

# Root traits and functioning: from individual plants to ecosystems

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Fine roots, the most distal portions of the root system, are responsible for the uptake of water and nutrients by plants, represent the main type of plant tissue contributing to soil organic matter accrual, and are key drivers of mineral weathering and soil microbial dynamics (Bardgett et al. 2014). Despite the overwhelming importance of fine root traits for plant and plant community functioning and biogeochemical cycles, basic information about their ecology is lacking, particularly compared to the wealth of information developed for leaves and stems. Testing hypotheses on how root traits underlie these ecosystem processes has been particularly hampered due to (1) a paucity of systematically collected data and (2) the complexity of the relationships between root traits and root, plant and ecosystem functioning. Nonetheless, the development of the field of root ecology in the last two decades has been outstanding, in particular in the compilation of belowground trait datasets (Iversen et al. 2017), methodological root ecological handbooks (Freschet et al. 2021b), novel conceptual frameworks to describe root trait diversity (Bergmann et al. 2020), its connection with belowground plant and community function (Bardgett et al. 2014, Freschet et al. 2021a), species' distributions (Laughlin et al. 2021), and scaling up traits from the individual root to the ecosystem level (McCormack et al. 2017). The papers that feature in this Special Issue on *Root traits and functioning: from individual plants to ecosystems* cover different climate regions, taxonomic and spatial scales, and a diversity of traits (Table 1) and form perfect examples of this upward moment of the belowground component in plant ecology.

## Expanding the “Root Economics Space”: New traits to characterize diverse belowground strategies across biomes

The efforts to describe the natural variation in root diversity led to the definition of the root economics space (RES), stating that interspecific variation in root traits can be framed along two key dimensions (Bergmann et al. 2020). First, a ‘collaboration axis’ organizes species based on how much they rely on mycorrhizal fungi for resource acquisition: on the one end, species produce thin roots with high specific root length (SRL, root length per unit root dry mass) through which plants acquire soil resources (i.e., the ‘do-it-yourself’ strategy), while species on the other end of this axis construct thick, low-SRL roots with ample colonization space for mycorrhizal fungi to which they outsource soil resource uptake (i.e., the ‘outsourcing’ strategy). A second, independent ‘conservation axis’, in turn, separates species with mass-dense (and presumably long-lived) roots that permits long-term resource conservation, from species with roots that are high in nitrogen concentration indicating active root metabolism and fast turnover. The establishment of this root economics space – and its four key traits (root diameter, SRL, root tissue density, and root nitrogen concentration) – provides novel and important insights into the formation of diverse belowground strategies and hence, species coexistence

and community diversity.

The studies in this Special Issue not only strengthen the concept of a RES, but expand it by focusing on novel, largely unexplored systems, traits, and (a)biotic drivers (Table 1). For example, while the pioneering work by Bergmann et al. (2020) encompasses species from around the globe, it mostly reflects trait variation across temperate species and builds on only sparse information on root trait data from the tropics. Thus far, it is not known to what extent similar dimensions underlie root trait variation across tropical species. This Special Issue presents important contributions to the discussion of how root systems may work at the tropics (Table 1). Two Forum articles in this Special Issue suggest that the RES might comprise different trait axes in tropical than temperate regions. Firstly, Weemstra et al. (2022) speculate that the ‘collaboration axis’ may be even more important for plants on highly weathered and phosphorus-limited tropical soils than in nitrogen-limited temperate systems, where the deposition of highly mobile (inorganic) nitrogen may reduce the need for investments in mycorrhizal symbiosis. Secondly, Dallstream et al. (2022) argue that phosphorus limitations in tropical regions may select for an even larger variety of root trait combinations than those reflected by the collaboration axis. For example, tropical trees may vary in the formation and traits of cluster roots, exudation rates and profiles, and root lifespan depending on the chemical forms in which phosphorus occurs in (tropical) soils. These conceptual advances highlight the need for exploring how and why a large variety of fine-root systems coexist in hyper-diverse tropical plant communities.

Besides adding information from underexplored biomes, this Special Issue further highlights the importance of incorporating additional traits covering all belowground trait categories (McCormack et al. 2017) – albeit to different extents – in the context of a RES (Table 1). For example, using meta-analyses, Stiblíková et al. (2022) report that root foraging precision (i.e., the percentage increment of root biomass in a nutrient-rich patch relative to a nutrient-poor patch) across 123 herbaceous species was unrelated to the expected traits based on the RES assumptions (i.e., SRL, root diameter, mycorrhizal colonization rate, root tissue density and root nitrogen concentration). Being able to rapidly exploit nutrient hotspots may thus be an important resource uptake strategy independent of current RES, for at least some herbaceous species. In contrast, among ten shrub species, root foraging precision was associated with the collaboration axis, as those species with thick roots and low SRL had lower foraging precision and this may be explained by the greater mycorrhizal dependency of thick-rooted species circumventing their need to produce highly exploitative, branched-out roots (Yang et al. 2021). In addition to root architectural traits, Mao and co-workers (2022) examine root mechanical traits among 12 herbaceous species in relation to the RES. Those species that displayed the do-it-yourself strategy also had more mechanically robust roots (e.g., higher tissue quality investment) than species that relied more on mycorrhizal colonization. The authors argue that species relying on their own roots rather than on fungal symbionts should develop stronger and tougher roots that are better protected against root herbivores and able to penetrate compact soils to ensure sufficient resource acquisition. These studies provide further evidence that a large variety of root traits might feature in the RES in order to understand e.g., how plants acquire resources (e.g., through root foraging success) or determine ecosystem processes such as soil stability (e.g., through root mechanical traits).

Whereas the work of Yang et al. (2021), Stiblíková et al. (2022), and Mao et al. (2022) in this issue expanded the RES with fine root traits, others delved further, beyond the absorptive roots traditionally emphasized in fine-root studies. Klimešová and Herben (2021) study non-acquisitive belowground plant organs, like rhizomes or bud-bearing roots, of close to 1500 herbaceous species with different lifespans and clonality. Here, non-clonal perennial species built roots with mass-denser tissue and a higher degree of mycorrhization than annual and clonal species. Weemstra et al. (2022) argue that besides mycorrhizal *root* traits, mycorrhizal *fungi* traits (e.g., specific hyphal length [i.e., hyphal length per unit hyphal dry mass]; the fungal analogue of specific root length) determine fungal resource uptake and thus, plant nutrition, but explicitly warn against treating and interpreting them similar to mycorrhizal *root* traits because mycorrhizal *fungi* traits serve fungal but not necessarily plant’s fitness interests. Emerging evidence further suggests that not only mycorrhizal but also soil-borne pathogenic interactions shape the RES (Xia et al. 2021). The work of Dai et al. (2022) shows that (arbuscular mycorrhizal) tree species adopting the do-it-yourself strategy had higher root pathogen richness than species exhibiting the outsourcing strategy, potentially because high-SRL roots

have greater investments in root mechanics (Mao et al. 2022) and thus lower investments in root chemical defense against infections by soilborne pathogens (Xia et al. 2021). Together, these studies focusing on interspecific variation in a broad array of belowground traits and functions highlight the multidimensionality of the belowground, and bring forward relevant candidate (biotic) traits that would play a prominent role in expanding the current RES.

### **Intraspecific patterns in root trait variation: insights towards predicting plant community responses to environmental change**

Fewer studies in this Special Issue examine how root traits vary *within* species (Table 1). Based on interspecific plant resource economics frameworks, it is widely expected that root traits shift along a conservation axis: in more adverse environments (*e.g.* , with low resource availability or high biotic stress), species would produce roots with resource-conservative traits that prolong root lifespan and retain plant resources. Evidence is mounting, however, that this prediction does not hold at the intraspecific level (Weemstra and Valverde-Barrantes 2022). Along a biotic gradient, Gagliardi et al. (2022) test whether coffee (*Coffea arabica*) plants altered their roots traits and associated endophytes along a biotic (coffee leaf rust) environmental gradient, but find that the root traits measured were not involved in foliar defenses. Such above-belowground decoupling may result from the different environmental factors that determine leaf disease development and belowground trait expressions (Gagliardi et al. 2022). Along an abiotic (elevational) environmental gradient, the study by Spitzer et al. (2022) on intraspecific variation in root traits across 16 tundra species highlights the variable ways through which different species alter a variety of root traits, or adjust the same root trait in different manners (both linearly and nonlinearly). This intraspecific trait variation (rather than species turnover) was also the main driver of root trait variation at the community level, in this study, emphasizing its importance for plant communities to cope with environmental change (Spitzer et al. 2022).

These species- and trait-specific changes in root attributes may result from the different root systems that plants can construe to handle environmental change. For example, when water availability decreases, plants can display multiple responses such as enhance their root mass fraction (i.e., root biomass per unit plant biomass), SRL, rooting depth, or investments in mycorrhizal symbiosis, to improve plant water uptake (Freschet et al. 2021a). This multitude of adaptive responses to a particular environmental cue would lead to highly idiosyncratic root trait patterns across species in response to the same stressor (Weemstra et al. 2021). This is further demonstrated by Slette and collaborators (2022) who show that the root morphological traits commonly measured and assumed to be involved in water uptake (e.g., SRL) did not change during or after droughts in their prairie grassland communities. In contrast, root productivity did significantly change (albeit in an opposite direction than generally assumed, i.e., it decreased in response to drought), but this trait is rarely measured, especially within species and in natural systems. Wang et al. (2021) arrive at similar conclusions when studying intraspecific variation in root traits in response to P limitations across different wheat genotypes. Their experimental work elucidates how different (above- and) belowground trait combinations allow plants from a single species to be equally productive under different levels of soil P, as also speculated by Dallstream et al. (2022).

The intraspecific insights that these studies raise have important implications for the interspecific RES framework. Not only can root traits be under strong plastic controls, thus changing the positions of species within the RES, but the direction in which species change is also contingent on the context, i.e., depending on species identity, environmental constraints, and temporal patterns (seasonality, ontogeny). For instance, species sampled in different seasons may display different root traits: under adverse conditions, acquisitive, lower-order roots may be shed, and only higher order roots (with distinct traits, such as higher root diameter; McCormack et al. 2015) may be sampled, and root traits themselves (like nitrogen concentration) may change over the seasons (Zadworny et al. 2015). Depending on root phenology, Species 1 (Figure 1) may appear to shift along the collaboration axis but this may not reflect a shift in the species' dependency on mycorrhizal fungi. Similarly, root traits may change with plant ontogeny, changing from thin to thick roots as plants grow bigger (Leroy et al. 2022) (Species 2; Figure 1). Guo et al. (2022) further showed that allometric relationships (and thus covariations) among root traits also changed as a function of tree size in a tropical

forest community. The position of species within the RES may thus change with time (at least, along the collaboration axis), but whether these shifts indeed reflect changes in the degree of mycorrhizal dependency is still controversial (see e.g., Leroy et al. (2022)). Temporal variation in root traits including mycorrhizal colonization rates, both at the intra-, interspecific and community level, will warrant future research.

Several studies here further demonstrate the various traits involved in belowground resource uptake strategies, which are thus relevant in the context of a RES and of species' responses to environmental change. These include, but are not restricted to, root foraging precision (Yang et al. 2021, Stiblíková et al. 2022), productivity (Yang et al. 2021, Slette et al. 2022), mechanical traits (Mao et al. 2022), exudation profiles (Dallstream et al. 2022) and enzymatic capacities (Wang et al. 2021), root biomass fractions and vertical distributions (Yang et al. 2021, Wang et al. 2021, Gagliardi et al. 2022), mycorrhizal fungal traits (Weemstra et al. 2022) or interactions with plant pathogens (Dai et al. 2022). If e.g., Species 3 in Figure 1 would adjust (combinations of) these traits whilst keeping the four key RES traits (root N, specific root length, root tissue density, and root diameter) constant, it may remain at the same position at the RES, but still display considerable belowground adjustments in their belowground strategies. At the same time, which traits are being adjusted could be species-specific (Spitzer et al. 2022), so that to conserve plant resources under environmental stress, Species 4 may enhance root diameter which in turn may enhance root lifespan (McCormack et al. 2012) whereas Species 5 increases root tissue density, as assumed by the RES framework. Together, the studies in this Species Issue provide highly important clues for the further development of the RES by identifying relevant additional traits that characterize species, their resource strategies, and coping mechanisms for environmental variation. They also show, however, that more work is needed at the intraspecific level, where root trait patterns are diverse but of great importance for predicting how plant communities cope with environmental change, and call for novel conceptual frameworks that capture this belowground plasticity (Weemstra and Valverde-Barrantes 2022).

### **Root trait variation at the plant community level: Linking belowground trait diversity to vegetation dynamics and ecosystem functioning**

Ultimately, both inter- and intraspecific variation in root traits characterize belowground strategies at the community level. In this Special Issue, root trait patterns within plant communities (Table 1) reiterate what is observed within and across species, namely, that plants can display a wide variety of root trait strategies to carry out their belowground functions. Pierick and collaborators (2022) study the variation in root traits in tropical montane forests along an altitudinal gradient in the Andes. In their case, although there were weak trends towards more conservative root trait syndromes on high altitudes with deteriorating soil conditions, all tropical forest communities showed high within-community variance in root traits at each altitude, confirming the importance of multiple strategies for resource capture in tropical forests. In addition, Kotowska et al. (2022) present compelling evidence that expected ecological trends in trait syndromes, like the dominance of “acquisitive traits” in secondary succession, were not supported after comparing mature and secondary forests in Indonesia, despite the large productivity of the secondary forests. Finally, Erktan and colleagues (2022) provide an in-depth view of root diameter distributions, where most of the temperate plant communities (including woody and non-woody species) they studied, showed a multimodal distribution of root diameter reflecting the distinct belowground strategies to exploit soil resources that exist within plant communities.

Such belowground trait diversity may in turn explain vegetation dynamics. Using a novel deep-learning approach to detect roots and analyze root growth images from a rhizobox, Alonso-Crespo et al. (2022) show that the vertical distribution of roots depended on which functional group was arrived first within a plant community. This may in turn determine competitive outcomes among plant species, and thus determine the overall coexistence and exclusion of species within plant communities. Furthermore, Schuster and co-workers (2022) find evidence for belowground overyielding (i.e., greater root standing biomass and root productivity in species' mixtures compared to monocultures) in temperate forest communities, especially among angiosperm trees. The authors argue that such differences in belowground productivity may occur due to the greater diversity in root systems in angiosperms compared to gymnosperms, reflecting belowground resource

partitioning, and thereby link diversity in belowground strategies to an important ecosystem function.

### **Extending the root system: incorporating microbial communities associated with roots**

The root-associated microbiome, i.e., the diverse community of micro-organisms tightly associated with roots (Alekklett and Hart 2013), is of particular interest to biodiversity research given the important functional roles played by root associated microbes in root and rhizosphere processes. In this issue, several studies look into the relationships between soil, rhizosphere and root endophytic microbial community composition, root functional traits, and soil properties. Mafa-Attoye et al. (2022) confirm a rhizosphere effect (i.e., microbial changes in the soil directly around the roots mediated by root activity (Hiltner 1904)), demonstrating substantial differentiation in terms of community composition and functioning between rhizosphere and bulk soil microbial communities (although only for bacterial and archaeal, but not fungal communities) across four agro-ecological systems. In contrast, Merino-Martín and collaborators (2022) only observed differences in fungal, but not bacterial communities, between rhizosphere and bulk soil along an elevation gradient. This rhizosphere effect is also partly related to variation in inter- (Mafa-Attoye et al. 2022, Merino-Martín et al. 2022) and intraspecific (Gagliardi et al. 2022, Leroy et al. 2022) variation in root morphological traits that are found here to predict the community composition of the root-associated microbiome.

Despite these important contributions, important open questions remain. For instance, the collaboration axis is a key dimension in the RES, but it only explicitly accounts for symbiotic and not pathogenic interactions, which may also drive (interspecific) differences in root traits (Dai et al. 2022). Furthermore, the RES framework predicts a greater abundance of symbiotic microbes in thick roots (i.e., representing the ‘outsourcing’ strategy) at the interspecific level, but Gagliardi and co-workers (2022) found the opposite pattern intra-specifically. Additional variables, such as plant ontogeny (see Leroy et al. (2022)); the spatial scale at which plant-microbe interactions are studied (see Merino-Martín et al. (2022)); and the necessity to invest in plant root pathogen defense (Dai et al. 2022) may provide valuable insights in unraveling the extent to which soil properties, root traits, and microbial communities (and associated functioning) interact (in)directly, and ultimately, shape plant community diversity and ecosystem functioning.

The publications in this Special Issue *Root traits and functioning: from individual plants to ecosystems* comprise a diversity of plant belowground traits (Table 1) that are involved in the different functional processes of plants (water and nutrient uptake; plant defenses against below- and aboveground pathogens; anchorage; competitive capacities; belowground symbioses) and ecosystems (soil stability; belowground productivity; vegetation dynamics). Building on different and novel methodological approaches (from meta-analyses and machine-learning to greenhouse experiments and field study) and systems (crops, agro-ecological settings and natural conditions), they expand our global belowground datasets (Table 1). Together, they underwrite the multidimensionality of the belowground world of plants across biomes (from alpine tundra vegetation to tropical forests); taxonomic (from the plant community to the intraspecific level) and spatial (from microbial processes, to the whole plant and ecosystem) scales and maintain the momentum of root ecology.

### **References**

- Alekklett, K. and Hart, M. 2013. The root microbiota—a fingerprint in the soil? - *Plant Soil* 370: 671–686.
- Alonso-Crespo, I. M. et al. 2022. Assembly history modulates vertical root distribution in a grassland experiment. - *Oikos* n/a: e08886.
- Bardgett, R. D. et al. 2014. Going underground: root traits as drivers of ecosystem processes. - *Trends in Ecology & Evolution* 29: 692–699.
- Bergmann, J. et al. 2020. The fungal collaboration gradient dominates the root economics space in plants. - *Sci Adv* 6: eaba3756.
- Dai, D. et al. 2022. Correlation between fine root traits and pathogen richness depends on plant mycorrhizal types. - *Oikos* n/a: e09354.

- Dallstream, C. et al. 2022. A framework for fine-root trait syndromes: syndrome coexistence may support phosphorus partitioning in tropical forests. - *Oikos*: e08908.
- Erktan, A. et al. 2022. Dissecting fine root diameter distribution at the community level captures root morphological diversity. - *Oikos*: oik.08907.
- Freschet, G. T. et al. 2021a. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. - *New Phytol*: nph.17072.
- Freschet, G. T. et al. 2021b. A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. - *New Phytol* 232: 973–1122.
- Gagliardi, S. et al. 2022. No evidence of foliar disease impact on crop root functional strategies and soil microbial communities: what does this mean for organic coffee? - *Oikos* in press.
- Guo, Z. et al. 2022. Are fine roots ‘leaves underground’ in terms of allometry? A test in a tropical forest successional series in southwest China. - *Oikos* in press.
- Hiltner, L. 1904. Über neuere Erfahrungen und Problem auf dem Gebiet der Bodenbakteriologie unter besonderer Berücksichtigung der Grundungung und Brache. - *Arbeiten der Deutsche Landwirtschaftliche Gesellschaft* 98: 59–78.
- Iversen, C. M. et al. 2017. A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. - *New Phytol* 215: 15–26.
- Klimešová, J. and Herben, T. 2021. The hidden half of the fine root differentiation in herbs: nonacquisitive belowground organs determine fine-root traits. - *Oikos*: oik.08794.
- Kotowska, M. M. et al. 2022. Consequences of tropical rainforest conversion to tree plantations on fine root dynamics and functional traits. - *Oikos* in press.
- Laughlin, D. C. et al. 2021. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. - *Nat Ecol Evol* in press.
- Leroy, C. et al. 2022. Ontogenetic changes in root traits and root-associated fungal community composition in a heteroblastic epiphytic bromeliad. - *Oikos* n/a: e09213.
- Mafa-Attoye, T. G. et al. 2022. Roots alter soil microbial diversity and interkingdom interactions in diversified agricultural landscapes. - *Oikos* in press.
- Mao, Z. et al. 2022. Intra- and inter-specific variation in root mechanical traits for twelve herbaceous plants and their link with the root economics space. - *Oikos* n/a: e09032.
- McCormack, M. L. et al. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. - *New Phytologist* 195: 823–831.
- McCormack, M. L. et al. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. - *New Phytol* 207: 505–518.
- McCormack, M. L. et al. 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. - *New Phytol* 215: 27–37.
- Merino-Martin, L. et al. 2022. Habitat partitioning of soil microbial communities along an elevation gradient: from plant root to landscape scale. - *Oikos* n/a: e09034.
- Pierick, K. et al. 2022. Elevational trends of tree fine root traits in species-rich tropical Andean forests. - *Oikos* n/a: e08975.
- Schuster, M. J. et al. 2022. Patterns of belowground overyielding and fine-root biomass in native and exotic angiosperms and gymnosperms. - *Oikos* n/a: e08877.

Slette, I. J. et al. 2022. Repeated extreme droughts decrease root production, but not the potential for post-drought recovery of root production, in a mesic grassland. - *Oikos* n/a: e08899.

Spitzer, C. M. et al. 2022. Root trait variation along a sub-arctic tundra elevational gradient. - *Oikos* n/a: e08903.

Stiblikova, P. et al. 2022. Interspecific differences in root foraging precision cannot be directly inferred from species' mycorrhizal status or fine root economics. - *Oikos* in press.

Wang, X.-X. et al. 2021. Plasticity and co-variation of root traits govern differential phosphorus acquisition among 20 wheat genotypes. - *Oikos* in press.

Weemstra, M. and Valverde-Barrantes, O. J. 2022. Above- and below- ground trait responses to environmental variation: the need to distinguish inter- and intraspecific variability. A commentary on 'Above and below-ground plant traits are not consistent in response to drought and competition treatments.' - *Annals of Botany*: 3.

Weemstra, M. et al. 2021. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. - *Functional Ecology* 35: 342–356.

Weemstra, M. et al. 2022. Incorporating belowground traits: avenues towards a whole-tree perspective on performance. - *Oikos* in press.

Xia, M. et al. 2021. Coordination between compound-specific chemistry and morphology in plant roots aligns with ancestral mycorrhizal association in woody angiosperms. - *New Phytologist* 232: 1259–1271.

Yang, Y. et al. 2021. Linking fine-root architecture, vertical distribution and growth rate in temperate mountain shrubs. - *Oikos* in press.

Zadworny, M. et al. 2015. Seasonal variation in chemistry, but not morphology, in roots of *Quercus robur* growing in different soil types. - *Tree Physiology* 35: 644–652.

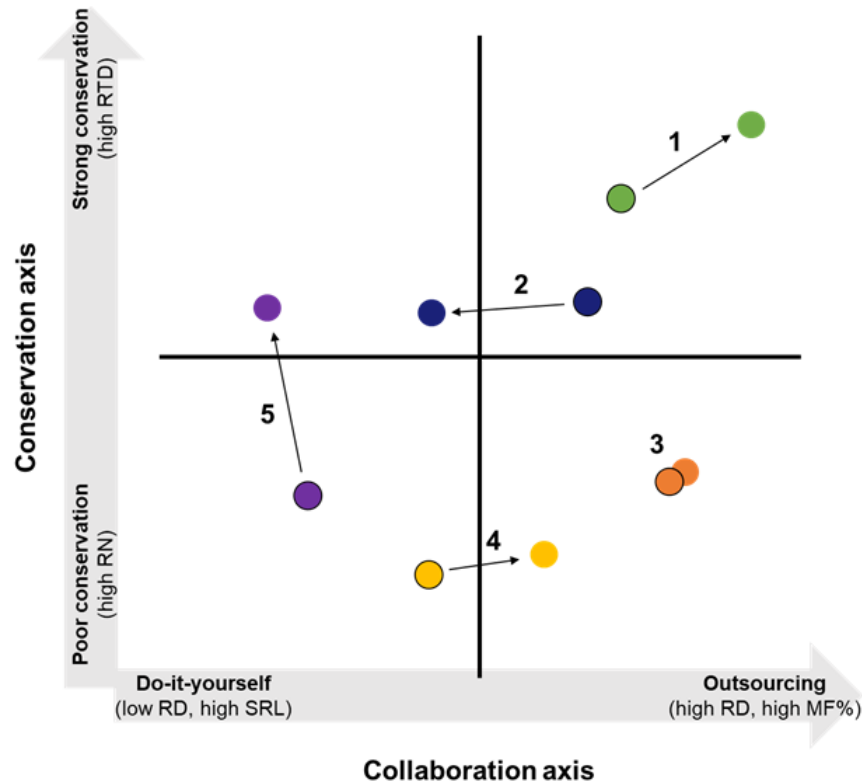
## Tables, Figures

**Table 1.** Overview of publications in this Special Issue and the biomes, taxonomic scales and belowground traits that they cover. Trait categories are derived from McCormack et al. (2017). For the trait overview: \*, references that did not measure traits but discuss these conceptually (i.e., in the two Forum papers) or used trait data from existing databases; other references include newly collected trait data.

Climate region	Reference in this Special Issue
Temperate	Alonso-Crespo et al. (2022); Erktan et al. (2022); Klimešová & Herben (2022); Mafa-Attoye et al. (2022); Mao et al. (2022); Merino-Martin et al. (2022); Schuster et al. (2022); Slette et al. (2022); Yang et al. (2022)
(Sub)Tropical	Dai et al. (2022); Dallstream et al. (2022); Gagliardi et al. (2022); Guo et al. (2022); Leroy et al. (2022); Kotowska et al. (2022); Pierick et al. (2022)
(Sub)Arctic	Spitzer et al. (2022)
Taxonomic scale	
Community	Alonso-Crespo et al. (2022); Erktan et al. (2022); Guo et al. (2022); Kotowska et al. (2022); Mafa-Attoye et al. (2022); Merino-Martin et al. (2022); Pierick et al. (2022); Schuster et al. (2022); Slette et al. (2022); Spitzer et al. (2022); Weemstra et al. (2022)*

Species	Dai et al. (2022); Dallstream et al. (2022)*; Klimešová et al. (2022)*; Mao et al. (2022); Spitzer et al. (2022); Stiblíková et al. (2022)*; Weemstra et al. (2022)*; Yang et al. (2022)
Individual (within species)	Gagliardi et al. (2022); Leroy et al. (2022); Mao et al. (2022); Spitzer et al. (2022); Wang et al. (2022)
<b>Root trait category</b>	
<i>Anatomy</i> (e.g., stele diameter, absence/presence of arbuscules)	Leroy et al. (2022)
<i>Architecture</i> (e.g., branching intensity, root tip density)	Leroy et al. (2022); Spitzer et al. (2022); Yang et al. (2022)
<i>Chemistry</i> (e.g., root concentration of nitrogen, secondary compounds)	Dallstream et al. (2022)*; Erktan et al. (2022); Gagliardi et al. (2022); Klimešová et al. (2022)*; Kotowska et al. (2022); Mafa-Attoye et al. (2022); Mao et al. (2022); Merino-Martin et al. (2022); Pierick et al. (2022); Stiblíková et al. (2022)*; Spitzer et al. (2022);
<i>Dynamics</i> (e.g., root lifespan, root production)	Alonso-Crespo et al. (2022); Dallstream et al. (2022)*; Kotowska et al. (2022); Schuster et al. (2022); Slette et al. (2022); Weemstra et al. (2022)*; Yang et al. (2022)
<i>Mechanics</i> (e.g., toughness, tensile strength)	Mao et al. (2022)
<i>Morphology</i> (e.g., specific root length, root diameter)	Dai et al. (2022); Dallstream et al. (2022)*; Erktan et al. (2022); Gagliardi et al. (2022); Guo et al. (2022); Klimešová et al. (2022)*; Kotowska et al. (2022); Leroy et al. (2022); Mafa-Attoye et al. (2022); Mao et al. (2022); Merino-Martin et al. (2022); Pierick et al. (2022); Stiblíková et al. (2022)*; Slette et al. (2022); Spitzer et al. (2022); Wang et al. (2022); Weemstra et al. (2022)*; Yang et al. (2022)
<i>Microbial</i> (e.g., mycorrhizal type, endosphere community composition)	Dai et al. (2022); Dallstream et al. (2022)*; Gagliardi et al. (2022); Klimešová et al. (2022)*; Leroy et al. (2022); Merino-Martin et al. (2022); Stiblíková et al. (2022)*; Weemstra et al. (2022)*
<i>Physiology</i> (e.g., enzyme activity, nutrient uptake)	Dallstream et al. (2022)*; Wang et al. (2022)
<i>System</i> (e.g., root mass fraction, maximum rooting depth)	Alonso-Crespo et al. (2022); Dallstream et al. (2022)*; Gagliardi et al. (2022); Klimešová et al. (2022); Leroy et al. (2022); Mafa-Attoye et al. (2022); Merino-Martin et al. (2022); Schuster et al. (2022); Stiblíková et al. (2022)*; Wang et al. (2022); Weemstra et al. (2022)*; Yang et al. (2022)





**Figure 1.** Implications of intraspecific variation in root traits for an interspecific Root Economics Space (RES). The graph shows a conceptual diagram of the interspecific RES with the collaboration gradient on the x-axis which ranges from species that rely on their own roots (i.e., the do-it-yourself strategy) to species that depend on mycorrhizal symbiosis (i.e., the outsourcing strategy) for soil resource uptake. The y-axis represents the conservation gradient separating species with root traits that permit poor to strong conservation of plant resources. These two axes are further explained in the main text. Each dot with a black outline represents a given species positioned in the RES depending on its root trait expressions (*RD* , root diameter; *SRL* , specific root length; *MF* %, mycorrhizal colonization rate; *RN* , root nitrogen concentration; *RTD* , root tissue density). Dots with the same color but without the black outline represent the same species after it shifted positions within the RES due to intraspecific variation in the corresponding root traits. Numbers in the graph refer to the hypothesized underlying cause of this shift further outlined in the main text.