A theoretical framework for the ecological role of three-dimensional structural diversity

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The three-dimensional (3D) physical aspects of ecosystems are intrinsically linked to ecological processes. Here, we describe structural diversity as the volumetric capacity, physical arrangement, and identity/traits of biotic components in an ecosystem. Despite being recognized in earlier ecological studies, structural diversity has been largely overlooked due to an absence of not only a theoretical foundation but also effective measurement tools. We present a framework for conceptualizing structural diversity and suggest how to facilitate its broader incorporation into ecological theory and practice. We also discuss how the interplay of genetic and environmental factors underpin structural diversity, allowing for a potentially unique synthetic approach to explain ecosystem function. A practical approach is then proposed in which scientists can test the ecological role of structural diversity at biotic–environmental interfaces, along with examples of structural diversity research and future directions for integrating structural diversity into ecological theory and management across scales.

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One of the fundamental goals in ecology is to understand the identity, abundance, and arrangement of life forms on Earth, because such variation underpins the emergence of ecological patterns and processes (Hooper 2002; Mace *et al*. 2010). For example, early research showed that the stratification of vegetation layers was correlated with niche partitioning in birds (MacArthur and MacArthur 1961). Many biological and ecological studies have sought to resolve structural attributes and variation in the arrangement of organisms from fine to broad spatial scales (Figure 1; Panel 1). At the spatial scale of molecules, biologists have linked protein structural attributes to critical cellular processes (Senior *et al*. 2020; Belteton *et al*. 2021); while at broad scales, landscape ecology and remote sensing have focused on characterizing land-cover heterogeneity and patch structure across landscapes or continents (McGarigal and Marks 1995). There is also a rich history in forestry linking stand structure with timber production (Reineke 1933), and ecologists have long been fascinated with describing habitat structure (McCoy and Bell 1991). Despite historical roots in forestry, remote sensing, and community and landscape ecology, there is still a relatively limited understanding of the linkages of three-dimensional (3D) structural diversity to broader ecological patterns and processes. The explicitly structural conception of diversity presented here, which incorporates physical structure – the volumetric capacity and the spatial arrangement of biotic components of different identities – may be as valuable, and complementary to, more widely applied biological diversity measures in characterizing ecological processes across space and time (LaRue *et al*. 2019; Hakkenberg and Goetz 2021; Zhai *et al*. 2022).

In a nutshell:

- Three-dimensional structural diversity describes the volumetric capacity, physical arrangement, and identity/traits of biotic components that arise through genetic and environmental factors and their interactions
- All biotic components of ecosystems occupy spatial volumes, arranged in relation to other components, which mediate the flow of energy and matter in ecological processes, making structural diversity an integral part of ecology
- We propose applying structural diversity at interfaces between Earth system layers for predicting ecosystem function
- A framework for understanding and characterizing structural diversity will facilitate its incorporation into theoretical and applied ecology

Descriptions of structural diversity have been inconsistent and often constrained to a narrow range of ecosystem components or spatial scales, and connections to a broader framework have been challenging (Golley 2000). Gaps in understanding of the ecological role of structural diversity have been partly related to a lack of efficient methods for measuring ecosystems in 3D space. Specifically, the difficulty of measuring the size and 3D location of small ecosystem components across large spatial

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Panel 1. A brief history of the conceptualization of structural diversity in ecology

The concept of structural diversity has evolved in the literature over the past century (Figure 1; WebTable 1), partly due to advances in technologies that became available to quantify ecosystem structural attributes (Figure 1; WebTable 2). Throughout most of the first half of the 20th century, tools for measuring the size and spatial location of ecosystem components were limited to labor-intensive field methods, and therefore conceptions of structural diversity were simpler. The emergence of advanced remote-sensing techniques in the 1990s that permitted three-dimensional (3D) quantification of vegetation and topography marked an important milestone in the ability to characterize 3D ecosystem components across scales of measurements. The concept of structural diversity continued to evolve into the early 21st century as 3D data from remote sensing became more readily available. Despite advances in remote-sensing technology, quantification of structural diversity has been mostly limited to tree canopies at the stand level.

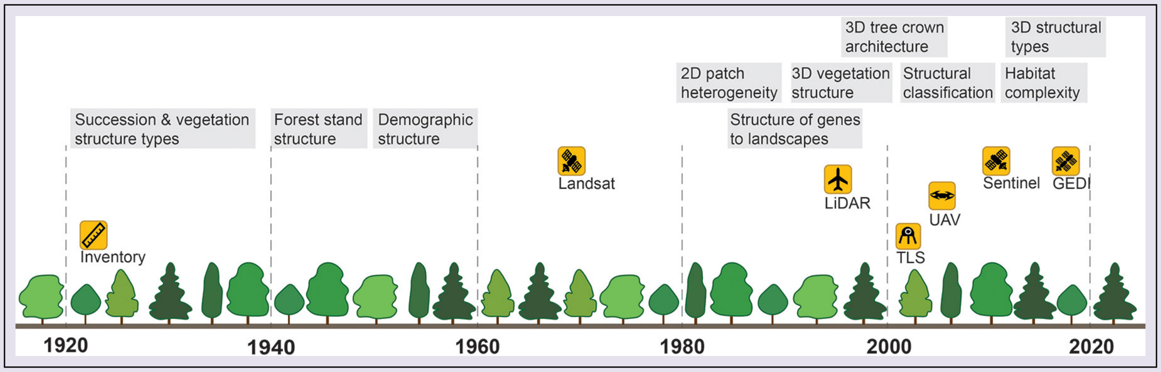

Figure 1. A timeline of previous enumerations of structural diversity and related concepts, along with examples of major technological advances in tools for its measurement: Inventory (for example, human-collected measurements in the field), Landsat (NASA/USGS Landsat satellite program), lidar (light detection and ranging), TLS (terrestrial laser scanning), UAV (unoccupied aerial vehicle), Sentinel (European Space Agency's Sentinel satellite program), and GEDI (Global Ecosystem Dynamics Investigation, installed on the International Space Station).

scales has limited the types of metrics available to ecologists to conduct detailed multi-scale analyses (Panel 1). However, emerging frontiers in remote sensing, geographic information systems, and computational science have converged (Lausch *et al*. 2016; Dubayah *et al*. 2020; Valbuena *et al*. 2020) to create a pathway for examining structural diversity across macrosystems. In addition to measurement constraints, the incorporation of structural diversity as a component of ecological studies has been limited by a lack of well-defined hypotheses and theories connecting it to ecological patterns and processes (but see literature in forestry for theory on tree architecture in ecosystem productivity; eg Ammer 2019). A comprehensive understanding of structural diversity is needed to advance ecological theory and inform management practices to improve ecosystem resilience and conservation efforts in an era of unprecedented global change. Indeed, structural diversity has been recognized in international initiatives for conservation and biodiversity monitoring that seek to track changes in diversity (essential biodiversity variables) (Pereira *et al*. 2013; Skidmore *et al*. 2021) across multiple levels of biological organization (genes to landscapes) (Noss 1990; Lausch *et al*. 2016).

A framework for structural diversity

Our primary objective here is to present a framework for structural diversity that can facilitate its characterization across space and time, and promote theory focused on understanding its role in ecology, including resolving inconsistencies in how the concept is defined. The main tenets of our framework are that structural diversity (1) is a key part of ecosystems that describes the volumetric capacity, physical arrangement, and identity/traits of biotic components in an ecosystem, and (2) is an integral part of ecological patterns and processes through its influence on the distribution and interactions of energy and matter. Structural diversity fits within the larger framework of ecological diversity because, like taxonomic diversity, it can be measured across all levels of biological organization, and at different spatial and temporal scales (Figure 2) (Noss 1990; Lausch *et al*. 2016). We first provide a broad overview of what structural diversity is and explore its role in driving ecological patterns and processes, and then discuss how structural diversity can be applied as a unique approach for predicting ecosystem function. Finally, we give examples of structural diversity research and discuss key challenges and future directions.

A definition for structural diversity

Our framework builds upon past enumerations of structural diversity (sometimes described as structural complexity or heterogeneity) to propose that it be conceptualized as the 3D space (volumetric capacity) that biotic components of different identities/traits take up and the physical arrangement of these components in 3D space (Figure 3). The measurement of structural diversity begins with the identification of the component of interest: a biotic object (dead or alive), a network (connected components), or the entire ecosystem itself, from a patch to the macroscale (Nadkarni *et al.* 2008). Each component has one or more identities or traits (eg moss species nested within the bryophyte division). These components can be represented across a variety of spatial scales (eg microbiomes to plant communities to landscapes) and levels of biological organization (eg organs to landscapes). We focus primarily on sessile organisms that are the dynamic and essential building blocks of physical structure in ecosystems (eg microbes, coral reefs, plants); although biotic components could also include non-sessile organisms, we do not emphasize them in detail here.

We propose a focus on the following three categories to describe structural diversity within and of ecosystems: volumetric capacity (occupied or unoccupied), physical arrangement, and the identity/traits of biotic components. First, volumetric capacity considers the proportion of the total space or volume in an ecosystem that a component (or more) encompasses and includes the occupied (how many components fit into the ecosystem) and unoccupied (how much space is unfilled) volume within the 3D space of interest. The presently occupied volume represents the "realized" volumetric capacity or niche space (ie geographic representation of niche space), whereas the unoccupied volumetric capacity represents the volume available for the emergence of additional components. For example, occupied volumetric capacity might include the volume represented by the plant canopy in wetlands and lake communities. However, where to establish the boundary for measuring ecosystem volume remains an open question. For example, the volume of a lake has a typically clear bottom and surface boundary, whereas for the forest ecosystem, the canopy boundary could be set as the height of the atmosphere directly above the tallest tree or average of all trees in the canopy. Furthermore, the measurement of unoccupied volume is possible but can be challenging in terrestrial systems. Research should focus more on the occupied and unoccupied volume for within and across system comparisons.

Second, physical arrangement considers how components are physically configured within space. There are many possible measurements of physical arrangement, including heterogeneity in vegetation height (Atkins *et al.* 2018), the distribution of different sized components such as stem area (McElhinny *et al.* 2005), or fractal surface geometry (Torres-Pulliza *et al.* 2020).

Third, the volumetric capacity or physical arrangement of groups of components that vary in their identity or traits can also be measured, such as the architecture of different phenotypes or ecotypes of a submerged aquatic plant or marine macroalgae (Santamaría *et al.* 2003; Coleman *et al.* 2019), or the vertical distribution of functional trait values throughout an ecosystem (Kamoske *et al.* 2021). We suggest that 3D volumetric capacity, physical arrangement, and the identity/traits of biotic components – in combination – describe the structural diversity of a given ecosystem (Figure 3). Like other diversity measures such as biodiversity and functional diversity, structural diversity provides a characterization of one dimension of the diversity of an ecosystem, allowing within and cross system/regional comparisons with the potential to aid conservation and restoration of various ecosystem types.

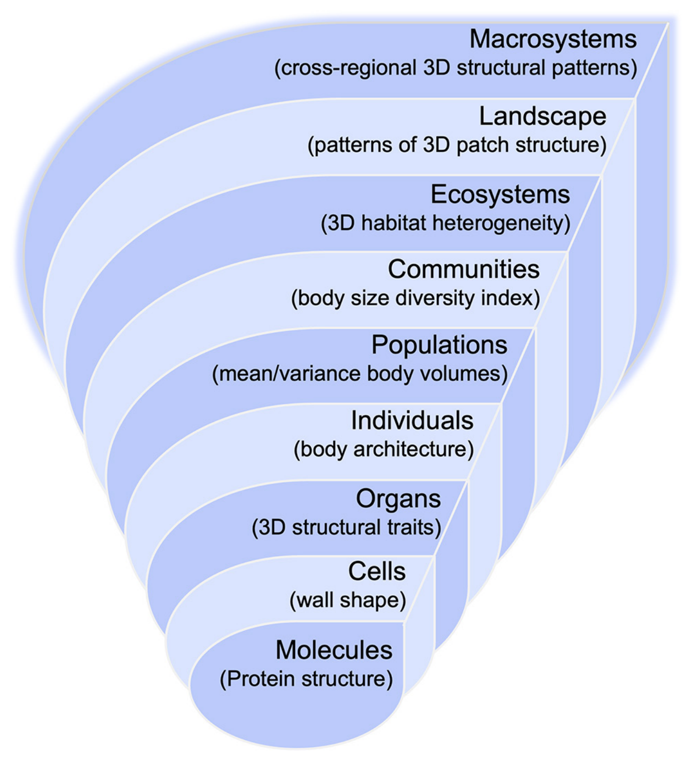

Figure 2. Structural diversity can be measured across multiple levels of biological organization, from molecules to macrosystems.

Quantification of structural diversity across spatial and temporal scales is very similar to approaches used in landscape ecology to measure two-dimensional (2D) land surface features (Table 1). Landscape ecology emphasizes interactions among spatial patterns and ecological processes at medium spatial scales (10–100s km^2), which parallels our attempts to connect descriptions of structural diversity to ecosystem functions (see "Structural diversity as a unique predictor of ecosystem function" section below). Landscape patch and surface metrics have been commonly used to describe the spatial composition and configuration of 2D landscapes (eg cover and arrangement; Fahrig 2003; Turner and Gardner 2015), which can be expanded to include 3D features (Lepczyk *et al.* 2021), including the volumetric capacity, physical arrangement, and identity/traits of ecosystem features across landscapes (Table 1). Furthermore, traditional landscape ecology comparisons of patterns within and among patches are also transferable to describing spatial patterns in structural diversity. For example, future research could investigate the utility of these 3D metrics to identify structural diversity hot spots across a region.

The ecological emergence of structural diversity and its dynamic nature

Like other aspects of diversity, the structural diversity of life forms and the communities they compose is determined by the interplay between the environment and genetics: from genes to regional processes. Intra- and interspecific genetic and epigenetic variation determines the phenotype of organisms, including their size and body architecture. Population genetic variation, biotic interactions, and regional species pools influence the combined structural diversity of communities. In addition, environmental conditions – defined here as an ecosystem's abiotic factors – at spatial scales ranging from microhabitats to regional climate affect the genetic composition of populations and regional species pools available to determine the structure of ecosystems. Finally, interactions between genetics and environmental factors affect the structural diversity of organisms, populations, and communities through phenotypic plasticity (the ability of a genotype to express different phenotypes in response to their environment). However, the relative contributions of genetic and environmental factors to structural diversity in single species and communities across ecosystem types have not been well quantified.

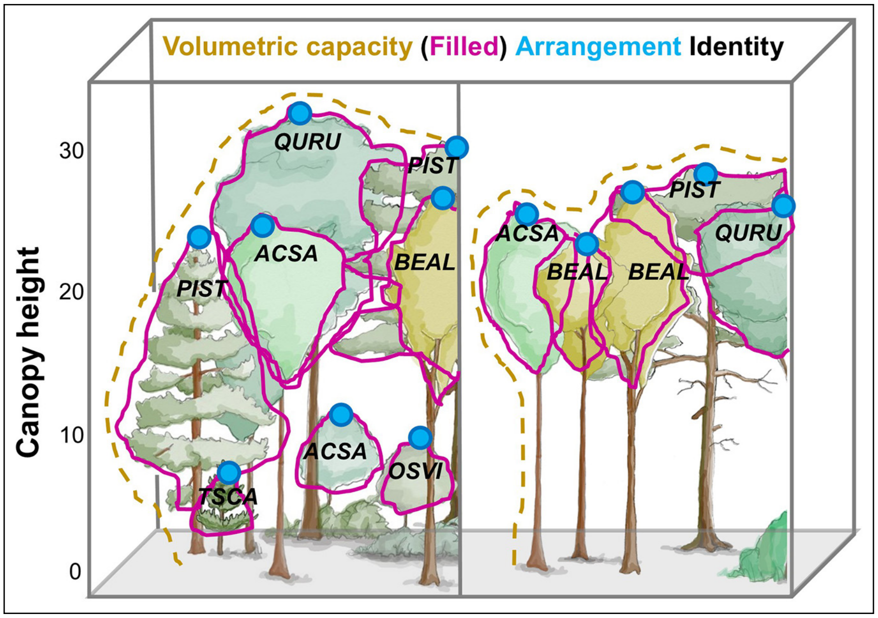

Figure 3. Structural diversity is defined as the three-dimensional (3D) volumetric capacity (eg occupied canopy volume, both overall and the space filled by crowns), physical arrangement (eg distribution of all biotic components in a canopy), and identity/traits of biotic components within ecosystems (eg varying positioning of crown peaks of different tree species). Structural diversity can be measured for components – living and dead biotic objects – ranging from the organs of an organism to the physical dimensions of the ecosystem itself. Acronyms indicate tree species identities: ACSA = *Acer saccharum*, BEAL = *Betula alleghaniensis*, OSVI = *Ostrya virginiana*, PIST = *Pinus strobus*, QURU = *Quercus rubra*, TSCA = *Tsuga canadensis*. Color shading indicates potential volumetric capacity (mustard brown), filled volumetric capacity (pink), arrangement (blue), and species identity (black).

Structural diversity is a dynamic property of ecosystems that can vary across space, linking it with a large body of work on landscape structure (McGarigal and Marks 1995). For example, in landscapes, structural diversity can be assessed within and among patches by describing diversity within a discrete patch (alpha diversity) or within regions (gamma diversity), or as turnover among patches (beta diversity) (Arellano and Halffter 2003). Endogenous or exogenous drivers and feedbacks with structural diversity may create heterogeneous patterns across space (Turner 2010). Because spatial patterns in structural diversity may vary at different scales, ecologists must first determine which scale is most relevant for the ecological process of focus when making cross-scale comparisons.

Table 1. Extension of two-dimensional landscape ecology patch and surface metrics to structural diversity across spatial scales

Category	Landscape ecology	Structural diversity
Volumetric capacity	Proportion of landscape filled by patches	Occupied proportion of ecosystem volume
	Contagion	Porosity
Physical arrangement	Patch size diversity/dominance	Foliage height diversity
	Amplitude	Heterogeneity of component heights
	Edge density	Canopy surface roughness
	Connectivity	–
	Fractal dimension	Fractal rugosity
	Radial surface pattern	Radial vertical surface pattern
Identity/traits	Spatial configuration of patch types	Spatial configuration of volume or arrangement of components of unique identity/traits

Notes: structural diversity can be measured at spatial scales (patch, class, landscape, macroscale) comparable to those addressed in landscape ecology. Definitions of metrics from landscape ecology taken from McGarigal *et al*. (2009); Turner and Gardner (2015); Lepczyk *et al*. (2021); names of structural diversity metrics taken from MacArthur and MacArthur (1961); Atkins *et al*. (2018); LaRue *et al*. (2020); Torres-Pulliza *et al*. (2020).

Structural diversity can also vary substantially across time (Campos *et al.* 2021), but the relevant temporal scale should be determined by the focal component or ecosystem. Components within ecosystems, along with the structural diversity that emerges from these components, can develop or degrade over time frames varying across orders of magnitude, from disturbances that last seconds to successional processes that play out over centuries. As a result, the temporal stability of structural diversity can be persistent (stable for years), periodic (daily or seasonally cyclic), or ephemeral (temporary structures occurring at irregular intervals). As with any diversity concept, the temporal organization of structural diversity and its constraints on other processes depends on the grain and extent of the study (Weins 1989).

Linkages between structural diversity and ecological patterns & processes

Structural diversity describes patterns that are explicitly linked to ecological and evolutionary processes. All biotic components in nature have a physical location in 3D space (*x*, *y*, *z* dimensions) that contributes to an ecosystem's structural diversity and influences how biotic components function and interact with each other to generate ecological patterns. For example, structural diversity can describe characteristics of vegetated ecosystems at varying stages of succession (eg primary versus secondary successional forest stands) (Spies and Franklin 1988) or resulting from different types of disturbances (Atkins *et al.* 2020; Smith *et al.* 2023). Structural diversity also describes spatial patterns of resource availability, which are linked to patterns of foraging by organisms (Théry 2001), such as woody vegetation arrangement due to herbivory in African savanna landscapes (Asner *et al.* 2009).

Structural diversity is further coupled with ecological processes because the volumetric capacity and arrangement of biotic components constrain the flow of energy and matter. Structural diversity constrains processes such as nutrient or hydrologic cycling, decomposition, and population dynamics because the physical arrangement of organisms in space partly determines how much energy and matter are allocated within an ecosystem (including decaying material) and how energy and matter interact. For instance, canopy openness impacts diurnal temperature range and thereby the vertical distribution of energy in the ecosystem (Ehbrecht *et al.* 2019). Structural diversity of forests can also dictate the horizontal distribution of snow depth across landscapes, influencing the hydrologic cycle (Hojatimalekshah *et al.* 2023). In addition, the volume and arrangement of biotic components constrain the maximum amount of energy and matter found within ecosystems and subsequently the flow of energy toward populations that determine their potential growth. Volume and arrangement are likewise linked to ecosystem services (such as the amount of available wildlife habitat within an ecosystem [Figure 4]) or community parameters (such as which species gain dominance). Previous research in fisheries biology has demonstrated the importance of seascape structural heterogeneity and foraging arenas for shaping predator–prey dynamics and food webs (Walters and Korman 1999; Hunsicker *et al.* 2011; Ahrens *et al.* 2012). Therefore, a central tenet of our framework is that structural diversity is a useful descriptor for ecological systems because of its fundamental role in influencing the distribution of energy and matter within ecosystems.

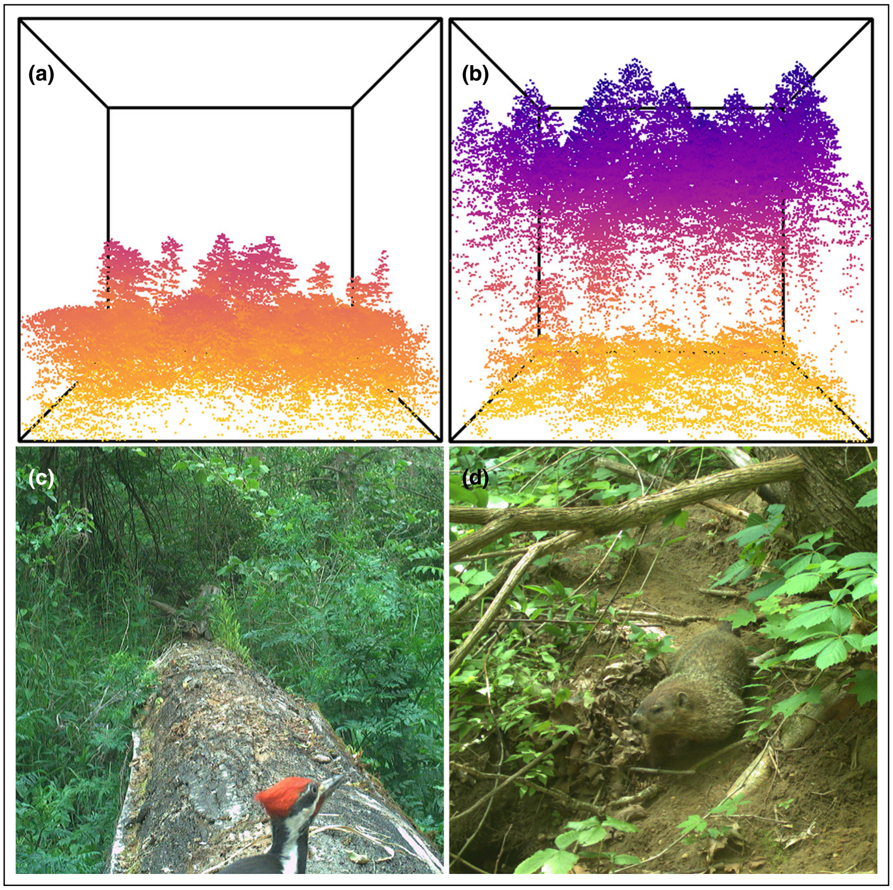

Figure 4. Advances in remote sensing, such as light detection and ranging (lidar), allow for detailed maps of structural diversity (NEON 2020) at (a) an early successional mixed forest and (b) a late successional conifer forest, and have demonstrated the importance of structural diversity as wildlife habitat for species, including (c) the pileated woodpecker (*Dryocopus pileatus*) and (d) groundhog (*Marmota monax*). Photo credits in (c and d): Purdue University Integrated Deer Management Project.

A closer look at the importance of structural diversity for ecosystem function

Structural diversity as a unique predictor of ecosystem function

Structural diversity can and should be integrated into subfields of ecological theory (eg Table 2), including but not limited to evolutionary ecology, population and

Table 2. Examples of classical hypotheses and applications in ecology for which a consistent way of measuring structural diversity can improve understanding of ecological systems

		Explanation
Hypothesis	Structural diversity begets diversity (Stein *et al.* 2014)	Structural diversity may facilitate increased levels of taxonomic, phylogenetic, or functional diversity via increased spatial resource heterogeneity and niche partitioning, or arise as a product of diversity
	Structural diversity improves ecosystem function (LaRue *et al.* 2023)	Structural diversity may be a more accurate proxy of realized niche space than taxonomic diversity, linking it closely to ecosystem function
	Structural diversity supports ecosystem stability (Mitchell *et al.* 2023)	Communities with certain structural diversity are more resistant to disturbances
Application	Ecophysiological and land surface models (Fischer *et al.* 2019)	Structural diversity underlies key ecophysiological processes and provides for more accurate dynamic vegetation models
	Wildlife habitat and natural resource management (Davies and Asner 2014)	Structural diversity can support more varied wildlife habitat and aid in natural resource monitoring
	Large-scale biodiversity mapping (Hakkenberg and Goetz 2021)	The relationship between structural diversity and biodiversity can be used as a proxy for mapping biodiversity

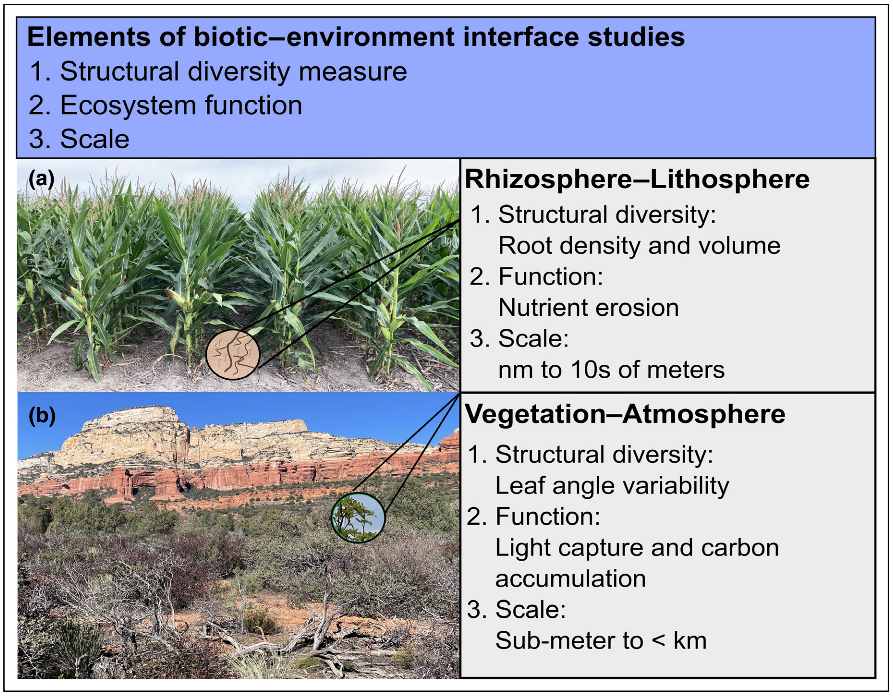

Figure 5. Linkages between structural diversity and ecosystem function are hypothesized to occur frequently at critical interfaces between the biotic system and environment, depicted here in (a) agricultural and (b) dryland ecosystems. To test for these linkages, investigators should identify relevant biotic–environmental interfaces, focal ecosystem functions, and metrics of structural diversity that would be hypothesized to drive functional outcomes, as well as the relevant spatial and temporal scales on which to measure these ecosystem characteristics. Photo credit in (a): S Oh.

community biology, and ecosystem ecology. Here, we examine how structural diversity might be used in ecosystem ecology and posit how it can provide a unique approach for predicting ecosystem function.

Structural diversity may provide a unique basis for predicting ecosystem function compared to other forms of ecological diversity that are not as directly shaped by phenotypic plasticity. Several aspects of ecological diversity that often underpin structural diversity, but typically exclude explicitly structural information, include taxonomic diversity, phylogenetic diversity, and functional diversity (Noss 1990; Swingland 2001). Taxonomic diversity refers to the assortment of the biotic identity of organisms, whereas phylogenetic diversity characterizes the relatedness of a group of organisms' genetic identity and evolutionary history. By definition, taxonomic and phylogenetic diversity are determined by genetics, with environmental factors filtering the local and regional species pool (Le Bagousse-Pinguet *et al.* 2017). Functional diversity characterizes the assortment of functional traits, either those represented by a suite of organisms or quantified through direct measurement of traits, and its variation is determined by genetics and phenotypic plasticity (Cianciaruso *et al.* 2009; Karbstein *et al.* 2020). Genetics and environmental factors undoubtedly influence all these types of diversity. However, we expect that, like functional diversity, interactions between genetics and the environment more directly shape structural diversity (ie a phenotypic rather than a genotypic measure). Therefore, we hypothesize that structural diversity may be a closer approximation of both fundamental and realized niche spaces within ecosystems than taxonomic or phylogenetic diversity alone. All of these types of ecological diversity have unique value for describing ecosystem function, and we suggest that structural diversity should be included and integrated alongside these other types of diversity. The integrative potential of structural diversity for predicting ecosystem function could be even more powerful when considering the relative spatial distribution of functional, biotic, and abiotic components within ecosystems (Kamoske *et al.* 2021). Furthermore, unlike other types of diversity, structural diversity can be readily measured with great precision and at large scales via remote sensing, making it particularly useful for predictions relating to ecosystem function.

Assessing linkages between structural diversity and ecosystem function in practice

We propose a biotic–environmental interface approach for effectively quantifying structural diversity and designing experiments to systematically examine its role in driving ecosystem function. Because the interaction of the biosphere with Earth's abiotic layers shapes the flow of energy and matter throughout ecosystems, we propose that quantifying structural diversity at interfaces between the Earth system's layers (eg biosphere with the lithosphere, atmosphere, or hydrosphere) is likely to be an especially pragmatic approach toward describing linkages between structural diversity and ecosystem function (Figure 5). To characterize structural diversity and its link with function at different interfaces within an ecosystem of interest, an investigator needs to first identify: (1) the primary component(s) composing the structural diversity, with the most appropriate measure(s) and indices of structural diversity that facilitate the combination of multiple ecological attributes including a simple mathematical formulation to combine multiple structural diversity categories into one ecologically meaningful index; (2) essential target ecosystem functions; and (3) relevant spatial (grain/extent) and temporal (time frame) scales (Figure 5). For example, a Pacific Ocean kelp forest at the biosphere–hydrosphere and biosphere–lithosphere interfaces might include: (1) components of individual kelp species, including different genotypes, described through the height stratification of individuals; (2) shoreline protection and nutrient cycling; and (3) plot (10–100 m^2) and landscape (1–100 km^2) spatial scales and an interannual time frame. Structural diversity can vary depending on which structural measurements are most closely linked to the population, community, or ecosystem process of interest; this may include a single component or incorporate nested hierarchical levels (Nadkarni *et al.* 2008). Qualification and quantification of a component will require identifying its suite of potential identities and traits to be measured, as well as an appropriate measure of structural diversity (eg Table 1) to be selected at one or more biotic–environmental interfaces. Finally, because ecosystems are dynamic across space and time, the spatial and temporal scale of interest may strongly influence quantification of structural diversity.

Examples of structural diversity research

Structural diversity research has already proven useful in ecological applications, such as wildlife management, forestry, and biodiversity conservation. To further illustrate its utility, we provide two examples to demonstrate structural diversity research through (1) assessing wildlife habitat use and (2) mapping landscape plant community composition. These examples illustrate how remote-sensing technologies and the biotic–environmental interfaces approach can be used to advance understanding of applied problems using structural diversity.

Quantifying habitat suitability is a central goal in wildlife management but characterizing habitat can be tedious without remote-sensing tools and suitable measures of structural diversity. Advances in remote sensing, such as light detection and ranging (lidar), have facilitated development of detailed 3D maps of ecosystem structure and demonstrated the importance of structural diversity for predicting wildlife habitat (Figure 4). The biosphere–atmosphere and biosphere–lithosphere interfaces are a focus of many wildlife management units. For example, small mammals may prefer high vertical complexity of vegetation (Jaime-González *et al.* 2017; Schooler and Zald 2019), and many woodpeckers and flycatchers may prefer high snag and understory shrub densities (Martinuzzi *et al.* 2009). Wildlife managers may discover that incorporating structural diversity metrics into habitat assessments can help promote and maintain wildlife populations. Cost can be an issue in obtaining remote-sensing data for wildlife management; however, as more remote-sensing data are becoming freely available (eg US Geological Survey 3DEP lidar data), these concerns can be dramatically alleviated.

The composition of plant communities in mountainous forest landscapes at the biosphere–atmosphere interface can be predicted with structural diversity. Recent work has shown that integrated suites of structural diversity, topography, and foliage reflectance measurements from airborne remote-sensing platforms provide strong predictive ability for plant community composition in a mountain forest landscape (Hakkenberg *et al.* 2018). Airborne lidar-derived canopy maximum height, foliage height diversity, and the vertical skewness of vegetation heights were able to predict not just overstory but also understory plant composition and diversity when integrated with hyperspectral reflectance indices and topography (Hakkenberg *et al.* 2018).

Key challenges and future directions

The proposed structural diversity framework can enhance the theoretical understanding of ecosystems through existing and novel research avenues (Table 2), especially if applied across a broad range of ecosystem types (ie beyond forests). However, more work is needed to enhance understanding of the relative contributions of the genetic and environmental factors that underpin structural diversity in different ecosystems. For instance, genomic approaches combined with experimental studies could improve our understanding of the genetic and environmental drivers of structural diversity (eg dendrogenomic approaches, Johnson *et al.* 2017). Biotic–environmental interfaces can be used to identify when and where strong linkages occur between structural diversity and ecosystem function. Furthermore, quantifying both above- and belowground components of structural diversity and linking these to function will be critical for a whole-ecosystem understanding of the role of structural diversity. It is also generally unknown whether high structural diversity typically leads to higher diversity across taxonomic groups or greater ecosystem functioning. Finally, these relationships may be scale-dependent and hierarchically organized, lending themselves to inquiry within a macrosystems biology framework (Heffernan *et al*. 2014).

The framework presented here could also promote the practical application of structural diversity measures for the development of conservation, restoration, and management practices (Table 2), including the sustainable use of natural resources and climate-change mitigation. The potential for using structural diversity to predict ecological and evolutionary processes in natural and human-dominated landscapes will be relevant for addressing ecosystem responses and adaptation to global change. More explicit manipulation of structural diversity in restored and managed ecosystems may achieve management objectives, and longitudinal monitoring of structural diversity could also aid in the documentation of management outcomes (Fahey *et al*. 2018). Finally, targeting specific structural diversity parameters may help conservation practitioners identify and preserve the critical habitat needed for endangered species.

Technological advances in remote sensing and computational infrastructure enable scientists to measure and model structural diversity in new ways, including increased detail of ecosystem components and potentially at global extents. Past remote-sensing technologies have primarily facilitated the quantification of structural diversity in forest ecosystems at the biosphere–atmosphere interface. Yet advances in measuring the hydrosphere (water) and lithosphere (soil) will enable investigation of ecosystem components that have previously been difficult or impossible to measure, such as roots and aquatic plants. The advent of fine-scale remote-sensing tools (Mitchell *et al*. 2015) provides detailed perspectives of many small ecosystem components. Moreover, increasingly available full-waveform lidar from the National Aeronautics and Space Administration (NASA) Global Ecosystem Dynamics Investigation (GEDI) offers a promising future avenue for research on near-global measurement of structural diversity (Dubayah *et al*. 2020; Hakkenberg *et al*. 2023). Integrating multi-sensor platforms and artificial intelligence to extract structural and other ecosystem features, such as biodiversity and functional traits, may even allow for simultaneous, whole-ecosystem characterization of ecological diversity and function. However, to aid in cross-study comparisons, future efforts to evaluate structural diversity should consider the comparability of measured components across sites and systems, and the metrics used to quantify them (Nadkarni *et al*. 2008; Hakkenberg and Goetz 2021). Many remote-sensing data products are becoming increasingly affordable and even free (eg NEON 2020). These computational and data advances will allow for the development of digital toolkits for practitioners.

Conclusions

Structural diversity is a critical but often overlooked aspect of ecosystems that, if appropriately characterized and quantified, could expand knowledge about how ecosystems and their component parts are organized in space and time, as well as how this arrangement drives ecological processes. We propose the adoption of a broad conceptual framework of structural diversity that will be flexible and compatible across ecosystem types and scales. Recent technological and computational advancements that promote the quantification of structural diversity across a range of spatial, temporal, and biological scales will facilitate this endeavor. We also highlight the hypothesis that, because structural diversity is the result of interactions between genetic and environmental factors, it is likely to be an effective predictor of ecosystem function. The linkage between structural diversity and function can be leveraged to improve conservation and management efforts, while practitioners can incorporate structural diversity into their toolkit to address global change at biotic–environmental interfaces.

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Data Availability Statement

No underlying unpublished data were used in the development of the paper.

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