REVIEW

Active Remote Sensing for Ecology and Ecosystem Conservation

Unravelling the relationship between plant diversity and vegetation structural complexity: A review and theoretical framework

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Abstract

1. Vegetation structural complexity (VSC)—the three-dimensional distribution of plants within an ecosystem—is an important ecological trait. To date, research has focused primarily on the *effects* of VSC on ecological patterns and processes, but comparatively little is known about what drives variation in VSC.

2. Recent advances in active remote sensing technology, particularly light detection and ranging and radio detection and ranging, have allowed the measurement of VSC at unprecedented spatial scales and resolutions. Out of this and earlier work has emerged evidence that VSC is typically associated with greater ecosystem functioning (especially microclimate regulation, productivity, faunal diversity and habitat provisioning), making restoration of vegetation complexity a potentially powerful restoration tool.

3. Recent studies of VSC across natural and experimental gradients of plant diversity have also revealed that more diverse plant communities tend to be more structurally complex. However, the shape and generality of this relationship—and the mechanism(s) by which phytodiversity might contribute to structural complexity—remain poorly understood.

4. Here, we review how active remote sensing has facilitated recent VSC research and shaped our understanding of the relationship between vegetation complexity and ecosystem function. We then present a theoretical framework for the relationship between phytodiversity and VSC based on classic biodiversity-ecosystem functioning principles. Finally, we evaluate the evidence for the notion that diverse plant assemblages tend to be more structurally complex and explore the shape of the relationship between phytodiversity and VSC using data from 13 recent remote sensing studies.

5. *Synthesis.* The relationship between phytodiversity and VSC appears to be almost universally positive. Preliminary evidence further suggests that the most common relationships between phytodiversity and VSC are linear or saturating, indicating that the extent of functional redundancy between species varies across plant communities and ecosystems. In contrast, we find little evidence for exponential or negative relationships between plant diversity and VSC, suggesting that even

modest increases in plant diversity could markedly increase structural complexity. Additional investigations of phytodiversity-VSC relationships are necessary to establish whether the observed positive relationships are causal (and, if so, in which direction) and to clarify the potential impact of plant community restoration on structural complexity and broader ecosystem function.

1 | INTRODUCTION

Structurally complex habitats tend to support more biodiverse communities due, in part, to the greater abundance and diversity of niches in heterogeneous environments (MacArthur & MacArthur, 1961). Indeed, the positive, causal relationship between heterogeneity and biodiversity underlies many of the most fundamental concepts and applications of ecology, including the beneficial effects of physical ecosystem engineers (Jones et al., 1997), the importance of keystone structures (Tews et al., 2004), and many methods in restoration ecology and management (Ricklefs & Schluter, 1993). Greater structural complexity is also directly linked to increased ecosystem function (sensu Schulze & Mooney, 1993) through effects on the distribution and abundance of species (Srivastava, 2006), and indirectly through its positive effects on biodiversity (Tilman et al., 2014).

Recent advances in remote sensing technology have allowed vegetation structure to be measured at greater spatial scales and resolutions than ever before (Atkins, Fahey, et al., 2018; Ishii et al., 2004; McElhinny et al., 2005; Walter et al., 2021). In particular, airborne and terrestrial light detection and ranging (LiDAR) and radio detection and ranging (RADAR) approaches have developed rapidly over the last two decades, and have now been widely adopted by ecologists, conservationists, and resource managers (Bae et al., 2022; Davies & Asner, 2014; Schimel & Schneider, 2019; Stepanian et al., 2014). As efforts to map habitat structure have grown, it has become increasingly clear that physical habitat structure varies considerably at local (e.g. Ehbrecht et al., 2017), regional (e.g. Bergen et al., 2009), and continental (e.g. Coops et al., 2018) scales, and that plant community traits underly many of these differences. Dozens of quantitative metrics have been developed to describe vegetation structural complexity (VSC; reviewed by Atkins, Fahey, et al., 2018; Bergen et al., 2009; McElhinny et al., 2005; Müllerová et al., 2021) though, to date, these have been primarily restricted to forest ecosystems (Davies & Asner, 2014). A small number of studies have investigated vegetation structure in non-forested habitats (e.g. McDonnell & Stiles, 1983; Mensah et al., 2020; Raizer & Amaral, 2001) but the adoption of active remote sensing has been slower in these systems (but see Guimarães-Steinicke et al., 2021). For examples of how active remote sensing technologies have been used to measure vegetation structure, to date, we point readers to recent reviews by Atkins, Bohrer, et al., 2018; terrestrial laser scanning and portable canopy LiDAR) and Camarretta et al. (2020; airborne LiDAR).

Although vegetation structure necessarily encompasses a variety of physical attributes (e.g. vegetation density, height and vertical variation in cover), standardised metrics allow for straightforward comparison of the structure of plant communities between habitats and over time (McElhinny et al., 2005). In the context of forestry management, such comparisons can elucidate the effects of different forestry practices on stand structure (Castro-Izaguirre et al., 2016; Chamberlain et al., 2021; Deere et al., 2020; Goode et al., 2020; Juchheim et al., 2020; Munro et al., 2009; Parrotta et al., 1997; Põldveer et al., 2021) and above-ground primary production (Dănescu et al., 2016; Hardiman et al., 2011; Ishii et al., 2004; LaRue et al., 2018; Mensah et al., 2020). Variation in vegetation structure—whether driven by human activity or arising naturally across biotic and abiotic gradients—has also been linked to variation in a number of important ecological functions, including cascading effects on faunal diversity (Iezzi et al., 2018; Ishii et al., 2004; Morante-Filho et al., 2018; Sukma et al., 2019), microclimate regulation (Ehbrecht et al., 2017; Guimarães-Steinicke et al., 2021; Rissanen et al., 2019) and species interactions (Kostenko et al., 2015; Langellotto & Denno, 2004; McDonnell & Stiles, 1983; Warfe & Barmuta, 2004). The strong, positive effect of vegetation structure on these (and other) ecological functions raises the intriguing possibility that vegetation structure, which is becoming comparatively straightforward to measure at high precision over large areas using active remote sensing, might be a useful proxy for ecological function, particularly in the context of restoration and conservation efforts (Chamberlain et al., 2021; LaRue et al., 2019).

While our understanding of the *effects* of vegetation structure on ecosystem function have improved rapidly—driven in large part by concurrent advances in remote sensing technology—comparatively little is known about what *causes* variation in the structure of vegetation communities. In part, this is a reflection of the inherent complexity of measuring physical structure: different metrics include unique combinations of structural traits, such that even defining the salient structural aspects of a single vegetation community can be challenging (Threlfall et al., 2016). Without broad consensus on what constitutes vegetation structure and how to measure it, it is difficult to determine what processes underly it.

Similarly, the choice of structural metric is typically constrained by the resolution and availability of field or remote-sensing data and can be strongly influenced by research or management goals. For example, Recher (2004) found that the identity and density of hollow-forming eucalypts had a strong effect on bird diversity in Australian forests; the same traits would likely be of little utility in estimating the effects of canopy structure on understory plant diversity or microclimate regulation, even in the same forest stands (see Larrieu et al., 2021 for additional examples of tree-related microhabitats). On the other hand, the three dimensional structure of vegetation communities is itself shaped by a complex suite of ecological interactions that resist generalisation across sites: the physical structure of an individual plant, for example, is shaped by a diverse collection of interactions with neighbouring plants, associated fauna, and the abiotic environment, and these small-scale processes can interact in complex and context-dependent ways to shape overall community structure (Langellotto & Denno, 2004).

Given that vegetation structure can strongly influence ecosystem function—and the possibility that vegetation structure could be used as a proxy for specific ecosystem functions in restoration contexts—there is an acute need to understand what drives variation in vegetation structure, how human impacts affect structural complexity, and how managers can increase VSC in degraded habitats. To date, a number of factors have been found to be positively correlated with vegetation structure, including soil water availability and fertility (Ali et al., 2019; de Souza et al., 2020), precipitation (Ehrbrecht et al., 2021), above-ground net primary productivity (ANPP; Fotis et al., 2018) and canopy height (Atkins et al., 2022; Gough et al., 2019). Active remote sensing approaches have been particularly useful in determining the drivers of vegetation structure at large spatial scales, but it remains difficult to determine whether the relationship between these factors and vegetation structure is causal, or whether they may be correlated with other biotic or abiotic drivers that are, in fact, the primary determinants of vegetation complexity. For example, Ali et al. (2019) report that plant diversity and structural complexity were positively correlated with one another across >900 tropical forest plots, but that both also increased with increasing water availability. Indeed, plant diversity is positively correlated with many of the factors (e.g. rainfall, ANPP, canopy height) known to be associated with greater structural complexity, raising the possibility that phytodiversity (which we hereafter use to refer broadly to any measure of plant taxonomic, functional, or phylogenetic diversity; see Section 5.1) may be a primary determinant of vegetation structure. Additional studies are necessary to test the generality of the above drivers, and experimental manipulations of plant diversity will be particularly useful in determining which driver(s) are ultimately responsible for observed variation in vegetation structure across spatial scales. These insights are also necessary for vegetation structure to be leveraged to restore ecosystem function in degraded habitats. In this review, we highlight how recent advances in active remote sensing technology have been used to measure and compare vegetation structure in natural and managed ecosystems. We discuss how remotely sensed structural complexity estimates are currently being used in ecological research by synthesising a rapidly growing body of literature on the effects of structural complexity on several broadly defined ecosystem functions. We then present a novel framework for predicting how phytodiversity might shape VSC based on classic biodiversity-ecosystem functioning principles and evaluate the preliminary evidence for several hypothesised relationships between phytodiversity and vegetation structure. Finally, we discuss current limitations on the broader adoption of remote sensing technology for the measurement and comparison of vegetation structure in ecology and identify promising areas for future research that address both applied and theoretical questions.

2 | WHAT IS VSC?

While VSC is an intuitive concept (Figure 1) with a long history of study in ecology, forestry management and conservation, a precise, universal definition of the term is elusive. For example, Ishii et al. (2004) define vegetation structure as "the variability of the three-dimensional spatial arrangement of trees and other structural elements within a forest". Related definitions that invoke heterogeneity in vegetation distribution are presented by Gough et al. (2019; "horizontal and vertical variation in vegetation density, height or distribution") and Ehrbrecht et al. (2021; "the degree of heterogeneity in biomass distribution in three-dimensional space"). Still other definitions are based on the positioning of vegetation in vertical or horizontal space: McElhinny et al. (2005) define vegetation structure as "the spatial arrangement of the various components of the ecosystem, such as the heights of different canopy levels and the spacing of trees", while Atkins, Bohrer, et al. (2018) consider structural complexity to reflect the distribution of canopy elements "and the complexity of a canopy beyond estimates of biomass or leaf area alone". Further complicating efforts to broadly define vegetation structure is the expansion of structural complexity research (partially facilitated by high-resolution active remote sensing technology) into nonforested systems, where definitions based on canopy architecture or tree spacing are not always applicable.

Although there are dozens of metrics used to describe various aspects of VSC, Atkins, Bohrer, et al. (2018) provide a useful taxonomy that encompasses five broad categories: leaf area and density, canopy height, canopy arrangement, canopy openness, and canopy variability. We direct readers to table 1 in Atkins, Bohrer, et al. (2018) for a more detailed discussion of structural metrics and their use in ecology, and provide only a brief overview here. Leaf area index (LAI; the ratio of one-sided leaf area to ground area) is among the most common metrics of leaf area and density, and previous studies have compared the mean, maximum and standard deviation of LAI across vegetation communities. Canopy height metrics include maximum, minimum and mean canopy height; since measures of canopy height can be derived from nearly any active remote sensing approach these are among the most commonly reported structual complexity metrics. Parameters describing the arrangement of vegetation
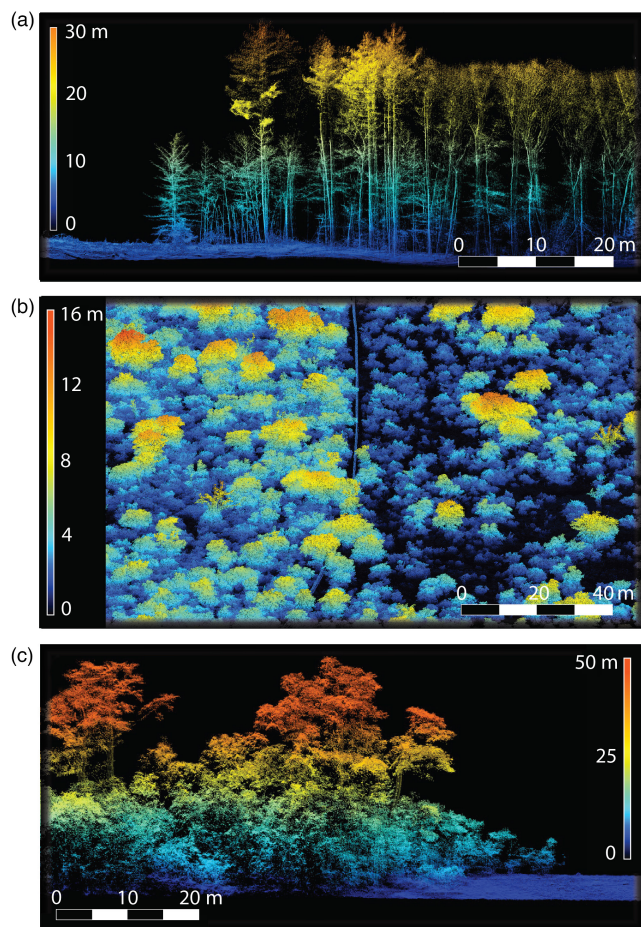
FIGURE 1 Examples of active remote sensing (unoccupied aerial vehicle-borne light detection and ranging) data for measurement of vegetation structural complexity using the Harvard Animal Landscape Observatory platform. (a) Cross-section of a temperate North American forest edge from Harvard Forest, United States during leaf-off stage. (b) Oblique view of large herbivore exclosure (left) and unfenced control (right) plots in the semi-arid savanna ecosystem of Kruger National Park, South Africa. Note the fence (thin blue line) in the middle of the image. (c) Transitional zone between tropical forest (left) and bai (forest clearing; right) habitats in Odzala-Kokoua National Park, Republic of Congo.

biomass within a habitat encompass both horizontal (e.g. clumping, tessellation, dispersion) and vertical (e.g. canopy porosity) metrics. Canopy openness, on the other hand, includes vertical measures of canopy density or presence/absence, including the density and distribution of deep canopy gaps as well as cover fraction (the ratio of leaf cover to total area). Finally, the heterogeneity of vegetation biomass in three-dimensional space is described by a family of metrics including rugosity, rumple and other measures of vertical and horizontal variance (e.g. effective number of layers).

Although it is beyond the scope of this review to address the etymology of vegetation structure, it is worth noting that at least two factors related to its definition currently hamper efforts to synthesise previous research in this area (Ishii et al., 2004). First, there is a large and rapidly growing list of terms used interchangeably to refer to various aspects of VSC, including canopy structural complexity

(sensu Atkins, Bohrer, et al., 2018), vegetation 3-D structure (sensu Bergen et al., 2009), forest structure (sensu Chamberlain et al., 2021), forest structural complexity (sensu Ehbrecht et al., 2021), canopy structure (sensu Ishii et al., 2004), stand structural complexity (sensu Kane et al., 2010), plant structural complexity (sensu Andow & Prokrym, 1990) and VSC (sensu Sukma et al., 2019). Stein and Kreft (2015) likewise report that dozens of metrics of vegetation structure have been used across studies, many of which are also used in broader studies of habitat (i.e. non-vegetation) heterogeneity. Second, even for a single term, there are often multiple, distinct metrics of vegetation structure that include various combinations of structural and compositional traits, which may be measured at a variety of spatial scales or resolutions. Many of these metrics, moreover, are highly correlated with one another, making it difficult to draw meaningful inferences about different aspects of vegetation structure. These issues have been previously reviewed elsewhere (Bergen et al., 2009; Chamberlain et al., 2021; McElhinny et al., 2005). Ishii et al. (2004) also present an excellent summary of the futility of adopting a single metric of vegetation structure given the often disparate goals of ecological, conservation, and management studies.

These factors notwithstanding, we encourage future researchers to consider using existing metrics of vegetation structure whenever possible to facilitate comparison across studies and to explicitly define their metrics to minimise confusion; care should also be taken to ensure that, when multiple metrics are reported, they are independent and capture different aspects of structural complexity (see Atkins, Bohrer, et al., 2018). For simplicity, we hereafter use the broad term "VSC" to refer to any aspect or metric of vegetation structure describing the three-dimensional distribution of vegetation within an ecosystem (i.e. leaf area and density, canopy height, canopy arrangement, canopy openness, and canopy variability; Atkins, Bohrer, et al., 2018). We favour this generic term because it is sufficiently broad to encompass forest and non-forest vegetation communities, all aspects of plant morphology, and the range of spatial scales at which complexity is typically measured (i.e. individuals to communities). For the purposes of our quantitative review (see Section 5.2), the breadth of this definition also allows us to include (and compare) studies that measure distinct aspects of vegetation structure (see *y*-axes in Figure 3), as well as studies that report VSC at spatial scales ranging from small ($<15\,m^2$) experimental plots to entire forest stands.

3 | REMOTE SENSING AND VSC

Early investigations of structural complexity in forests, which date to at least the 1940s, typically estimated VSC using a combination of spatially explicit forestry surveys and demographic information (e.g. stand age distribution) as proxies for direct measurement of three-dimensional structure; these approaches were based on the assumption that individual demographic variation was correlated with stand structural heterogeneity (e.g. variation in height or canopy cover; Cooper, 1960; Watt, 1947). In the decades that followed,

and motivated in part by growing interest in the link between structural complexity and ecosystem function, numerous methods were developed to more directly quantify VSC. These included field-based measurements of physical structure (e.g. MacArthur & MacArthur, 1961), spatial tessellation based on georeferenced ground surveys (e.g. Zenner & Hibbs, 2000), hemispherical photography (e.g. Morante-Filho et al., 2018), and other modelling, functional trait, and survey approaches (e.g. Iezzi et al., 2018; Kissling et al., 2008; Rissanen et al., 2019; Sukma et al., 2019). Outside forest systems, where direct measurement of individual or community structure can be less logistically challenging, comparable methods have also been developed to quantify the distribution of vegetation at smaller scales (e.g. Guimarães-Steinicke et al., 2021; McDonnell & Stiles, 1983), including in aquatic ecosystems (Raizer & Amaral, 2001).

The adoption of active remote sensing approaches (i.e. LiDAR and RADAR) by ecologists in the last two decades has revolutionised the study of numerous fields, including spatial (Anderson & Gaston, 2013), animal (Davies & Asner, 2014), and ecosystem ecology (Cohen & Goward, 2004). The same is true for the study of VSC (Atkins, Bohrer, et al., 2018; Bergen et al., 2009; McElhinny et al., 2005), where remote sensing approaches have proven particularly useful for several reasons. First, relative to field surveys, remote sensing methods are typically (but not always) more cost effective (Rhodes et al., 2015), particularly at larger spatial scales or when repeat sampling is necessary. At the same time as the costs of collecting or purchasing remote sensing data across multiple modalities—including unoccupied aerial vehicles (UAVs), terrestrial scanning systems, and plane- and satellite-borne sensors—have decreased, the spatial and temporal coverage of remote sensing datasets have increased. As a result, remote sensing data suitable for estimating VSC at large scales (e.g. Global Ecosystem Dynamic Investigation) are now available for much of the world (Rose et al., 2015). Second, remote sensing has significantly broadened the spatial scales at which VSC can be measured relative to field-based methods. For example, terrestrial, airborne and spaceborne LiDAR have recently been used to characterise tree structure at the scale of individual branches (c. 0.1–1.0 m; Lau et al., 2018), trees (c. 1.0–10 m; Jung et al., 2011), forest stands (c. 10 m–10 km; Kane et al., 2010), landscapes (c. 10 km–100 km; Zellweger et al., 2019), and the globe (c. 1,000 km–10,000 km; Lefsky, 2010). Third, as advanced remote sensing methods have become increasingly accessible to ecologists, the spatial resolution of structural data has increased dramatically: many UAV-borne LiDAR sensors, for example, are capable of achieving sub-centimetre accuracies, with point densities exceeding 1000 points/m^2 (Lin et al., 2011). With this data resolution, VSC can even be quantified in non-forest ecosystems with significantly lower vertical vegetation heterogeneity (Figure 1b). Moreover, many remote sensing platforms are capable of providing high data resolution over increasingly large areas (e.g. Asner et al., 2012), reducing the trade-off between spatial coverage and resolution that previously constrained both field- and remote sensing-based studies of vegetation structure. Finally, remote sensing methods have proven

especially useful for the estimation of *vertical* vegetation structure, particularly in forest ecosystems where tree height often precludes direct measurement in the field (Lenoir et al., 2022). Remote sensing approaches, for example, can return three-dimensional estimates of canopy complexity even through tightly packed canopies (Rissanen et al., 2019), whereas field-based methods (e.g. LAI) typically involve reducing data dimensionality due to logistical constraints (Lefsky et al., 1999). Importantly, despite the dissimilarities between field- and remote sensing-based measures of vegetation complexity, multiple studies have found strong congruence between estimates of VSC using different techniques (e.g. Bergen et al., 2009; Ishii et al., 2004; Kane et al., 2010; Müllerová et al., 2021), including field- and remote sensing-based approaches. Collectively, these advantages suggest that remote sensing holds the promise to allow ecologists to measure VSC in ways directly comparable to previous field-based methods, but at unprecedented spatial scales and resolutions; the recent proliferation of studies using remote sensing to investigate the effects of VSC on ecological processes is one indication of this potential (Table 1).

To date, a variety of LiDAR and RADAR platforms have been used to investigate VSC. The technical constraints, capabilities, and application of these technologies for ecology, conservation, and management have been previously reviewed (Atkins, Bohrer, et al., 2018; Bergen et al., 2009; Davies & Asner, 2014; Leite et al., 2022; Lenoir et al., 2022; Müllerová et al., 2021; Wang et al., 2010), so here we briefly highlight constraints and capabilities of different remote sensing approaches as they pertain to the estimation of VSC. Generally, LiDAR has proven to be especially useful for fine-scale quantification of VSC due to the ability to parse laser waveforms to gather additional information about leaf traits (e.g. leaf water content), the inclusion of trees below size thresholds typically excluded from field surveys, and the ability of LiDAR to penetrate even dense vegetation canopies (Lenoir et al., 2022). Many aerial LiDAR systems, however, are unable to penetrate dense cloud cover, making them suboptimal for regions with regularly overcast weather (though UAV-borne LiDAR systems flown at lower altitudes are not subject to the same constraints). Terrestrial laser scanners (TLS), in contrast, are not limited by cloud cover and can provide the high point densities necessary for branch- or individual-scale mapping of plant structure (Atkins, Fahey, et al., 2018), though this capability comes with the trade-off of lower spatial coverage. Advantages of RADAR include the ability of satellite-borne RADAR arrays to penetrate cloud cover, to more finely parse structural characteristics (e.g. leaf size and orientation) based on backscatter wavelength and polarisation, and to simultaneously assess the density and water content of leaves (Bergen et al., 2009); RADAR can also be used to investigate ecological phenomena (e.g. insect outbreaks) where high temporal resolution is critical (Bae et al., 2022). However, a key limitation of radar for measuring VSC is that it typically (though not always) provides lower spatial resolution than LiDAR. Optical and spectral data can be useful in combination with active remote sensing approaches for differentiating living and dead plant tissue, identifying vegetation to species or functional groups, and correlating vegetation structural

TABLE 1   Examples of studies that use active remote sensing (light detection and ranging [LiDAR]) to investigate effects of vegetation structural complexity (VSC) on four broad categories of ecological traits: (i) faunal diversity, (ii) forest productivity and carbon storage, (iii) microclimate regulation, and (iv) species interactions and animal movement.

Faunal biodiversity: The diversity of associated fauna tends to be positively correlated with VSC, though the effects of VSC are more complex for species or guilds with specific habitat requirements

Reference	LiDAR type	Taxa	Synopsis
Deere et al. (2020)	Fixed wing	Mammals	Mammals prefer vertically and horizontally complex forests
Melin et al. (2018)	Fixed wing	Birds	Positive correlation between woodland bird diversity and VSC
Müller et al. (2010)	Helicopter	Birds	VSC is a better predictor of bird diversity than plant species composition
Müller et al. (2014)	Fixed wing	Invertebrates	Different components of VSC drive patterns of arthropod diversity across spatial scales
Müller et al. (2018)	Fixed wing	Invertebrates	Positive effect of vertical biomass distribution on arthropod density
Schooler and Zald (2019)	Fixed wing	Mammals	Structural complexity is positively associated with small mammal diversity
Traylor et al. (2022)	Handheld	Invertebrates	Insect functional groups respond differently to various aspects of VSC
Zellweger et al. (2013)	Satellite	Birds	VSC is a strong predictor of bird occurrence for species with structural habitat requirements

Forest productivity and carbon storage: above-ground carbon storage is positively correlated with structural attributes in forests, and VSC can be a better predictor of productivity than phytodiversity

Reference	LiDAR type	Forest type	Synopsis
Gough et al. (2019)	Terrestrial	Temperate/subtropical NEON sites	Maximum canopy height is a strong predictor of VSC
Kane et al. (2010)	Fixed wing	Temperate forest	VSC accurately predicts forest successional age
Kent et al. (2015)	Fixed wing	Tropical forest	Historical effects of logging activity on forest VSC are detectable using LiDAR
LaRue et al. (2018)	Terrestrial	Temperate/subtropical NEON sites	Canopy reflectance, greenness, and brightness are correlated with VSC
Milodowski et al. (2021)	Fixed wing	Tropical forest	Logging reduces VSC by selectively removing upper canopy trees

Microclimate regulation: structurally complex vegetation communities tend to reduce maximum temperature and increase humidity, potentially buffering associated species from climate change

Reference	LiDAR type	Microclimate variable	Synopsis
Davis et al. (2019)	Fixed wing	Temperature	Canopy cover affects surface temperature in temperate savannas and conifer forests
Ehbrecht et al. (2017)	Terrestrial	Temperature/ humidity	Remotely sensed VSC accurately predicted forest temperature and humidity
Frey et al. (2016)	Fixed wing	Temperature	The effects of VSC on subcanopy temperature in montane forests may mitigate the effects of climate change
George et al. (2015)	Fixed wing	Temperature	VSC affects air temperature in temperate, deciduous forests
Guimarães-Steinicke et al. (2021)	Terrestrial	Temperature	Vertical vegetation biomass distribution affects canopy surface temperature in grassland communities
Stickley and Fraterrigo (2021)	Fixed wing	Temperature	Understory vegetation structure contributes to variation in forest temperature

Species interactions and animal movement: species' preferences for structurally complex (or simple) habitats drives idiosyncratic variation in the strength and direction of species interactions

Reference	LiDAR type	Interaction type	Synopsis
Cho et al. (2017)	Fixed wing	Pollination	Understory honey plant diversity is negatively correlated with overstory canopy density
Davies et al. (2016)	Fixed wing	Predation	Vegetation structure is an imporant predictor of predation risk in African sub-tropical succulent thicket
Davies et al. (2019)	Fixed wing	Habitat selection	Orangutan (*Pongo pygmaeus*) nest site selection is mediated by VSC
Ewald et al. (2014)	Fixed wing	Habitat selection	Roe deer (*Capreolus capreolus*) habitat selection is mediated by VSC and climate

(Continues)

TABLE 1 (Continued)

Species interactions and animal movement: species' preferences for structurally complex (or simple) habitats drives idiosyncratic variation in the strength and direction of species interactions			
Reference	LiDAR type	Interaction type	Synopsis
Klein et al. (2020)	Fixed wing	Habitat selection/ predation	Siberian jay (*Perisoreus infaustus*) nest predation is negatively correlated with understory vegetation density
McLean et al. (2016)	Fixed wing	Animal movement	Movement decisions in three primate species are shaped by forest complexity
Olsoy et al. (2015)	Terrestrial	Predation	Heterogenous vegetation structure creates "fearscapes" with areas of higher and lower predation risk
Palminteri et al. (2012)	Fixed wing	Habitat selection	Saki monkeys (*Pithecia irrorata*) select home ranges with tall, uniform canopies
Paolucci et al. (2019)	Fixed wing	Seed dispersal/ animal movement	Seed dispersal by tapirs (*Tapirus terrestris*) is higher in open, degraded forests
van Hoesel et al. (2019)	Fixed wing	Disease transmission	Forest management practices affect disease transmission through effects on VSC and habitat selection

characteristics with vegetation condition (e.g. NDVI; Camarretta et al., 2020 and citations therein); photogrammetry methods can also produce 3D estimates of vegetation structure that can be analysed in comparable ways to LiDAR point clouds (Cao et al., 2019).

4 | ECOLOGICAL EFFECTS OF VSC

One of the key motivations behind the study of VSC in ecology is the strong linkage between vegetation structure and various ecological patterns and processes. Although some of these effects have been known for decades—for example, the positive effect of vertical vegetation structure on bird diversity (MacArthur & MacArthur, 1961)—recent advances in remote sensing technology have facilitated efforts to better understand the link between VSC and ecosystem function (Atkins, Bohrer, et al., 2018; Vierling et al., 2011). In particular, remote sensing has shed light on the effects of VSC on (i) animal diversity and movement (reviewed by Bergen et al., 2009), (ii) forest productivity and carbon storage (reviewed by Ishii et al., 2004), (iii) microclimate regulation (reviewed by Zellweger et al., 2019), and (iv) species interactions. Since each of these topics (with the exception of VSC effects on species interactions) has been previously reviewed, we provide a representative list of recent studies using various LiDAR approaches to investigate the ecological effects of VSC in Table 1. Broadly speaking, VSC tends to have a positive effect on faunal diversity (e.g. birds; Barrett et al., 2008), though the responses of individual species or guilds with specific habitat requirements (e.g. woodboring beetles; Traylor et al., 2022) can be more complex and shaped by abiotic factors (Seibold et al., 2016). Nonlinear and/or negative relationships between faunal diversity and VSC can also arise as a result of decreased average population size or habitat area (and thus greater risk of stochastic extinction) in complex environments (Heidrich et al., 2020). The relationship between VSC and forest productivity also tends to be positive (but see

Ehrbrecht et al., 2021; Patton et al., 2022), in part because many VSC metrics include measures of (or proxies for) above-ground biomass, productivity, or height (Atkins, Bohrer, et al., 2018). However, positive VSC-productivity relationships persist across climatic, nutrient, and disturbance gradients even when measures of productivity are not included in VSC metrics, suggesting that more structurally complex forests may have a greater capacity for carbon storage through more efficient light capture and canopy packing (Castro-Izaguirre et al., 2016; Hardiman et al., 2011). With respect to microclimate regulation, the effects of VSC are more straightforward: structurally complex vegetation almost universally reduces temperature by more completely intercepting solar radiation, and also tends to locally increase humidity. Finally, VSC appears to have wide-ranging effects on the strength and direction of multiple species interactions (e.g. predation, pollination, seed dispersal), though the nature of this relationship is idiosyncratic and reflective of the physiology and habitat preferences of the species involved.

Understanding the relationship between VSC and ecologically and economically important functions is particularly critical in the context of restoration (Camarretta et al., 2020). A fundamental assumption of restoration ecology is that ecosystem degradation is temporary and reversible, though determining which aspects of degraded ecosystem structure, function, or composition are most critical to meet restoration goals remains a challenge (Perring et al., 2015). Given the growing evidence of the positive effects of VSC on numerous ecological functions (Table 1), it is not surprising that restoring VSC has recently emerged as a promising approach to simultaneously improve multiple ecosystem functions and increase biodiversity. Indeed, the strength of the tripartite relationship between ecosystem structure, function and biodiversity has recently been underscored by numerous successful efforts to restore ecosystem function and biodiversity by increasing structural complexity (reviewed by Lengyel et al., 2020). Broader adoption of remote sensing technology to measure ecosystem structure thus promises to

significantly improve our understanding of the relationship between ecosystem structure and function, and to inform future restoration efforts (Atkins, Fahey, et al., 2018).

5 | RELATIONSHIP BETWEEN PHYTODIVERSITY AND VSC

Biodiversity is widely accepted as a major determinant of ecosystem function (Loreau et al., 2001). The effects of biodiversity on various ecological functions—including ecosystem stability, nutrient cycling, resistance to invasion, and primary productivity—are caused by the greater functional complementarity of diverse communities, more efficient use of resources, and feedbacks that, over time, increase the overall availability of nutrients and/or habitat (Hooper et al., 2005; Tilman et al., 2014). While it is clear that both phytodiversity and vegetation complexity have a positive effect on a number of important ecological dynamics and functions (Table 1), comparatively little is known about how plant diversity affects VSC. Given that increasing vegetation complexity is a promising approach to restore degraded habitats and lost ecosystem function, a better understanding of the relationship between plant diversity and VSC is critical for the development of effective restoration interventions. Theory suggests that the effects of plant diversity on VSC may be governed by many of the same mechanisms that have been implicated in broader investigations of the relationship between biodiversity and ecosystem function: functional complementarity, increased resource-use efficiency and feedbacks that increase resource availability. In line with these predictions, there is growing evidence that the relationship between phytodiversity and VSC tends to be positive, though the shape and generality of this relationship remains poorly understood. Below, we propose a simple framework for predicting the effects of phytodiversity on VSC based on classic biodiversity-ecosystem functioning theory. We then evaluate the strength of evidence for several alternative hypotheses using data from studies that use active remote sensing to measure VSC across natural and experimental phytodiversity gradients.

5.1 | A theoretical framework for phytodiversity-structural complexity relationships

Understanding the relationship between biodiversity and ecosystem function has been a central focus of ecological research for at least three decades (Tilman et al., 2014) and has been the subject of a number of comprehensive reviews. Here, we provide a brief summary of biodiversity-ecosystem functioning theory as it pertains to VSC (more detailed information can be found in Hooper et al., 2005; Loreau et al., 2001; Naeem et al., 2002; Schulze & Mooney, 1993; Srivastava & Vellend, 2005). Out of this work, a consensus has emerged that biodiversity tends to be positively correlated with ecosystem function, although negative and neutral relationships between these traits have also been reported (see,

for example, Isbell et al., 2015; Strong et al., 2015). While, in theory, the relationship between biodiversity and ecosystem function can take nearly any form, most studies report relationships that fit within four broad categories (Figure 2): (i) linear positive, (ii) saturating positive (i.e. Michaelis–Menten), (iii) exponential positive and (iv) linear and nonlinear negative (Naeem & Wright, 2003). Below, we present a simple theoretical framework that describes how each of these forms might arise in the context of a unidirectional, causal relationship between phytodiversity and VSC. A key underlying assumption in our framework is that VSC is an ecosystem function and, by extension, that it may be predictably shaped by mechanisms linking it to underlying biodiversity. While there is no universally accepted definition of "ecosystem function", we suggest that VSC falls firmly within the broad definition offered by De Groot et al. (2002). Specifically, VSC clearly encompasses aspects of both "habitat function" (e.g. the provisioning of refuge and reproduction habitat) and "regulation function" (e.g. regulation of essential ecological processes, including resource fluxes); as discussed in Section 4, VSC affects numerous ecological dynamics and patterns, from species interactions to microclimate and primary productivity to biodiversity.

Our framework comprises four distinct relationships (Figure 2), each of which implies a different underlying mechanism behind the effects of phytodiversity on VSC. A positive linear relationship between phytodiversity and VSC is consistent with a "proportional gain" (sensu Strong et al., 2015) model where each species' contribution to VSC is positive and roughly equal. This relationship also implies limited redundancy across species, since functional redundancy typically results in nonlinear relationships between diversity and functioning (Naeem et al., 2002). However, linearity can also be indicative of complementarity or transgressive overyielding, where
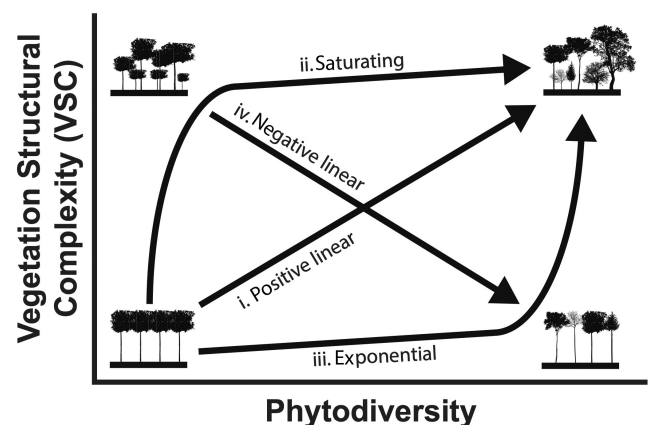

FIGURE 2 Theoretical framework for the relationship between phytodiversity and vegetation structural complexity (VSC) based on classic biodiversity-ecosystem function principles. Four possible relationships are predicted: (i) positive linear, (ii) saturating (Michaelis–Menten), (iii) exponential, and (iv) negative linear. Schematic illustrations of different VSC-phytodiversity combinations are illustrative and not intended to reflect changes in plant communities over time (i.e. succession).
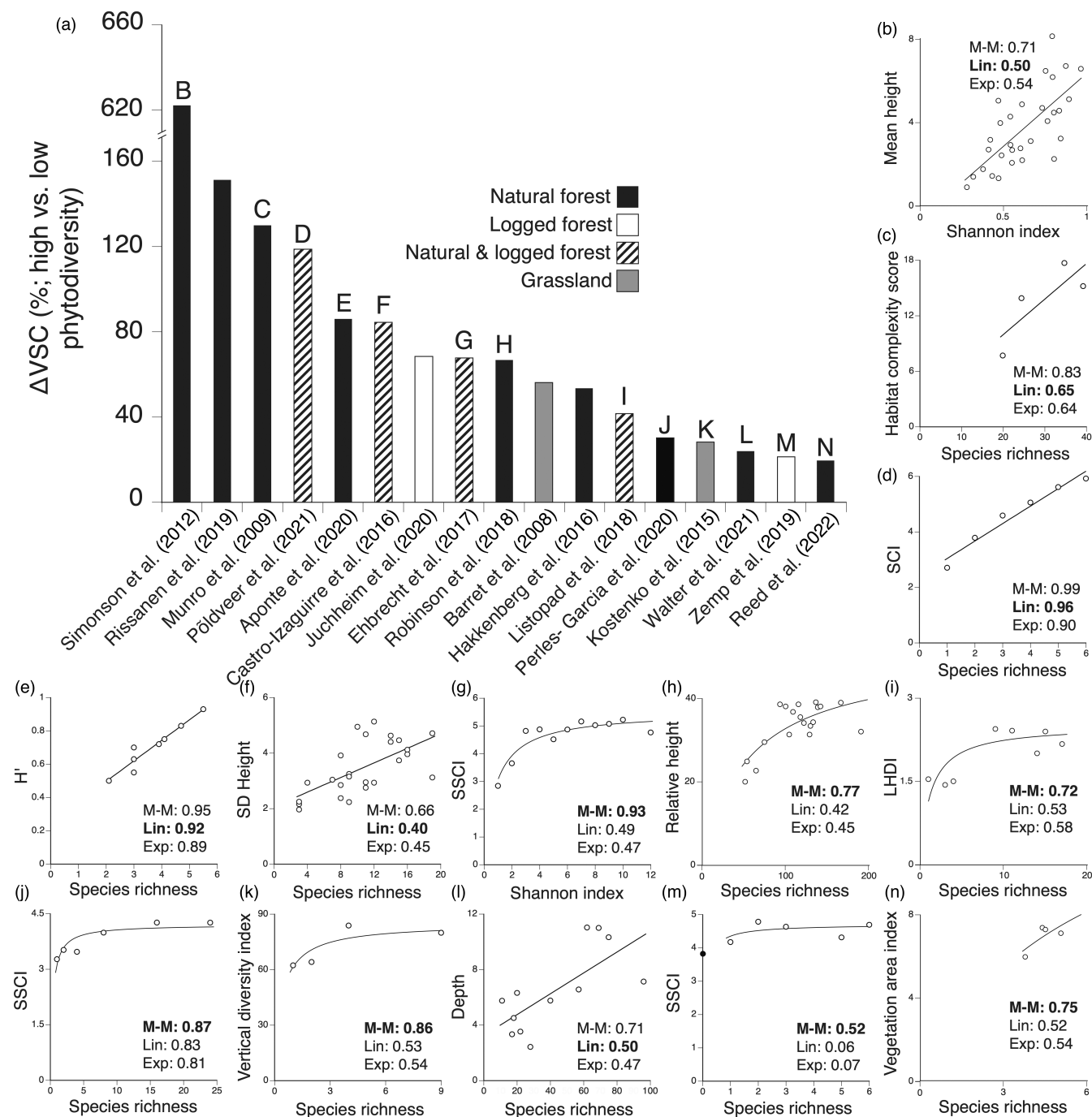
FIGURE 3 Preliminary evidence for the shape of the relationship between phytodiversity and vegetation structural complexity (VSC). (a) Percent change in VSC between the single highest and lowest phytodiversity sites from 17 recent studies. Letters above bars correspond to panels b–n. Studies were classified as occurring in "logged forest" if all sites were logged (or actively in plantation) within 10 years of the time of the study. (b–n) Variation in VSC as a function of phytodiversity. Lines are best-fit models. Inset text shows R^2 values for saturating ("M-M"; Michaelis–Menten), linear ("Lin"), and exponential ("Exp") curves; bold text denotes the selected model for each study. The best fit model was determined by comparing R^2 values but, because the M-M model can approach linearity, we selected the linear fit for panels b–f, l, and n despite the lower R^2 for the Lin model (see text for details). Note that the black point in panel j (zero realised phytodiversity, corresponding to no native tree addition to plots of oil palm) is included for illustrative purposes but was excluded from the analyses. LHDI, LiDAR height diversity index; SCI, structural complexity index; SSCI, stand structural complexity index. Full references are provided in Table S1.

the contribution of each successive species to VSC is increased (relative to their contributions in monoculture) in more diverse communities (Tilman et al., 2014). In the context of VSC, phenotypic plasticity driven by heterospecific neighbours (i.e. canopy packing)

might also cause otherwise exponential complexity curves to become more linear across increasing levels of biodiversity (Rissanen et al., 2019). From a management perspective, a linear relationship between phytodiversity and VSC suggests that efforts to restore a

greater proportion of lost phytodiversity should be rewarded with greater increases in VSC.

Saturating (or Michaelis–Menten) relationships between diversity and function are common and are almost always indicative of high functional redundancy among species. In the context of managing structural complexity, saturating relationships suggest that maximum complexity is achieved by the co-existence of a small number of species (relative to the broader species pool), and that the effect of restoring additional species will be small due to overlap in their contributions to complexity. Metrics of VSC that prioritise traits that are common across plant species (e.g. the presence of suitable perches for birds; Iezzi et al., 2018) may also bias otherwise linear or exponential relationships towards saturating curves. Saturating relationships may also be more common in plant communities with only single canopies (or lower overall height) since species in these settings are more likely to have overlapping (i.e. redundant) vertical profiles (Ishii et al., 2004).

Positive exponential relationships, in contrast, are typically found in communities with low functional redundancy and can be indicative of synergistic effects of diversity on ecosystem function and/or the presence of keystone species with outsized effects on function (Scherer-Lorenzen, 2005). Exponential relationships between phytodiversity and VSC might be expected in successional communities, for example, where the establishment of structurally complex, woody species is dependent on the presence of (often more structurally simple) earlier colonisers. Early successional forest communities may also have high phytodiversity despite low structural complexity (particularly for VSC metrics based on maximum canopy height or canopy height variation) due to their consistently low overall height (Horn, 1975); the same pattern may also be common in grasslands, though fewer studies have investigated patterns of vegetation structure for non-woody vegetation in these systems (Kahmen & Poschlod, 2004). Plant communities with exponential relationships between phytodiversity and VSC may be more resistant to restoration because the contributions of species with large impacts on VSC are dependent on the presence of other species. Idiosyncratic or stepwise variations on saturating and exponential curves may also arise in plant communities where single species have large effects on VSC, or where species' contributions are strongly context-dependent (Emmerson et al., 2001; Strong et al., 2015).

Finally, negative linear (and nonlinear) functions can arise when competitive dominant species contribute less to the function of interest than rarer species (Jiang et al., 2008). While possible, we consider such negative relationships between phytodiversity and VSC unlikely relative to the three positive relationships described above since they require numeric dominance of structurally simple species without the loss (i.e. local extinction or replacement) of more complex, rare species. One exception to this prediction may be experimental studies where natural community assembly processes are bypassed and novel or no-analogue plant communities can be maintained. While some previous reviews of the effects of biodiversity on ecosystem function also include the possibility of a neutral relationship between these traits (e.g. Strong et al., 2015),

we do not consider such a relationship in our framework. Most parsimoniously, a neutral relationship between diversity and function suggests that species do not contribute to the measured function; this is not possible in the context of phytodiversity-VSC relationships since VSC is, by definition, zero in the absence of vegetation and positive in its presence. One notable exception to this rule are VSC metrics focused narrowly on specific traits (e.g. deadwood snags) that may only occur in a small proportion of plant species (Larrieu et al., 2021).

From an ecological perspective, the nature of the relationship between phytodiversity and VSC can shed light on underlying mechanisms that could be difficult to measure directly. For example, the two non-linear positive relationships in our framework suggest fundamental differences in species redundancy and/or context-dependence. The nature of the relationship between phytodiversity and VSC should similarly inform conservation and restoration practice. For example, the most effective intervention to restore VSC in degraded ecosystems varies considerably across the same two positive relationships: a saturating relationship suggests that function can be restored with just a fraction of historic phytodiversity, while an exponential relationship suggests that a greater proportion of phytodiversity (and potentially positive plant–plant interactions) must be restored to regain complexity. As quantification of VSC becomes increasingly feasible via active remote sensing, we encourage researchers to consider the role of phytodiversity in driving patterns of VSC; the use of remote sensing to make such comparisons at larger (e.g. continental) spatial scales will likely be a particularly fruitful area for research. As our understanding of the relationship between VSC and phytodiversity improves, it may also become possible to infer patterns of phytodiversity from remotely sensed vegetation structure.

Two additional observations regarding how the definitions of phytodiversity and VSC can potentially affect the relationship between these variables bear brief mention. First, we note that the choice of VSC metric can significantly shape the exact strength and form of the reported relationship between phytodiversity and complexity. For example, in a tightly packed, hyper-diverse tropical forest, phytodiversity may be negatively correlated with canopy porosity (due to canopy packing and the absence of canopy gaps), but positively correlated with LAI (due to the presence of multiple, distinct canopy layers). Changes in VSC across successional stages similarly illustrate this point: biodiverse but short-statured early successional forests are often classified as structurally simple due to their low canopy height, but these plant communities may provide a more dense and heterogeneous habitat for ground-dwelling species than old-growth forests with taller canopies but sparser understories. While it is beyond the scope of this review, it is also worth noting that different data acquisition methods (e.g. terrestrial laser scanning vs. airborne LiDAR) and resolutions can also affect estimates of VSC in ways that may affect the nature of the phytodiversity-VSC relationship (see, for example, Hilker et al., 2010; Popescu et al., 2011). Since these differences are more reflective of methodological choices than real

ecological differences, we do not consider them further here other than to highlight the importance of choosing, measuring, and interpreting VSC metrics with care.

Second, relationships between biodiversity and ecosystem function can similarly be influenced by which aspects (or metrics) of biodiversity are considered, and we suggest that this almost assuredly applies to the relationship between phytodiversity and VSC (Flynn et al., 2011; Reiss et al., 2009). At present, there is an insufficient number of studies to draw generalisations about the impact of various biodiversity metrics on phytodiversity-VSC relationships, but based on broader reviews of biodiversity-ecosystem functioning (e.g. Cadotte et al., 2011; Chao et al., 2014), we offer a brief comparison of how several of the most commonly used classes of biodiversity metrics might be used for future studies of vegetation structure. In this review, the majority of studies we identified that compared biodiversity and VSC reported biodiversity in terms of species richness (the total number of species) or, more accurately, species density (the total number of species per unit area; Gotelli & Colwell, 2001). While species richness is a coarse metric of biodiversity, it is widely used and has the advantage of being intuitive and broadly comparable across studies and ecosystems, and over time in designs with repeat sampling. The main limitation of species richness in this context is that it does not account for the relative abundance of species, making it difficult to determine species-specific contributions to VSC and to compare plant communities with similar species richness but different composition (the latter being particularly problematic for communities with numerous rare species). Indexes (e.g. Shannon Index, Simpson Index) of species evenness, in contrast, are less sensitive to sampling effects and so may be more appropriate in communities where a small number of species have a disproportionate effect on VSC (Wilsey & Potvin, 2000). Functional diversity, on the other hand, reflects "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). Metrics of functional diversity—which at their core involve measurement of functional traits (Petchey & Gaston, 2006)—have the benefit of more mechanistically linking biodiversity to ecosystem function and provide greater insight into the redundancy of species' contributions to functions like VSC. Growth form (e.g. grass vs. shrub vs. tree) is a particularly useful classification scheme for investigations of biodiversity contributions to vegetation structure. Functional diversity metrics can also account for intraspecific variation in phenotype, as occurs in mixed-age stands and treefall gaps; intraspecific phenotypic variation can contribute significantly to VSC but is not captured by non-functional metrics of biodiversity such as species richness. Finally, phylogenetic diversity ("the distinct evolutionary history in a community"; sensu Flynn et al., 2011) may be useful in the context of VSC if phylogenetic diversity is strongly correlated with functional diversity. As with the choice of VSC metrics, care should be taken to select an appropriate measure of phytodiversity that accurately reflects the true diversity of species, forms, or types in a community. Explicit comparison of the relationship between different VSC and biodiversity metrics within a single plant community is a worthwhile direction for future research, and will help elucidate the specific limitations of various diversity metrics in predicting vegetation structure (and vice versa; Hakkenberg et al., 2016; Marselis et al., 2019).

5.2 | Preliminary evidence: Does greater phytodiversity increase VSC?

To evaluate the potential causal relationship between phytodiversity and vegetation complexity, we conducted a literature search using Web of Science to find peer-reviewed studies comparing phytodiversity and VSC. Additional references were collected from citations within these articles, and articles identified during the preparation of this review were also included if they met search criteria. The Web of Science search yielded 236 articles. From these studies (and citations therein) we identified 29 articles that met the minimum criterion of comparing VSC across at least two sites that differed in phytodiversity. The majority of studies we identified focused on forestry management, restoration, or biodiversity detection (20 of 29 studies), with the remaining studies comprising investigations of reciprocal interactions between VSC and associated fauna or climate (9 of 29 studies). Two studies (Guimarães-Steinicke et al., 2021; Kostenko et al., 2015) quantified VSC in grasslands, while the rest were conducted in temperate, subtropical, or tropical forests. Mensurative studies, in which cross-site comparisons were made without experimental manipulation of phytodiversity, were the most common (21 of 29 studies), although eight studies involved manipulations of plant diversity in plantations, experimental forests, or as a result of herbivore exclosure. Complete search and inclusion criteria are detailed in the Supporting Information (Appendix S1), and a complete list of all 29 studies can be found in Table S1 and Appendix S2.

Our first goal was to determine the *direction* and *strength* of the relationship between phytodiversity and VSC across studies. Twelve studies compared VSC across sites that differed in phytodiversity, but either did not provide site-level measures of phytodiversity beyond categorical descriptions (i.e. high vs. low) or presented only pairwise path coefficients between phytodiversity and VSC in structural equation models (e.g. Kissling et al., 2008; Mensah et al., 2020; Schuldt et al., 2019). From these, we were able to determine the direction of the relationship between phytodiversity and VSC, but not the shape. Seven of these studies reported exclusively positive relationships between phytodiversity and VSC; an additional three studies (Fricker et al., 2015; Hakkenberg & Goetz, 2021; Kamoske et al., 2022) compared multiple metrics of phytodiversity and VSC, and found positive relationships between some and mixed (i.e. neutral and/or negative) relationships between others. The other two studies in this group reported exclusively neutral (de Almeida et al., 2020) or negative (Hardiman et al., 2011) relationships. Although a majority (83%) of these studies report positive relationships between phytodiversity and VSC, the exceptions also shed light on the nature of the relationship between plant diversity and structure. For example, Hardiman et al. (2011) suggested that the negative relationship between Simpson's diversity index and

canopy rugosity in their study may have been due to the relatively low overall variation in VSC across the primarily early successional plots. They also predicted that the nature of this relationship might become more positive over time. Indeed, in an unrelated study of experimental tree plantations in China, Perles-Garcia et al. (2021) reported an increasingly positive relationship between tree species richness and canopy complexity over time. Together, these studies lend support to the notion that disturbance and successional age influences the strength (and direction) of the relationship between phytodiversity and VSC. Forest type can also affect the strength of the relationship between phytodiversity and VSC: Mensah et al. (2020), for example, detected a strong, positive effect of tree diversity on VSC in mixed plantations and woodlands, but neutral effects in savannas and gallery forests. The mixed results reported by Hakkenberg and Goetz (2021)—that tree species richness, but not herbaceous species richness, was positively correlated with canopy height heterogeneity—also underscores the importance of aligning the scales at which VSC and phytodiversity are measured.

For the remaining 17 studies—all of which reported positive relationships between phytodiversity and VSC—we were also able to extract quantitative VSC estimates for at least two levels of reported phytodiversity. From these, we calculated the average change in VSC between the lowest and highest phytodiversity sites (Figure 3a) to determine the relative strength (% change) of positive relationships between phytodiversity and VSC. High phytodiversity sites were, on average, 98% more structurally complex than low phytodiversity sites (range: 19%–622%). Differences in phytodiversity similarly varied across studies, with the average high diversity site having 6-fold more phytodiversity (or species richness) than the paired low diversity site (range: 0.32- to 23-fold). Overall, these results suggest that more diverse plant communities are nearly always more structurally complex (Figure 3a; Table S1).

Our second goal was to determine the *shape* of the relationship between phytodiversity and VSC across studies. Thirteen studies reported VSC estimates across four or more levels of phytodiversity, which allowed us to investigate variation in the shape of the relationship between phytodiversity and VSC (Figure 3b–n). Because we were typically only able to extract summary data (i.e. VSC estimates averaged across multiple experimental replicates with identical phytodiversity), we averaged replicated VSC estimates at the same level of phytodiversity for those studies that provided raw data to ensure that datasets were comparable across all studies. This conservative approach resulted in low replication ($N < 10$ levels of phytodiversity) for eight of the studies we investigated, which may have reduced the likelihood of detecting true, non-linear dynamics. We also note that one study (Zemp et al., 2019) reported results from a native tree addition experiment within an oil palm plantation, one treatment of which consisted of no native tree addition; this treatment was reported as containing zero realised species richness, so we excluded it from the analysis (but included it in Figure 3m for illustrative purposes). Likewise, Robinson et al. (2018) contained a single outlying value with diversity <30% of the next smallest value; we excluded this point from subsequent analyses. These limitations notwithstanding,

we followed Gamfeldt et al. (2015) and regressed VSC against phytodiversity using three alternative models: linear, exponential, and saturating (Michaelis–Menten); all analyses were performed in R (v. 4.0.3; R Core Development Team, 2015). We compared model fit by calculating R^2 values for each model and found that the saturating model had the highest correlation coefficient for all datasets; the linear and exponential fits were broadly comparable (all R^2 values presented in Figure 3b–n). Because the saturating model can approach linearity across the narrow values of phytodiversity in our set of studies (for example, when the Michaelis–Menten constant, K_M, is large relative to mean phytodiversity), and because few studies included sites with very low levels of phytodiversity, we tested for true non-linearity by comparing the K_M and mean phytodiversity for each study: we classified phytodiversity-VSC relationships as saturating if mean phytodiversity was at least 5× greater than K_M and linear if K_M was less than 5× greater than mean diversity.

Using these model selection criteria, we found that data from six studies (Aponte et al., 2020; Castro-Izaguirre et al., 2016; Munro et al., 2009; Põldveer et al., 2021; Simonson et al., 2012; Walter et al., 2021) were best described by a positive linear relationship. The remaining seven studies (Ehbrecht et al., 2017; Kostenko et al., 2015; Listopad et al., 2018; Perles-Garcia et al., 2021; Reed et al., 2022; Robinson et al., 2018; Zemp et al., 2019) were best fit by a saturating (Michaelis–Menten) relationship. No studies exhibited an exponential relationship between phytodiversity and VSC. While additional studies will be necessary to resolve the generality of the relationship between phytodiversity and VSC—and how the shape of this relationship varies across a more diverse suite of ecosystems—these results are broadly consistent with the expectations that diversity is positively correlated with ecosystem function and that the degree of functional redundancy in species' contributions to ecosystem function (in this case, VSC) can vary across diverse plant assemblages (Tilman et al., 2014).

For the seven studies that exhibited a saturating relationship between phytodiversity and VSC, our framework suggests that this may be due to significant functional redundancy between species. Consistent with this notion, three of the seven studies that exhibited saturating relationships between phytodiversity and VSC investigated the latter in plantation or logged forest settings; another of these studies investigated VSC in long-term experimental forest plots that included plantation monocultures. Increased structural complexity can reduce the value and efficiency of timber harvest, and many forests used for lumber extraction are therefore managed for reduced structural complexity (e.g. by maintaining even-aged stands and/or planting species with similar vertical profiles; Hardiman et al., 2011; Milodowski et al., 2021). Accordingly, higher diversity sites in these studies may have been less likely to include structurally dissimilar (i.e. functionally unique) species than studies where communities were allowed to assemble naturally. One other study (Kostenko et al., 2015) was one of only two to investigate VSC in a non-forest ecosystem (grassland), where the constraints on VSC are less well understood. Although a majority of studies report results consistent with limited functional redundancy, these results

should be interpreted conservatively due to the reliance of all but two studies on species richness (or species density) as a metric of phytodiversity; to fully elucidate the extent of functional redundancy among species' contributions to VSC, future studies should use phytodiversity metrics that also encompass functional or phylogenetic variation in plant communities.

In contrast, the limited functional redundancy across species implied by a positive, linear relationship between phytodiversity and VSC is consistent with the theory of niche complementarity, which predicts that the co-existence of plants in naturally assembling (and recovering) communities is driven, in part, by morphological divergence (Naeem et al., 2002; Tilman et al., 2014). Of the six studies that exhibited such a relationship, four included only natural (i.e. non-logged) sites, and the two remaining studies (Castro-Izaguirre et al., 2016; Põldveer et al., 2021) compared logged and non-logged forest stands. Vertical stratification in forests (e.g. figure 3 in Ishii et al., 2004) is a near-universal mechanism by which diverse tree communities co-exist, and heterogeneity in vertical biomass distribution is a key factor in a number of VSC metrics (but see Parker & Brown, 2000 for a discussion of the limitations of stratification in classifying forest structure). The same complementarity dynamics may also contribute to positive phytodiversity-VSC relationships at smaller scales in non-forested ecosystems, including among aquatic plants (Raizer & Amaral, 2001) and old-field vegetation (Guimarães-Steinicke et al., 2021). Determining whether natural and managed ecosystems differ systematically in the shape of the phytodiversity-VSC relationship is a promising direction for future research and one that will benefit from the use of remote sensing technology to measure VSC at greater spatial scales and resolutions.

5.3 | Conclusions and future directions

Preliminary evidence (Figure 3) suggests that the effects of phytodiversity on VSC are almost universally positive, a result consistent with the observation that species-rich, intact forests tend to be more complex than plantations and degraded forest fragments (Ishii et al., 2004). Combined with the growing evidence of positive effects of VSC on broader ecosystem dynamics (Table 1), our review suggests that increasing VSC by conserving and restoring phytodiversity is a promising approach for maintaining ecosystem function, restoring lost faunal diversity, and increasing resilience to anthropogenic impacts. Identifying best practices for phytodiversity restoration will require a better understanding of the nature of the phytodiversity-VSC relationship, and particularly the extent to which species are (or are not) functionally redundant in their contribution to structural complexity. Our theoretical framework should help guide future studies in this area.

One key challenge to leveraging VSC for restoration will be disentangling the potentially bidirectional relationship (or feedback) between phytodiversity and VSC: phytodiversity may enhance VSC due to architectural diversity among species (as we suggest here), but VSC may also enhance phytodiversity by creating niche space for additional plant species (Walter et al., 2021). We consider it likely that phytodiversity and VSC interact in both directions, and a more complete understanding of these dynamics is also critical for restoration. For example, although we did not find evidence for an exponential relationship between phytodiversity and VSC in the limited number of studies on the topic to date, such a relationship would be consistent with positive effects of VSC on phytodiversity and might suggest that a threshold level of structural complexity is necessary to maintain high biodiversity. More complex relationships than those we present here (e.g. hump-shaped curves) may also occur due to bidirectional feedbacks between phytodiversity and VSC (e.g. increased stochastic extinction risk at high VSC; Heidrich et al., 2020). Experimental manipulation of phytodiversity is one promising approach for resolving the direction and shape of the relationship between phytodiversity and VSC. It is also critical that studies investigating the nature of the phytodiversity-VSC relationship span large phytodiversity gradients (particularly high diversity sites) to distinguish between linear and non-linear relationships. We also encourage researchers to consider investigating phytodiversity-VSC relationships in non-forest ecosystems, where high-resolution active remote sensing may be particularly useful in quantifying the complexity of short-statured vegetation (Figure 1b); broader investigation of intact forests will also help overcome the difficulty of determining whether variation in VSC in logged forests is reflective of changes in phytodiversity or the direct impacts (e.g. selective removal of large individuals and increased fragmentation) of timber extraction.

Technology to measure VSC has improved dramatically over the past six decades: from MacArthur and MacArthur's (1961) "foliage height diversity" calculated using a stiff vertical wire, to the hemispherical photography approach employed by Morante-Filho et al. (2018), to more recent efforts that use LiDAR (Melin et al., 2018) or RADAR (Bae et al., 2019). Active remote sensing—particularly LiDAR—has significantly increased the spatial scale and resolution at which vegetation structure can be measured, unlocking new avenues for research into the causes and consequences of structural variation at local, regional, and global scales. Although remote sensing technology has been widely adopted by ecologists, field-based methods including forest inventories and individual plant surveys are still commonly used to estimate VSC. Remote sensing is not a panacea: researchers must still determine which structural attributes to measure, identify suitable VSC metrics, and ensure that the spatial and temporal resolution of data collection are appropriate and feasible. However, to the extent that it is practical, we encourage future researchers to employ active remote sensing techniques to measure 3D ecosystem structure. Remote sensing allows for direct measurement of 3D structure (as opposed to extrapolation from 2D or non-dimensional data), is often more accurate than field-based surveys, and can quantify VSC at the spatial scales necessary to inform restoration efforts and understand ecosystem dynamics (Davies & Asner, 2014). With decades of study having shown that VSC can have far-reaching,

positive effects on many aspects of ecosystem function, we encourage researchers to turn their attention to understanding what causes variation in vegetation structure so that restoration of VSC can be added to the toolbox of approaches to fight the ongoing biodiversity and climate crises.

AUTHOR CONTRIBUTIONS

Tyler C. Coverdae conceived the idea for the review and drafted the first manuscript. Both authors contributed critically to subsequent drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data presented in this review were extracted from previously published studies (see Supplementary Information for a complete list).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of studies included in quantitative review.

Appendix S1. Details of literature search and selection criteria.

Appendix S2. Full references for 29 studies included in quantitative review.