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An integrated framework of plant form and function: the belowground perspective

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Summary

Plant trait variation drives plant function, community composition and ecosystem processes. However, our current understanding of trait variation disproportionately relies on aboveground observations. Here we integrate root traits into the global framework of plant form and function. We developed and tested an overarching conceptual framework that integrates two recently identified root trait gradients with a well-established aboveground plant trait framework. We confronted our novel framework with published relationships between above- and belowground trait analogues and with multivariate analyses of above- and belowground traits of 2510 species. Our traits represent the leaf and root conservation gradients (specific leaf area, leaf and root nitrogen concentration, and root tissue density), the root collaboration gradient (root diameter and specific root length) and the plant size gradient (plant height and rooting depth). We found that an integrated, whole-plant trait space required as much as four axes. The two main axes represented the fast–slow 'conservation' gradient on which leaf and fine-root traits were well aligned, and the 'collaboration' gradient in roots. The two additional axes were separate, orthogonal plant size axes for height and rooting depth. This perspective on the multidimensional nature of plant trait variation better encompasses plant function and influence on the surrounding environment.

I. Introduction

Vascular plants began to colonize the Earth's land surface *c.* 430 million yr ago (Harrison & Morris, 2017; Morris *et al.*, 2018) and emerged as the dominant primary producers in terrestrial systems (Field *et al.*, 1998). Over time, land plants evolved different strategies and growth forms to survive and compete for limited resources. The plant kingdom now spans plants ranging from tiny, short-lived sidewalk weeds (e.g. *Poa annua* L.) with a maximum height of only 30 cm to mighty, long-lived redwood trees (*Sequoia sempervirens* (D. Don) Endl) which stand over 100 m in height and can live for over 2000 yr. Seeking to better understand this diversity in plant strategies, ecologists widely adopted trait-based approaches to quantify and interpret global diversity in plant growth, survival and reproduction of individuals in different habitats (Grime, 1977; Westoby *et al.*, 2002; Violle *et al.*, 2014; Bruelheide *et al.*, 2018; Freschet *et al.*, 2021).

Plant strategies for success have been interpreted in the light of economic theory, but rather than money, plants spend and save the currencies of carbon, nutrients and water (Box 1). Economic theory suggests that plants invest in organ construction in ways that reflect strategies for rapid growth or enhanced survival and life span (Grime, 1977; Orians & Solbrig, 1977; Tilman, 1982; Lambers & Poorter, 1992). This growth–survival trade-off was further developed following observations on foliar tissues, where the spectrum of strategies ranging from fast-growing, but short-lived, acquisitive leaves to slow-growing but long-lived and therefore more conservative leaves. This gradient was later termed the 'leaf economics spectrum' (LES) (Reich *et al.*, 1992; Wright *et al.*, 2004). Variation in leaf strategies along the LES has been linked to differences in plant performance (Davis *et al.*, 1998; Poorter & Bongers, 2006), species distributions, interactions (Sterck *et al.*, 2006) and ecosystem processes (Reich *et al.*, 1997; Diaz *et al.*, 2004, 2007; Grigulis *et al.*, 2013).

The success of the LES in explaining variation in leaf traits inspired further application of economic theory in other plant organs such as stems (Poorter & Bongers, 2006; Chave *et al.*, 2009; Zanne *et al.*, 2010) and flowers (Roddy *et al.*, 2020). These investigations largely confirmed trade-offs among investments in tissue construction, longevity and growth (Niklas, 1995; Poorter *et al.*, 2008; Chave *et al.*, 2009), and led to the conjecture of other gradients of trait variation representing alternate plant strategies. For example, in a large study covering six aboveground traits of *c.* 46 000 species, Diaz *et al.* (2016) observed another important

Box 1 Terminology in plant economics.

The sROOT working group had extensive discussions at the iDiv Synthesis Center on the meanings of plant trait terminology. Some of us initially perceived these discussions as tedious, but later realized that taking the time to reflect on the terms and their meaning would deepen our understanding of the trait framework concept we were building. It was doubly important to make sure we were all on the same page given that among the core group of 22 participants, we spoke seven different languages. We decided to share some of our thoughts here so that it might help others to understand our reasoning and conceptual framework.

Axis, gradient, spectrum or space?

Wright *et al*. (2004) introduced the leaf economics spectrum (LES). Following the *Oxford English Dictionary*, the word spectrum is used to classify the position of an object on a scale between two extreme points. The LES is therefore considered to be unidimensional, and mathematically a spectrum is described by one axis. In this paper, we only use the term spectrum when referring to the LES, and the term PC axis when referring to the axes of a principal component analysis. In other, more generalized discussions, we use the term gradient to describe gradual linear changes between two opposed ecological strategies.

The next question was how to address multidimensional trait coordination. A spectrum is a single gradient from A to B, so that term does not suffice. Bergmann *et al*. (2020) therefore decided to term two-dimensional root trait coordination the 'root economics space', where we think of space as an area or volume that is spanned by two or more unidimensional gradients. Confusingly, both the root economics spectrum (as in Weemstra *et al*., 2016) and the root economics space (Bergmann *et al*., 2020) are abbreviated as RES. We use RES to abbreviate root economics space and will refer to RESpectrum otherwise. The RESpectrum, as an analog of the fast–slow LES, is just one aspect of RES.

The naming of the axes in the RES

As long as there was just one axis described, the terminology was simple: LESpectrum or RESpectrum was sufficient to refer to the fast–slow or acquisitive–conservative gradient. Now that there were two or more independent axes defining the trait space we needed additional names.

Our rationale to name the fast–slow spectrum the conservation gradient was based on the strong functional link to life span. Despite a comparably low initial investment, the fast strategy comes with the expense of short-lived structures; in turn, the slow strategy allows a longer rate of return on investments by conserving invested carbon in better-protected structures.

The second spectrum – which we only observe below ground – reflects on the importance of collaboration with mycorrhizal fungi. Collaboration strategies range from 'do it yourself' resource acquisition to outsourcing a large portion of resource acquisition to mycorrhizal fungi. The conservation and collaboration gradients vary along orthogonal principal component axes in global root trait variation (Bergmann *et al*., 2020) and are hence independent, meaning that a fast or slow plant strategy can be combined with a range of collaboration strategies with mycorrhizal fungi.

Reflections on plant economics

Plant trait coordination is based on economic theory, where the currency is not money but instead photoassimilates, nutrients and water – the building blocks of plant tissues. We discussed two aspects regarding this concept.

How to interpret the term 'economy' in plants? Some considered the economy as optimizing the absolute scarcity of resources (i.e. the most limiting factor). Others coined it as the 'decisions' that plants have to make towards investing resources in different tissues with a certain return on investments (i.e. more the operational level). If the term economy related to the actual limiting factor that needs optimization in trait space, it would require a debate on the most limiting resource for plant growth (e.g. carbon, nitrogen or other resources such as phosphorus or water). As there is an ongoing discussion about the extent to which carbon currently is, and under future climate change will be, limiting plant growth (Prescott *et al*., 2020; Millard *et al*., 2007), the framing of the whole-plant economics space as a carbon economy would potentially be problematic. Therefore, it seemed more relevant to coin the term 'economy' as plant investment in tissue construction with a return on investment of resource acquisition. Along the conservation gradient, the returns on investment range from fast to slow, and along the collaboration gradient, carbon is either invested in a high root surface area or traded for resource acquisition with mycorrhizal fungi.

axis first highlighted by Westoby (1998) representing maximum plant size. The possibility that multiple organ strategies would align at the whole-plant level is often referred to as the 'plant economics spectrum' (PES; e.g. Wright & Westoby, 1999; Craine, 2005; Kerkhoff *et al.*, 2006; Freschet *et al.*, 2010) or the 'spectrum of plant form and function' (Díaz *et al.*, 2016). In his 'traits manifesto' Reich (2014) hypothesized that 'strong selection along trait trade-offs must result in convergence for any taxon on a uniformly fast, medium or slow strategy for all organs (leaves, stems and roots) and all resources (carbon, nitrogen, water)'. However, not all traits seem to fully align with the concept of a whole-plant economy (Brodribb & Feild, 2010; Sack *et al.*, 2013; Kröber *et al.*, 2015; Li *et al.*, 2015; Weemstra *et al.*, 2016).

Furthermore, our understanding of how function follows form in the plant kingdom has developed with a strong bias towards aboveground traits. Several notable studies indicate that belowground trait variation may not follow predictions established above ground (e.g. Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016). Using an extensive, global database of root trait observations (Guerrero-Ramírez *et al.*, 2021), Bergmann *et al.* (2020) recently expanded the expected unidimensional economic spectrum to two main functional gradients below ground. One gradient is defined as the conservation gradient and represents the 'classical' fast–slow trade-off between traits associated with high metabolic activity, such as root nitrogen concentration, and those associated with tissue investment, such as root tissue density. The other, but equally important, gradient

– the collaboration gradient – relates to resource acquisition and varies from a 'do it yourself' strategy to an 'outsourcing' strategy, where resource acquisition is primarily delegated to arbuscular mycorrhizal (AM) fungal partners. Together, the conservation and the collaboration gradients explain 77% of root trait variation and encompass the so-called root economics space (RES; Box 1).

Here we ask how the two recently discovered dimensions of the RES (Bergmann *et al.*, 2020) relate to aboveground trait variation, that is, to both the LES and to the wider framework of global plant form and function *sensu* Díaz *et al.* (2016). First, we present an economic framework that integrates root traits into the global framework of plant form and function by linking the multiple known gradients of plant trait variation – the conservation gradient, the collaboration gradient and the plant size gradient (Section II). Second, we use a qualitative literature review to reassess the relationships between above- and belowground traits predicted in our framework, focusing on trait pairs that are often intuitively considered functionally equivalent (e.g. leaf and root tissue density; Sections III and IV). Third, we test our framework with a new analysis, where existing plant trait databases (TRY, Kattge *et al.*, 2020; GRooT, Guerrero-Ramírez *et al.*, 2021) are combined to assess above- and belowground trait relationships across species (Section V). Fourth, we mirror this global-scale analysis with measurements made within the same individuals or plots to further test the robustness of the trait coordination at the individual plant level (Section VI). Finally, we discuss the implications of our integrated framework and consider future research directions (Section VII).

II. An integrated framework of plant form and function – linking above- and belowground traits

We developed a conceptual framework linking above- and belowground trait variation across species. We envisage three gradients – conservation, collaboration and plant size – which we expand on in the following.

1. Conservation gradient

The economy along the conservation gradient is a central component of both the LES and the RES, as both concepts share a trade-off in traits related to a slow vs fast return on resource investment (see Box 1 for terminology). This trade-off differentiates between acquisitive species with short tissue life span, high metabolic activity and/or high rates of resource acquisition, and conservative species with longer tissue life span, lower metabolic activity and greater protection from herbivory, but slower rates of resource acquisition. The root traits traditionally used to represent this functional trade-off are root nitrogen concentration (RN) as a measure of overall nutrient concentration, physiological activity and palatability (Freschet *et al.*, 2021) and root tissue density (RTD; fine root mass per unit volume), which represents carbon-based construction costs per unit mass (Freschet *et al.*, 2020) including lignification to ensure long life span and limited herbivory. Acquisitive or 'fast' roots are characterized by high RN concentration and low RTD. The leaf traits traditionally used to represent this functional trade-off are: leaf nitrogen concentration (LN) (Wright *et al.*, 2004; Díaz *et al.*, 2016), as fast growth requires high nitrogen concentration to accommodate high photosynthesis rates via high concentrations of proteins associated with light harvesting, CO_2 capture and bioenergetics (Evans & Seemann, 1989); and leaf mass per area (LMA, leaf mass per unit leaf area – the inverse of specific leaf area (SLA)), where acquisitive species show low LMA (or high SLA) providing limited construction cost per unit leaf area to achieve a large leaf area and thus 'fast' return of carbon on investment. By contrast, conservative, 'slow' species are characterized by long-lived leaves with thick cell walls and high construction costs per area (high LMA, low SLA) but low rates of herbivory (low LN) (Poorter *et al.*, 2009). Previous studies have often assumed that SLA (1/LMA) is functionally analogous to specific root length (SRL) because both traits reflect a strategy of cheap construction of absorptive surface area (Reich, 2014). However, recent work from Bergmann *et al.* (2020) has shown that SRL reflects, to a large extent, an orthogonal belowground collaboration gradient influenced by association with mycorrhizal fungi.

Table 1 Above- and belowground traits included in the current analyses.

Traits	Abbreviation	Units	Associated gradient
Leaf mass per area	LMA	$mg\ mm^{-2}$	Leaf conservation
Leaf tissue density	LTD	$g\ cm^{-3}$	Leaf conservation
Leaf thickness	Lth	mm	Leaf conservation
Leaf nitrogen concentration	LN	$mg\ g^{-1}$	Leaf conservation
Leaf phosphorus concentration	LP	$mg\ g^{-1}$	Leaf conservation
Leaf lignin concentration	LL	$mg\ g^{-1}$	Leaf conservation
Specific stem density	SSD	$kg\ m^{-3}$	Plant size
Maximum vegetative plant height	Height	m	Plant size
Maximum rooting depth	Rdep	m	Plant size
Root tissue density	RTD	$g\ cm^{-3}$	Root conservation
Root nitrogen concentration	RN	$mg\ g^{-1}$	Root conservation
Root phosphorus concentration	RP	$mg\ g^{-1}$	Root conservation
Root lignin concentration	RL	$mg\ g^{-1}$	Root conservation
Root diameter	RD	mm	Root collaboration
Specific root length	SRL	$m\ g^{-1}$	Root collaboration
Mycorrhizal colonization intensity	%M	%	Root collaboration
Root cortex fraction	CF	ratio	Root collaboration

Next to these key traits, there are additional traits related to the conservation gradient (Table 1). The core of the LES *sensu* Reich *et al.* (1992) and Wright *et al.* (2004) contrasts fast and slow return on carbon and nutrient investment. The basis for fast return are both high mass-based photosynthetic rates and high leaf respiration rates (Lambers & Poorter, 1992; Reich *et al.*, 1997; Wright *et al.*, 2004), linked with both high LN and leaf phosphorus (LP) concentrations, which determine the energy available for plant metabolism (Güsewell, 2004; Wright *et al.*, 2004; Ågren, 2008). By contrast, slow, conservative plants construct dense tissues with thick cell walls that are physically and chemically well-protected from damage and decay. The ‘slow’ end of the conservation spectrum should thus be positively related to tissue density, lignin concentration and life span in both leaves and roots. Given the large overlap in conceptual arguments and functioning of both leaf and root conservation gradients, we hypothesize that the traits on the gradients for conservation should be aligned between leaves and roots (Fig. 1). In addition, we hypothesize significant bivariate correlations between leaf and root traits that are assumed to be functionally analogous (Westoby & Wright, 2006; Withington *et al.*, 2006; Freschet *et al.*, 2010; Reich, 2014) such as leaf and root nitrogen or phosphorus concentration and leaf and root tissue density.

2. Collaboration gradient

Recently, Bergmann *et al.* (2020) demonstrated that SRL is not positioned on the root conservation gradient but on an independent PC axis related to the ‘collaboration gradient’ that has evolved in concert with symbiosis with mycorrhizal fungi. This novel global conceptualization of belowground trait space has now also been observed in more local and regional studies (Spitzer *et al.*, 2021; Stock *et al.*, 2021; Sun *et al.*, 2021; Sweeney *et al.*, 2021; Williams *et al.*, 2021). The key traits along this gradient are mean root diameter (RD) and SRL. These traits reflect that thick-rooted species with low SRL are more readily colonized by AM fungi as a result of the larger fungal habitat in the root cortex (Brundrett & Tedersoo, 2018; Ma *et al.*, 2018; Kong *et al.*, 2019; Sweeney *et al.*, 2021). This relationship most likely dominates the root collaboration gradient as *c.* 80% of plant species worldwide are AM species (Tedersoo *et al.*, 2020). Other mycorrhizal associations, such as ectomycorrhiza or ericoid mycorrhiza (ErM), tend to colonize moderate to thin roots with higher SRL, while nonmycorrhizal species have the highest SRL through the construction of very small-diameter roots to maximize the volume of soil that roots explore and exploit by themselves (Bergmann *et al.*, 2020; Freschet *et al.*, 2021).

Inherently related to the functional importance of the collaboration gradient for the symbiosis with mycorrhizal fungi, colonization rates of AM fungi are positively correlated with root diameter (Brundrett, 2002). This is a result of an increased fraction of root cortical tissue in thicker roots, providing improved conditions for mycorrhizal association (Kong *et al.*, 2014, 2019; Valverde-Barrantes *et al.*, 2016). This axis of root collaboration leads us to hypothesize that there is no direct functional analog to SRL and root diameter above ground and that this axis should therefore be independent of the conservation PC axis of plant leaves and roots (Fig. 1). Accordingly, we hypothesize that there is no bivariate correlation between SRL and LMA or a functional pairing for thinner leaves (LTh) and thinner root diameter.

3. Plant size

Plants are more than leaves and fine roots. The analyses of several large datasets have demonstrated that the axis of plant aboveground size forms another independent gradient in multivariate trait space (Diaz *et al.*, 2004, 2016; Wright *et al.*, 2007). Plant height and overall size represent a coupling of time to reproduction and longevity (Westoby *et al.*, 2002), and is to some extent related to a wide range of differences associated with the dichotomy among herbaceous and woody plants (Díaz *et al.*, 2016). Plants with taller shoots have a greater capacity to compete for light along its predictable vertical gradient (Price *et al.*, 2014). Much in the same way, deeper root systems can be associated with an increased capacity to successfully acquire water and, to a limited extent, nutrients as well, especially phosphorus, from deeper soil layers (Fort *et al.*, 2013; Maeght *et al.*, 2013; Freschet *et al.*, 2020; Mackay *et al.*, 2020). However, whether maximum rooting depth is directly related to the overall amount of water uptake or merely related to the accessibility of water in deeper soil layers, for example, under drought conditions, is less clear (Brunner *et al.*, 2015). Further, many belowground resources do not increase with soil depth, as nutrient and oxygen availability are often higher in the topsoil (Jobbagy & Jackson, 2001). Successful competition for soil resources may therefore depend to a large extent on horizontal root extent and total root length rather than rooting depth (Postma *et al.*, 2020), but other strategies of soil exploitation may also determine soil resource competition (e.g. Lambers *et al.*, 2008). Ultimately, horizontal extent and total root length are linked to the balance between above- and belowground biomass (e.g. Freschet *et al.*, 2015b; Weemstra *et al.*, 2020) and we thus hypothesize that plant maximum height and maximum root system depth are positively but weakly related and do not necessarily reflect a single coupled gradient of plant size. Furthermore, both plant maximum height and rooting depth should be independent of leaf and root functional traits (Jiang *et al.*, 2020).

We depicted the main gradients of plant form and function in conceptual Fig. 1, which graphically represents our three main hypotheses.

Hypothesis 1

Above- and belowground gradients related to resource investment (conservation gradients) align as a whole-plant fast–slow gradient. Functionally analogous leaf and root traits are well-correlated across this gradient.

Hypothesis 2

Root traits that vary along the belowground collaboration gradient form an orthogonal, independent gradient to the conservation gradient of whole-plant fast–slow traits.

Hypothesis 3

Traits related to overall plant size such as maximum plant height or rooting depth are independent of leaf and root functional trait gradients and form additional gradients in the framework of plant form and function.

III. Methods for current evidence and the analysis of above- and belowground linkages

A detailed methodological description is provided in the Supporting Information Methods S1.

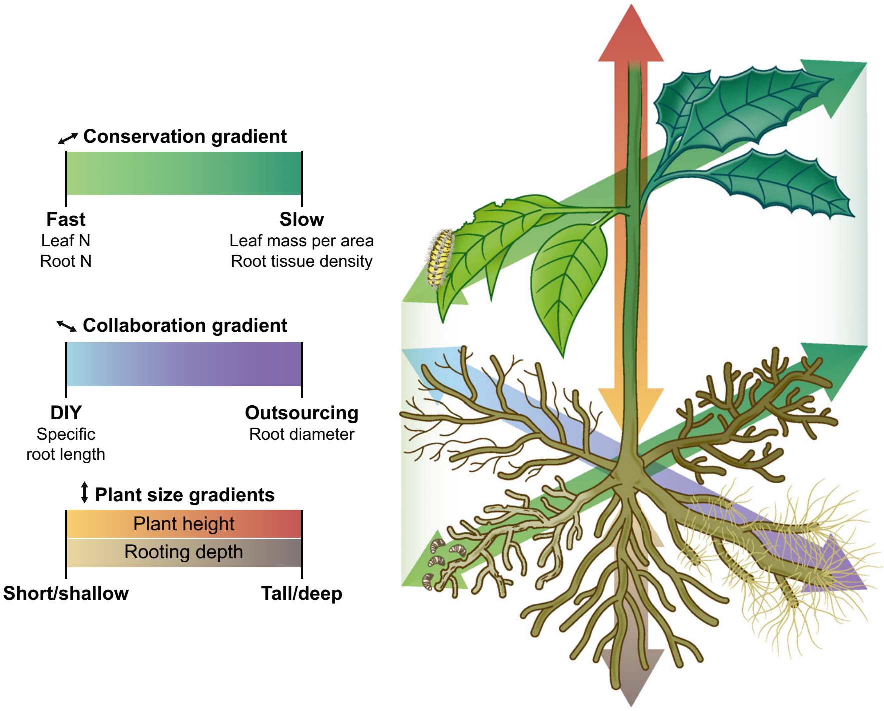

Fig. 1 The integrated framework of plant form and function based on knowledge and expectations from separate findings of the leaf economics spectrum (LES), the root economics space (RES) and the spectrum of whole-plant form and function. We hypothesize a strong coordination of leaf and root conservation gradients representing a gradient of species from fast resource return on investment to slow resource return on investment both above and below ground. Further we expect an orthogonal collaboration gradient of root traits representing a gradient of species from 'do it yourself' resource uptake strategies to strategies where resource acquisition is outsourced to collaborative fungal partners. We do not necessarily expect a single gradient of plant size for maximum height and rooting depth. Figure courtesy of Nathan Armistead, ORNL Graphics, based on Kramer-Walter *et al*. (2016).

1. Qualitative literature review assessing functional trait pairs

We found nearly 100 papers that examined trait correlations among different organs (leaf, stem, root). We selected core traits with key ecological relevance, representing plant chemistry (leaf nitrogen concentration, leaf phosphorus concentration, root nitrogen concentration, root phosphorus concentration), morphology (leaf tissue density, stem tissue density, leaf thickness, specific leaf area, root tissue density, root diameter, specific root length), physiology (leaf photosynthetic capacity, leaf and root respiration), life span (leaf and root life span), size (maximum plant height, maximum rooting depth) and mycorrhizal colonization (i.e. mycorrhizal colonization rate). We use 1/LMA (equal to SLA) in the literature review as this is most often reported in the literature and is expected to be positively correlated to SRL; in turn we refer to LMA in the remainder of our paper as it is ecologically more intuitive and better reflects the spectrum of plant form and function by Diaz *et al.* (2016).

In summarizing our results, we counted: the total number of studies reporting a correlation for each trait pair irrespective of the significance of the relationship; the number of studies showing a significantly positive relationship; and the number of studies showing a significantly negative relationship. We report data on 90 bivariate trait pairs in Fig. S1 (see also Methods S2 and Table S1). In the main text, we focus on the set of six above- and belowground traits which we expected to be functional analogs as described in Section II (RN-LN, RP-LP, RTD-LTD, RD-LTh, SRL-SLA, depth-height; see abbreviations in Table 1). This detailed review relies on a more conservative selection of 59 studies, that is, only those reporting species-specific trait relationships for a minimum of 15 species (see Methods S2). We tested alternative arbitrary cutoff values for a minimum species number (three or 20), but the overall outcome was the same (data not shown).

2. Analysis of two global trait datasets to test our conceptual framework

Main database We used two types of dataset: species-specific mean trait values (804 species) based on global databases (TRY, Kattge *et al*., 2020; GRooT, Guerrero-Ramírez *et al*., 2021; additional datasets, Table S2); and species-specific individual trait data (455 species) where root and shoot traits were measured on the same plant individual or plot to test our inference from global trait databases. However, we did not focus on intraspecific trait variation in our analysis. Our full dataset of species-specific mean traits included all data from the individual trait dataset and all species with data on at least one aboveground and one belowground trait (2510 species). Table S3 provides an overview of the full dataset.

We took a three-step approach in our multivariate analyses. First, we focused on species with full data on six traits defining the gradients of leaf and root trait variation, with two traits per gradient: the leaf conservation gradient (LMA, LN), the root conservation gradient (RTD, RN) and the root collaboration gradient (RD, SRL). We performed this analysis for both the species' mean trait dataset and the individual dataset. Second, we included maximum plant height (height; Kattge *et al.*, 2020) and maximum rooting depth (Rdep; Fan *et al.*, 2017) to represent plant stature. There were no species that had observations corresponding to all of the additional traits, so we performed this analysis on the dataset of species with mean trait data for at least one aboveground and one belowground trait of the mentioned traits (2510 species). We used the FungalRoot Database (Soudzilovskaia *et al.*, 2020) and the nodDB Database (Tedersoo *et al.*, 2018) to obtain additional information on mycorrhizal association and nitrogen fixation ability, respectively. Third, we broadened our analysis to include additional leaf traits characterizing species on the 'fast' (leaf phosphorus concentration (LP)) and 'slow' (leaf tissue density (LTD), leaf lignin concentration (LL), leaf thickness (Lth)) side of the leaf conservation gradient as well as root traits characterizing species that align with the 'fast' (root phosphorus concentration (RP)) and 'slow' (root lignin concentration (RL)) ends of the conservation gradient. Further, we added traits characterizing 'outsourcing' species on the root collaboration gradient (AM colonization rate (%M), root cortex fraction (CF)).

Data processing All data processing and analyses were done using R 4.0.3 (R Core Team, 2020). Before analysis, all trait records were standardized by calculating *z*-scores. In order to correct trait values for study design and source of publication, we calculated residuals using a linear mixed model for each trait. Scientific names were standardized and matched among datasets using the Taxonomic Name Resolution Service v.4.0 (http://tnrs.iplantcollaborative.org/), The Plant List (The Plant List, 2013, v.1.1), and the Leipzig Catalogue of Vascular Plants (LCVP; Freiberg *et al.*, 2020). Using the backbone phylogeny from Zanne *et al.* (2014) we constructed a phylogenetic tree including all species using the function 'phylomatic' from the package BRANCHING (v.0.6.0; Chamberlain, 2020).

Statistical analysis We used phylogenetically informed methods for all analyses presented in the main paper and provide results for nonphylogenetically informed analyses in the Supporting Information. First, we assessed bivariate relationships among the six core traits (RD, SRL, RTD, RN, LMA and LN), where sample sizes ranged from 866 (for RTD vs RN) to 1497 (for SRL vs LMA) depending on the number of species with respective trait information. We fitted phylogenetic generalized least-squares models to each pair of traits and calculated phylogenetically corrected correlation coefficients. Second, we performed one phylogenetically informed principal component analysis (PCA) for all six core traits. In addition, we performed phylogenetically informed PCAs for subsets of species (mycorrhizal association type, woodiness or ability to fix atmospheric nitrogen) and used permutational multivariate ANOVA (PERMANOVA) to identify significant differences between these subsets. Third, we investigated multiple trait relationships between root traits (RD, SRL, RTD, RN), leaf traits (LMA, LN) and plant size traits (max height and Rdep). Fourth, we broadened our analysis to include additional root traits (RP, RL, CF and %M), leaf traits (LL, LP, Lth, LTD) and one stem trait (SSD). We performed a PCA based on pairwise complete correlations using a regularized covariance matrix, where negative eigenvalues were set to small positive values. We used mean trait data of all 2510 species to calculate the correlation matrix and subsequently performed a nonphylogenetically corrected PCA.

IV. Current evidence for trait correlations above- and belowground in published literature

First, we tested our integrated framework using a comprehensive literature review to ask to what extent functional analogs, such as, for example, LN-RN, LTD-RTD, LTh-RD, SLA-SRL, were supported in previous studies.

1. Results

Our literature review documented root–shoot relationships across 36 trait pairs, including 147 (53%) nonsignificant, 86 (31%) significantly positive, and 43 (16%) significantly negative correlations. However, in only 12 out of the 36 trait pairs were the majority of reported relationships significant; no consistent relationship was detected for the other 24 trait pairs (Fig. 2).

On the 'fast' end of the conservation gradient, high LN or LP concentrations were significantly positively correlated to high RN or RP concentrations, as expected based on functional analogues (e.g. Kerkhoff *et al.*, 2006; Geng *et al.*, 2014). On the 'slow' end of the conservation gradient, high LTD and RTD were significantly positively correlated in more than half of the studies reporting this relationship (e.g. Bergmann *et al.*, 2017; Wang M *et al.*, 2017). In addition, we found that acquisitive species with high SLA were significantly positively correlated with roots of high RN and RP concentrations (e.g. Holdaway *et al.*, 2011; Kleyer *et al.*, 2019). Further, we found that the majority of reported relationships were significantly negative for RTD compared with LN, LP and SLA (e.g. Shen *et al.*, 2019). Other functional pairs related to the conservation gradient showed mixed results. While leaf and root respiration rates were significantly positively correlated in the majority of studies, we had no data to support potential correlations for leaf and root life span (Fig. S1).

Correlations among root traits representing the collaboration gradient (SRL and RD) and purported analogous leaf traits (SLA and LTh) were less clear. Despite 33 studies reporting SRL–SLA correlations on datasets with more than 15 species each, the results were ambiguous: 13 studies reported positive correlations (e.g. Wang R. *et al.*, 2017), 17 were nonsignificant (e.g. Geng *et al.*, 2014), and three were negative (e.g. Li & Bao, 2015). The relationship between SRL and other leaf traits representing the conservation gradient (LN, LP, LTD, LTh) were mostly nonsignificant, as was the relationship between RD and LTh (Fig. 2). As SRL and SLA are composite traits of RD and RTD and LTh and LTD, respectively, the positive correlation between LTD and RTD appeared to be the underlying reason for the correlation between SRL and SLA, whereas the absence of correlation between RD and LTh appeared to weaken this correlation. The relationships between RD and other aboveground traits were mixed and provided little support for strong coordination between traits along the root collaboration gradient and leaf economics conservation traits. Colonization intensity with mycorrhizal fungi, another

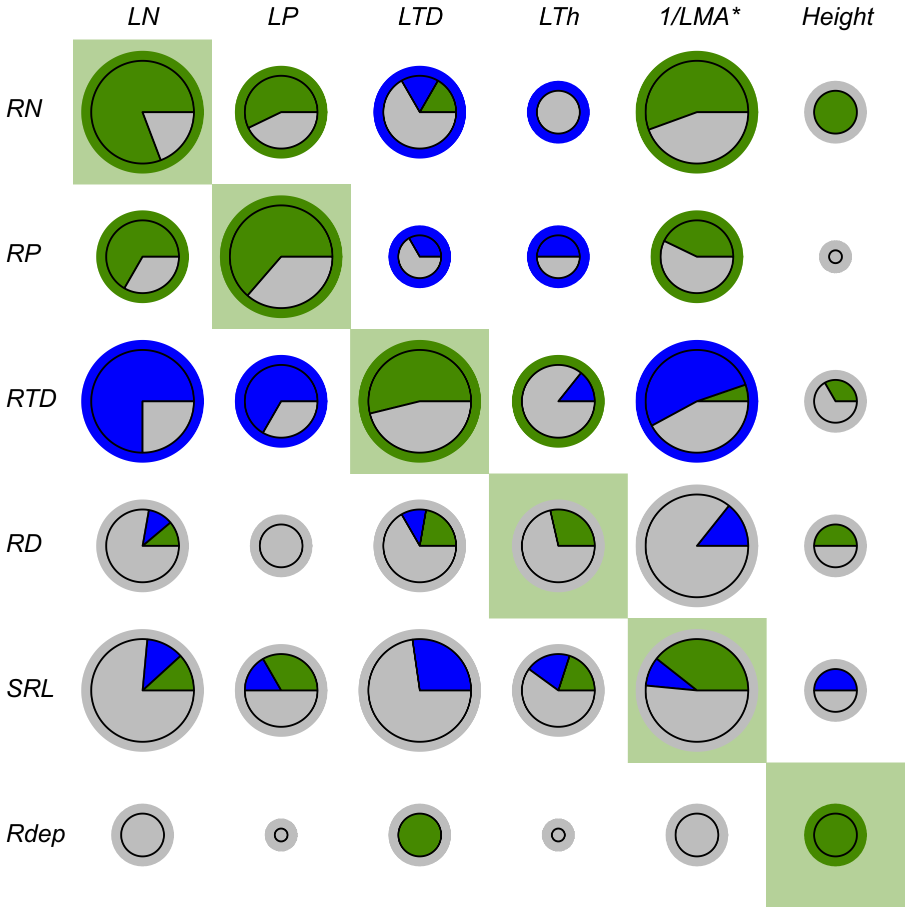

Fig. 2 Results of qualitative literature review of 59 papers with 276 reported root-leaf trait relationships among a minimum of 15 species presented as pie charts. LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; LTD, leaf tissue density or leaf dry matter content; Lth, leaf thickness; LMA, leaf mass per area; height, maximum vegetative plant height; RN, root nitrogen concentration; RP, root phosphorus concentration; RTD, root tissue density or root dry matter content; RD, average root diameter; SRL, specific root length; Rdep, maximum rooting depth. * We use 1/LMA (equal to SLA) as this is most often reported in the literature and is expected to be positively correlated to SRL. Pie legend: gray, percentage of overall studies with nonsignificant relationship; blue, percentage of overall studies with significantly negative correlations; green, percentage of overall studies with significant positive correlation. The green box color highlights the diagonal root–shoot trait pairs which are assumed to be functional analogs and positively correlated. The outer ring color of the pie indicates the direction of hypothesized relationships based on our new framework of plant form and function (see Fig. 1); gray if no significant correlation was expected, blue for negative and green for positive expected correlations between trait pairs. Where the color of the outer ring matches the main color of the pie content, our new framework is supported by a majority of studies in the literature. The size of the pie relates to the number of studies reporting a correlation between the trait pair: smallest size is zero studies, the second smalles size is one to five studies, the third smalles size is six to 10 studies, and the largest size is ≥ 10 studies. As an example, leaf and root nitrogen are expected to be functionally analogues (green box). A trait correlation between the pair was reported in 26 studies (biggest circle), 21 of which were significantly positive (81% green); no study was significantly negative (0% blue), and five studies reported nonsignificant results (19% gray). See Supporting Information Fig. S1 for full results.

important trait characterizing the root collaboration gradient, also showed no significant relationships with leaf traits; however, there was an overall lack of data assessing these relationships (Fig. S1).

Our literature review provided limited evidence to broaden our perspective on plant form and function to include the relationship between plant height and rooting depth as suggested functional analogs. In fact, our survey, focusing on reports containing more than 15 species per study, resulted in only one study reporting a positive correlation between plant height and rooting depth (Burton *et al.*, 2020), although we are aware of some other studies – particularly in smaller stature plants – that have also found positive correlations between height and rooting depth (Violle *et al.*, 2009). Our full database contained two additional studies analyzing plant height and rooting depth (Leuschner & Meier, 2018; Miedema *et al.*, 2019), both with nonsignificant results (Fig. S1). Clearly, any generalization regarding this trait pair based on our survey would be premature.

From this literature review we conclude that reported bivariate correlations provided some evidence that traits along the conservation gradient of the RES are correlated with traits of the LES. Yet, many of the root–shoot pair correlations were nonsignificant, except for leaf and root chemical traits, leaf chemical traits and RTD, and LTD and RTD. Bivariate correlations between root traits along the collaboration gradient (SRL and RD) and all leaf traits were mostly nonsignificant, except perhaps the correlation between SRL and SLA – although there was no consensus on whether the correlation was positive or negative, and conclusions remain ambiguous despite the large amount of studies. Overall, our literature review provided some evidence for relationships between

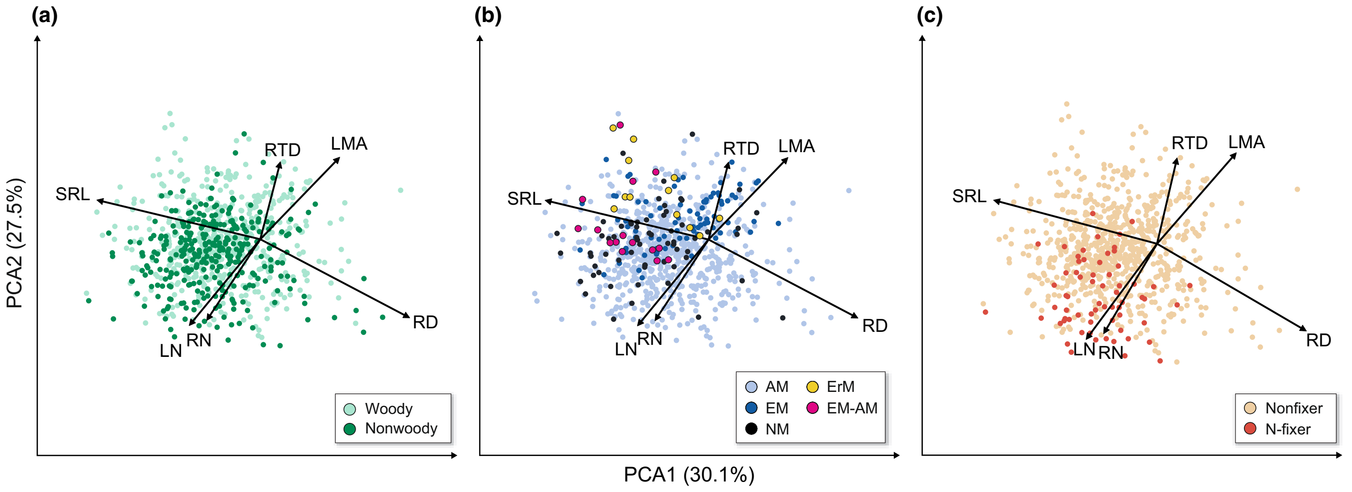

Fig. 3 Phylogenetically informed principal component analyses of the core species set (*n* = 804) based on species' mean trait values for (a) woody (*n* = 480) and nonwoody (*n* = 324) plant species; (b) arbuscular mycorrhizal species (AM, *n* = 630), ectomycorrhizal species (EM, *n* = 84), arbuscular and ectomycorrhizal species (EM-AM, *n* = 15), ericoid mycorrhizal species (ErM, *n* = 12), or nonmycorrhizal species (NM, *n* = 63); (c) nonN-fixing (*n* = 739) and N-fixing plant species (*n* = 65, corresponding data in Supporting Information Table S4). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length. Permutational multivariate analysis reveals significant differences between all subgroups and can be found in Table S7.

above- and belowground traits, but they seemed less straightforward than expected from previous synthesis papers (Reich, 2014), presumably because of the multidimensional trait space below ground (Bergmann *et al.*, 2020).

V. The global spectrum of plant form and function – evidence from a global dataset of above- and belowground species' mean trait values

In the second step, testing our integrated framework for global form and function in plants, we utilized a dataset of six core traits quantified as species means for each of 804 species. The six traits selected represented the leaf and root conservation gradients (LN, LMA, RTD, RN) and the root collaboration gradient (RD, SRL). Results of the PCA (Fig. 3; Table S4) supported our conceptual framework. The belowground root conservation PC axis was closely aligned with the aboveground leaf conservation PC axis (Hypothesis 1), while the collaboration-related root traits belowground (RD and SRL) formed a separate PC axis that was orthogonal to the conservation-associated traits (Hypothesis 2). Although most traits were best captured by PC1 and PC2, RTD most strongly loaded onto PC3, indicating that in addition to its relevance for root economics, RTD shows additional variation potentially related to other root functions that is not captured elsewhere (see also Fig. S2 for pairwise trait correlations, and Fig. S3 and Table S5 for nonphylogenetically informed results).

Results from the main PCA were consistent when conducted separately within woody and nonwoody plants (Fig. S4). The main difference between the two growth forms is that RTD was less strongly loaded on PC1 in the nonwoody plants, leading to a weakening of the correlation between LMA and RTD in these species compared with trees and shrubs (Fig. S4; Table S6). Although there was substantial overlap, there were significant differences in the trait space occupied by common subgroups, including growth form, mycorrhizal association and N-fixing status (Fig. 3; Table S7). Woody species generally encompassed a larger trait space while nonwoody species were more concentrated towards the acquisitive side of the leaf and root conservation axes. Probably reflecting their large global diversity and wide distribution, plants forming relationships with AM fungi encompassed the full trait space. Plants that formed relationships with ectomycorrhizal species (EM) and ericoid mycorrhizal species (ErM) were more were more concentrated around higher RTD and LMA values. While the species in our dataset with AM associations spanned the plant kingdom, the species with EM and ErM associations were limited to three plant orders: the Fagales (EM), Pinales (EM) and the Ericales (ErM). As a result, the more conservative leaf and root traits associated with these groups may be related to both their mycorrhizal association and their phylogeny. Nonmycorrhizal plants were more concentrated towards higher SRL on the collaboration axis, representing smaller-diameter roots that maximize their absorptive surface area in order to exploit soil resources by themselves (Fig. 3b; Table S7). Finally, N-fixers were strongly associated with higher LN and RN (Fig. 3c; Table S7).

Next, we extended our dataset to include measures of plant size, namely plant height and rooting depth, using a PCA based on a matrix of pairwise relationships across 2510 species. Here we focused initially on 8 traits so that each gradient proposed in our conceptual framework would be equally represented by two traits. The addition of plant size traits did not alter the alignment of leaf and root traits (Figs 4, S5). Consistent with our conceptual framework, rooting depth and plant height were unrelated to all other traits and were poorly related to PC1 and PC2 (Hypothesis 3; Figs 4, S5; Table S8). Rooting depth and plant height were instead

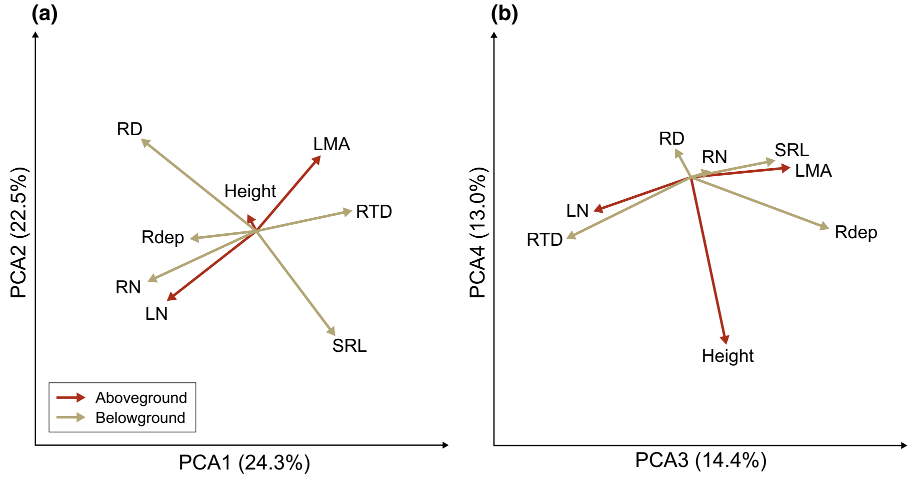

Fig. 4 Principal component analysis (PCA) based on a correlation matrix of species' mean values of root and leaf traits (species $n = 2510$) representing the six core traits (see Fig. 3) together with overall plant size for the first and second axes (a) and the third and fourth axes (b) (corresponding data in Supporting Information Table S8). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length; height, maximum vegetative plant height; Rdep, maximum rooting depth. A three-dimensional version of this figure is available as Fig. S5. A PCA of all 17 traits based on pairwise correlations (Fig. S7; Tables S10) very closely resembled the result of 14 traits as in Fig. S6.

best captured by PC3 and PC4, respectively. As expected, these traits were only weakly aligned, demonstrating a significant bivariate correlation ($P = 0.03$, data not shown) but without meaningful predictive power ($r = 0.09$).

In a final step of our analysis we used an expanded set of 14 leaf and root traits to determine if these traits aligned with the conservation or collaboration gradient as hypothesized in our conceptual framework (Fig. 1). High CF and %M were closely associated with high RD on the 'outsourcing' end of the collaboration PC axis, opposite from greater SRL (Fig. S6; Table S9). The inclusion of additional leaf and root conservation traits was generally consistent with our expectations as high phosphorous concentrations (LP and RP) remained aligned with high LN and RN, representing a 'fast' strategy, while high lignin concentrations (LL and RL), LMA and LTD were oriented along the same PC axis, representing a 'slow' strategy. One notable exception to these trends was that leaf thickness (LTh) was partly separated from the traditional LES, being most strongly associated with PC3 and PC4 (Table S9). As in the literature review, the bivariate relationship between composite traits LMA and SRL appeared to be driven more by the association between LTD and RTD than between RD and LTh (Fig. S6). Results from this expanded set of 14 leaf and root traits were consistent with results that also included size-related traits (17 traits; Fig. S7; Table S10; see also Fig. S8 and Tables S11, S12 for a sensitivity analysis of this data).

VI. The robustness of above- and belowground trait coordination at the level of individual plants: are individual-based measurements consistent with database composites of species mean traits?

The comparison of mean trait values calculated from observations across different environments and sites is highly useful to allow standardized species comparisons over large, spatial scales (Section V). However, local site conditions drive within-species phenotypic variation in traits and may thus obscure global patterns of trait relationships as well as above/belowground coordination, which might be coadapted to a local environment. To account for potential cross-site variation we conducted an additional set of tests utilizing trait values, where above- and belowground traits were measured within individuals or within the same plot across individuals experiencing the same edaphic and climatic conditions for 455 species. Results of our individual-based analysis are consistent with those made using the global, species-mean database and support the robustness of our conceptual framework (Fig. 1). The overall pattern of trait alignment in our individual-based analysis (Fig. 5; Table S13) was consistent with that observed using the larger species' mean datasets with six core traits (Fig. 3) and the expanded set of 14 root and leaf traits (Fig. S6). In the individual-based analysis, RD and SRL formed a clear PC axis representing the root collaboration gradient that was orthogonal to a separate PC axis where both leaf and root conservation traits were reasonably well aligned (Fig. 5; Table S13; see also Fig. S9 and Table S14 for nonphylogenetically informed results).

Permutational multivariate analysis again highlighted distinct differences among common plant groups, although these differences were less consistent and less striking compared with the global species-averaged dataset (see Figs 3, 5). Plants associated with N_2-fixing bacteria differed significantly from plants without this symbiosis (Table S15). There were also significant differences between the most common types of mycorrhizal associations (Fig. 5, Table S15). However, unlike the species-averaged dataset, the difference between woody and nonwoody species in the individual-based dataset was not significant (Table S15).

VII. Conclusions and ecological considerations

After years of vigorous scientific debate, we asked whether above- and belowground plant traits were coordinated across the whole plant using a qualitative literature review combined with analyses of

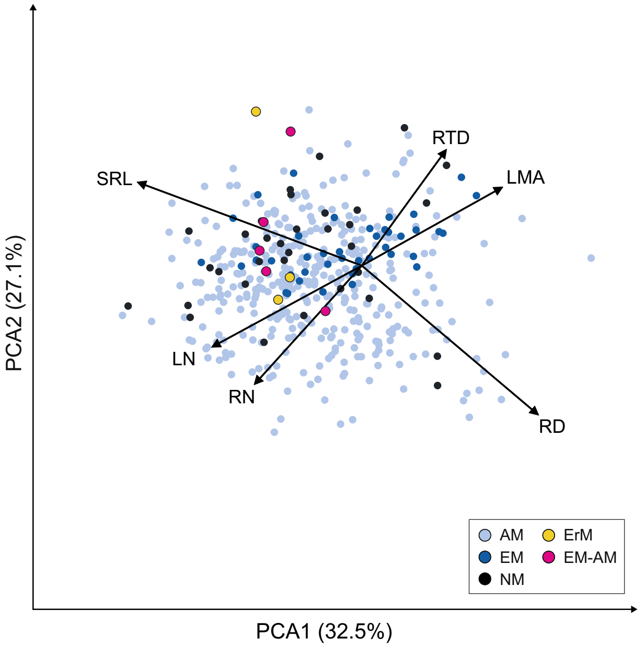

Fig. 5 Phylogenetically informed principal component analysis of traits measured on the same individual showing arbuscular mycorrhizal species (AM, $n = 372$), ericoid mycorrhizal species (ErM, $n = 3$), ectomycorrhizal species (EM, $n = 42$), arbuscular and ectomycorrhizal species (EM-AM, $n = 5$) or nonmycorrhizal species (NM, $n = 33$) (total $n = 455$, corresponding data in Supporting Information Tables S13, S15). LMA, leaf mass per area; LN, leaf nitrogen concentration; RN, root nitrogen concentration; RD, average root diameter; RTD, root tissue density; SRL, specific root length.

a global plant trait database spanning leaf, stem and fine-root traits. We found that key leaf and fine-root traits were aligned along the expected 'conservation' gradient of plant economic investment, but decoupled from an additional 'collaboration' gradient for fine roots, explaining a similar amount of trait variation. Together the two respective PCA axes explained 58% of the variation across leaf and root traits. In turn, whole-plant traits such as plant height and rooting depth each formed additional, separate gradients; we observed similar patterns using both species trait means and above- and belowground trait data collected from individual plants. This large-scale data synthesis and analysis highlight the fact that the trait space for whole-plant form and function is multidimensional, and that the capability of fine roots to collaborate with mycorrhizal fungi for plant resource acquisition adds an important and ecologically relevant dimension to this trait space.

1. Traits along the 'conservation' gradient

The currencies of economics in plants are the carbon, water and nutrient inputs required to construct and maintain tissues that explore the environment for a resource return on this investment. Plants with an acquisitive strategy – a high metabolic rate, fast growth and fast turnover – need to invest in leaves and roots that are capable of delivering high amounts of resources. We observed that these strategies – as reflected in leaf and root traits – are coordinated in air and soil within a plant, as predicted by Reich (2014) and shown by many others as documented in the literature review (Section IV).

The higher metabolic activity that comes with higher mass-based rates of leaf photosynthesis, root nutrient uptake and growth in both organs should be reflected in the respiration rates of leaves and stems (Reich *et al.*, 1998a,b). Although root respiration measurements are complicated, especially *in situ*, we found good agreement between leaf and root respiration rates (Fig. S1). However, studies comparing the physiology of leaves and roots are scarce (but see Loveys *et al.*, 2003; Reich *et al.*, 2008) and limited by methodological constraints to quantify traits such as nutrient uptake capacity and root respiration accurately (Freschet *et al.*, 2020). We hope the near future will see improved capabilities to scale up physiological root measurements, both in laboratory and field measurements (Griffiths & York, 2020).

However, this fast–slow continuum does not capture all of the variation in plant strategies, and not all above/belowground trait analogues were well coordinated. In particular, the composite traits of LMA and SRL have previously been assumed to be functionally analogous. However, our analyses indicate that SRL is related to the collaboration gradient (Kong *et al.*, 2019; Bergmann *et al.*, 2020; Sweeney *et al.*, 2021), and ambiguous relationships between LMA and SRL observed in previous studies are probably confounded by positive correlation between functional analogs LTD and RTD, yet no correlation between LTh and RD.

2. Traits along the 'collaboration' gradient

The collaboration gradient refers to the symbiosis with mycorrhizal fungi via the investment of carbon in a fungal partner for the return of limiting soil resources (Kong *et al.*, 2019; Bergmann *et al.*, 2020). Separate from the conservation graient, plant collaboration strategies range from 'do it yourself', with thin, high SRL roots for efficient resource uptake, to 'outsourcing' with more cortex volume and hence a larger root diameter to harbor fungal structures. While a parallel can be made with the microbial phyllosphere communities of leaves above ground, which can fix atmospheric N_2 to the benefit of the plant (Stone *et al.*, 2018), the magnitude of this outsourcing strategy is unique to the soil environment.

Apart from increasing SRL, there are other conceivable options to realize a 'do it yourself' resource acquisition. Eissenstat *et al.* (2015) found root branching to be positively correlated with SRL and negatively correlated with mycorrhizal colonization, although evidence for linked architectural and morphological traits is mixed (Comas & Eissenstat, 2009; Kong *et al.*, 2014; Liese *et al.*, 2017). Plants can also release exudates to chemically enhance inorganic phosphorus availability (Lambers *et al.*, 2006). Furthermore, root hairs are known as major structure for resource uptake (Peterson & Farquhar, 1996). They mimic the beneficial effect of mycorrhizal fungi (Schweiger *et al.*, 1995; Maherali, 2017) and could conceptually be linked to a 'do it yourself' strategy (e.g. Yang *et al.*, 2017).

3. Traits along the 'size' gradients

We found that traits related to plant size, above- and belowground, were independent of the conservation and collaboration gradients (as in Díaz *et al.*, 2016). Further, plant height and rooting depth were aligned on separate PC axes from one another, and the assumption that tall plants also root deeply was not supported by our data. This lack of correlation may be expected for several reasons. First, while greater height achieves greater access to light, changes in rooting depth can be important for multiple returns on investment, including water acquisition, nutrient uptake and anchorage. Furthermore, these belowground functions can also be achieved by adjustments in other traits, potentially diluting singular relationships above and below ground (Ennos & Pellerin, 2000; Lambers *et al.*, 2006; Maeght *et al.*, 2013; Freschet *et al.*, 2021). Second, while growing taller may be associated with increased transpiration-induced water demand and photosynthesis-related nutrient demand, growing deeper does not necessarily improve access to water if water is not limiting, nor does it increase nutrient uptake if nutrients are concentrated in shallow soil layers. However, other metrics of plant size may be more closely aligned. For example, above- and belowground biomass pools (e.g. root : shoot ratios) may reveal more consistent coordination in whole-plant size (see the following section).

Although seed mass has received considerable attention in the trait literature (Westoby, 1998; Moles & Westoby, 2004; Díaz *et al.*, 2016) and has been suggested to be closely linked to plant size (Díaz *et al.*, 2016; but see Westoby, 1998), we did not focus on this trait here because there was no first approximation of a logical belowground analog. However, recent evidence indicates that seed mass may be associated with the belowground collaboration axis (Bergmann *et al.*, 2017) and this is a tantalizing avenue for further study.

4. Further widening of the traits capturing plant form and function

Although the traits of individual roots and leaves are crucially important, how these structures are displayed (i.e. their branching architecture; Lynch, 2005) or deployed through the soil (vertical and lateral distribution; Niinemets, 2010), together with total biomass allocated to different plant tissues (Poorter *et al.*, 2012), will ultimately determine the growth and functioning of a plant. Biomass allocation over different organs is a highly plastic trait as plants adapt and respond to local conditions (Poorter *et al.*, 2012; Freschet *et al.*, 2018). However, allocation is challenging to measure in the field, particularly below ground (Freschet *et al.*, 2020), but revealing relationships between biomass pools of fine roots vs leaves (or total belowground vs aboveground biomass) could lead to more consistent trait coordination in whole-plant size than we observed between plant height and rooting depth (but see Freschet *et al.*, 2015a).

Coordination of hydraulic traits above and below ground seems vital to ensure efficient overall plant hydraulic conductance, photosynthetic rates and plant growth (Brodribb *et al.*, 2002; Fan *et al.*, 2012; Smith & Sperry, 2014). Indeed, recent reviews have compiled strong evidence for correlations between rooting depth and root conductivity, and leaf and stem conductivity in woody species (Bartlett *et al.*, 2016; Brum *et al.*, 2017; Mursinna *et al.*, 2018; McCulloh *et al.*, 2019). However, data on herbaceous species and the importance of other root hydraulic traits for leaf hydraulic traits are limited (Zhou *et al.*, 2021). Furthermore, hydraulic traits tend to be decoupled from the LES and RESpectrum (Kong *et al.*, 2014; Li *et al.*, 2015) and work on hydraulic trait coordination merits more attention from the trait research community.

5. Constraints on and potential limitations of plant form and function

There are a number of factors with the potential to alter the aboveground–belowground trait correlations predicted by our conceptual thinking (Fig. 1), but in our view three stand out: trait correlations potentially differ between species' mean traits and those measured on individual plants; traits and trait correlations can change in different environments; and trait correlations probably manifest in different ways across the phylogenetic tree.

Comparison of global mean vs individual-based trait data Trait variation driven by local conditions and within-species phenotypic diversity may obscure global patterns. At the same time, global averages may also mask important above/belowground relationships that are only observed when trait sets are adapted to a common environment. Here, we observed very similar trade-offs between global species means and individual-based datasets. Although we deem our results to be generally robust, there remains substantial uncertainty surrounding the amount and importance of intraspecific variation and plasticity in trait analyses (Sultan, 2000; Weemstra *et al.*, 2021). Additional work is needed to investigate the ranges of variation within and across species and, given the focus of the current study, it would be particularly interesting to know whether there is more variation in above- or belowground traits.

Environmental constraints can synchronize or decouple plant form and function Aboveground–belowground trait correlations may shift under different environmental constraints given that traits vary along environmental and climatic gradients. Trait–environment variation is well known for aboveground traits (e.g. in responses to light (Reich *et al.*, 1998a,b; Poorter & Bongers, 2006), temperature and precipitation (Moles *et al.*, 2014; Maire *et al.*, 2015)), but also for root traits along changing soil resource availability (Holdaway *et al.*, 2011; Freschet *et al.*, 2017; de la Riva *et al.*, 2018; Fort & Freschet, 2020). Yet, evidence on whether above/belowground traits are coordinated or decoupled along environmental gradients is mixed and depends on the traits (e.g. Craine & Lee, 2003; Freschet *et al.*, 2013; Chen *et al.*, 2016; de la Riva *et al.*, 2016; Kramer-Walter *et al.*, 2016; Hu *et al.*, 2019; Zadworny *et al.*, 2021). Overall, shifting environmental constraints will probably cause trait adjustments within organs or shifts in allocation to different organs (e.g. Prescott *et al.*, 2020) and both changes could strengthen, weaken or fully decouple aboveground–belowground trait correlations. With the whole-plant trait framework developed here, we hope to inspire new work to unravel patterns of trait coordination across environmental gradients more effectively.

Trait variation among clades and across phylogenetic scales Patterns of trait variation observed across all higher plant groups will probably vary among individual clades and at different phylogenetic scales. For example, variations in leaf and root nitrogen content are decoupled in monocots and caryophyllales, yet are closely coupled within other major plant clades (Kerkhoff *et al.*, 2006; Valverde-Barrantes *et al.*, 2017). Similarly, root and leaf trait relationships observed within a genus or single species (e.g. Isaac *et al.*, 2017; McCormack *et al.*, 2020) often differ from those reported here and other studies based on more diverse cross-species surveys. Moreover, strong phylogenetic conservatism observed in many collaboration-related traits (e.g. RD, SRL, root cortex, mycorrhizal colonization; (Kong *et al.*, 2014; Ma *et al.*, 2018)) and the comparatively weak phylogenetic conservatism of LMA (Flores *et al.*, 2014) make it more likely that these trait pairs are not tightly coupled. Importantly, the degree to which traits are conserved also varies widely among different groups. For example, root diameter is highly conserved in some groups, with species in the Fagaceae often having relatively thin roots and those in the Magnoliaceae having relatively thick roots. Yet Kong *et al.* (2014) observed a greater range in first-order root diameter in the family Euphorbiaceae alone than across all other families of surveyed subtropical plants. Here again, targeted studies are needed to untangle how phylogeny and evolution have shaped above- and belowground trait coordination.

6. Future directions

Our study provides a comprehensive understanding of how plant trait variation above and below ground can be integrated at the whole-plant level. Still, despite our best efforts, we were able to assemble root trait data for only *c.* 2500 species with at least one trait measured above and below ground. In comparison, the most comprehensive aboveground trait analysis included *c.* 46 000 species (Díaz *et al.*, 2016). This illustrates the need to focus our attention on the neglected ‘hidden half’ of the plant. Yet, future efforts should not only broaden the number of observations in global root trait databases (e.g. Iversen *et al.*, 2017), but deliberately strive to fill gaps identified in this review. One such gap is the need to better understand belowground physiological processes (i.e. actual measurements of root functions such as root respiration or resource uptake that we aim to predict based on root form) where true progress is currently limited by methodological constraints.

Our framework opens up a range of perspectives in plant ecology and plant biology. Future studies should scrutinize the relevance of trait gradients for individual plant performance and upscale these findings to the community level. Past attempts to verify the ecological value of traits on different scales were of mixed success (Robinson *et al.*, 1999; Schroeder-Georgi *et al.*, 2016; Ravenek *et al.*, 2016; Fort *et al.*, 2017; van der Plas *et al.*, 2020), but the new framework might provide new insights. These insights could also help to unravel the importance of trait gradients for stress responses as shown for flooding (Mommer *et al.*, 2006; Wright *et al.*, 2017), drought (Gupta *et al.*, 2020), herbivore attack (Stam *et al.*, 2014) or interactions thereof (Pierik *et al.*, 2013; de Vries *et al.*, 2019). In particular, community-level gradients of plant trait variation might allow us to more accurately predict ecosystem functioning under climate change.

Another challenge is to reveal how environmental gradients drive trait changes. So far, studies on regional or global scales were restricted to climatic gradients for leaves (e.g. Bruelheide *et al.*, 2018) or roots (Holdaway *et al.*, 2011; Laughlin *et al.*, 2021) because we lack the data to link traits with local environmental conditions, especially soil physical and chemical properties. Abiotic conditions drive plant form and function and underpin integrated trait variation and coordination. In order to advance our understanding of trait–environment relationships, we encourage all to provide metadata on abiotic parameters together with trait information.

Our work provides the plant trait community with an integrated above- and belowground framework to build on and better understand plant growth and function under different conditions in a changing world. This framework hopefully moves beyond the trait community *per se*, as it has implications for agronomists developing crop systems, breeders incorporating root traits into breeding programs, forestry, plant growth and climate modelers who are connecting above- and belowground worlds.

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Data availability

The RCode to compile the final dataset as well as the RCode and data to reproduce all figures and analyses of this paper can be accessed at http://doi.org/10.5281/zenodo.5006671

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Results of the full quantitative literature review of 98 papers with 550 reported root–leaf–stem trait relationships presented as pie charts.

Fig. S2 Pairwise correlation of all traits used in the analysis based on the full dataset ($n = 2510$ species).

Fig. S3 Nonphylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species' mean trait data (corresponding to phylogenetically informed Fig. 3(b), with corresponding data in Table S5).

Fig. S4 Phylogenetically informed PCA on the core species set ($n = 804$) separated for nonwoody and woody plant species for the six core traits based on species' mean trait data (corresponding to Fig. 3, with corresponding data in Table S6).

Fig. S5 Three-dimensional representation of Fig. 4.

Fig. S6 PCA based on correlation matrix of species' mean traits ($n = 2510$) expanding the six core traits (see Fig. 3) to a set of 14 leaf and root traits (corresponding data in Table S9).

Fig. S7 PCA based on correlation matrix based on species' mean trait data of all traits ($n = 2510$, with corresponding data in Table S10).

Fig. S8 Sensitivity analysis for data shown in Fig. 3 to test if using different combinations of species' numbers and traits would affect the results (corresponding data in Tables S11 and S12).

Fig. S9 Nonphylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (corresponding to phylogenetically informed Fig. 5, with corresponding data in Table S14).

Methods S1 Detailed description of all methods for sections III, IV and V.

Methods S2 PRISMA flowchart of qualitative literature review.

Table S1 List of 140 papers and extracted information used for qualitative literature review.

Table S2 List of additional data sources for the main database.

Table S3 Quantitative description of all plant traits in the main database.

Table S4 Results of the phylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species' mean trait data (as shown in Fig. 3).

Table S5 Results of the nonphylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species' mean trait data (as shown in Fig. S3).

Table S6 Results of the phylogenetically informed PCA on the core species set ($n = 804$) for the six core traits based on species' mean trait data of woody and nonwoody species (as shown in Fig. S4).

Table S7 Results of the permutational multivariate analysis on the core species set ($n = 804$) including variation between different groups of species based on species' mean trait data (as shown in Fig. 3).

Table S8 Results of the PCA based on the correlation matrix of all species ($n = 2510$) for the six core traits and plant height and rooting depth (as shown in Fig. 4).

Table S9 Results of the PCA based on the correlation matrix using complete pairwise data of all species ($n = 2510$) expanding the six core traits to a set of 14 leaf and root traits (as shown in Fig. S6).

Table S10 Results of the PCA based on the correlation matrix using complete pairwise data of all species ($n = 2510$) for all traits (as shown in Fig. S7).

Table S11 Results of the PCA based on the correlation matrix using complete pairwise data for species corresponding to the full dataset ($n = 804$) for all traits (as shown in Fig. S8a).

Table S12 Results of the PCA based on the correlation matrix using complete pairwise data for all species ($n = 2510$) for only the six core traits (as shown in Fig. S8b).

Table S13 Results of the phylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (as shown in Fig. 5).

Table S14 Results of the nonphylogenetically informed PCA of traits measured on the individual plant level ($n = 455$) for the six core traits (as shown in Fig. S9).

Table S15 Results of the permutational multivariate analysis of traits measured on the individual plant level ($n = 455$) for the six core traits, including variation between different mycorrhizal types (as shown in Fig. 5).