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Opinion

Plant Trait Networks: Improved Resolution of the Dimensionality of Adaptation

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Functional traits are frequently used to evaluate plant adaptation across environments. Yet, traits tend to have multiple functions and interactions, which cannot be accounted for in traditional correlation analyses. Plant trait networks (PTNs) clarify complex relationships among traits, enable the calculation of metrics for the topology of trait coordination and the importance of given traits in PTNs, and how they shift across communities. Recent studies of PTNs provide new insights into some important topics, including trait dimensionality, trait spectra (including the leaf economic spectrum), stoichiometric principles, and the variation of phenotypic integration along gradients of resource availability. PTNs provide improved resolution of the multiple dimensions of plant adaptation across scales and responses to shifting resources, disturbance regimes, and global change.

Rapid Advances in Data, Analyses, and Applications of Trait-Based Plant Ecology

Plant functional traits, defined as those that influence growth, reproduction, and survival [1,2], are important indices for predicting how plants respond and adapt to changing environments across levels of organization, that is, from organs, to species, and to ecosystems [3,4]. Indeed, functional traits can contribute to the prediction of species' distributions, vital rates, and responses to climate change [5].

As many traits are intercorrelated, the relationships among multiple traits has become a strong focus in studies of plant adaptation and environmental responses for the past several decades [6–8]. Recent studies have considered extensive suites of functional traits [9,10], including leaf, stem, root, reproductive, and whole-plant integrative traits. Positive or negative trait correlations are generally considered to represent trade-offs, co-optimization, and/or allometric relationships based on biomechanical and/or physiological requirements [11,12]. Indeed, many of these trait relationships have proven common, or even general, across diverse sets of species within and among communities and biomes, and even across global databases. One prominent example is the well-recognized set of relationships among leaf economic traits, including specific leaf area, leaf nitrogen concentration, leaf longevity, and net photosynthesis, known as the leaf economics spectrum (LES) [13,14]. Indeed, LES traits have been linked to other traits related to resource acquisition and resource retention across plant life history, including plant height, stem density, seed mass, and leaf area [15]. The generality of LES trait relationships has led to the exploration and definition of analogous correlative frameworks for different organs, including wood and root economic spectra [16,17], and whole-plant economic spectra [18,19]. Furthermore, correlative frameworks have been proposed among other sets of traits, including hydraulics [20,21], drought tolerance [22], biomechanics [23], and plant defense traits [24]. Despite their commonness, these trait constellations frequently shift across functional groups and environments, providing useful insights in numerous specific contexts [25,26].

Highlights

Most functional traits are multifunctional and adaptations to multiple selective pressures, complicating the use of traditional correlation and clustering approaches to establish their integration and relative mechanistic importance.

New developments in the analysis and application of plant trait networks (PTNs) increase the resolution and inference of adaptations and responses of plants across scales.

Communities vary in their constraints on given traits, resulting in variation in PTN topology, and the relative importance of component traits.

PTNs provide a multidimensional approach for evaluating the adaptations and response of plants across lineages, life forms, ontogenetic stages, and environments.

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This increasing focus on suites of correlated traits has led to a reductionist tendency toward simplicity, that is, to reduced dimensionality. Thus, if traits are strongly correlated, they can be considered as a single spectrum, and analyses such as principal components analysis can provide a quantitative basis. Thus, plant economic spectra are often considered to vary along a single axis, from traits related to rapid growth and short tissue lifespans, to traits related to slow growth, stress tolerance, and long tissue longevities [14]. However, recent studies have highlighted how such simplified dimensionality can obscure overall patterns of adaptation, because individual traits often contribute in a combined way to multiple functional systems [6–8,27], thereby contributing to vital rates and their resiliency to stress, and thus competitive ability and fitness in different environments (Figure 1). Accounting for these complex relationships holds promise to clarify the integration of the phenotype and constraints on its adaptation, and to assess traits of particular importance to given functions and to overall fitness, and how these vary across species, habitats, and environments.

Theoretical Basis for Plant Trait Networks and Their Numerous Ecological Applications

Network theory presents an effective approach toward resolving the relationships among multiple plant traits and their significance. Network analysis was developed from graph theory, and resulted in small-world network models and scale-free network models [28–30]. Theoretically, a network can be any collection of units potentially interacting as a system that is represented as a set of nodes connected by edges. Networks have been widely used for analyses of social groups [31], microbial communities [32], metabolic pathways [33], transport systems [34,35], and gene interactions [36]. The application of network analysis to complex systems of plant traits in nature can enable the explicit consideration of the interdependent relationships among multiple

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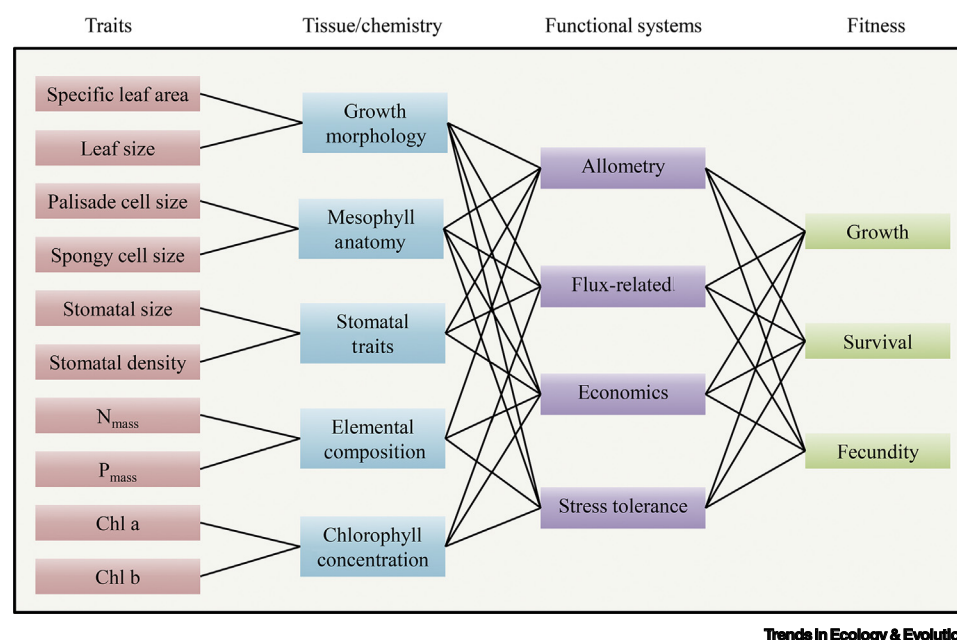
Figure 1. The Complexity of Correlations among Multiple Traits, within and among Organs and Functional Systems, and Their Contribution to Fitness. This figure emphasizes the importance of traits on higher level processes, a hierarchy that may inform the topology of plant trait networks, depending on the traits included and their inter-relationships. N_{mass}, and P_{mass} are mass-based expressions of leaf nitrogen and phosphorus concentrations, respectively. Chl a and Chl b are chlorophyll a and chlorophyll b concentrations, respectively.

traits. Indeed, for more than two decades studies have suggested that the relationships among plant traits may be visualized as a network or correlogram, and sometimes analyzed using path analysis or structural equation models [21,26,37–43]. Recent studies [40,44] have quantified parameters to describe the network topology and the interdependency of traits.

Plant trait networks (PTNs) have potential to capture comprehensively and enable the visualization of the associations among plant traits, that is, as a set of nodes (traits) connected by edges (trait–trait relationships). PTNs can be applied across individuals of a species, or across species within or across communities, and can highlight the multivariate responses and adaptive mechanisms of plants to the environment. In principle, PTNs could also be used to resolve the key traits and trait combinations that influence important components of fitness or other aspects of function (e.g., productivity) across plant communities. PTNs have fundamental properties that can highlight important details of functional ecology, and provide novel insights. For example, (i) each trait has the potential to become a key node, that is, a hub with special importance in a given environment; (ii) interactions among particular traits can have disproportionate ecological significance; and (iii) the properties of an ensemble of traits can yield specific functions beyond simply considering one or few traits and their relationships. PTNs can be subdivided by organ (i.e., leaf or root trait networks), functional system (e.g., photosynthetic, economic, hydraulic, or signaling trait networks), or other classification criteria.

Some ecological theories can also be explicitly framed using PTNs. For instance, networks among elemental composition variables (i.e., ionomics [45,46]) could reflect Liebig's law of the
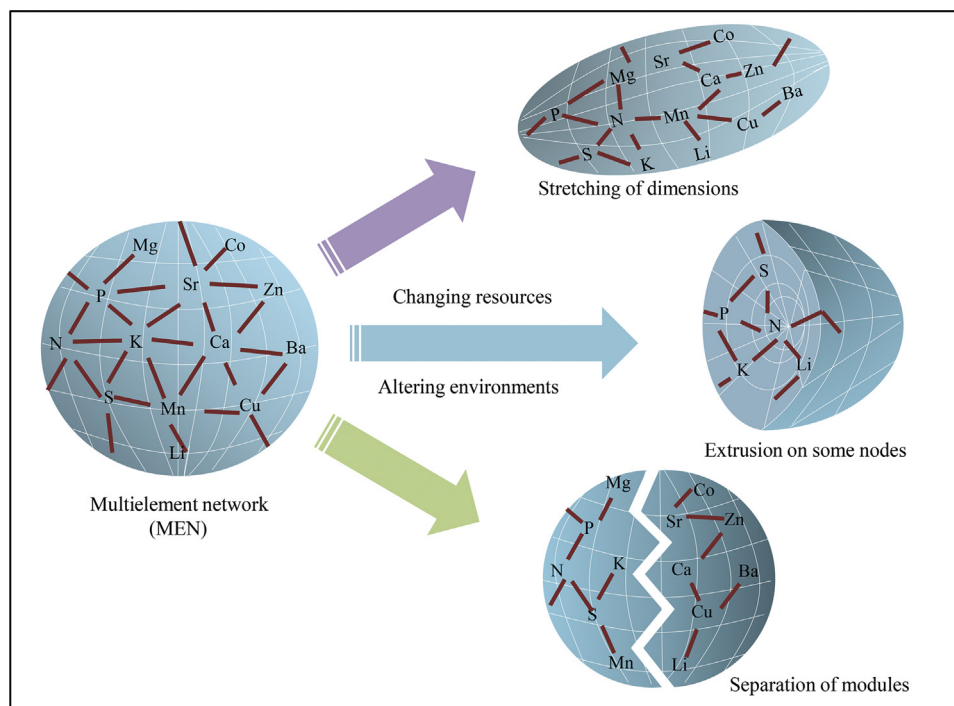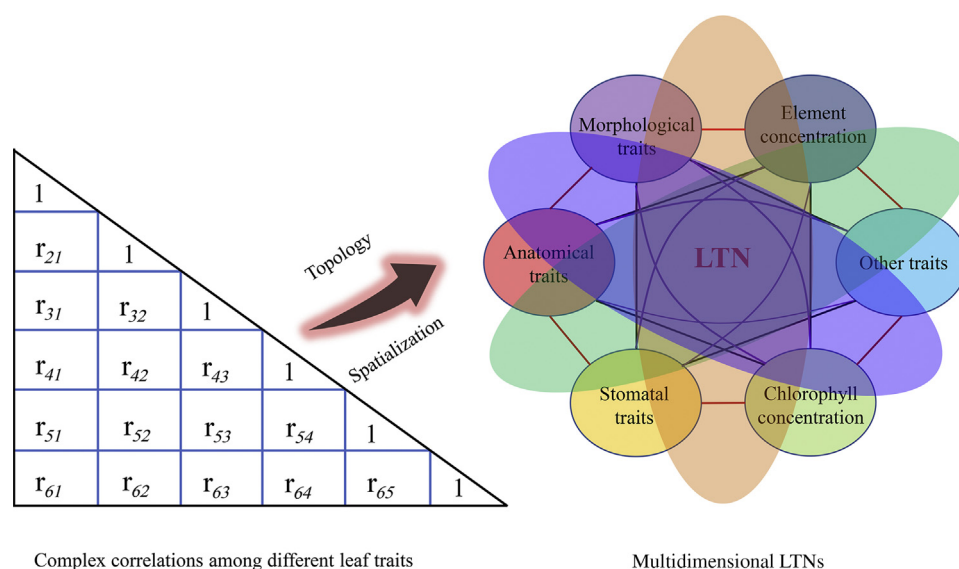

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Figure 2. Multielement Networks of the Leaf and Potential Responses to Changing Resources and Environments. 3D diagrams are used to highlight the relationships between multiple plant traits and their variation with the environment. For example, where nitrogen limitation becomes stronger, the network may reflect stretching of dimensions, extrusion on some nodes, or separation of modules. Note that all nodes are not necessarily shown in each graph, and the apparent absence of a given element in any panel does not imply its actual loss or that plants do not require the element.

minimum [47] and the theory of ecological stoichiometry (relating to element limitation using elemental ratios) [48,49]. In general, the adaptation of plants to limiting factors (e.g., nutrient availabilities) may be resolved by testing the shifts of trait networks (Figure 2). Thus, in principle, shifting key nodes and deforming ionomic networks could reflect changes in the limiting resource, with functional consequences for the performance of plants in given environments.

Additionally, PTNs can enable clearer resolution and greater expansion of trait constellation frameworks than have been afforded by the consideration of single or few dimensions of plant function (Figure 3). For example, PTNs can enable moving beyond simple 'economics' frameworks [14,50] to considering multiple modules of plant function, including, economics, 'flux traits', and tolerances of multiple resource shortages. Thus, PTNs allow us to clarify multiple spectra or leading dimensions simultaneously, and their inter-relationships, as strongly correlated traits (or trait spectra), might be aggregated to a module corresponding to a higher-level function, such as productivity. Indeed, PTNs enable the quantification of the interdependency of multiple traits. Plant traits can be biologically or statistically correlated; however, not all traits directly connect in all PTNs. Consequently, PTNs with higher edge density, shorter average path length, and shorter diameter imply a stronger coordination among multiple traits [44] (Y. Li, dissertation, Beijing Forestry University, 2020).

Within PTNs, the importance of given traits can be assessed. Traits with higher connectivity to other traits are hub traits, whereas traits with higher centrality (i.e., betweenness) are mediators. While a given trait can be both a hub and a mediator, these are distinct qualities; a hub trait interacts with many other traits, thus having a high degree, and likely plays a central regulatory role that influences the whole phenotype, whereas a mediator trait has high betweenness, and likely coordinates several subnetworks. Several studies have tested the expectation that leaf economics traits should be hub traits (Box 1). However, the test for the identity of hub traits might depend on plant functional groups and/or the overall combination of traits considered within the PTNs, and their relative variation in the

Complex correlations among different leaf traits

Multidimensional LTNs

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Figure 3. Establishing Multiple Dimensions of Leaf Trait Networks (LTNs) Based on the Correlations among Leaf Traits. In the left panel, r_{ij} is the coefficient of correlation (or other tests) to present trait–trait relationship; here i an j are different traits, respectively. In the right panel, the trait modules are connected with lines of different colors, emphasizing that different processes that can underlie the linkages of modules; the shading represents the expectation of variation in the strength of interconnection of modules.

Box 1. Parameters of PTNs

Parameters Describing the Overall Topology of PTNs

Three parameters can be used to quantify the tightness of the PTN, that is, the edge density (*ED*), diameter (*D*), and average path length (*AL*); and two parameters to quantify the complexity of the PTN, that is, the average clustering coefficient (*AC*), and modularity (*Q*) (Figure I).

ED describes the density of the connected edges between nodes in a network, that is, the proportion of actual connections among traits out of all possible connections.

$$ED = \frac{2L}{n \cdot (n-1)} \tag{I}$$

where *L* is the number of actual edges of the network, and *n* is the number of node traits. *D* is the maximum shortest distance between any two connected node traits in the network, and *AL* is the mean shortest path between all node traits in the network. PTNs with higher *D* and *AL* have greater overall independence among traits.

$$D = max \{d_{ij}\} \ (i \neq j) \tag{II}$$

$$AL = \frac{1}{n \cdot (n-1)} \sum_{i \neq j} d_{ij} \tag{III}$$

where d_{ij} is the shortest distance between focal node trait vi and node trait v_j, and *n* is the number of node traits.

AC is the average of the clustering coefficients of all traits in PTNs. PTNs with higher *AC* are more extensively divided into several different components.

$$AC = \frac{1}{n} \sum_{i=1}^{n} CC_i \tag{IV}$$

where CC_i is the clustering coefficient of focal node trait v_i (see Equation IX), and *n* is the number of traits.

Modules are defined as clusters of traits that exhibit covariation among themselves, relatively independently of other clusters [60]. The modularity of the network measures the separation of trait clusters within the network (Equation IX).

$$Q = \frac{\sum \left[\left(A_{ij} - \frac{k_i * k_j}{2m} \right) \delta(c_i, c_j) \right]}{2m} \tag{V}$$

where *m* is the number of edges, A_{ij} is the element of the A adjacency matrix in row *i* and column *j*, k_i is the degree of *i*, k_j is the degree of *j*, c_i is the component of *i*, c_j is that of *j*, the sum encompasses all *i* and c pairs of vertices, and δ(x, y) is 1 if x = y and 0 [61].

Parameters Describing the Properties of Nodes within PTNs

Two parameters can be used to quantify the connectedness of each trait, that is, the degree (*k*) and closeness (*C*); and two parameters to quantify the centrality of each trait, that is, the betweenness (*B*), and clustering coefficient (*CC*).

k is the number of edges that connect a focal node trait to other nodes. Plant traits that have a high *k* can be considered as overall hub traits.

$$k_i = \sum_{j \neq i} a_{ij} \tag{VI}$$

where a_{ij} is the connection between the focal node trait v_i and node trait v_j.

C is the reciprocal of the mean shortest path between a focal node trait and all other nodes. Traits with high closeness are closely related to other traits.

$$C_i = \frac{n-1}{\sum_{j=1}^{n-1} d_{ij}} \ (i \neq j) \tag{VII}$$

where d_{ij} is the shortest distance between focal node trait v_i and node trait v_j, and *n* is the number of node traits.

B is the number of shortest paths passing through a focal node trait. Traits with high betweenness values serve as mediators in the PTN.

$$B_i = \sum_{jk} \sigma(j, i, k)$$ [VIII]

where (j, i, k) is the number of shortest paths between the focal node trait v_j, and node trait v_k that crossed node v_i.

CC describes how a complete node trait is connected to its neighbors. If a node trait is fully connected to its neighbors, the clustering coefficient is 1. A value close to 0 signifies few connections with neighbors. Traits with high CC values represent centers of different specific functional modules in PTNs.

$$CC_i = \frac{2l_i}{t_i(t_i-1)}$$ [IX]

where l_i is the number of links between neighbors of node trait v_i, and t_i is the number of neighbors of node trait v_i.
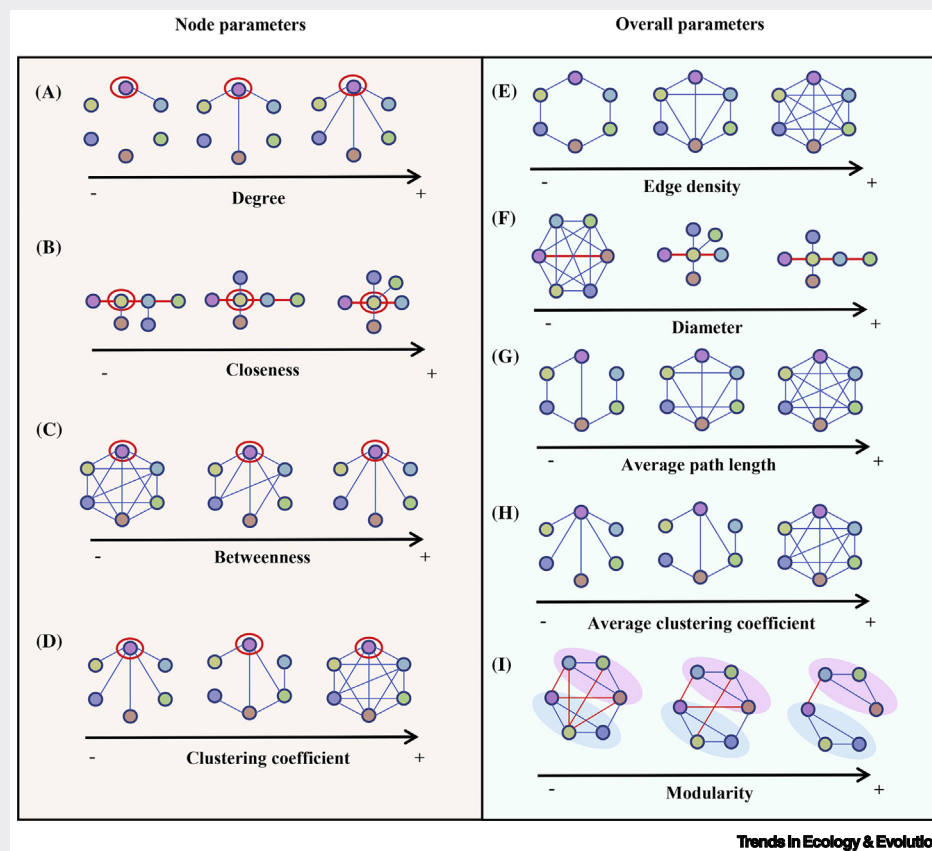

Figure I. Key Parameters of Plant Trait Networks (PTNs). Network metrics were used to assess the interdependence among traits in PTNs. The individual parameters of PTNs are degree (k), closeness (C), betweenness (B) and clustering coefficient (CC) as shown in A–D. The overall parameters of PTNs are edge density (ED), diameter (D), average path length (AL), average clustering coefficient (AC), and modularity (M) as shown in E–I.

dataset. Thus, a trait correlation network based on a compilation of relationships across the literature found that specific leaf area was a hub trait [40]. However, the same authors, in an empirical assessment of herbaceous perennial plants, observed that biomass allocation traits and stem specific length were stronger hubs in that system [40]. PTNs can also enable tests of shifts of correlative trait suites across environments. For example, economic and hydraulic traits are decoupled in moister regions, but are coupled in drier regions [8,20,51].

Finally, PTNs enable the quantification of overall phenotypic integration. Phenotypic integration has long been considered as a key topic in ecology [52], with approaches largely focusing on ascertaining the correlations among traits contributing to functional units (modules), and identifying correlations among modules [53]. PTNs enable a more comprehensive and detailed characterization of trait modules, and investigation of their biological significance, and thus, higher resolution of overall phenotypic integration [44,53] (Y. Li, dissertation, Beijing Forestry University, 2020).

Methods for Constructing PTNs and Typical Examples
Methods for Constructing PTNs
A network consists of a series of nodes and edges. In PTNs, plant traits are nodes and trait–trait relationships are edges. First, a matrix of trait–trait relationships is calculated (Figure 3). Trait–trait relationships (r) can be quantified using Pearson correlations [40], Spearman correlation coefficients, phylogenetic correlations, or other tests [44]. Trait–trait relationships can arise for various reasons [21,54]. First, some trait–trait relationships may be directly mechanistic (i.e., physiological structure–function relationships), where, for instance, the size or number of a given structure determines the physiological output of a process. Second, some trait–trait relationships arise owing to their coselection through optimal design, that is, each trait independently contributes structurally either positively or negatively (in the case of a trade-off) to an overarching function. Third, some trait–trait relationships arise owing to the concerted convergence of the two traits, that is, each trait contributes independently and is selected for their advantage in the given environment. To avoid considering spurious correlations among traits, a threshold can be applied to determine whether there is a correlation among traits, for example, $|r| > 0.2$, $P < 0.05$ [40], although a different threshold may be chosen as appropriate for a given study design. Then, an adjacency matrix $A = [a_{i,\,j}]$ with $a_{i,\,j} \in [0,1]$ is established by assigning above threshold as 1 and below threshold as 0; thus, A only shows the presence and absence of connections between pairs of plant traits. Finally, PTNs are visualized and the parameters of PTNs are calculated, for example, using the package igraph in R Software (Box 1).

An Example of PTNs: Leaf Trait Networks
Plants adapt to changing environments by shifting multiple traits and their relationships. PTNs are an especially useful approach to resolve these shifts across bioregions or life forms. Given the importance of leaves in overall plant function, we focus on leaf trait networks (LTNs) as an illustrative example. We compiled data for 34 traits of 394 tree species across nine typical forests, all measured in standard ways, which enabled the construction of LTNs (Y. Li, dissertation, Beijing Forestry University, 2020). As expected, the parameters of LTNs enabled the quantification of the shifts in leaf traits to varied environments at the biome scale (Box 2). Communities in colder biomes are less differentiated into clusters, that is, have fewer modular LTNs. Furthermore, plants adapted to stressful conditions are constrained in certain traits, which tend to be uncorrelated with the rest of the integrated phenotype, leading to a looser overall network.

Outlook and Challenges of PTNs
PTNs provide an integrative perspective on plant adaptation and ecology, highlighting new approaches to elucidating the response of the total phenotype to changing environments and resources, with many potential applications. First, PTNs can clarify the variation of trait correlative structure, within and across organs, within given species across ontogenetic stages, or across species of different lineages, or across communities of varying environments or successional stages. PTNs could also be used to compare trait correlations across different scales, that is,

Box 2. Examples of Applying PTNs

Changes in LTNs from Tropical to Cold-Temperate Forests

To quantify spatial variation in LTNs, we investigated 34 leaf traits of 394 tree species in nine forests along the 3700 km north–south transect of eastern China (NSTEC) as part of the 15th standard transect of the International Geosphere Biosphere Program. This transect extends from tropical to cold-temperate forests, ranging from 18.7° N to 51.8° N [19,20,54]. Details on the traits and their measurements are provided in Table S1 in the supplemental information online.

The LTNs provided new insights (Figure I, adapted from Y. Li, dissertation, Beijing Forestry University, 2020). LTNs shifted to a simpler topology from tropical to cold-temperate forests, reflecting the cooler climate and reduction of soil nutrient availability. LTNs were tight and complex in tropical forest and loose assemblages of few modules in cold-temperate forests. Leaf thickness and its associated leaf economic traits were generally identified as key traits in LTNs, with greater connectivity than that among other peripheral traits.
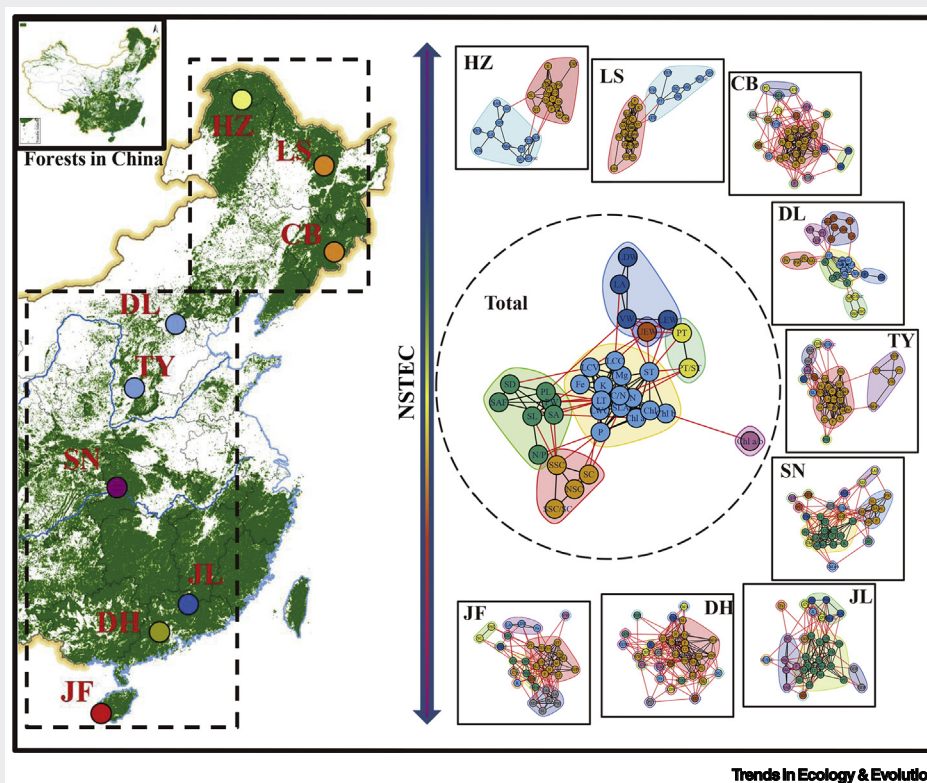

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Figure I. Shifts in Leaf Trait Networks (LTNs) from Tropical to Cold–Temperate Forests along the North–South Transect of Eastern China (NSTEC). The nine forests are Huzhong (HZ), Liangshui (LS), Changbai (CB), Dongling (DL), Taiyue (TY), Shennongjia (SN), Jiulian (JL), Dinghu (DH), and Jianfengling (JF). The colors in the left panel represent different forest types. In the right panel the nodes represent different traits, and LTNs are divided into different modules, indicated by colors of the circles and of the shaded regions. The black and red lines represent the connections respectively between nodes of the same modules, and between nodes of different modules.

for organ-level traits (e.g., photosynthesis per leaf area, nitrogen per leaf area, and leaf mass per area), plant-level traits (e.g., relative growth rate with plant nitrogen concentration and phosphorus concentration), or ecosystem level traits (e.g., net ecosystem exchange, total plant nitrogen, leaf area index, and number of stomata per unit land area). For such an approach, it is key to scale variables thoughtfully from organs to communities, even to ecosystems [4]. Furthermore, shifts in PTNs for given communities should be considered with ongoing climate change, as these may be impacted by atmospheric N deposition, acid deposition, climate change, land-use change, and

even environmental pollution. This information will clarify the current status and predict future scenarios. As future work clarifies the specific significance of the network parameters across different ecological contexts, new applications can be developed to improve trait-based modeling. For example, the resolution of hub traits will lead to a better understanding of traits that should be included in models of species distributions, as well as vegetation models, and understanding the separation of modules will indicate which traits should be considered independently within such models.

Although PTNs can be used as a tool to better characterize trait relationships, their current limitations require analysis. For example, the selection of traits may influence the structure of PTNs, to an extent that will need to be clarified. Indeed, such future work must evaluate the ability of PTNs to disentangle the importance of given traits and their topology for contrasting types of traits sets, for example, for a large number of closely related traits (such as, anatomical variables), relative to a set of traits representing a mix of state variables and rates (such as morphological variables, physiological rates, and biomass ratios) or for traits representing given organs or spanning different organs. Furthermore, given that trait correlations may arise due to causal relationships, or indirect relationships, the identification of important traits using PTNs must also be compared with those known to play a causal role in driving processes such as adaptation to a given environment, or contribution to fitness. We expect that future work to further clarify the opportunities and limitations of PTNs will provide important insights. For example, we hypothesize that the greatest shift in PTN topology will arise from the addition or removal of hub traits that have important connectivity with and causal impacts on other traits in the network. Indeed, in general, scale-free networks are tolerant to the addition or removal of peripheral nodes, and sensitive to new hub nodes [40,55,56]. In the example described in Box 2, trait networks composed of different numbers of subsampled traits showed same trends with climate variables.

The new development and applications of PTNs are timely, given the removal of impediments to their determination. First, the Plant Trait Database TRY (https://www.try-db.org), the largest and best-known database, contains 148 000 plant taxa and 6.9 million trait records. This database could provide a good foundation for constructing PTNs [44]. Recently, TRY has enhanced its coverage and become open access [57]. Second, the sPlot database (https://www.idiv.de/en) contains more than 1.1 million vegetation plots and 279 000 plant species with trait information [7,58], scaling traits from the species to the community level. This database could be used to construct PTNs at the community level. However, data matching between TRY and sPlot is poor; thus, constructing PTNs requires filling in trait gaps, which might introduce large amounts of error or bias. If possible, traits must be consistently measured with the same methods, and even on the same individual plants [59].

Concluding Remarks

PTNs provide valuable tools and insights for clarifying many aspects of functional ecology for a wide range of plants and their adaptations. Priority areas are the determination of PTNs and their variation among (i) plant traits with different functions and/or multifunctions; (ii) different plant organs (i.e., leaf, stem, trunk, and roots); (iii) contrasting phases of growth from seedlings to mature plants; (iv) communities reflecting phases of succession from early to climate-mature; (v) different types of disturbance; and (vi) climates. Such information will be useful to expand and optimize our ability to observe and predict the responses of plants, communities, and ecosystems (see Outstanding Questions). We anticipate that the conceptual and methodological development of PTNs will facilitate the accelerated collection of systematic and consistent trait data, which will be widely applied across different ecological scales.

Outstanding Questions

Plant functional traits enable us to quantify adaptation to different environments. Given many traits of plants are adaptations to multiple selective pressures, how can these be considered together and how can we disentangle them?

How can we quantify the complex relationships among multiple traits with metrics for their integration, modularity, and the topology of their coordination?

How can we consider the multiple dimensions of plant adaptation and response to changing environments, resources, disturbance, and global change?

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Supplemental Information

Supplemental information associated with this article can be found online https://doi.org/10.1016/j.tree.2020.06.003.

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