

Opinion

Ecosystem Traits Linking Functional Traits to Macroecology

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As the range of studies on macroecology and functional traits expands, integration of traits into higher-level approaches offers new opportunities to improve clarification of larger-scale patterns and their mechanisms and predictions using models. Here, we propose a framework for quantifying ‘ecosystem traits’ and means to address the challenges of broadening the applicability of functional traits to macroecology. Ecosystem traits are traits or quantitative characteristics of organisms (plants, animals, and microbes) at the community level expressed as the intensity (or density) normalized per unit land area. Ecosystem traits can inter-relate and integrate data from field trait surveys, eddy-flux observation, remote sensing, and ecological models, and thereby provide new resolution of the responses and feedback at regional to global scale.

Requirement to Bridge Traditional Traits to Macroecology

The **functional traits** (see [Glossary](#)) of a plant, animal, or microbe are measurable properties related to productivity or adaptation to the environment. For species within and across communities, functional traits contain information on many patterns and processes, including phylogenetic signal, correlations with physiological function, and information on environmental constraints, at a wide range of scales [1,2]. Thus, there has been a steep increase in the number of studies investigating spatial and temporal variation in traits [3,4], trait–trait correlations [5,6], traits as indicators of resource utilization strategies [7,8], and traits as mechanistic drivers of function [9–11].

Although classic advances in **macroecology** and **biogeography** tend to focus on the relationships between organisms and their environment by characterizing and explaining statistical patterns of abundance, distribution, and diversity at large scales [12], trait-based macroecology has already begun to emerge. For example, Elser *et al.* [13] used nitrogen (N) and phosphorous (P) stoichiometry to explore nutritional constraints at regional and global scales. Hessen *et al.* [14] developed a concept to estimate the effect of atmospheric N deposition on carbon (C) sequestration in ecosystems using stoichiometric principles. Recently, Kunstler *et al.* [15] demonstrated that plant functional traits have globally consistent effects on competition for light, water, and nutrients. These studies highlighted the inherent potential in linking macroecology to traditional traits for the exploration of large-scale ecological patterns and processes and functional biogeography.

Under global change scenarios, climate change, land-use change, and atmospheric N and acid deposition have strong ecological and environmental effects at the widest range of scales, from

Highlights

Most processes related to effects of global change must be understood and dealt with at regional or global scales, requiring the linkage between traditional traits and macroecology.

We propose a framework for quantifying ecosystem traits to broaden the applicability of functional traits to macroecology.

Ecosystem traits are quantities informative of environmental adaptation and the optimization function of organisms at whole community or ecosystem, standardized on the intensity (or density) per unit land area.

Using data sets from tropical to cold-temperate forests, we developed an approach for scaling up and scale-matching traits measured for use as ecosystem traits per land area.

Ecosystem traits can integrate data from field investigations, eddy-flux, remote sensing, and ecological models, and provide new resolution of the responses and feedback at regional to global change.

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regional to global. While many studies at the organ or species levels have focused on global change phenomena, there are real difficulties in scaling up such data [16]. To accomplish this, we need to systematically collect the traits or characteristics of organisms in entire communities and to fully exploit these data with the most powerful approaches in macroecology (e.g., **ecological modeling, eddy-flux observation, remote sensing**, integrative analysis, and others). Several studies have explored the possibility of incorporating traits into models to enhance the accuracy of predictions for forest function [17–19]; however, this application is often limited by the availability of trait databases at suitable scales. Croft *et al.* [20] proposed using leaf chlorophyll concentration (*Chl*) as a proxy for leaf photosynthetic capacity at a large scale, and potentially combining this trait with remote sensing in the future. While the demand to link functional traits and macroecology is escalating, there remains a major conceptual gap that has led to confusion about the applicability of trait data within large-scale macroecological studies, and a lack of clear approaches to apply traits measured at the organ level to broader spatial scales.

Current Gaps between Traditional Traits and Macroecology

It is important to identify the gaps that separate traditional traits from macroecology. Trait databases based on field investigations are rapidly expanding. For instance, the TRY Plant Trait Database (<https://www.try-db.org>) contains 148 000 plant taxa and 6.9 million trait records [21], allowing community-level trait statistics to be explored [6–8]. However, a series of conceptual challenges must be overcome. New approaches are needed for scaling up, that is, translating functional traits measured at the organ level for individuals to represent the natural community. Data for traits measured at the organ level must be available for a sufficient number of species to represent complex natural communities, in which community composition and the relative contribution of each plant species are highly variable. Even in the TRY database, some shortcomings are clear. In most communities, the traits of several plant species are measured, with a strong focus on dominant species, excluding less dominant species [2]. In general, systematic measurements of plant traits have been made for relatively few species, focusing on the leaf, branch, stem, and fine roots, or even on detailed leaf traits (i.e., morphology, stomata, venation, anatomy, elemental composition, and hydraulic and photosynthetic function). Using data compiled from different studies may lead to uncertainty, owing to incompatible protocols, and the unquantified effects of ecotypic and plastic variation influencing traits for different populations of given species [22]. Finally, only a few traits have been investigated in relation to actual community structure, such as height, density, biomass of each plant species. Many authors acknowledge the importance of scaling traits to community or ecosystem level; however, lack of data availability makes it difficult to scale-up with satisfactory accuracy and precision.

A second challenge is scale matching, that is, relating these traits to higher-level processes, such as eddy-flux observations, regional-scale climate models, and remotely sensed variables. Previous studies have developed equations to scale-up traits from the organ to the community levels, such as Equations 1 [2] and 2 [11] for the community-weighted mean (CWM).

$$\text{CWM} = \sum_i p_i T_i \quad [1]$$

$$\text{CWM} = \frac{\sum_i p_i \sum_{j=1}^{\text{NIV}_i} (t_j / \text{NIV}_i)}{P_{\text{Cover}}} (\text{NIV}_i \geq 1) \quad [2]$$

where p_i is the relative abundance of species i in the community, T_i is the trait value of species i observed in the plot, NIV is the number of individual values of the trait under consideration in the

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database for species i , t_{ij} is the value j of a given trait of species i in the database, and P_{Cover} is the proportional cumulative relative abundance of all species of a given community for which the trait value is available in the database.

In principle, Equations 1 and 2 can be used to explore the distributions of functional traits and their causes and consequences for higher-level processes across ecosystems. However, a new vital challenge emerges when linking such CWMs to regional processes. The CWM represents a community-aggregated value based on community composition (relative biomass or relative abundance), and reflects the mean species behavior, not necessarily the behavior of the community or ecosystem [2]. Further, the units of traits remain the same for the measured organs, such as elemental concentrations (g kg^{-1} for leaf C, N, and P concentration), specific leaf area ($\text{mm}^2 \text{mg}^{-1}$), and leaf stomatal density (number cm^{-2}). From the perspective of physiological ecology, some functional parameters, such as photosynthetic rate, transpiration rate, or hydraulic conductance, are generally measured at the organ scale and normalized by its dimensions (i.e., for leaves or stem segments). Yet, the functions at the ecosystem level are generally modeled on basis of land area, through eddy-flux observations, remote sensing, and ecological modeling. Consequently, these mismatched units (i.e., spatial scale) represent a second gap between traditional traits and macroecology. In principle, such mismatched units could lead to the misinterpretations of correlations and interactions among plants, animals, microbes, and biotic and abiotic factors at large scales.

Toward Defining Ecosystem Traits

An increasing number of studies on traits and macroecology are focusing on using communities and ecosystems to explore ecological problems at regional or global scales. For progress to be made on this topic, new concepts must be developed to integrate traits measured at the organ level, to meet the requirements of the main technologies of macroecology, especially by matching them at the same spatial scale. We propose that the concept of 'ecosystem traits' could be used to address these gaps. Ecosystem traits are traits representing characteristics of plants, animals, soil microbes, or other organisms, calculated as the intensity (or density) normalized per unit land area. Our hypothesis is that these traits would therefore contain information on variation in community species composition and structure, including adaptation and sorting of species according to the biotic and abiotic environment, as well as their plasticity, and would reflect optimization of processes that occur during evolution and ecological assembly.

Ecosystem traits have the following characteristics: (i) they represent community-scale information for plants, animals, and soil microbes (Figure S1 in the supplemental information online); (ii) they are calculated or normalized per unit land area to enable scale matching; (iii) they can be derived from trait measurements at organ or individual levels, and typically require community structural variables to enable scaling up; (iv) they have specific ecological significance, and enable tests of adaptation or optimization of traits at community or ecosystem levels. For example, scaling leaf area up to community level gives the ecosystem trait leaf area index (LAI), and scaling up leaf dry mass gives leaf mass index (LMI). Consequently, LAI and LMI are important ecosystem scaling variables, as ecosystem-scale versions of leaf area-based traits (e.g., leaf stomatal density) per land area are calculated as the products of LAI and specific leaf area-based traits, and ecosystem-scale versions of leaf mass-based traits (e.g., leaf N and P concentrations) are calculated as the products of LMI and specific leaf mass-based traits. Thus, LAI and LMI are central ecosystem traits, consistent with them being recognized as essential in macroecology, though without being explicitly named this way previously [23,24]. The calculation and use of ecosystem traits enable scale matching and integrating trait information for

Glossary

Biogeography: the study of the distribution of species and ecosystems in geographic space and through geological time [36].

Ecological modeling: an abstract, usually mathematical, representation of an ecological system (ranging in scale from an individual population, to a community, or even an entire biome), which is studied to better understand the real system [37].

Eddy-flux observation: a key atmospheric measurement technique to measure and calculate vertical turbulent fluxes within atmospheric boundary layers [38].

Functional trait: morpho-physio-phenological traits that impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance [2].

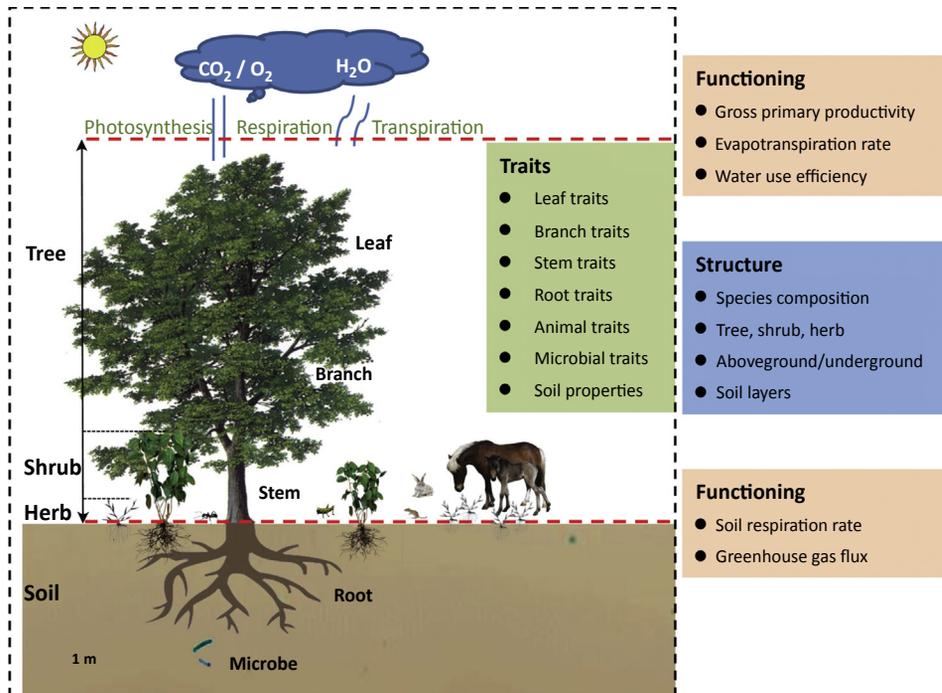
Macroecology: the subfield of ecology that deals with the study of relationships between organisms and their environment at large spatial scales to characterize or explain statistical patterns of productivity, abundance, distribution, and diversity [12,39].

Remote sensing: the use of satellite- or aircraft-based sensor technologies to detect and classify objects on Earth, including on the surface and in the atmosphere and oceans, based on propagated signals (e.g., electromagnetic radiation) [40].

comparisons across ecosystems and regions, such that these traits can be used as an interface among ecological modeling, eddy-flux observations, and remote sensing. We note that many organ-level traits have not been sufficiently measured to scale-up to the ecosystem level. For example, leaf optical properties (reflectance or hue) can play important role in energy balance and surface warming, and such data, although currently lacking, could have importance if scaled up as ecosystem traits. Further, we note that there may be additional key challenges to be resolved in scaling up important qualitative traits to the ecosystem level (e.g., serrated versus non-serrated leaves; single versus compound leaves; evergreen versus deciduous).

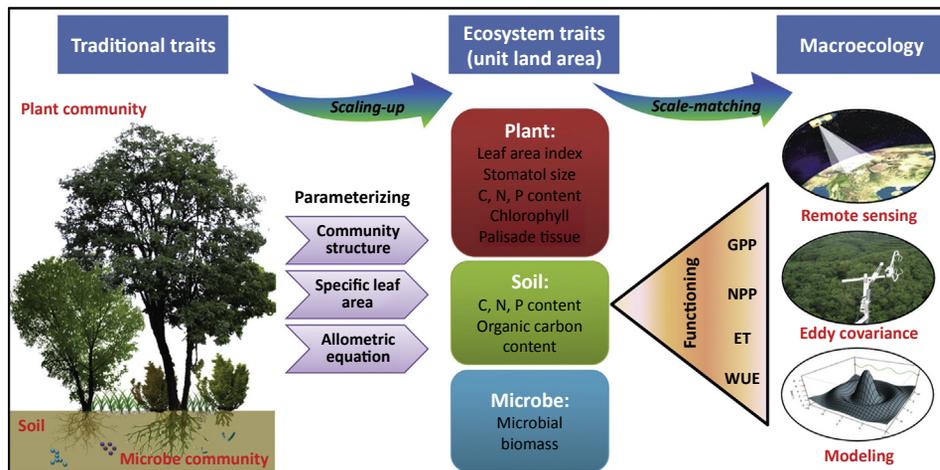
Figure 1 demonstrates the general relationships among structure, trait, and function at the ecosystem scale. All parameters are measured by different approaches. Thus, traits are sampled and measured at the organ level, whereas function is mainly measured or simulated by eddy-flux observation, remote sensing, and ecological models at the ecosystem level, and structure is derived through field investigation or radar [25]. By integrating organ-level traits and stand structure to derive ecosystem traits, one may fill the gaps and establish links across spatial scales.

There are complexities that remain to be resolved in calculating ecosystem traits from measurements at the organ or species level, even when trait values are available for all species present in a given area, along with details on plant community structure and other important parameters for each species (such as specific leaf area, and allometric equations for biomass allocation). Extending from the concept of the CWM (Equations 1 and 2; Figure 2), we developed new



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Figure 1. Conceptual Framework of Ecosystem Traits Based on Organ-Level Traits and Stand Structure, Functioning, and Environmental Factors in a Forest. Ecosystem traits are traits representing characteristics of plants, animals, soil microbes, or other organisms, calculated as the intensity (or density) normalized per unit land area. Abbreviations: GPP, gross primary productivity; WUE, water-use efficiency.



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Figure 2. Scaling up and Scale Matching of Traits Measured at the Organ Level and Ecosystem Traits per Land Area. We can first scale-up traits measured at the organ level with the help of data on community structure, allometric equation, specific leaf area, and others, and standardized on per land area, and then try to establish the quantitative relationship with these parameters of remote sensing, ecological modeling, and eddy-flux observation. These are the important foundations to linking traditional traits to macroecology. Abbreviations: ET, evapotranspiration; GPP, gross primary productivity; NPP, net primary productivity; WUE, water-use efficiency.

approaches to calculate these ecosystem traits on the basis of land area as Equation 3 (normalized by mass) and Equation 4 (normalized by area).

$$\text{Trait}_{\text{ecosystem}} = \sum_{j=1}^4 \sum_{i=1}^n \text{OMI}_{ij} \times \text{Trait}_{ij} \quad [3]$$

$$\text{Trait}_{\text{ecosystem}} = \sum_{i=1}^n \text{LAI}_i \times \text{Trait}_i \quad [4]$$

where n is the number of species in the forest community; j ($= 1, 2, 3, \text{ and } 4$) represents leaf, branch, stem, and root, respectively, excluding any organ without specific traits; OMI_i is the organ (leaf, branch, stem, and root) biomass per land area of the i th species in the specific community; and LAI_i is the leaf area index of i th species in the specific community. This formulation in terms of OMI (which is typically LMI) and LAI is based on Wang *et al.* [26] and Liu *et al.* [27]. It is worth emphasizing the variable relationship between an ecosystem trait expressed per land area, as calculated from Equations 3 and 4, and the CWM trait, which is typically an organ-scale trait. Ecosystem traits that are ratios of other ecosystem traits (e.g., N:P ratio) are equivalent to the CWM of traits.

We thus propose the calculation of ecosystem traits according to specific methods for scaling up (Table S1). We have investigated ecosystem-scale versions of key leaf traits, including morphology (leaf size, leaf thickness, leaf dry mass, and leaf specific area), stomata (stomatal size, stomatal density, and stomatal area fraction), cross-sectional anatomy [adaxial and abaxial epidermis thickness, leaf thickness, and spongy tissue thickness, and elemental composition (C, N, P, K, Ca, Mg, and S)] (Figure S1). All of these traits indicate potential mechanisms for the adaptations of species across each community and potential controls on the community productivity. Additional traits, such as *Chl* and leaf vein density, could be considered as the field of macroecology develops.

In practice, ecosystem traits could represent any aspect of the structure and function of plants (standing live, leaf litter, or seed rain), animals, insects, soil microbes, and other organisms at the community level (Figure S2). We measured specific traits at the organ level and scaled them up to the community level using a framework similar to that shown in Figure 2. Such ecosystem traits provide new insights about processes that affect interactions among organisms and the environment at different scales. Box 1 presents some examples of ecosystem traits.

Future Direction for Linking Ecosystem Traits to Macroecology

Establishing the quantitative relationships between ecosystem traits and the functioning of natural ecosystems is a vital challenge [9,11,28,29]. Recent analyses of the database constructed along the North–South Transect of Eastern China (NSTEC) transect from tropical to cold-temperate forests have allowed the derivation of ecosystem traits from the measured data at the organ level, and linked to ecosystem functioning based on ecological modeling, eddy-flux observations, or remote sensing. As hypothesized, stomatal density at the community level was positively associated with net primary productivity (NPP) in natural forests, explaining 51% of variation in NPP, where NPP data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) products in a 1 × 1-km grid [26]. In addition, Liu *et al.* [27] found that stomatal area fraction was positively correlated with water-use efficiency of the ecosystem. Furthermore, *Chl* at the community level was correlated with gross primary productivity (GPP; $R^2 = 0.31$, $P < 0.05$; Figure S4). These results demonstrate major links between ecosystem traits and functioning in natural forest ecosystems [30]. Given that ecosystem traits are derived using LAI and LMI, it is important to note that these indices themselves might drive part of the relationships with higher-level processes. Therefore, further progress is required to resolve the underlying mechanistic relationships between ecosystem traits and landscape gas fluxes across regions.

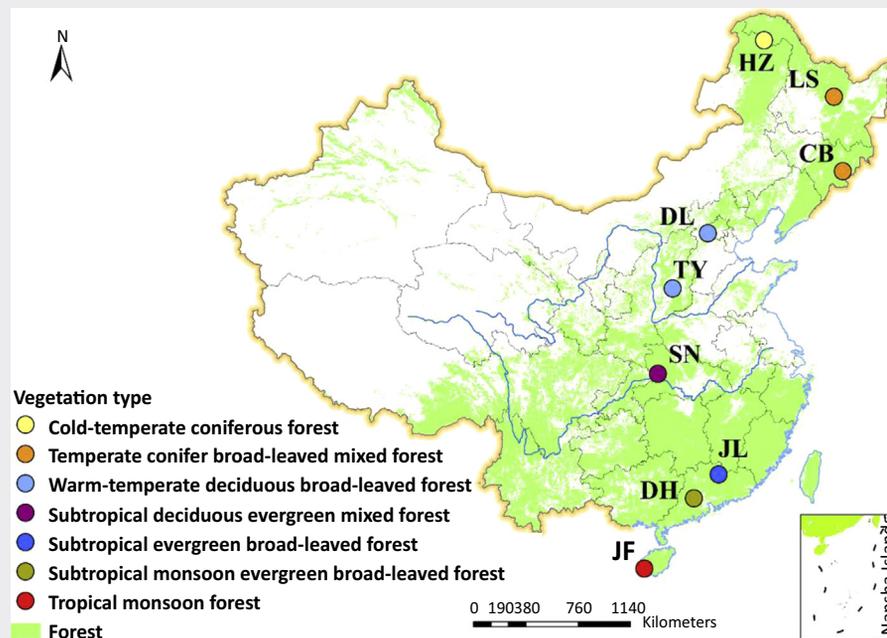
Box 1. Examples of Scaling up Organ-Level Traits to Ecosystem Traits

Recently, we conducted field studies exploring the spatial patterns of multiple functional traits (e.g., leaf, branch, trunk, root, soil, and soil microbe traits) in forests along the 3700-km NSTEC, which is the 15th standard transect of the International Geosphere Biosphere Programme [41]. This transect extends from tropical to cold-temperate forests, ranging from 18.7° N to 51.8° N (Figure 1 and Table I). The data sets collected within this framework encompass all forest types observed in the Northern Hemisphere, and represent almost all types of forests globally. Along the transect, we measured 36 plots across nine forest types, including 1100 plant species [4,42]. These comprehensive data sets on plants, soils, microbes, and community structure in each plot provide a key example system for developing ecosystem traits for diverse forests at regional and continental scales.

Based on the principles presented in Figure 2 (main text), we developed an approach to scaling up and scale matching between traits measured at the organ level to ecosystem traits per land area. This goal was achieved by integrating the traits of all plant species present in each plot, with detailed data on plant community composition and several key transferring parameters for each plant species (e.g., specific leaf area and allometric equations for biomass allocation). This analysis produced examples of ecosystem traits per land area (Table II), including leaf stomatal density and length [26], *Chl* [30], and the stoichiometric properties of leaf, branch, stem, and fine roots (C:N:P) [43]. Thereafter, the spatial patterns of these traits and their correlation with ecosystem processes were tested.

There was strong variation in ecosystem traits at the regional scale. Stomatal density and stomatal length per land area at the ecosystem scale varied strongly among the nine forest communities along the NSTEC, showing a quadratic relationship with increasing latitude from tropical to cold-temperate forests [26]. Leaf *Chl* per land area at the ecosystem scale ranged from 7.09 g m⁻² in tropical forest to 2.26 g m⁻² in cold-temperate forests, and decreased with increasing latitude [30]. The ecosystem-scale C:N, N:P, and N:P of the leaf, branch, stem, and fine roots [43] differed significantly from previously published mean values based on sparsely collected data that did not comprehensively represent the communities [44,45]. The only ecosystem stoichiometric trait that varied with latitude was P per land area, which decreased with increasing latitude, supporting the idea that P would be more limiting in forests located at lower latitudes [13,46].

These results are examples of major patterns that can be resolved using ecosystem traits across regions. For this approach, it is necessary to conduct an extensive and systematic field investigation of plant traits, community structure, and parameters of soil and microbe to expand the existing trait databases. Once determined, these ecosystem trait values can be interfaced with remote sensing and ecological models [47], an overall integration that will be invaluable for studies of macroecology and future modeling at larger spatial scales.



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Figure 1. The Nine Forests along the North–South Transect of Eastern China. Abbreviations: CB, Changbai; DH, Dinghu; DL, Dongling; HZ, Huzhong; JF, Jianfeng; JL, Jiulian; LS, Liangshui; SN, Shennong; TY, Taiyue.

Table 1. Selected Information on Nine Forest Ecosystems along the North–South Transect of Eastern China^a

Sites	Longitude (E)	Latitude (N)	MAT (°C)	MAP (mm)	Vegetation type	Dominant species	Soil type
JF	108°51'26"	18°44'18"	23.15	2265.8	Tropical mountain rain forest	<i>Schoepfia jasminodora</i> Sieb., <i>Ficus vasculosa</i> Wall., <i>Madhuca hainanensis</i> Chun.	Lateritic yellow earth
DH	112°32'14"	23°10'25"	21.83	1927	South subtropical evergreen broad-leaved forest	<i>Schima superba</i> Gardn., <i>Cryptocarya chinensis</i> Hemsl., <i>Pinus massoniana</i> Lamb.	Laterite
JL	114°26'28"	24°35'05"	18.22	1769.93	Subtropical evergreen broad-leaved forest	<i>S. superba</i> Gardn., <i>Castanopsis fargesii</i> Franch., <i>Castanopsis cartesii</i> Hayata	Red earth
SN	110°29'43"	31°19'15"	8.50	1446.71	North subtropical evergreen deciduous mixed forest	<i>Fagus engleriana</i> Seemen., <i>Quercus serrata</i> Thunb., <i>Cyclobalanopsis oxyodon</i> Oerst.	Yellow-brown earth
TY	112°04'39"	36°41'43"	5.98	644.38	Warm temperate deciduous and broadleaf mixed forest	<i>Quercus wutaishanica</i> Mayr., <i>Pinus tabulaeformis</i> Carr., <i>Populus davidiana</i> Dode	Cinnamon soil
DL	115°25'24"	39°57'27"	6.55	539.07	Warm temperate deciduous and broadleaf mixed forest	<i>P. tabulaeformis</i> Carr., <i>Q. wutaishanica</i> Mayr., <i>Larix principis-rupprechtii</i> Mayr.	Brown soil
CB	128°05'27"	42°24'16"	2.79	691.00	Temperate conifer broadleaf mixed forest	<i>Pinus koraiensis</i> Siebold., <i>Larix gmelinii</i> Rupr., <i>Quercus mongolica</i> Fisch.	Dark brown soil
LS	128°53'51"	47°11'06"	0.01	648.34	Temperate conifer broadleaf mixed forest	<i>P. koraiensis</i> Siebold., <i>L. gmelinii</i> Rupr., <i>Betula platyphylla</i> Suk.	Dark brown soil
HZ	123°01'12"	51°46'48"	-3.67	472.96	Cold-temperate coniferous forest	<i>L. gmelinii</i> Rupr., <i>Pinus sylvestris</i> L., <i>B. platyphylla</i> Suk.	Grey forest soil

^aAbbreviations: CB, Changbai; DH, Dinghu; DL, Dongling; HZ, Huzhong; JF, Jianfeng; JL, Jiulian; LS, Liangshui; MAP, mean annual precipitation; MAT, mean annual temperature; SN, Shennong; TY, Taiyue.

Table II. Examples of Ecosystem Traits Derived from the Measured Data at the Organ Level along the North–South Transect of Eastern China (NSTEC), with Mean Values \pm Standard Error^a

	Ecosystem traits	HZ	LS	CB	DL	TY	SN	JL	DH	JF	Refs
Leaf	Stomatal traits										[26]
	Stomatal density (N mm ⁻²)	352.2 \pm 120.8 ^b	852.2 \pm 267.1	1752.9 \pm 239.3	1632.5 \pm 219.8	1533.9 \pm 222.8	1761.6 \pm 427.9	2050.8 \pm 684.9	1718.8 \pm 242.5	2685.4 \pm 595.9	
	Stomatal length (μ m mm ⁻²)	10 132 \pm 3439	26 994 \pm 8241	44 935 \pm 6302	41 638 \pm 7507	34 461 \pm 4287	42 255 \pm 7850	44 831 \pm 14 837	40 592 \pm 6506	53 986 \pm 12 086	
	Leaf chlorophyll concentration (g m ⁻²)	2.26 \pm 0.13	5.20 \pm 0.07	5.57 \pm 0.19	4.22 \pm 0.22	3.60 \pm 0.24	7.29 \pm 0.04	5.54 \pm 0.12	4.66 \pm 0.15	7.09 \pm 0.29	[30]
Element stoichiometry											[43]
	C:N	24.81 \pm 0.06	20.97 \pm 0.58	18.40 \pm 0.80	18.35 \pm 0.25	27.65 \pm 2.48	23.80 \pm 1.55	27.06 \pm 0.45	28.25 \pm 0.38	24.86 \pm 0.32	
	N:P	9.56 \pm 0.10	14.63 \pm 0.18	14.92 \pm 0.37	21.35 \pm 0.14	16.65 \pm 0.53	17.51 \pm 0.56	22.44 \pm 0.96	26.04 \pm 1.49	24.77 \pm 0.37	
	C:P	237.17 \pm 2.96	307.06 \pm 11.10	274.99 \pm 16.24	391.78 \pm 5.60	456.47 \pm 24.66	417.14 \pm 32.97	606.89 \pm 25.31	735.64 \pm 43.66	616.05 \pm 16.51	
Branch	Element stoichiometry										[43]
	C:N	68.76 \pm 1.85	67.67 \pm 2.81	55.70 \pm 1.58	53.53 \pm 0.05	62.36 \pm 1.71	50.42 \pm 4.46	61.96 \pm 2.03	60.51 \pm 4.16	–	
	N:P	6.02 \pm 0.02	8.16 \pm 0.07	7.90 \pm 0.39	13.56 \pm 0.11	11.35 \pm 0.13	9.16 \pm 0.45	12.24 \pm 1.30	15.92 \pm 1.45	–	
	C: P	413.77 \pm 9.96	552.16 \pm 23.24	438.89 \pm 17.71	725.93 \pm 6.26	707.95 \pm 25.07	459.01 \pm 31.32	753.71 \pm 55.67	945.33 \pm 11.04	–	
Stem	Element stoichiometry										[43]
	C:N	853.30 \pm 34.63	181.74 \pm 16.22	298.65 \pm 55.63	375.85 \pm 19.66	362.11 \pm 87.82	172.74 \pm 31.29	335.58 \pm 29.37	441.82 \pm 59.17	–	
	N:P	12.37 \pm 0.38	10.17 \pm 0.18	13.34 \pm 1.82	16.32 \pm 0.04	13.22 \pm 0.46	9.38 \pm 0.15	17.31 \pm 3.95	20.40 \pm 2.87	–	
	C:P	10 583.6 \pm 765.4	1855.2 \pm 196.0	4224.1 \pm 1083.0	6132.0 \pm 313.2	4679.0 \pm 965.2	1618.9 \pm 289.9	5935.5 \pm 1579.5	8610.9 \pm 735.6	–	
Root	Element stoichiometry										[43]
	C:N	56.55 \pm 1.58	52.80 \pm 1.88	43.36 \pm 1.90	32.28 \pm 0.13	43.57 \pm 1.93	71.20 \pm 14.50	56.64 \pm 8.04	56.21 \pm 2.84	–	
	N:P	8.60 \pm 0.15	6.83 \pm 0.15	10.38 \pm 0.44	22.67 \pm 0.21	20.93 \pm 1.15	7.42 \pm 0.57	15.89 \pm 1.12	22.65 \pm 1.99	–	
	C:P	485.82 \pm 5.55	359.62 \pm 5.61	450.65 \pm 29.51	731.71 \pm 8.86	905.50 \pm 10.45	516.31 \pm 87.18	883.20 \pm 75.83	1256.37 \pm 39.9	–	

^aAbbreviations: CB, Changbai; DH, Dinghu; DL, Dongling; HZ, Huzhong; JF, Jianfeng; JL, Jiulian; LS, Liangshui; SN, Shennongjia; TY, Taiyue.

^bEach trait has been scaled up from the data measured at the organ level to the community level on the basis of land area.

Notably, the divergence of trait–trait relationships determined at the organ level from those among ecosystem trait relationships also requires further investigation. One illustrative example is the importance of *Chl* as a leaf-scale trait versus as an ecosystem trait. Using data for four deciduous tree species, Croft *et al.* [20] reported that the relationship between the maximum rate of carboxylation ($V_{\text{cmax}25}$) and *Chl* was stronger than that between $V_{\text{cmax}25}$ and leaf N concentration. As a result, the authors concluded that *Chl* would be a better proxy for leaf photosynthetic capacity compared to leaf N, due to the large and dynamic investment of N in nonphotosynthetic pools. An additional advantage of this approach is that *Chl* can be modeled accurately from remotely sensed data [31], and it could thus be used to model leaf photosynthetic capacity at a global scale [32]. Although this concept was innovative, the use of *Chl* as a proxy for leaf photosynthetic capacity is only appropriate at the species level under ideal conditions (Figure S3 and S4). Across natural forest communities, in which the vertical structure of plant communities is inherently complex (e.g., tree layer, shrub layer, and herb layer), these traits might be decoupled. For instance, even within a single layer, there are significant differences among leaves with respect to exposure to sunlight, with measurement of *Chl* potentially overestimating photosynthetic capacity, due to self-shading effects. Further, the shading effect might differ among natural forests, because of variation in community structure. In addition, in any given leaf, much of the *Chl* is functionally redundant in light-harvesting antennae. Ultimately, if *Chl* accurately estimates the photosynthetic capacity of natural forest communities, the ecosystem trait *Chl* per land area should have a strong relationship with photosynthetic capacity or GPP (Figure S4). We examined the relationship between ecosystem-scale *Chl* and GPP in natural forest communities along the NSTEC transect. This was achieved by measuring leaf-scale *Chl* data for 937 common plant species in nine natural forests [30], integrated with data for specific leaf area, allometric equations for biomass allocation, and community structure. In addition, the *Chl* for all tree species and all plant species (including tree, shrub, and grass) was scaled up from the organ or species level to per land area [30]. We found that *Chl* at the tree and forest community level was only weakly correlated with GPP ($R^2 = 0.31$ and 0.32 , respectively; Figure S3). Therefore, *Chl* alone is not appropriate as a close proxy for ecosystem-scale leaf photosynthetic capacity in natural forests.

Concluding Remarks

The concept of ecosystem trait is valuable, due to its benefits for scale matching, and for relating to ecological processes across regions. Consequently, this new concept could be used in a wide range of studies on macroecology and functional biogeography, particularly as data sets grow and technologies advance (Figure 3). The proposed ecosystem traits could be applied to: (i) functional traits of plants, animals, and microbes to determine trait–environmental relationships at large scales; (ii) relationships among the traits of plants, animals, and microbes at large scales; (iii) quantitative relationships between traits and functioning at ecosystem or region scales; (iv) maps of ecosystem traits across the globe, similar to those recently advanced for mean trait values plotted on map pixels, which will enable resolution of their continental-scale variation and latitudinal, elevational, and climatic associations [33–35]; and (v) incorporating ecosystem traits (e.g., C, N, P, C:N, N:P, *Chl*, specific leaf area, and stomatal traits) into ecological models, and interfacing with eddy-flux observations, and remotely sensed variables. Such information would expand or optimize our ability to observe and predict the responses of these terrestrial ecosystems to global change (see Outstanding Questions). With the conceptual development of ecosystem traits, field survey data (community structure and traits) can be integrated rapidly and combined with remote sensing and radar toward offering a wide availability of ecosystem traits at global scales.

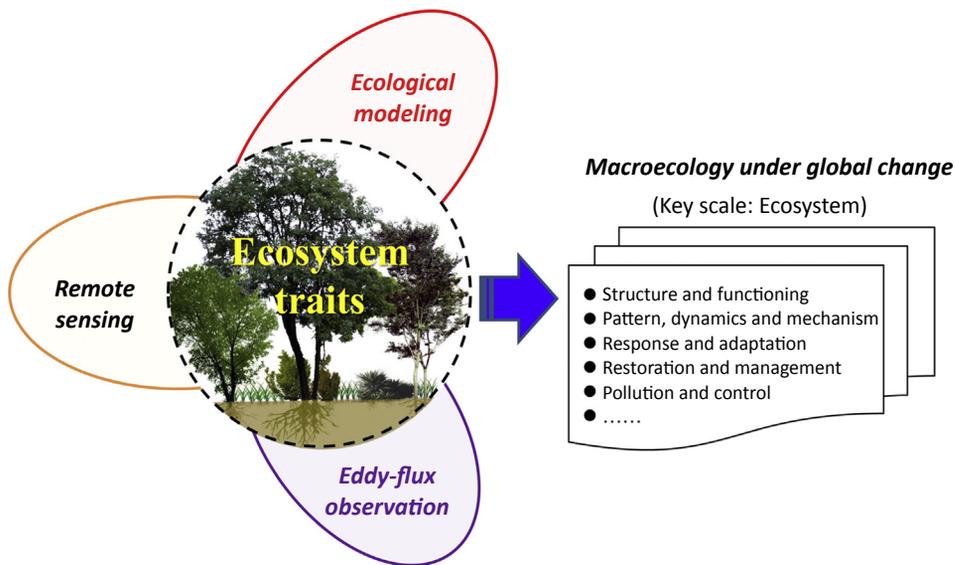
Outstanding Questions

Traditional traits measured at the organ or species level need integration into higher-level approaches to improve predictive models, because most processes and effects related to global change and regional problems must be understood and addressed at a regional or global scale.

How can we scientifically scale-up functional traits measured at organ level to represent the natural community?

How can we relate ecosystem-scale traits to higher-level processes or function at large spatial scales, such as eddy-flux observations, regional-scale climate models, and remotely sensed variables reflecting vegetation structure and function?

How can we implement our conceptual framework of ecosystem traits to wider aspects of macroecology?



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Figure 3. The Importance of Ecosystem Traits for Macroecological Studies under Global Change. Ecosystem traits are keystone to link the relationship between trait and functioning parameters observed by these advanced technologies (remote sensing, ecological modeling, and eddy-flux observation), or to improve their prediction accuracy.

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Author Contributions

N.H. and G.Y. conceived the original idea. N.H., C.L., S.P., S.L., and L.X. wrote the manuscript. Y.L., X.H., G.Z., X.Z., Y.L., Q.Y., S.L., S.N., L.S., S.W., and J.Z. edited the manuscript.

Data Accessibility Statement

All data used here have published in previous papers and presented in Table II in Box 1 and supplementary files. For further data sharing, please contact the corresponding authors (henp@igsnr.ac.cn or yugr@igsnr.ac.cn).

Disclaimer Statement

There are no conflicts of interest to declare.

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tree.2018.11.004>.

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