them pertain to herbaceous species, but their geographical distribution was not limited to Northwest Europe (Supporting Information Table S2.1). Consequently, the studies covered different species and different environments. The direction of the reported correlation was included as additional information but did not influence the network calculation. When several studies reported opposing directions for a given relationship, we considered the most frequently reported direction. Cases with equal numbers of studies reporting positive and negative directions for the same trait combination did not occur.

2.2 | Sites, species selection, and trait measurements for the network of observed trait correlations

The study sites comprised dry semi-natural grasslands, heaths, mesic and wet pastures and meadows, reeds, and saltmarshes,

TABLE 1 Description of study sites with location (Lat: latitude, Lon: longitude), mean annual temperature (MAT), mean annual rainfall (MAR), and main plant communities

Location	Lat.	Lon	MAT (°C)	MAR (mm)	Number of plots	Main plant communities
Swabian Alb, DE	48°24'	9°36'	8.8	921	8	Calcareous, dry semi-natural grasslands
Basel, CH	47°35'	7°35'	10.0	778	18	Dry ruderal grasslands
Cloppenburg, DE	52°55'	7°55'	8.6	799	20	Pastures, heathlands
Western Pommerania, DE	54°20'	12°42'	8.2	553	48	Fens, wet and mesic pastures
Müritz, DE	53°19'	12°45'	8.1	568	28	Fens, wet and mesic pastures, dry acidic grasslands
Aarhus, DK	56°10'	10°41'	7.8	605	44	Salt marsh, dry coastal grasslands, wet and mesic pastures
Zeeland, NL	51°28'	3°41'	10.1	733	39	Salt marsh, reeds, wet and mesic pastures
East Frisia, DE	53°24'	7°06'	8.8	786	183	Salt marsh, reeds, wet and mesic pastures

geographically ranging from Switzerland to Germany, The Netherlands and Denmark (Table 1). Herbaceous understorey plants of forests were not included in the dataset. Consequently, trade-offs due to light limitation may be underrepresented in this study.

Several plots were established at each location (see Table 1). The vegetation was either recorded in 1-m^2 plots with frequency counts, or in 25-m^2 plots with abundance estimations using the Braun–Blanquet scale (Braun-Blanquet, 1964). From the species list in the vegetation tables, we selected the most abundant herbaceous species that collectively added up to *c.* 80% of the plot biomass (Garnier et al., 2007). To collect their traits, 6–10 individuals of these species were dug out from different plots to account for intraspecific variability. We aimed at collecting size, area, density, and mass traits (Table 2) from all organs of each individual, that is, seeds, leaves, stems, roots, and rhizomes (when applicable). Altogether, we collected 23 different traits from 2,530 plant individuals on 381 plots. For 550 individuals, we obtained a full trait matrix. The traits of the remaining individuals had missing values. Trait data of individuals were averaged at the species level, resulting in a full matrix comprising 126 herbaceous species and 23 traits. Of the 126 species, 11 were annuals. For the detailed trait collection and measurement protocol, see Supporting Information S1.

2.3 | Statistical analysis

Most statistical analyses were conducted in R version 3.3.3 (R Development Core Team, 2011). To account for non-normality, biomass data were log-transformed, biomass fractions were logit-transformed (Warton & Hui, 2011), and other traits were either box-cox or log-transformed, based on the results of a Shapiro–Wilk normality test (Table 2).

2.4 | Phylogeny

To account for the phylogenetic relationship between species, we used Daphne, a dated phylogenetic tree comprising 4,685 species

TABLE 2 Plant traits and their units, identifiers, means, minimum and maximum values, and transformations. Identifiers refer to the Thesaurus of Plant Characteristics for Ecology and Evolution (https://top-thesaurus.org/home, Garnier et al., 2017). This resource provides general trait definitions. For trait collection and measurement standards, see Supporting Information Appendix S1. NA, not available

Trait	Abbreviation	Unit	Trait Identifier	Mean	Maximum	Minimum	Transformation
Seed number	SN	*n*	NA	4,144	141,812	0	log
Seed mass	SM	mg	TOP112	1.50	30.67	0.01	log
Reproductive mass	RepM	mg	NA	953.54	26,935.38	0.18	log
Onset of seed ripening	ONSET	Julian day	TOP293	195.26	268.17	146	—
Leaf area	LA	mm^2	TOP25	754.89	6,910.80	2.69	box-cox
Specific leaf area	SLA	mm^2/mg	TOP50	23.13	73.83	6.35	box-cox
Leaf dry matter content	LDMC	mg/g	TOP45	250.68	618.83	51.10	box-cox
Specific stem length	SSL	mm/mg	NA	3.44	20.93	0.32	box-cox
Specific root length	SRL	mm/mg	TOP935	33.58	1,112.26	0.38	box-cox
Plant leaf dry mass	LBM	mg	TOP76	599.88	5,471.10	2.50	log
Plant stem dry mass	SBM	mg	NA	1,307.42	17,259.26	18.19	log
Plant root and rhizome dry mass	BIBM	mg	NA	1,171.66	24,798.98	14.96	log
Plant height vegetative	PCH	cm	TOP69	36.95	151.61	0.50	box-cox
Leaf carbon concentration per mass	LCC	%	TOP452	44.16	68.64	28.39	logit
Leaf nitrogen concentration per mass	LNC	%	TOP462	1.90	4.07	0.59	logit
Stem carbon concentration per mass	SCC	%	TOP491	44.92	53.45	29.79	logit
Stem nitrogen concentration per mass	SNC	%	TOP501	0.93	2.29	0.21	logit
Root carbon concentration per mass	RCC	%	TOP713	44.37	57.96	33.67	logit
Root nitrogen concentration per mass	RNC	%	TOP723	1.08	3.03	0.43	logit
Leaf mass fraction	LMF	Proportion	NA	0.23	0.61	0.01	logit
Stem mass fraction	SMF	Proportion	NA	0.43	0.84	0.04	logit
Below-ground mass fraction	BIMF	Proportion	NA	0.34	0.90	0.03	logit

of the northwest European flora (Durka & Michalski, 2012). This tree was pruned to the species in our dataset using the R function treedata (in geiger; Pennell et al., 2014; Supporting Information Figure S3.1). First, we calculated Blomberg's K (Blomberg, Garland, Ives, & Crespi, 2003) to assess the phylogenetic signal in each trait (multiPhylosignal in picante; Kembel, 2010) and Pagel's λ (fitContinuous in Geiger; Pennell et al., 2014). Both statistics compare the observed signal in a trait to a signal under a Brownian Motion model of trait evolution. Values close to 1 indicate a strong phylogenetic signal (Münkemüller et al., 2012). Subsequently, we calculated phylogenetically corrected trait correlations using phylogenetic GLM (pgls in caper; Freckleton, Harvey, & Pagel, 2002). The resulting phylogenetically corrected correlation matrix was compared to an uncorrected Pearson correlation matrix using a Mantel test to assess the effect of the phylogenetic signal on the trait correlations.

2.5 | Network analysis

To calculate the observed trait correlation network, we used significant Pearson correlations. A threshold of $r > 0.2$ marked pairwise correlations that were significant at $p < 0.05$. All correlations below this threshold were set to zero, yielding the adjacency matrix $A = [a_{i,j}]$ with $a_{i,j} \in [0,1]$. Additionally, network connections between any pair of traits are weighted by the absolute correlation strength, $|r_{ij}|$ (adjacency in WGCNA; Langfelder & Horvath, 2008). For the literature-based adjacency matrix, we could not use Pearson correlations because different metrics and procedures were used in the 27 studies, ranging from bivariate correlations and principal components analyses to regression techniques and structural equation models (Supporting Information Table S2.1). Therefore, a value of ±1.0 was assigned when a source reported any positive or negative relationship between two traits and 0.0 for no relationship found in the literature. Because all relationships were either set to ±1.0 or 0.0, the resulting literature-based network is unweighted, that is, only shows presences and absences of connections. Both networks were visualized in Cytoscape 3.4.0, using the preinstalled Prefuse Force Directed OpenCL layout (www.prefuse.org).

To compute centrality measures, we used CentiScaPe 2.2 as a Cytoscape plugin (Scardoni, Petterlini, & Laudanna, 2009). We report the weighted degree and betweenness centrality for each trait (Figure 1). The weighted degree C_D of a trait t is determined as the sum of the weights, i.e., the absolute value of correlation strength $|r_{ts}|$, over all neighbours s of trait t in the network.

$$C_D(t) = \sum_{s=1}^{n} |r_{ts}| a_{ts}, \tag{1}$$

where n is the total number of traits (Dong & Horvath, 2007). Betweenness C_B of a focal trait t is computed as the normalized number of all shortest paths in the weighted network between pairs of traits that include the focal trait.

$$C_B(t) = \sum\nolimits_{s \neq t \neq u} \frac{p(s,t,u)}{p(s,u)}. \tag{2}$$

Here, $p(s,u)$ is the total number of shortest paths from node s to node u and $p(s,t,u)$ is the number of those paths that pass through t. A path is a sequence of traits each connected by edges with the next. The shortest path from node s to node u is the path for which the weighted network distance is minimized.

$$dist(s,u) = \min\left(\frac{1}{|r_{sh}|} + \cdots + \frac{1}{|r_{hu}|}\right). \tag{3}$$

Here, the sum runs over all connections along a path, each connection is weighted by the inverse of the absolute correlation of traits, and the minimum is taken over all possible paths connecting nodes node s and u. A trait with high betweenness joins many other trait pairs and thus controls interactions between subnetworks or modules globally, that is on larger distances, in the network.

In a second step, we decomposed the observed network into subnetworks of several strongly correlated traits, following recent approaches in gene co-expression network analysis (Villa-Vialaneix et al., 2013). We transformed the adjacency matrix (A) into a distance matrix $D = 1 - A$ and used average linkage hierarchical clustering to detect trait clusters of highly correlated traits (hclust in stats). Optimal cluster size was determined with function cutreeDynamic in dynamicTreeCut (Langfelder & Horvath, 2016). The traits belonging to a given cluster were then aggregated using a principal components analysis to yield trait modules. The module values were the scores of the first PCA axis. Trait modules correspond to trait dimensions, but are based on observed correlations, rather than concepts. To provide an alternative approach with network modularization methods, we also used ModuLand 2.0 as CytoScape plugin (Szalay-Bekő et al., 2012) to determine modules. ModuLand uses the LinkLand influence zone determination method and the ProportionalHill module assignment method (Kovács, Palotai, Szalay, & Csermely, 2010). Instead of the LinkLand centrality calculation, we used the correlation strengths as weights for module assignments.

3 | RESULTS

3.1 | Variation and phylogenetic signal in the observed trait dataset

Trait values showed large variation (Table 2), reflecting the large variation in environmental conditions of the plots where we sampled the individuals. The means and ranges for SLA, leaf nitrogen content (LNC), plant canopy height (PCH), and seed mass (SM) were similar to the values of herbaceous plants in the global TRY trait database (Kattge et al., 2011). The phylogenetic signal was weak in almost all traits despite being non-random in most of them (Supporting Information Table S2.2). The results from the phylogenetically corrected correlation analysis did not differ significantly from the uncorrected analysis (Mantel test $r_M = 0.995$, $p = 0.001$; see Messier et al., 2017 for similar results). We therefore used the uncorrected correlation table for further analyses. The low phylogenetic signal was probably dependent on the grassland species investigated in this study. More than half of all species belonged

to a few large families, such as Poaceae, Cyperaceae, Juncaceae, Asteraceae, and Ranunculaceae, known for strong intrafamily variation in traits and ecological specialization (Supporting Information Figure S3.1).

3.2 | The observed network versus the literature-based network

In the literature-based network (Figure 2), the traits exhibiting the highest connectedness were SLA and PCH, followed by SRL, stem mass (SBM), leaf *N* (LNC), leaf dry matter content (LDMC), and leaf C (LCC). These traits also exhibited a high betweenness, by connecting other groups of traits belonging to the biomass, stoichiometry, or seed dimension.

The observed trait network displayed more and other connections than the literature-based network (Figure 3). In addition, the hub traits were different. The most connected, most central traits were stem mass (SBM), stem specific length (SSL), leaf mass (LBM), below-ground mass (BIBM), PCH, and reproductive mass (RepM) (Figure 3, Supporting Information Table S2.3). These central traits were also connected to leaf economics and seed traits, as well as to PCH and leaf area (LA). Below-ground mass fraction (BIMF) showed the highest betweenness, connecting a root, stem, and leaf carbon subnetwork with the central network and, via stem mass fraction (SMF), with the stem, leaf, and root nitrogen subnetwork. In contrast to the literature-based network, the centrality of SLA was relatively minor. Altogether, 26 edges in the literature-based network were confirmed by our observations, 20 did not exceed a correlation of $r = 0.3$, and 39 edges were new and not present in the literature-based network (Supporting Information Table S2.4).

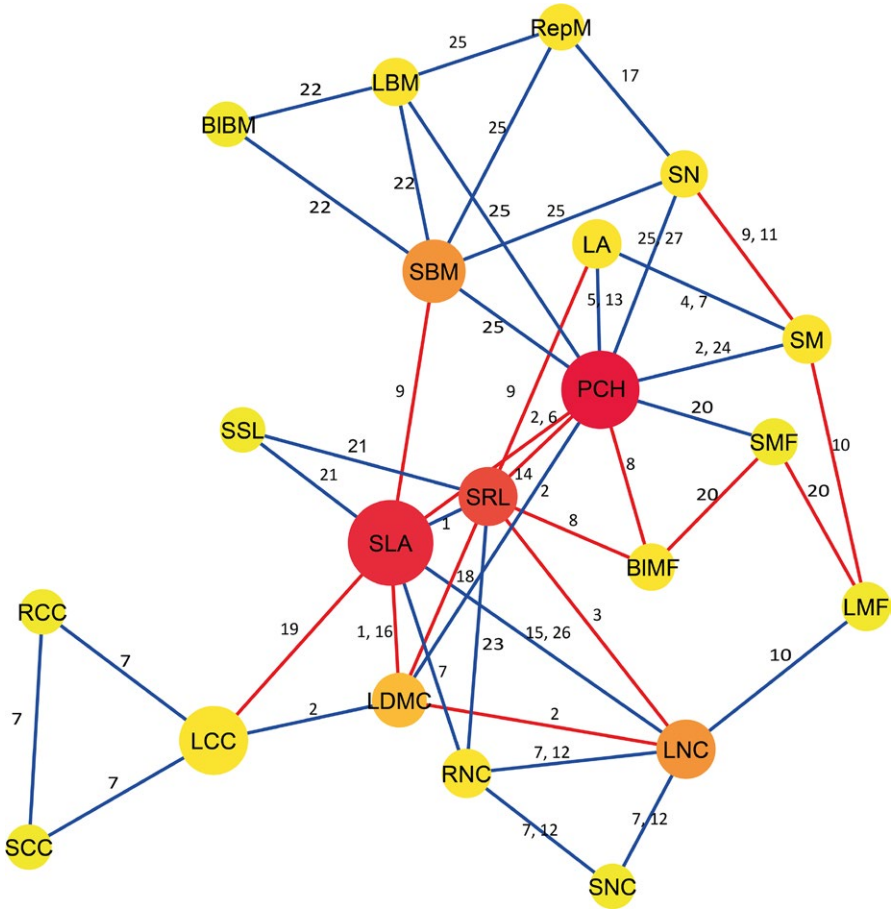

FIGURE 2 Trait correlation network based on literature sources. Node colours from yellow to red illustrate increasing degree, whereas node size shows betweenness. Blue and red edges represent positive and negative correlations, respectively. For trait abbreviations, see Table 2. Numbers indicate references: 1—Craine et al. (2001); 2—de Bello et al. (2012); 3—de Vries and Bardgett (2016); 4—Diaz et al. (2004); 5—Díaz et al. (2016); 6—Fonseca, Overton, Collins, and Westoby (2000); 7—Freschet et al. (2010); 8—Funk and Wolf (2016); 9—Garnier and Navas (2012); 10—Grime et al. (1997); 11—Jakobsson and Eriksson (2003); 12—Kerkhoff et al. (2006); 13—Laliberté, Shipley, Norton, and Scott (2012); 14—Laughlin, Leppert, Moore, and Sieg (2010); 15—Lavorel et al. (2007); 16—Lienin and Kleyer (2011); 17—Pierce et al. (2014); 18—Garnier et al. (2016); 19—Poorter, Niinemets, Poorter, Wright, and Villar (2009); 20—Poorter et al. (2012); 21—Bloor and Grubb (2003); 22—Poorter et al. (2015); 23—Roumet et al. (2016); 24—Leishman, Westoby, and Jurado (1995); 25—Vile, Shipley, and Garnier (2006); 26—Wright et al. (2004); 27—Moles and Leishman (2008). [Colour figure can be viewed at wileyonlinelibrary.com]

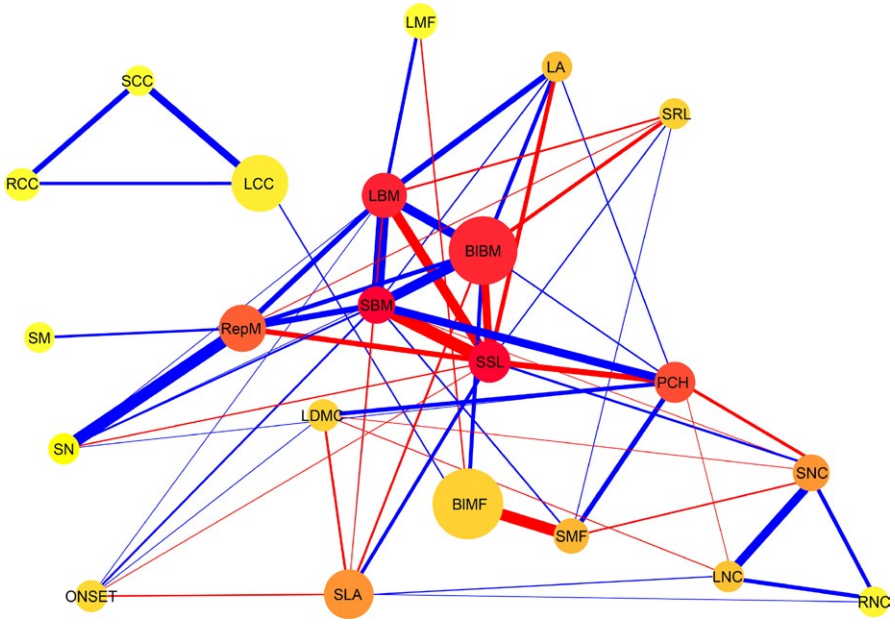

FIGURE 3 The observed network. Red and blue edges show negative and positive correlations, respectively. Correlation strength (0.3–0.8) is shown by line thickness and distance among traits. Node colours from yellow to red illustrate increasing degree, whereas node size shows betweenness. Trait abbreviations see Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Trait modules and trait dimensions

A cluster analysis decomposed the network into seven clusters of strongly correlated traits (Figure 4, Table 3). LA, SSL, SRL, LBM, SBM, and BIBM were grouped to a "size" cluster. The scores of first PCA axis of these traits represent the size module. Seed number (SN), SM, and RepM formed a "seed" cluster, albeit with strong connections to the size module (Table 3). Carbon and nitrogen concentrations of leaves, stems, and below-ground organs formed the clusters "C" and "N." Likewise, the fractions of leaf, stem, and below-ground biomasses formed a single cluster here called "fractions." LDMC and PCH as well as SLA and ONSET were grouped into two clusters named "height" and "SLA." The corresponding modules were also correlated with the traits of the "size" and "N" clusters (Table 3, Figure 3). An alternative approach using modularization techniques yielded a large module composed of the size, seed, height, and SLA clusters (Supporting Information Figure S3.3). Three other modules were similar to the fractions, C, and N clusters.

Within the size module, bivariate relationships of LBM, SBM, and BIBM were close to isometry, whereas RepM versus LBM, SBM, and BIBM followed a 2/3 power law (Supporting Information Table S2.5, Supporting Information Figure S3.4). Carbon and nitrogen concentrations of leaves, stems, and roots also scaled close to isometry, except for carbon relations of stems with roots and leaves.

4 | DISCUSSION

Correlations between traits assumed to belong to different leading dimensions were much stronger and more numerous than previously reported. Our results support the view that the traits of any plant organ are constrained by the resources allocated to the other plant organs, and that plant size, plant economics, plant regeneration, and elemental concentrations are to some extent all coordinated. Furthermore, some traits have a central regulatory position in the network. When these hub traits change, they will influence many other traits or, if characterized by a high betweenness, several subnetworks. Despite the loose discrimination of leading dimensions, some dimensions emerged from our analyses, such as the biomass allocation dimension and the elemental concentrations.

4.1 | The observed network differs from the literature-based network

The literature-based network reflects the emphasis placed on plant canopy height and the LES traits in current functional plant ecology. Surprisingly, other traits were of central importance in the observed trait network, where the centre was formed by the tight coordination of leaf, stem, below-ground and reproductive biomass, closely associated with specific stem and root length. These traits held the largest number of connections in the network. Hence, an environmental factor such as mowing frequency selecting on stem biomass will likely affect multiple other traits, thus changing the plant phenotype as a whole. Conversely, a factor selecting on seed mass should not change the entire phenotype. The relationships between root, leaf, and stem mass indicated isometry rather than scaling to the three-quarter power known from woody species (Enquist & Niklas, 2002; Minden & Kleyer, 2011; Niklas, 2006; Poorter et al., 2012). Reproductive mass scaled close to the three-quarters power with the masses of all vegetative organs, meaning that an increase in vegetative mass was accompanied by a smaller increase in reproductive mass, probably as a result of expenses in structural tissue (Weiner, Campbell, Pino, & Echarte, 2009).

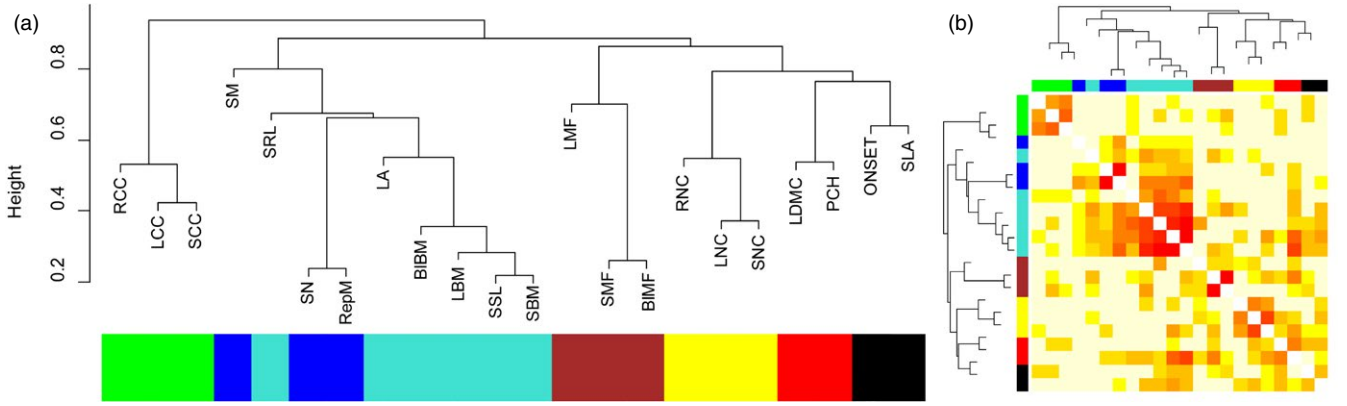

FIGURE 4 Trait correlation dendrogram (left) and heatmap (right). The coloured bar below the dendrogram represents the seven trait modules (turquoise: "size"; blue: "seed"; brown: "fractions"; yellow: "N"; green: "C"; red: "height"; black: "SLA"). The heatmap shows the correlation strength, increasing from light yellow to red [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Pearson correlations of traits with module scores, that is, the scores of the 1st PCA axes of each trait cluster (only significant correlations at $p < 0.05$ are shown, coloured cells indicate module affiliation as in Figure 4, trait abbreviations as in Table 1). LMF did not correlate and SM only marginally correlated with the 1st axis of their respective module. These traits correlated with the 2nd PCA axis [Colour table can be viewed at wileyonlinelibrary.com]

Traits	Size	Seed	Fractions	N	C	Height	SLA
Explained variance by 1st PCA axes	0.60	0.59	0.58	0.68	0.67	0.78	0.68
LA	0.63				−0.26	0.20	
SSL	−0.86	−0.48	−0.20	0.33	0.21	−0.44	0.47
RSL	−0.53	−0.33	0.31				
LBM	0.88	0.47			−0.20	0.19	−0.41
SBM	0.87	0.51	0.35	−0.24	−0.22	0.47	−0.43
BIBM	0.83	0.44	−0.40			0.27	−0.31
SN	0.36	0.88		−0.26		0.19	
SM	0.28	0.22					
RepM	0.55	0.98				0.19	−0.21
LMF				0.26		−0.29	
SMF			0.92	−0.24	−0.22	0.45	
BIMF			−0.94		0.31		
LNC				0.86		−0.38	0.30
SNCt	−0.23	−0.24	−0.28	0.85		−0.42	0.28
RNC	−0.22			0.75			
LCC			−0.32		0.82		0.24
SCC			−0.20		0.86		
RCC			−0.20		0.78		0.26
LDMC				−0.33	0.21	0.85	−0.44
PCH	0.50	0.33	0.37	−0.35		0.85	−0.25
ONSET	0.26		0.28		−0.27	0.31	−0.82
SLA	−0.40	−0.26		0.36		−0.35	0.82

Mass fractions were not strongly connected in the network, except the below-ground mass fraction that connects the leaf, stem and root carbon subnetwork with the central isometric network of stem, leaf, and below-ground mass. In particular, we did not find a negative relationship between stem and leaf mass fraction, as suggested by Poorter et al. (2012), whereas stem mass fraction was strongly negatively correlated with below-ground mass fraction.

SSL was the hub trait with the second highest connectivity in the network, in contrast to its low importance in the literature-based

network. Any increase in plant biomass was associated with a decrease in SSL, because of the increasing structural resources necessary to ensure the stability of a larger stem. Herbaceous plants do not have secondary growth, making SSL a suitable indicator of the trade-off between stem length and stability. SSL and specific stem density can both be seen as proxies for biomechanical stability, construction costs, pace of vertical expansion, and hydraulic safety (Pérez-Harguindeguy et al., 2013; Poorter et al., 2012). Replacing thin-walled stem tissue by dense, lignified tissue allows plants to increase in height before collapsing under their own weight (Niklas, 1994). Buckling risk depends on stem density, elasticity, and diameter (McMahon, 1973). Because of biomass investments to avoid buckling, increasing canopy height required a much larger increase in stem mass (RMA regression: SBM–PCH, log-transformed, slope 0.63, intercept −0.25, $r = 0.55$). SSL also had connections to traits of all other dimensions, showing that the trade-off between stem expansion and stability affects many other functions related to carbon gain, nutrient acquisition, growth, and reproduction. Although it is a rather easy trait to measure in herbaceous plants, SSL is still rarely used in functional trait analysis.

Like SSL, SRL scaled negatively with the other traits of the mass—size module, particularly below-ground biomass. This indicates a trade-off between investing in forage for nutrient and water resources and investing in anchorage and storage when plants become larger (Violle et al., 2009). Our network analysis does not support a RES or a close link between RES and LES traits as suggested by Craine, Froehle, Tilman, Wedin, and Chapin (2001), Freschet et al. (2010), and Roumet et al. (2016).

In the literature-based network, SLA and LNC took prominent roles, because they are known to covary with other traits of the leaf economics spectrum (Wright et al., 2004). SLA is the trait most often used to identify the position of species on the resource acquisition–conservation spectrum (Garnier et al., 2016). Why is SLA not as prominent in the observed network? First, Funk and Cornwell (2013) and Messier et al. (2017) showed that correlations between SLA, photosynthetic rate and leaf nitrogen concentration tend to be weak, when (a) the species pool consists of few growth forms, (b) leaf life span is constrained by climatic seasonality, and (c) variation in shade tolerance is low, as in our set of species that did not contain species from forest understoreys. Second, Minden, Andratschke, Spalke, Timmermann, and Kleyer (2012) found that SLA–LNC and SLA–LDMC relationships in salt marsh species deviate from the LES spectrum, due to investments in nitrogen-rich osmoprotectants and succulent growth forms, which alters SLA (Vendramini et al., 2002). Seventeen percent of our species are salt marsh species that actually show a negative relationship between SLA and LNC, compared to a positive relationship in the non-saltmarsh species. Hence, including salt marsh species may have distorted trait connections based on the LES. Low network connectivity does not invalidate functional relevance (e.g. Lienin & Kleyer, 2011). Weak connections facilitate many different trait combinations and thus multiple plant phenotypes, when compared to a single axis of variation (Messier et al., 2017).

4.2 | Observed modules and overlap with a priori defined dimensions

The broadly integrated network does not support the notion of independent dimensions. A recent study by Messier et al. (2017) on trait networks of a local tree community found similar results. Nevertheless, the cluster analysis revealed seven modules or subnetworks that partly overlap with the a priori dimensions described in the literature. In terms of connectedness and centrality, the most important spectrum is composed of SBM, SSL, BIBM, SRL, LBM, and LA. These traits stand for the trade-off between fast stem extension and stem stability associated with a below-ground trade-off of fast root and rhizome extension with anchorage and storage of nutrients. Leaf mass increases isometrically with stem mass as well as root and rhizome mass. Additionally, leaf area increases with leaf mass, and plant canopy height with stem mass.

Although the seed traits form their own module in the cluster analysis, modularization shows that they are associated with the size cluster. Likewise, the PCH–LDMC cluster could become part of this cluster. The covariation of size and reproduction is well known (Hodgson et al., 2017; Moles & Leishman, 2008; Obeso, 2002; Pierce, Bottinelli, Bassani, Ceriani, & Cerabolini, 2014). However, the larger the plant, the lower is the relative amount of biomass allocated to reproduction, according to the scaling exponent reported above. The covariation between plant canopy height and LDMC may be explained by the fact that the largest plants in our dataset are wetland species featuring high LDMC values, such as *Phragmites australis*, *Glyceria maxima*, and *Carex acutiformis*.

SLA and onset of reproduction represent another dimension, because herbaceous plants often terminate their vegetative expansion with the onset of generative reproduction, and relocate nutrients. With an earlier onset, plants need higher SLA to grow faster to attain their flowering height. Again, modularization shows that the SLA–ONSET trade-off is connected to the central size cluster (Supporting Information Figure S3.3). In temperate biomes, herbaceous species need to grow from the soil surface up to reproductive height within a few months, because regenerative buds are formed either near the surface (hemicryptophytes) or deeper in the soil (geophytes). This distinguishes herbaceous plants from trees, in which flowers and regenerative buds occur at the same height. The necessary expansion to reach reproductive height within a few months should require a tight integration of size and mass allocation traits with traits describing resource acquisition, storage and biomechanical stability across plant organs.

C and N concentrations form two separate modules, each of them integrated among roots, stems and leaves, and only loosely connected to the rest of the network. Positive scaling of N concentrations between leaves, stems, and roots has already been shown by Minden and Kleyer (2014). In our dataset, these relationships are close to isometry. Likewise, carbon relationships are close to isometry, except stem versus leaf and root. Correlation strengths

of carbon and nitrogen concentrations among organs are similar, in contrast to the study by Freschet et al. (2010), yet much lower than those among organ masses. It has been argued that carbon dioxide acquired by leaves, and nutrients acquired by roots may vary at different rates, leading to large variation of nutrient elements in these organs (Hillebrand, Cowles, Lewandowska, Van de Waal, & Plum, 2014; Kerkhoff et al., 2006).

4.3 | Network robustness

Networks of interacting species are often discussed in terms of robustness and stability, for example, the consequences of removing or replacing species in a food web (Proulx et al., 2005). These questions have little biological meaning in trait networks, because traits cannot be removed from plants. If traits are relevant for a research question and the data available, removing these traits is not reasonable, except for methodological analyses. Including new traits may change the overall network structure, depending on their connectedness with the present traits (Laughlin, 2014). The betweenness centrality may change strongly if the new trait is a hub trait connecting several subnetworks of traits. However, the probability of including a new hub trait is much lower than including peripheral traits. In general, scale-free networks are tolerant to the addition or removal of peripheral nodes, but sensitive to new hub nodes (Albert, Jeong, & Barabási, 2000). Furthermore, all bipartite correlations will change when new species become included in the dataset (Laughlin, 2014). This change will likely be minor if the new species belonged to the same growth forms and broad habitat types. Inclusion of tree species, evergreen species, forest understorey species, epiphytes, or macrophytes in our dataset would change the trait correlation structure more profoundly. For instance, the leaf economics spectrum might become more prominent in the network (see Díaz et al., 2016). To assess the significance of these changes, a Mantel test could be used (see e.g. Messier et al., 2017).

5 | CONCLUSIONS

Network techniques provide a suitable tool to study correlation patterns in functional traits. Beyond simple bivariate analyses, they allow the identification of key traits in terms of connectivity, regulation, and coherence of the whole network and its subnetworks. To determine networks, it is crucial that traits are measured with the same methodology, and, if possible, on the same individual (Westoby et al., 2002). Using large trait databases, with their inherent mixture of methods and species sets per trait, increases uncertainty and the need for imputation of missing data, which brings circularity into the analysis, as imputation itself is often based on correlations.

The observed trait network of herbaceous plants displays more correlations than previously known, supporting the notion of the plant as a coordinated system of biological functions. Size-related traits have the highest centrality in the network, where size not only denotes the mass and extension of leaves, stems, and roots, but also the mass investment per unit length or area to ensure the vital functions of leaves, stems, and roots. Common LES trait relationships cannot be clearly reproduced in our dataset. Furthermore, leaves, stems, and roots are remarkably integrated, as they form subnetworks in the size and element dimensions, although each of these organs have different functions. All in all, our results suggest that herbaceous perennial plants are organized along size- and nutrient spectra, but probably not along a plant economics spectrum.

Further research is needed to understand how responses of a given trait to environmental changes propagate in the network as a result of the connectedness of this trait, and how they may ultimately change the whole phenotype. Likewise, the effects of a given trait on ecosystem functions lead to changes in other traits, which may either dampen or increase changes in ecosystem functions such as productivity or decomposition. Ultimately, there is a latent need to abandon treating traits as single, independent entities in functional ecology and acknowledge their connectedness. Using modules, that is, PCA scores of highly connected trait clusters, as response "traits" may be helpful to reduce the effects of multicollinearity imposed by trait correlations.

Our results imply a general warning not to rely entirely on existing trait dimensions. Although we found support for several trait dimensions, the observed trait network deviated significantly from current knowledge. In particular, stem traits such as specific stem length warrant more consideration as core traits in herbaceous plants.

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AUTHORS' CONTRIBUTIONS

M.K. designed the project, the methodology, and the manuscript, together with J.T., and V.M. J.T., and T.J.B. collected species and traits in the Netherlands, V.M. and M.A.C.P. in northwest Germany, M.A.C.P., C.F., and R.E. in Denmark, A.T. and J.M.C. in western Pommerania, M.K. with students in the other regions. J.T. and M.A.C.P. carried out the trait analysis in the laboratory work. MM maintained the trait database. D.C.A. and B.B. assisted with the phylogenetic and network analyses respectively. M.K. was responsible for the statistical analysis. All authors contributed valuably to the drafts of the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.251q438 (Kleyer et al., 2018).

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