Review

Size matters for linking traits to ecosystem multifunctionality

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A priority research field addresses how to optimize diverse ecosystem services to people, including biodiversity support, regulatory, utilitarian and cultural services. This field may benefit from linking ecosystem services to the sizes of different body parts of organisms, with functional traits as the go-between. Using woody ecosystems to explore such linkages, we hypothesize that across stem diameter classes from trunk via branches to twigs, key wood and bark functional traits (especially those defining size-shape and resource economics spectra) vary both within individual trees and shrubs and across woody species, thereby together boosting ecosystem multifunctionality. While we focus on woody plants aboveground, we discuss promising extensions to belowground organs of trees and shrubs and analogs with other organisms, for example, vertebrate animals.

How size may matter to multiple ecosystem functions and services via trait variations

Plants provide important services to support the lives of many other organisms including people, both during the plants' life and afterlife (Figure 1A). For instance, trees and shrubs regulate essential climate and soil properties and provide habitat and food resources that support biodiversity, as well as other regulatory, utilitarian, esthetic, cultural, and supporting services; these services benefit human livelihood and wellbeing [1–6]. Quantifying and valorizing these ecosystem services, and finding the best balance in terms of **ecosystem multifunctionality** (see Glossary) [3,7–11], has become booming business and a fast expanding research field among social scientists, ecologists, economists, and policymakers. A field of study apparently unrelated to that of ecosystem multifunctionality deals with the relationships between the sizes of different parts or entire bodies of organisms, and how such body size variation relates to different morphologies and important functions such as physical strength, metabolic rates, and transport of resources [12–17]. Such size patterns can be studied both within individuals and species and across species of plant or animal. Here we show (i) how we can gain new insights into ecosystem multifunctionality by explicitly linking the sizes of different body parts of organisms to ecosystem services; and (ii) how we can achieve this by using **functional traits** to link these above-mentioned, currently disparate research fields of ecosystem services and body size biology and ecology. These linkages can be understood nicely by taking trees as our study object. Stems are the skeleton, the resource transport infrastructure, and the bearers of organs for photosynthesis and reproduction of the plant. They range in length from a few millimeters (e.g., in seedlings) to hundreds of meters per individual. They also range in diameter by three or four orders of magnitude, both across organs within individual trees and across plant species. Importantly, stems of trees and shrubs generally taper in diameter from base to tip, that is, from the wide trunk or main stems via the branches to the narrow twigs (Figure 1) [14,17]. This tapering in stem diameter is associated with the tapering of xylem vessel diameters to optimize the water and nutrient transport function of the tree [18]. Here we introduce our main point, that is, the size (i.e., diameter) differences and/or size diversity of different woody organs (main stem, branches, twigs) within plants and among species is

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associated with important variation in functional traits; and that, thereby, variation in stem size is important for providing many functions and services of the ecosystems.

For instance, the flowers and fruits of most shrubs and trees are mostly borne only on the thinner branches and twigs, making especially the outer canopy important to a great diversity of pollinating and frugivorous invertebrate and vertebrate animals (including people) that can access the canopy. However, especially in the tropics some cauliflorous trees, for example, cocoa (*Theobroma cacao*), produce big fruits on their coarse main stem (as they are too heavy to be supported by thinner stems [19]), thereby providing food to large mammals (including people) that cannot easily access the fruits in the tree canopy. Also, many tree and shrub taxa perform substantial photosynthesis with the green bark of their thinner branches and twigs but not their coarse branches and trunks [20,21]. These photosynthetic bark tissues must be relatively high in nitrogen [N, in RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase)] and carbohydrates [22,23], making them a palatable food source to certain herbivores. Others, especially mammalian herbivores, browse the bark of the trunk of the same or different trees, depending on the bark nutritional value.

Also, the stems of different diameters themselves lead to different functions to the ecosystem and different services to people (Figure 1B). For example, beavers cut down big trees and use their trunks for building dams (thereby regulating ecosystem hydrology), big branches for building their castle, and twigs for food. Some bird species build nests (in some cases containing twig litter) on or between branches, while woodpeckers make nest holes in trunks, which in turn can be used by multiple other cavity-breeding bird species as an example of (biodiversity) supporting services [24]. The same is true for humans; as examples of utilitarian services, we use tree trunks or big branches to construct buildings or furniture but small branches and twigs to weave baskets. We can extend these size differences to belowground organs and dead trees or abscised dead stems, as different size classes of roots and deadwood provide very different ecosystem functions and services, as discussed in Boxes 1 and 2, respectively. The examples above have emphasized the overall differences in traits and services between trunks, branches, and twigs within and across tree species. Moreover, following the ontogenetic development of tree individuals, the diameters of main stems and branches also increase as trees grow from seedling via sapling to adulthood and these changes will be associated with changes in functional traits. Here we add to all this the important trait variance that can be observed among woody species within a given diameter class, that is, within trunks, branches, or twigs. Together, these and further observations (Figure 1B) lead us to the hypothesis that trait variation across stem diameter classes within individuals, and how such 'vertical' trait patterns vary 'horizontally' between species and individuals, together regulate ecosystem services and promote multifunctionality. Below, we will discuss key aspects of this hypothesis, by linking organ size of trees and shrubs, via two groups of functional traits, to ecosystem multifunctionality. While focusing initially on living aboveground parts of trees and shrubs, we will discuss laterally whether and how this concept may also apply to belowground plant parts (Box1), to dead plant parts (Box 2), and to other types of organisms of very distant evolutionary position (Box 3).

Linking stem size variation to ecosystem multifunctionality

It is useful to distinguish between traits related to the resource economy of plants and morphological, that is, size- and shape-related traits, as they play very different roles in ecosystem functions and services (Figure 2). First, based on evidence from a substantial body of previous research, the provisioning of multiple ecosystem services is linked to interspecific variation in traits associated with the carbon and nutrient economy of plants, together forming the plant economic spectrum (PES) [25,26] or **resource economic spectrum (RES)** [27]. For example, plant traits affect

Glossary

Brown food web: a food web that depends on the afterlife of primary producers or their parts, where dead plant biomass provides the source of energy for decomposers and their consumers [35].
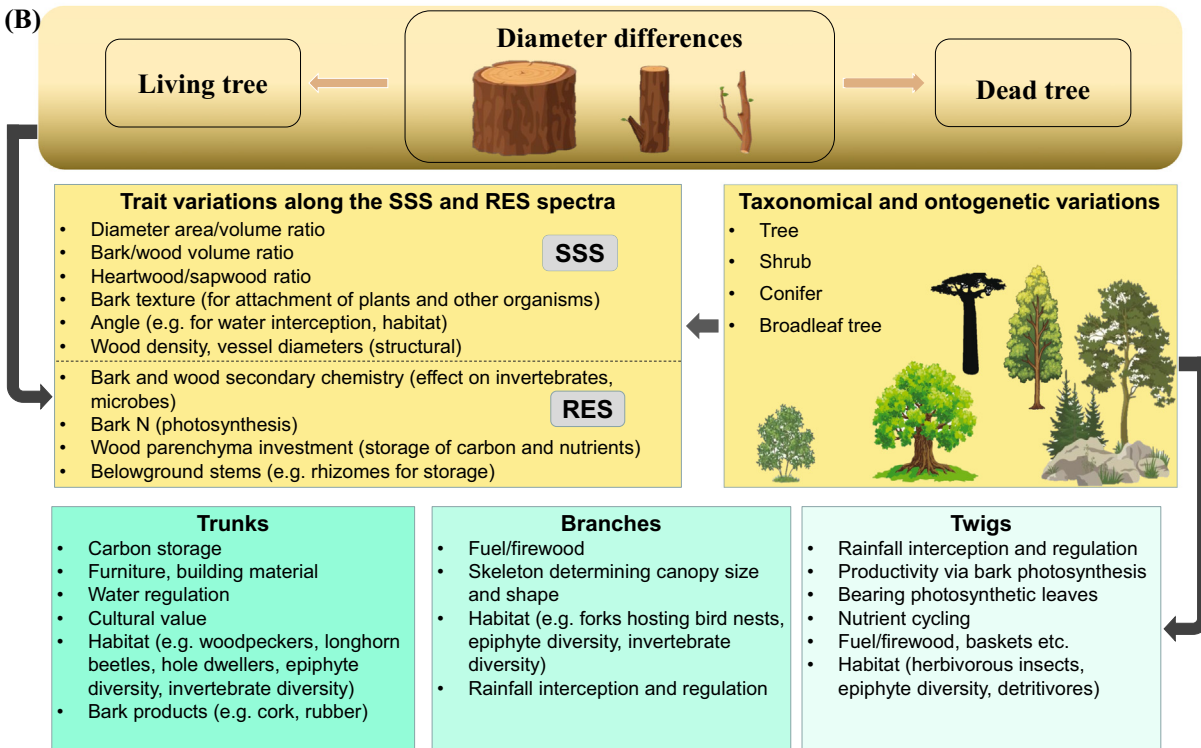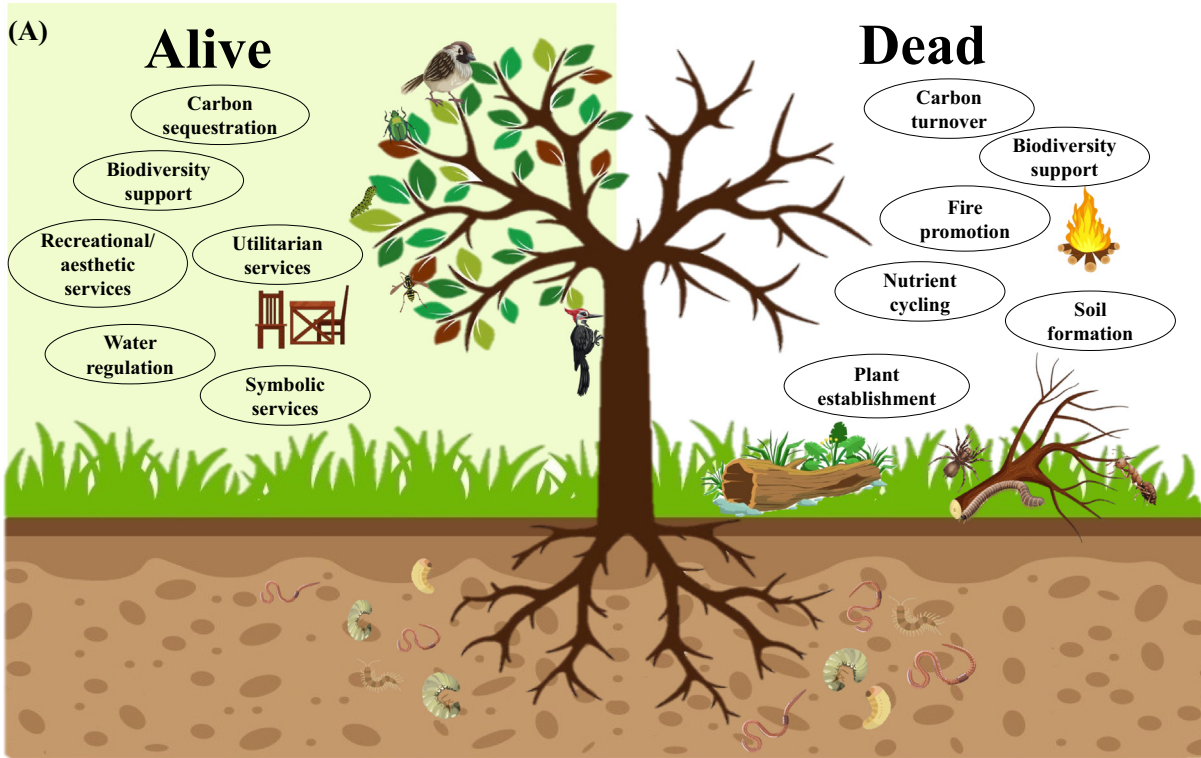
Ecosystem multifunctionality: the multiple ways in which ecosystems can simultaneously provide different functions and, thereby, services that are of socioeconomic value to humanity. Multifunctionality is defined here according to stakeholder priorities, ranging from regulatory to utilitarian, esthetic, cultural, and supporting services [6].

Functional traits: any morphological, anatomical, physiological, or phenological characteristics measurable at the individual level. Functional traits reflect the adaptation of plants to their living environments and their potential influence on ecosystem functions and services [29].

Green food web: a food web in which the primary producers, while alive, provide energy that flows through different trophic levels [35].

Resource economic spectrum (RES): a multivariate continuum encompassing the information of plant structural and biochemical trait tradeoffs and covariations related to the uptake, processing, and turnover of resources such as carbon, nutrient, and water; each position along this continuum represents one of many possible strategies associated with relative investment in resource acquisition versus resource conservation [27].

Size and shape spectrum (SSS): a multivariate trait continuum encompassing the information of the functional variation in the size and shape of plant parts ranging from small and simple in shape to large with more intricate shape [27].

(A) Alive

- Carbon sequestration
- Biodiversity support
- Recreational/aesthetic services
- Utilitarian services
- Water regulation
- Symbolic services

Dead

- Carbon turnover
- Biodiversity support
- Fire promotion
- Nutrient cycling
- Soil formation
- Plant establishment

(B)

Diameter differences

Living tree ← Diameter differences → Dead tree

Trait variations along the SSS and RES spectra

SSS
- Diameter area/volume ratio
- Bark/wood volume ratio
- Heartwood/sapwood ratio
- Bark texture (for attachment of plants and other organisms)
- Angle (e.g. for water interception, habitat)
- Wood density, vessel diameters (structural)

RES
- Bark and wood secondary chemistry (effect on invertebrates, microbes)
- Bark N (photosynthesis)
- Wood parenchyma investment (storage of carbon and nutrients)
- Belowground stems (e.g. rhizomes for storage)

Taxonomical and ontogenetic variations
- Tree
- Shrub
- Conifer
- Broadleaf tree

Trunks
- Carbon storage
- Furniture, building material
- Water regulation
- Cultural value
- Habitat (e.g. woodpeckers, longhorn beetles, hole dwellers, epiphyte diversity, invertebrate diversity)
- Bark products (e.g. cork, rubber)

Branches
- Fuel/firewood
- Skeleton determining canopy size and shape
- Habitat (e.g. forks hosting bird nests, epiphyte diversity, invertebrate diversity)
- Rainfall interception and regulation

Twigs
- Rainfall interception and regulation
- Productivity via bark photosynthesis
- Bearing photosynthetic leaves
- Nutrient cycling
- Fuel/firewood, baskets etc.
- Habitat (herbivorous insects, epiphyte diversity, detritivores)

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(See figure legend at the bottom of the next page.)

Box 1. Extending the concept of plant organ size, functional traits, and ecosystem multifunctionality to belowground organs

In analogy with the aboveground tree organs, variation in the functional traits of different belowground organs of different size classes may further add to ecosystem multifunctionality. For instance, the proportions of plants' belowground resource investment, and their physical structure, chemical form, and recalcitrance, vary across root diameters. Above-ground and belowground organs are allometrically connected: wider trunks are generally supported by thicker coarse roots and rhizomes (belowground stems). Coarse roots and rhizomes tend to store much mobile carbohydrate while supporting extensive root systems to promote soil stability and water extraction from deeper layers. By contrast, fine roots are the actual sites for water and nutrient uptake. They also contribute importantly to the long-term soil carbon pool [44]. First, root litter decomposability (see Box 2) is low compared with that of leaves, while it shows large interspecific variation based on structural and chemical traits [45,46]. Moreover, hyphal networks of mycorrhizal fungi associated with fine roots [47] are a predominant contributor to (relatively stable) soil carbon in colder biomes, partly because of the recalcitrant fungal chemistry [48,49]. There is enormous variation in this mycorrhizal contribution to soil carbon, for example, ectomycorrhizal ecosystems store much more belowground carbon than arbuscular mycorrhizal ones [49].

Also, dicot plants tend to have thicker fine roots with stronger mycorrhizal dependency than monocots [50], likely resulting in greater carbon accumulation per unit root mass, while within these plant taxa there is great interspecific variation in mycorrhizal colonization [51]. In general, plant root diameter plays an important role in driving rhizosphere fungal community composition, with important implications for belowground biodiversity and associated services such as carbon sequestration, nutrient provisioning, and pest control [52]. It is poorly understood how root diameters relate to communities of other organisms like bacteria, protists, and invertebrates and their associated belowground ecosystem functions (but see [53]).

A remarkable phenomenon of root diameter and ecosystem function are the snow roots of *Corydalis conorhiza* in the Caucasus Mountains [54]. These extremely fine roots, complementary to the much coarser, soil-borne roots of itself and coexisting species, grow upward into snowfields, thereby taking up 'new'N that would otherwise run off downslope and which instead enriches N-limited snowbed communities. Important for ecosystem multifunctionality is how the combinations of different trait values and functions across root diameters of coexisting species complement the functions and services provided by the same species aboveground. This research gap is in strong need of empirical investigation.

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ecosystem carbon and nutrient cycling through their role in plant growth and dead matter turnover (Figure 1 and Box 2). Across species, fast cycles (fast growth and fast litter decomposition) are linked with large specific leaf area and high concentrations of N and phosphorus (P) of living plant parts involved in photosynthesis and nutrient acquisition, while slow cycles (slow growth and slow litter decomposition) tend to be linked to high tissue dry matter content (DMC), high lignin content, and C:N ratio [28–31]. Furthermore, mixed-species tree canopies support high biodiversity by providing myriad habitats and food sources for the '**green food web**'. The tissue quality of leaves and stems (e.g., contents of N, P, carbohydrates, and secondary compounds) determines the palatability to wide-ranging insects [32–34], while these insects in turn support populations of predators [35], for example, insectivorous birds.

Recently, interspecific variation in the size and shape of leaves and twigs, summarized as the **size and shape spectrum (SSS)**, has been linked conceptually to ecosystem functions and services as well, both during the life and afterlife of plant organs [27,36]. For instance, bark fissuredness varies greatly both among species and stem diameters, thereby determining the diversity and composition of invertebrate communities [37–39]. An additional aspect of the SSS is the tree architecture, which also involves the degree of ramification, branch densities in the canopy and the angles (from vertical to horizontal) of the trunks, branches, and twigs, respectively. The main stem may be unbranched, like that of a palm tree, slightly branched, like that of a conifer tree, or richly branched, like that of the sacred fig (*Ficus religiosa*). These aspects of SSS impact on biodiversity (e.g., via nesting sites), while they may also cause spatial heterogeneity in rainfall

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Figure 1. Summary of the main ways in which trees, from trunk to twig, determine ecosystem services. (A) Cartoon showing the ecosystem services determined by living and dead (parts of) trees in the ecosystem. (B) Diagram summarizing how evolutionary and ontogenetic differences in diameter classes of trunks, branches, and twigs of living and dead trees link with ecosystem functions and services directly and indirectly through trait variation along the size and shape spectrum (SSS), and the resource economic spectrum (RES).

Box 2. The afterlife legacy of the stem size–trait–ecosystem multifunctionality linkages

The functional traits that are important for ecosystem functions and services during the lifetime of organisms or their body parts, often leave an important legacy on (often different) ecosystem functions and services once these organisms or their body parts die (see Figures 1 and 2Aiii,Biii in main text). In the case of trees and shrubs, for instance, depending on the tree species' traits, trunks can be important for carbon sequestration and, thereby, regulation of global temperatures, while twigs with certain trait makeup can play a key role in surface litter ignition and wildfire spread. In central China, people traditionally collect foliated twigs of the conifer *Cunninghammia lanceolata* for fire-making, a utilitarian service. In general, RES-related traits of dead plant parts are important for the '**brown food web**'. For example N, P, DMC, lignin content, and C:N ratio indicate the litter substrate quality, and determine the composition and activity of the decomposer community and the animals feeding on them [31,35,55] and, thereby, the associated rates of carbon and nutrient cycling and soil fertility [45]. Along the RES spectrum, larger stems with denser tissues (higher DMC) will decompose slowly [28,56] and thereby provide a long-term habitat, while in low DMC, more decomposable dead stems will provide a good albeit transient habitat to invertebrates [31,57] (cf. [55] for leaves). Litter traits belonging to the SSS influence the compaction and cohesion of the soil organic layer, thereby potentially regulating soil surface water retention [27], surface flammability [36], and soil fauna composition [55]. As an alternative carbon release process besides fire, wood decomposition is an important control on atmospheric CO_2 concentrations and thereby climate [42,58].

Deadwood diameter tends to be negatively related to decomposition rate for given tree species [28,59] and for trunks across different tree species [60]. However, the diameter effect on wood decomposition is not merely a matter of the surface area to volume ratio, determining the accessibility to decomposers. A key finding from a stem litterbag study in shrubby steppe in China was that wider stems had slower litter decomposition rates not only via greater relative surface exposure, but also indirectly via their higher wood DMC or lower wood N content [61]. Thus, wood decomposition is driven by both SSS traits and RES traits from tree logs via dead branches to twig litter. These relationships will also affect biodiversity as a key ecosystem service. Logs with larger diameter and/or more complex wood and bark structure (high SSS trait values) will provide more habitat options to larger invertebrate species, while logs with smaller diameter and/or denser tissue with smaller lumens will provide less hospitable habitat space [62].

Ontogeny also has consequences for ecosystem services in the tree's afterlife. For instance, with tree age, more refractory secondary compounds accumulate in heartwood of coarse woody parts such as the trunk, and the proportion of heartwood to sapwood increases [63], resulting in a higher proportion of recalcitrant compounds and, after tree death, slower decomposition [42,58]. This ontogenetic contribution to decomposability is closely linked to size distribution, as trunk diameters of a given individual increase with age. All of the above afterlife effects of stem size-related trait variation on ecosystem functions and services will add to the stem size–trait effects on ecosystem functions and services during the lifetime of trees and shrubs, thereby promoting overall ecosystem multifunctionality (see Figure 2Aiii,Biii in main text).

interception rates [40], thereby regulating soil hydrology and potentially creating microclimatic niche diversity both in the canopy layer and on the forest floor. Large variance in stem SSS and RES traits from trunk via branches to twigs may also promote esthetic services (e.g., the visual attractiveness of diverse architectures and bark textures) and utilitarian ones (e.g., twig bark of some species used for spices like cinnamon, trunk bark used for rubber, frankincense, or cork). Regulatory service effects are exemplified by the interspecific variation in bark flammability in Australian eucalypts; in some species only the trunks (not the small branches and twigs) produce large amounts of bark flakes, either hanging from the trunk or accumulating on the forest floor, thereby promoting wildfires [41]. The proportion and density of tree individuals of such fire-promoting species in a stand will greatly affect fire regimes and thereby people's livelihoods and biodiversity.

Thus far, the available studies on the RES and SSS have focused mostly on leaf traits and have largely overlooked that stems, especially those of trees and shrubs, vary greatly in their traits, not only among different species for a given diameter, but also across the different stem diameters of a given plant. This variation, and its hypothesized consequences for ecosystem multifunctionality, are illustrated in Figure 2. At the functionally poor end of trait variance, for instance, a monospecific stand of similarly aged trees (Figure 2Ai), a given organ (trunk, branch, twig) will not vary by much among individuals in diameter (SSS), bark texture (SSS), or chemical composition (RES), leading to low ecosystem multifunctionality (Figure 2Aii,iii). Adding another tree species to such a stand
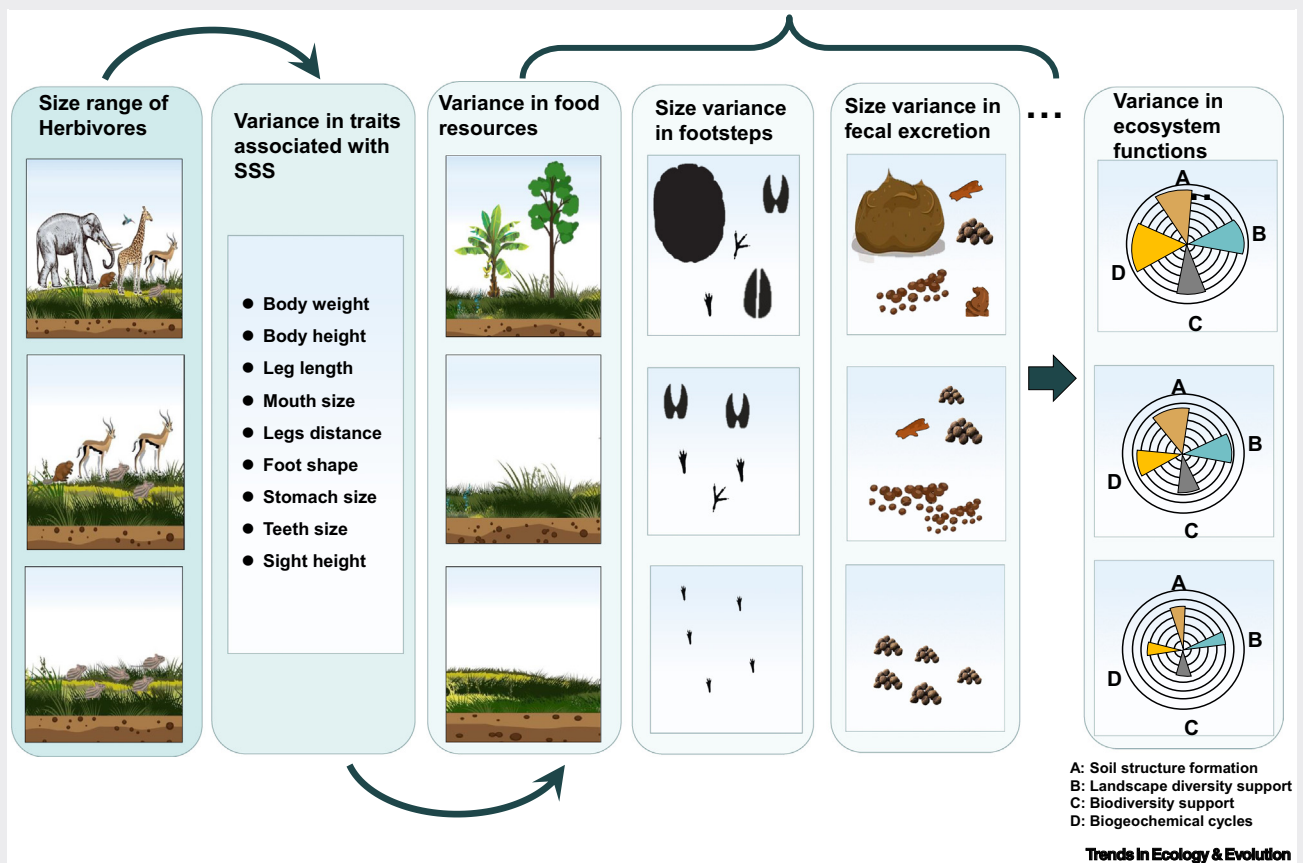
Box 3. Extending linkages between sizes, traits, and ecosystem multifunctionality to animals

Relationships between size diversity/variance and ecosystem multifunctionality may tentatively be extended to other organisms than plants, including animals (Figure I). Widely reported allometric relations between body size, metabolic rate, and gut capacity indicate that larger herbivores can survive on lower quality food but require higher bulk intake diets compared with smaller species [64], with important implications for multiple ecosystem functions. First, herbivore size may affect ecosystem productivity and support plant biodiversity [65], for example, by reducing light competition by dominant plant species and increasing light availability for germination and seedling establishment.

Second, animal body size is correlated with the amount and nutritional quality of waste products (feces, urine, urea), thereby affecting primary productivity. For example, herbivores take in nutrients in set stoichiometric (e.g., N:P) ratios that vary with body size, thereby driving the ratios of their dung [66]. This in turn adds to spatial heterogeneity in soil fertility, which drives biodiversity. Body size variation in herbivores also promotes food resource partitioning among herbivores, thereby supporting species coexistence and biodiversity [67].

Third, due to body size and foot shape variation, species may differ in the area they trample per footprint, and in the body mass per footprint area, and hence in their environmental impact [68]. Also, larger herbivores have relatively shorter legs and take relatively shorter steps per body mass than small herbivores, and so trample a greater area of ground per unit distance traveled, with implications for vegetation structure and habitat modification for other organisms [68,69]. The extent and rate of trampling, via soil compaction, can strongly affect other ecosystem functions and services, for example, soil stability and water and oxygen infiltration and thereby productivity [68]. One can only try to imagine the great impact the footsteps of giant herbivorous dinosaurs, like sauropods, must have had on the functioning of Mesozoic ecosystems.

Identifying analogies and differences in organ size–trait–ecosystem function relations between organisms from very distant evolutionary positions is important for combining different taxa to assess ecosystem multifunctionality comprehensively.
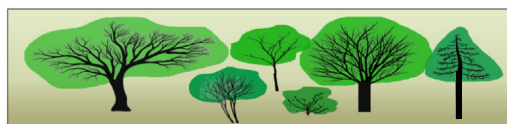

A: Soil structure formation
B: Landscape diversity support
C: Biodiversity support
D: Biogeochemical cycles

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Figure I. Relationship between size diversity and ecosystem multifunctionality in the animal world. The range of animal body (organ) size; the variance in traits in the SSS related to body (organ) size; the variance in food resources, home range, and in body mass per footstep area; and animals' metabolic rate and gut capacity may contribute to ecosystem multifunctionality. To give a specific example, in a savanna ecosystem composed of herbivores, variance in body size (related to interspecific and intraspecific variation and ontogenetic stages) leads to variance in SSS-related traits. In an ecosystem with body size ranging from low to high size diversity, the diversity of organ sizes (organ SSS traits) also increases, and leads to large diversity in food resources, activity ranges, footprints and soil compaction, and the quantity and quality of their excrements. Together, such trait variance will affect ecosystem multifunctionality.
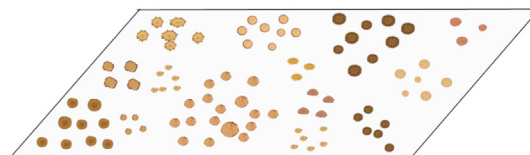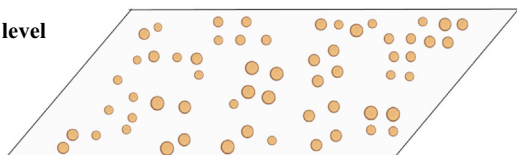
Stem size variance in forest

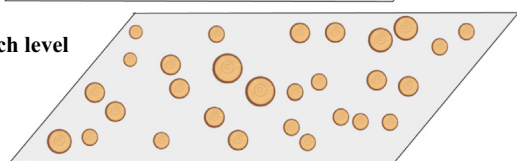**(Ai) Low stem traits variance within woody organs**
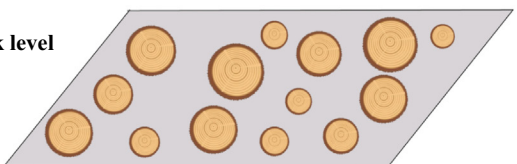
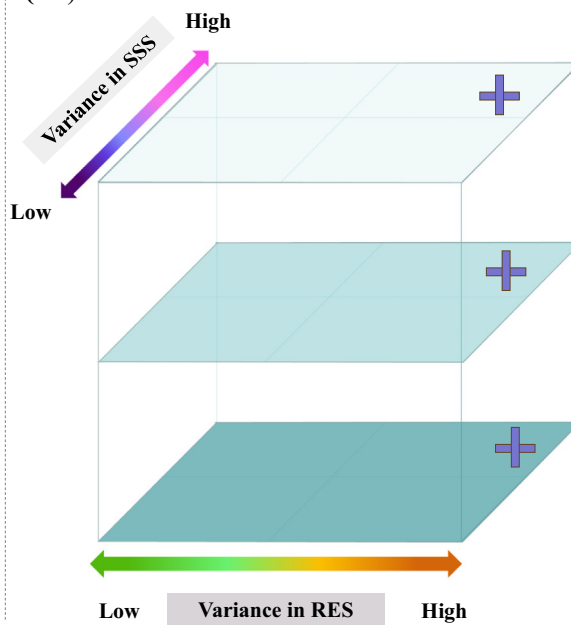**(Bi) High stem traits variance within woody organs**

Twig level

Branch level

Trunk level

(Aii)

Variance in SSS — High / Low

Woody organ

Twig

Branch

Trunk

Variance in RES — Low / High

(Bii)

Variance in SSS — High / Low

Variance in RES — Low / High

Ecosystem multifunctionality — Low / High

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(Aiii)

Stem variance of living tree ➕ Stem variance of dead tree

Ecosystem functions and services

(Biii)

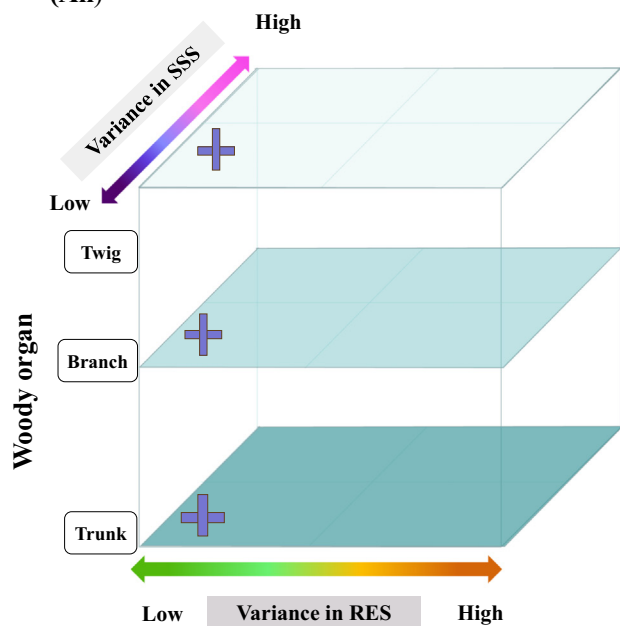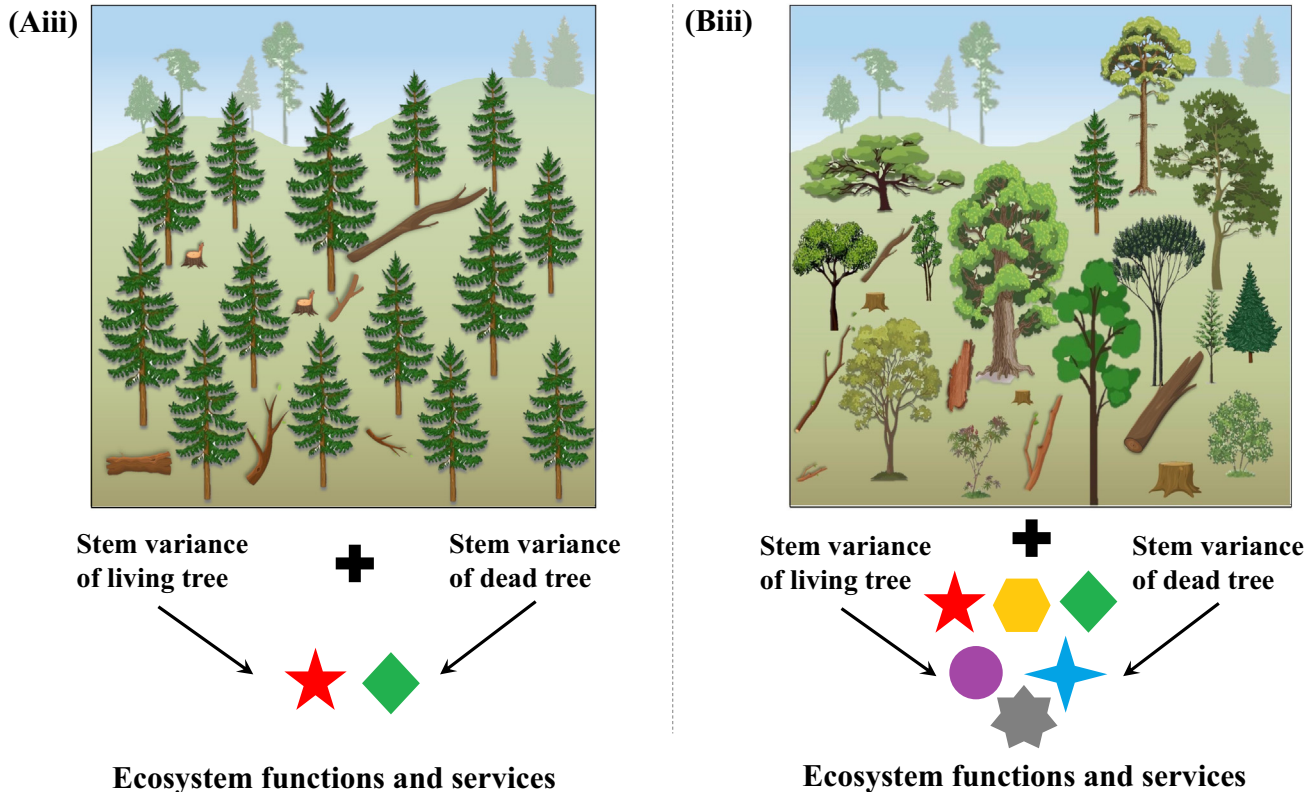Stem variance of living tree ➕ Stem variance of dead tree

Ecosystem functions and services

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Figure 2. Graphical illustration of hypothesized differences in trait variance (of stems themselves or their appendages like leaves, flowers, fruits) along tree size variance across woody species in forest, and their effects on ecosystem multifunctionality. Continuous variation in stem diameter is simply represented here by trunks versus branches versus twigs for clarity. (Ai–iii)A scenario with low stem size (diameter) and shape (SSS) variance and low variance in resource economics traits (RES) within each diameter class; this is common in monoculture plantations. (Bi–iii)A high SSS trait variance and high RES trait variance within each diameter class; this scenario should be common in multispecies, multistory forests. (Ai and B,i)The two contrasting scenarios, with variance in SSS-related and RES-related traits visualized through the range from light brown to dark brown colors of different stem disk size. (A,ii) and (B,ii) These contrasting scenarios are illustrated. Hypothetical trait variance in SSS is plotted along the *Y* axis and trait variance in the RES along the *X* axis. Note that the variance in angles of stems from vertical to horizontal (not shown here) across the tree organ also has important implications for ecosystem multifunctionality. (A,iii and B,iii) The importance of combining traits and stem size variance of both living and organs of trees and shrubs is emphasized, as well as those of other organs such as leaves, for ecosystem multifunctionality. See also Box 1 for including belowground organs in the size–trait–ecosystem multifunctionality linkages.

will add to functional trait variance proportionally to its difference in SSS and RES traits of each diameter class when compared with the first species (Figure 2Bi). Such variance in SSS and RES traits will in turn boost ecosystem services (Figure 2Bii,Biii).

The functionally rich end of trait variance within trunks, branches, and twigs (Figure 2Bi), for instance, a mature multispecies, multilayered forest with low human interference, likely features a high variance of both SSS and RES traits for a given organ. Such a forest is likely to host a much richer stem-associated invertebrate fauna within and across forest strata than the mono-specific stand, to mention just one of the many ecosystem functions and services it will promote.

In general, greater variance in SSS- and RES-related stem traits across woody species, both across and within forest strata and woody tree organs, should lead to greater overall ecosystem multifunctionality (Figure 2Aii–Bii). Variation in the traits of leaves, reproductive organs (see above),

and belowground organs (Box 1) and how they combine with variation in stem traits across different aboveground woody organs of different species, as well as the afterlife effects of such trait variation (Box 2) will determine further services to the overall ecosystem multifunctionality (Figure 2Aiii–Biii).

All of the above aspects of size contributions of trees, via stem traits to ecosystem services, are only partly or not at all quantified pieces of the big multifunctionality puzzle. In addition, while we focus here on ecosystem multifunctionality as regulated by variation in SSS and PES traits across different woody organs, other organisms (e.g., herbaceous plants, animals) also play an important role in support ecosystem services and functions. We illustrate this (Box 3) by discussing how the organ size–trait concept may relate to multiple ecosystem functions and services provided by animals. Testing size–traitmultifunctionality linkages empirically, in different woody ecosystems (e.g., forests, woodlands, tree plantations, shrublands, savannas) in different parts of the world, represents a major research challenge. Below we will give some specific methodological guidelines for how this challenge could be taken on in practice.

How to combine size and functional traits to assess ecosystem multifunctionality

Here we propose a sequence of six steps of how in general one may assess ecosystem multifunctionality (e.g., comparing forest A vs. B in Figure 2), as follows:

(i) List key ecosystem functions/services of interest, focusing on ecosystem functions *per se* (EF multifunctionality) or ecosystem services to people (ES multifunctionality) [6]. Weight the importance of the respective functions/services depending on the environmental/social context, the default being similar weighting for each function/service.

(ii) Determine which functional trait(s) make(s) a good proxy for the function/service targeted, for example, seven bark traits belonging to RES and PES could predict deadwood macro-invertebrate diversity in logs of temperate tree species [42].

(iii) Treat trunks, branches, and twigs, respectively, as if they are separate species, so assess the traits of interest on each tree organ–species combination.

(iv) Rank each function/service from 1 (minimal) to 10 (maximal function/service). Decide whether to weight the different tree organ–species combinations by the relative abundance or biomass of the species in the community. This will depend on the type of service targeted. Define objective standards for what qualifies as rank 1 and what as rank 10 in the context of a wider set of studies/ecosystems or within a study itself [5].

(v) How to rank will depend on the type of service:
- For biodiversity support, the functional wood/bark trait diversity across all tree organ–species combinations could be a proxy for invertebrate diversity in the living and dead parts of trees, respectively. Invertebrates associated with leaves or reproductive parts could be included under the woody organs that bear them.
- For cultural/symbolic and utilitarian services, tabulate all important cases (see main text) in a tree species by organ matrix. Rank the services simply as the total number of cases or weight different cases by importance.
- For regulatory services, often the weighted mean or total trait value may be appropriate. For instance, wood decomposability (relative mass loss) is negatively correlated with initial wood density across wide-ranging tropical trees species and diameter classes [43], so the sum of biomass-weighted wood densities of deadwood per unit forest plot area may be a good proxy for forest floor carbon storage.

(vi) The simplest calculation of ecosystem multifunctionality is to take the (non-weighted) mean or total of all the rankings of individual functions/services assessed under (iv). For a more advanced method the 'threshold approach' is recommended [3,6]. Irrespective of metric used, forest type B would always come out as higher in multifunctionality than forest type A in Figure 2.

Concluding remarks

We propose that the sizes of different body parts within individual trees and shrubs and across woody species matter for linking traits to ecosystem multifunctionality. To do so effectively (see also above), we need to define and quantify the SSS axis by collecting morphological woody organs' trait data (see Figure 1B) across the different woody organs (see Outstanding questions). In addition, for the renowned suite of RES-related traits (Figure 1B), we should collect data systematically along the different diameter classes of both living and dead trees (Box 2). Sufficient trait datasets measured on different body parts within and across species will help to test how ecosystem multifunctionality is determined by the combination of trait variation both horizontally between species and individuals, and vertically across diameter classes within individuals. Moreover, while this framework focuses on ecosystem multifunctionality as regulated by woody organ size and their associated SSS and RES trait variation, future extensions of the framework should also include other organisms that play important roles in supporting ecosystem services and functions, thereby embracing more of the real-world complexity in an even broader ecological and evolutionary context. While big challenges are ahead both in terms of developing further theory and collecting field data, the conceptual and actual linkages between sizes, traits, and ecosystem multifunctionality presented here are likely to improve assessments of the overall value of services provided by ecosystems.

Declaration of interests

No interests are declared.

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Outstanding questions

Which combinations of SSS-related traits and RES-related traits across the size classes (trunks, branches, and twigs) of woody plant species are the most effective for predicting ecosystem multifunctionality?

How can we collect trait data along the different diameter classes of both living and dead trees, and data for the ecosystem services they relate to, across woody ecosystems in a standardized way?

Can we find out which stem diameter diversity configurations can reach the highest ecosystem multifunctionality based on the functional traits across stem diameter classes, and what ecosystem management is needed to achieve this?

How does the relationship between the organ size–trait spectrum and ecosystem multifunctionality, and the role of specific SSS and RES traits, change along the temporal dimension, for example, with forest succession?

How do possible size–trait relationships of other organisms [e.g., animals (Box 2), fungi, bacteria, protists] affect ecosystem multifunctionality, and how could these be incorporated in the plant-centered framework in an effective way?

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