ECOGRAPHY

Research article

Diversity – volume relationships: adding structural arrangement and volume to species – area relationships across forest macrosystems

EDITOR'S CHOICE

Elizabeth A. LaRue, Anna G. Downing, Sheila Saucedo, Arturo Rocha, Sergio A. Vargas Zesati, Vicente Mata-Silva and Michael G. Harvey

Department of Biological Sciences, The University of Texas at El Paso, El Paso, TX, USA

Correspondence: Elizabeth A. LaRue (ealarue@utep.edu)

Ecography
2023: e06723
doi: 10.1111/ecog.06723
Subject Editor: Henrique Pereira
Editor-in-Chief: Miguel Araújo
Accepted 12 June 2023

The species – area relationship (SAR) is a common pattern in which diversity increases with the area sampled, but ecosystems are three-dimensional (3D) and diversity – volume relationships (DVRs) may exist in ecosystems that vary substantially in their vegetation volume. We tested whether forest vegetation volume, as a 3D extension of area in SARs, was a significant predictor of taxonomic (species) and structural (arrangement) diversity in five groups of organisms across the National Ecological Observatory Network (NEON). Vegetation volume and four structural arrangement metrics within the area of NEON plots were measured using NEON's discrete return lidar. Species richness was measured as the number of species within the respective NEON plot sampling area for understory plants, trees, breeding land birds, small mammals, and ground beetles. We found that volume negatively predicted understory plants and positively predicted tree and beetle species richness across the USA forest macrosystem, but not bird and small mammal species richness. Furthermore, volume was a significant predictor of several metrics that describe the internal and external heterogeneity of vegetation in forests (structural arrangement) within the ecosystem across the USA forest macrosystem. There were several significant within site-level relationships, but not at all sites, between volume and species richness or structural arrangement in organism groups. Our study indicates that previous work that has focused on a 2D conceptualization of habitat can be expanded to 3D habitat space, but that the strength and the positive or negative direction of DVRs may vary taxonomically or geographically.

Keywords: habitat volume, lidar, national ecological observatory network, species area – curve, vegetation structure

NORDIC SOCIETY OIKOS

www.ecography.org

Introduction

The species–area relationship (SAR) describes the common pattern in which the number of species increases with the size of the area sampled (Matthews et al. 2021, Tjorve et al. 2021a), but SARs consider two-dimensional (2D) area when ecosystems are three-dimensional (3D) in nature. Traditional tests for SARs have focused extensively on the importance of the amount of the spatial area of habitat for supporting a diverse community (Fattorini et al. 2021, Tjorve et al. 2021b). However, the vertical aspect of ecosystems is also important for meeting the habitat requirements of organisms (Gámez and Harris 2022). Therefore, the 3D space of ecosystems may exhibit similar relationships with biodiversity to those observed with spatial area (van der Gast et al. 2006). In forest ecosystems, the 3D aspects of volume – the outer envelope around the vegetation surface that includes both the open and filled spaces of the inner canopy – represents an important component of habitat. New advances in remote sensing tools make it easier to quantify 3D aspects of habitat across space and thereby measuring ecosystems characteristics such as the volume of forest vegetation (Lausch et al. 2016, Dubayah et al. 2020, Valbuena et al. 2020).

The volume of vegetation is hypothesized to restrict the amount of niche space that can be filled by plants and habitat for different taxa, especially in forests. In general, more volume available in a forest should allow for a greater number and more complex arrangement of different vegetation layers. A plant community with a greater stratification of vegetation layers has the potential to stratify resource use vertically (West et al. 2009, Atkins et al. 2018, Luo et al. 2019) and to create more vertical habitat for other organisms (MacArthur et al. 1966, Tews et al. 2004, Bergen et al. 2009). It is therefore expected that the biological diversity will scale with volume – in organisms that have a need for vertical niche space – even when horizontal area is kept constant, because there are more niche spaces to be filled vertically.

The expected relationship between increasing forest volume and taxonomic diversity may vary across organism groups (see Table 1 for predicted relationships), because of the different needs for vertical habitat among organisms. The volume of the forest influences how resources such as light can reach different members of the community and the ability for those different members to obtain these resources through mechanisms such as competition or facilitation (Westoby 1998, McElhinny et al. 2005, Kunstler et al. 2016). For example, an increase in forest volume may enhance the niche space available for organisms that use the middle to upper levels of the canopy, such as trees or birds more than the forest floor. At the same time, an increase in overstory volume can cause a reduction in light that reaches the understory plant community, thereby reducing the niche space available for organisms occurring at those levels. Accordingly, some previous studies have found opposite relationships between forest or plant volume and taxonomic diversity (i.e. birds and beetles, Table 1). New research is showing that other types of diversity, aside from species richness, may also exhibit positive relationships with sampling area (Matthews et al. 2021, Mazel and Thuiller 2021). For instance, two types of diversity, phylogenetic and functional, have been shown to exhibit a positive relationship with area (Mazel and Thuiller 2021). This may also extend to a historically overlooked type of diversity, structural diversity, which is described as the volumetric capacity, physical arrangement, and identity/traits of biotic components within an ecosystem (LaRue et al. 2023b) and is representative of architectural functional traits. Structural diversity metrics that describe the 3D physical arrangement of vegetation are hypothesized to predict realized niche space, because structural

Table 1. Predicted direction of relationships between the aspects of vegetation volume and structural arrangement of forests with the species richness of plant and animal organisms.

	Aspects of forest volume	Aspects of structural arrangement
Birds	+ Goetz et al. 2007, Redolfi De Zan et al. 2014 – Goetz et al. 2007	+ MacArthur and MacArthur 1961
Small mammals	- Schooler and Zald 2019	+ Sullivan et al. 2001, Ehlers Smith et al. 2017, Schooler and Zald 2019
Beetles	+ Redolfi De Zan et al. 2014 – Boutaud et al. 2022	+ Knuff et al. 2020, Müller and Brandl 2009
Trees	+ Gough et al. 2020	+ Gough et al. 2020, Hakkenberg and Goetz 2021, LaRue et al. 2023c
Understory plants	– Hakkenberg and Goetz 2021, Zheng et al. 2022	+ Hakkenberg and Goetz 2021, Coverdale and Davies 2023

arrangement influences the occupancy of niche axes such as available light (Adams et al. 2007, Vieilledent et al. 2010, Forrester and Bauhus 2016, LaRue et al. 2023c) and habitat selection for other trophic levels (Théry 2001). Structural diversity is an overlooked but critical type of ecological diversity (LaRue et al. 2023b). However, recent advances in the ability to measure 3D aspects of ecosystems have only now allowed for it to become feasible to quantify at larger spatial scales (LaRue et al. 2019, Aponte et al. 2020, Ehbrecht et al. 2021). Despite early work on the subject (MacArthur and MacArthur 1961), it is not well known how structural diversity fits within SARs theory. We may find that it follows similar patterns across macrosystems as has been observed with taxonomic, phylogenetic and functional diversity (Mazel and Thuiller 2021). For example, recent work has shown that the number of vegetation layers increases with the height of the canopy in different forest types due to layering and in-filling (Gough et al. 2020, Atkins et al. 2022).

Volume may cause increases in species richness of plants and animals directly or may do so indirectly through the alteration of the structural arrangement of vegetation such that it supports greater or less habitat for plants and animals. The volume of vegetation may increase niche space directly by adding more vertical space to the ecosystem, which allows for greater species packing (Coverdale and Davies 2023). However, volume may indirectly influence taxonomic diversity through the addition of new habitats via the stratification of layers or structural diversity because structural diversity may not always increase with higher forest volume. Structural diversity of sessile biotic ecosystem components (e.g. plants, corals) can have a positive relationship with the taxonomic or trait diversity of species (Helder et al. 2022), but may not always have a strong effect on a particular taxonomic group of plant or animals (Drag et al. 2023). Finally, there has been recent interest in quantifying the 3D niche of ecosystems and how this influences wildlife behavior, habitat use, population dynamics, and community diversity (e.g. see several recent reviews on the topic, Gámez and Harris 2022, Russo et al. 2022).

As diversity is being lost at unprecedented rates and the functioning of forest ecosystems is imperiled by global change threats (Pereira et al. 2013, Jetz et al. 2019), understanding how different dimensions of diversity are influenced by the volume of available habitat will advance our ability to make more accurate and informed management plans about habitat availability across macroscales (Fahey et al. 2018, Valbuena et al. 2020, LaRue et al. 2023b). Our objective was to test if forest volume constrains species richness of dif- ferent organism groups and vegetation structural diversity across macrosystems (diversity volume – relationships or DVRs). We hypothesized that the maximum volume of the forest vegetation will restrict the amount of niche space that can be filled by vegetation (structural diversity) and habitat that is available to support different plant and animal species (species richness). However, the importance of vertical niche space will vary by organism group. Therefore, we predict that species richness and structural arrangement metrics will be related to the volume of the vegetation in the ecosystem due to higher availability of niche space with more volume, and that volume constraints on structural diversity will also explain variation in the species richness of different organism groups but the strength and direction of the relationship will differ by organism group (Table 1). We evaluated these predictions by coupling forest volume and structural diversity metrics that describe the structural arrangement of vegetation within the canopy, (hereafter referred to as structural arrangement), using airborne light detection and ranging (lidar) and species richness for five different groups (understory plants, trees, breeding land birds, small mammals, ground beetles) across forested NEON sites in the USA from airborne light detection and ranging (lidar) and species richness from five different organism groups across forested NEON sites in the USA.

Material and methods

NEON site descriptions

To test for DVRs across the USA forest macrosystem, we used data products from 26 NEON sites (Fig. 1a, Supporting information) (Kampe 2010). Sites were chosen based upon those that had an average vegetation height of at least 3 m and the availability of lidar and taxonomic identification and abundance surveys. The 26 sites span a forest vegetation volume gradient (Fig. 1a) and span 15 ecoclimatic domains across the conterminous USA, Alaska, Hawaii and Puerto Rico (Supporting information).

Structural diversity measurements from NEON lidar: volume and structural arrangement

We used NEON Aerial Observation Platform (AOP) discrete return lidar, collected during peak growing season greenness (Krause and Goulden 2015), to estimate forest vegetation volume and four structural arrangement metrics within three types of NEON taxonomic survey plots. Three plot sizes were used: 40 × 40 m (tree, understory plant, and beetle), 90 × 90 m (small mammal), and 500 × 500 m (land breeding bird). The 2D area of our plots is kept consistent for each organism group studied here per the NEON spatial sampling design, to allow us to focus on how variation in forest vegetation vol- ume within that area is related to species richness and struc- tural arrangement.

We obtained the level 1 discrete return lidar from NEON (product no. DP1.30003.001) (NEON a,b) (Supporting information), removed outlier points, and corrected each plot's point-cloud for ground elevation to get vegetation heights. The 1 km^2 lidar .laz tiles were downloaded using the 'neonUtilities' R package (www.r-project.org, National Ecological Observatory Network 2020). We clipped at least a 20-m square buffer beyond the width of each plot. Outliers were filtered by removing points six standard deviations above and below the mean height for bird plots and four

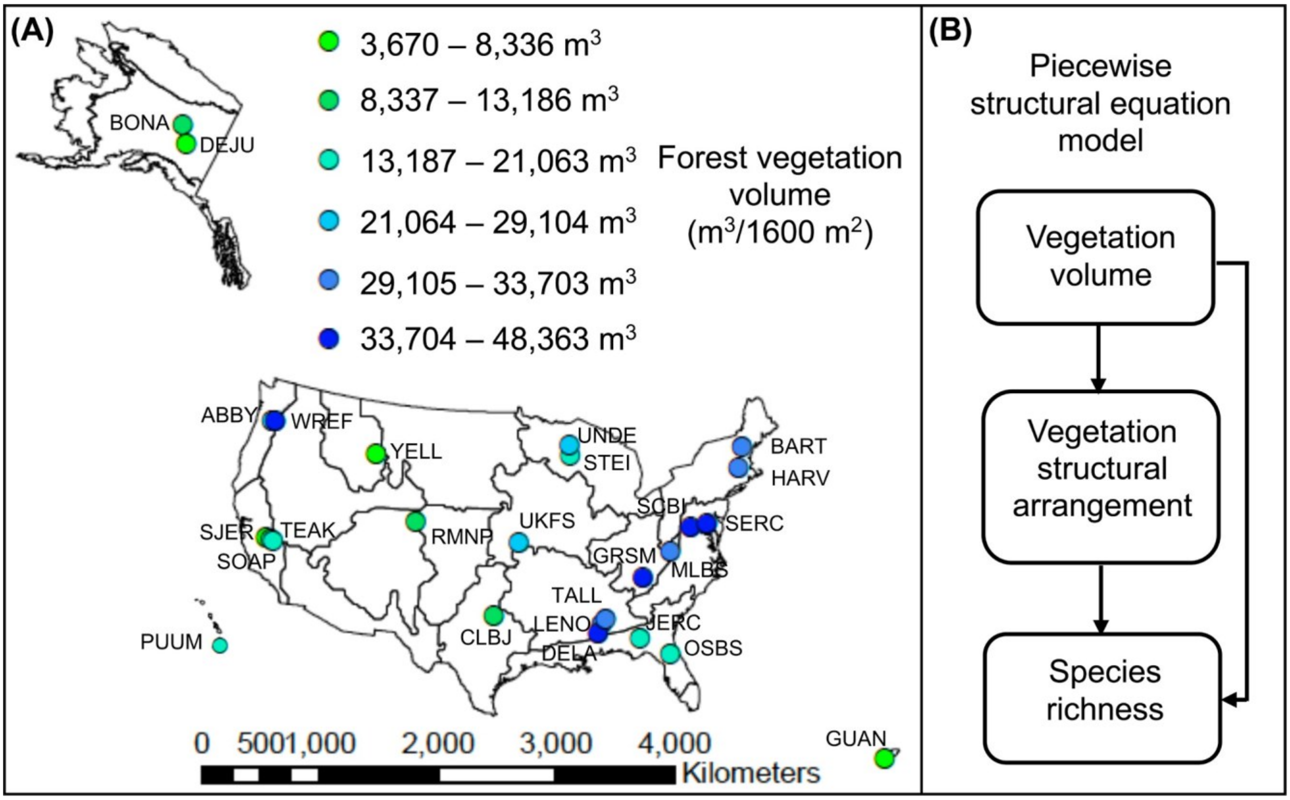

Figure 1. Average forest volume of NEON study sites across the USA (volume average for an area of 1600 m^2 taken across base plots from the tree organism group) (A) and hypothesized relationships between vegetation volume, structural arrangement, and species richness tested in the piecewise structural equation model (B). ABBY - Abby Road, BART - Bartlett Experimental Forest, BONA - Caribou-Poker Creeks Research Watershed, CLBJ - Lyndon B. Johnson National Grassland, DEJU - Delta Junction, DELA - Dead Lake, GRSM - Great Smoky Mountains, GUAN - Guanica Forest, HARV - Harvard Forest, JERC -Jones Center, LENO - Lenoir Landing, MLBS - Mountain Lake Biological Station, OSBS - Ordway-Swisher Biological Station, PUUM - Pu'u Maka'ala Natural Area Reserve, RMNP - Rocky Mountains, SERC - Smithsonian Environmental Research Center, SJER - San Joaquin Experimental Range, SOAP - Soaproot Saddle, STEI - Steigerwaldt-Chequamegon, TALL - Talladega National Forest, TEAK - Lower Teakettle, UKFS - University of Kansas Field Station, UNDE - University of Notre Dame Environmental Research Center, WREF - Wind River Experimental Forest, YELL - Yellowstone.

standard deviations for the other two smaller plot sizes and using the *classify_noise* function with the isolated voxels filter algorithm; all functions to process lidar came from the 'lidR' ver. 3.1.2 R package (www.r-project.org) unless otherwise noted (Roussel et al. 2020). The buffer area was corrected for ground elevation with a Delaunay triangulation using the *normalize()* function. Each buffer was then clipped to the corresponding plot area.

Forest canopy volume and four structural arrangement metrics that describe the 3D internal (variation in vegetation height inside the canopy) and external heterogeneity (variation in height of vegetation at canopy surface) of forest canopy vegetation were calculated (Supporting information). We point out that our measurement of volume and structural arrangement metrics are both measured using lidar data, however lidar provides reliable measurements of different structural dimensions of forest canopies, including metrics used here (Gough et al. 2020, LaRue et al. 2020, 2022, Atkins et al. 2022). Plots had a minimum canopy height of 3 m or taller. We used all returns to calculate: volume, rumple, CV(ht), CV(CV(ht)), and FHD (Supporting information); metrics were calculated using functions in the 'lidR' package unless noted otherwise. For rumple and volume, points < 3 m were converted to zero in the point cloud. Points below 0.5 m were filtered out of the point cloud for the remaining metrics. Volume was calculated as the sum of the forest vegetation volume (m^3) of each 1-m^2 cell in the plot raster grid for the area of each NEON plot type from a canopy height model (*grid_canopy()* function), which provides a measure of the outer envelope around the vegetation surface that includes both the open and filled spaces of the inner canopy. To remove potential outlier plots with few trees that were taller than 3 m, we removed plots with a volume of $<$ 2000 m^3 and shrub land cover types (only forest land cover types were used at the plot-level). A measure of surface canopy roughness, rumple (*rumple_index()* function) was calculated as the ratio of the outer surface area of the height of the canopy within a 1-m^2 grid (i.e. canopy height model) to the ground area of the plot. A measure of internal canopy vegetation height heterogeneity, CV(ht), was calculated as the coefficient of variation (CV) of vegetation heights across the entire point cloud with the *cloud_metrics()* function. A measure of the spatial variation in vertical vegetation height heterogeneity, CV(CV(ht)), was calculated as the CV of vegetation heights (points) within 9-m^2 voxels across the plot and then the plot-level CV across each voxel's CV value was calculated using the *grid_metrics()* function. Finally, foliage height diversity, a measure of the richness and evenness of vertical stratification of vegetation layers, was calculated using the *FHD()* function in the 'leafR' R package (www.r-project.org, de Almeida et al. 2019), which uses abundances as per-vowel-relative LAD values as described in MacArthur and MacArthur (1961).

Species richness from NEON products

We used five NEON TOS data products (Thorpe et al. 2016, Barnett et al. 2019b) to measure the species richness and Shannon's diversity index of five different organism groups (understory plants, trees, breeding land birds, small mammals and ground beetles). We used the most recent year of plot-level data that were sampled that was closest to the year of AOP lidar used. We removed individuals not identified to at least the species level.

Understory plant and tree taxonomic diversity

We used the plant presence and abundance (NEON.DP1.10058.001) (NEON c, d) and vegetation structure data products (NEON.DPI.10098.001) (NEON e, f) to measure the taxonomic diversity of understory plant and tree communities, respectively. We used the 1-m^2 nested subplots aggregated at the plot level (i.e. 40 × 40 m) from the plant presence and abundance product to calculate taxonomic richness and Shannon's diversity index of the understory plant community (individuals of height $<$ 3 m), because it is the only sampling subplot that includes the percent cover of each species (Barnett et al. 2019a). The vegetation structure includes the tree and shrub species identification of all individual trees with a stem diameter 10 cm or greater and a height of 1.3 m or taller. We used the live individuals from the 400-m^2 sampled area across base plots at each site to estimate species richness and Shannon's diversity index of the tree community within each plot.

Breeding land bird taxonomic diversity

We used the individual counts of identified land breeding birds observed within the bird observation plots from the NEON breeding land bird point counts product (NEON.DP1.10003.001) (NEON g, h) to calculate species richness and Shannon's diversity index of birds. Breeding land birds are counted within a 6 min interval at nine different points within the 500 × 500 m plot over the growing season. Land breeding birds include non-aquatic species and typically exclude raptors, aquatic, or upland game birds; these other groups were removed. In addition, we removed any birds sighted outside of a count period.

Small mammal taxonomic diversity

We used the NEON small mammal box trapping product (NEON.DP1.10072.001) (NEON i, j) to estimate species richness and Shannon's diversity index of small mammal communities that utilize the plot areas sampled. The box trapping is done across 3–8 arrays spaced at least 10 m apart within 90 × 90 m plots. Sherman folding traps are set for multiple nights per year and recapture is recorded by using ear and PIT markings. Only individuals with a trap capture status were used. Repeat captures of tagged individuals were removed at the plot level so as not to influence the frequency of individual species when calculating Shannon's diversity index.

Ground beetle taxonomic diversity

We used the NEON ground beetles (Coleoptera: Carabidae) product that were sampled from pitfall traps (NEON. DP1.10022.001) (NEON l, k) to estimate beetle species richness and Shannon's diversity index. The sampling method consists of four pitfall traps placed at each cardinal direction 20 m from the center of a base plot and sampled weekly throughout the growing season.

Statistical analyses

All variables were $\log_{10}(1+x)$ transformed prior to analysis. Additionally, variables were standardized using $[x - \text{mean}\{x\}]/2 \times \text{SD}[x])$ to make variable effect sizes comparable. Before testing for the presence of DVRs, we removed highly correlated (repetitive) variables using the Spearman correlation coefficient within our five different organism group datasets (Supporting information). We chose to use species richness in our analyses but dropped Shannon's diversity index from our analyses because it was highly correlated with species richness of each taxonomic group (r = 0.81– 0.97). The four structural arrangement metrics were retained. We tested for DVRs using a power function, which has been found to be one of the most common models to fit a SAR (Dengler 2009, Triantis et al. 2012) and previous work has also observed a power-law relationship between forest height and structural complexity metrics (Atkins et al. 2022). The power law describes a relationship where diversity increases with increasing area (or volume), but diversity may reach a threshold at higher values of area (or volume). We used the lognormal version of the power law, because the response and the predictor variable were $\log_{10}(1+x)$ transformed prior to all analyses. We employed a linear model with the lmer() function in the 'lme4' ver. 1.1.30 R package (www.r-project.org, Bates et al. 2015) to test for the lognormal power law relationship between volume and five diversity metrics across the five taxonomic groups. First, a linear model was fit for each dataset with volume as a fixed effect (predictor) and each diversity metric as a response variable for the different models. The linear model was run with a fixed intercept (C) representing the mean of the response variable across all plots and a random site intercept (C_{Site}) to account for across site-level variation in the species richness or structural arrangement response variable. The linear model was in the form of

$$\log_{10}(1 + \text{diversity}) = \log_{10} \text{C} + \log_{10} \text{C}_{\text{Site}} + Z\, \xi \log_{10}(1 + \text{volume}). \quad (1)$$

Separate models were fit for each diversity metric and organism group combination for a total of 25 models. A Wald χ^2 test that had a p-value < 0.05 was used to determine if forest volume was significantly associated with the diversity response variable. To investigate site-level relationships, we ran equivalent simple linear regression models for sites that had eight or more plots and used a bootstrapped 95% confidence interval that did not overlap with zero to assess significance of the site-level DVR.

We expected that volume would directly predict species richness, but that volume constraints on structural arrangement would indirectly explain variation in the species. To test for direct relationships of volume with species richness and indirectly through structural arrangement, we used a piecewise structural equation model approach (piecewise SEM) with the 'piecewiseSEM' ver. 2.1.2 R package (www.r-project.org, Lefcheck 2016). We fit the saturated model, which had two parts 1) volume as a direct predictor of a structural arrangement variable and species richness and 2) volume as an indirect predictor of species richness through a structural arrangement variable (Fig. 1b). A random site intercept was included into the piecewise SEM. Each model included volume, one structural arrangement metric, and species richness (four models per organism group, because there were four structural arrangement metrics).

Results

DVRs: species richness

The direction of the relationship between forest volume and the species richness of five organism groups varied by taxon (Table 2, Fig. 2). The organism groups that exhibited a significant relationship with forest volume were composed of plant and beetle taxa. We found a positive regression coefficient (power law) between volume and tree species richness ($Z_{Tree} = 0.41$ with Wald $\chi^2 = 90.15$, p-value = < 0.01), but a negative regression coefficient with understory plant species richness ($Z_{Understory\ plant} = -0.11$ with Wald $\chi^2 = 6.53$, p-value = 0.01). There was a positive regression coefficient between volume and ground beetle species richness ($Z_{Beetle} = 0.19$ with Wald $\chi^2 = 7.02$, p-value = < 0.01). The other two animal groups did not have a significant relationship with forest volume across sites (Table 2). At the site level, we found significant DVRs (Z coefficient) at 10 of 25, 10 of 25, 2 of 12, 0 of 2, and 3 of 19 sites for understory plants, trees, birds, small mammal, and beetle groups, respectively (Supporting information, most small mammal sites had < 8 plots, so most of the site-level regressions were not included).

DVRs: structural arrangement

The volume of forest vegetation was a predictor of four different dimensions of the structural arrangement of vegetation within the ecosystem (Table 2, Fig. 3), but the direction and magnitude of site-level relationships varied (Supporting information). Forest volume was significantly positively correlated with rumple and FHD, negatively with CV(ht), but there was typically an insignificant association for CV(CV(ht)) (Table 2). Generally, the direction of the relationships between volume and the structural diversity metrics was consistent across the datasets for the five organism groups with two exceptions: for rumple insignificant in the small mammal dataset and CV(CV(ht)) being significantly positively correlated in the bird dataset (Table 2). At the site-level, we found that for FHD, that all or nearly all sites had significant slopes across the taxonomic groups (Supporting information). Whereas, rumple, CVCV(ht), and CV(ht) exhibited around 1/4 to 1/2 of the sites showing significant relationships between volume and the structural arrangement metric (Supporting information).

Table 2. DVRs across the USA forest macrosystem modeled as $\log_{10}$ diversity = $\log_{10}$ C + $\log_{10}$ Z volume with a fixed and random site intercept. A significant volume regression coefficient is bolded when the p-value of a Wald χ^2 test had an alpha < 0.05. All variables were $\log_{10}$ (1 + x) transformed before analysis and standardized to make variable effect sizes comparable.

Taxa	Coefficient	Species richness	Rumple	CV(CV(ht))	CV(ht)	FHD
Understory plant **($N_{Plots} = 636$)**	log C (random intercept)	0.00 (0.15)	0.00 (0.13)	−0.01 (0.14)	0.00 (0.07)	0.00 (0.05)
	Z (χ^2, p-value)	**−0.11 (6.53, 0.01)**	**0.29 (44.63, < 0.01)**	0.06 (2.01, 0.15)	**−0.45 (88.55, < 0.01)**	**0.78 (1135.02, < 0.01)**
Trees **($N_{Plots} = 812$)**	log C (random intercept)	−0.02 (0.06)	0.02 (0.14)	−0.02 (0.15)	0.01 (0.09)	0.00 (0.06)
	Z (χ^2, p-value)	**0.41 (90.15, < 0.01)**	**0.31 (54.50, < 0.01)**	0.00 (0, 0.99)	**−0.47 (100.46, < 0.01)**	**0.78 (1239.98, < 0.01)**
Birds **($N_{Plots} = 118$)**	log C (random intercept)	−0.01 (0.23)	−0.01 (0.17)	−0.01 (0.11)	−0.00 (0.10)	−0.00 (0.04)
	Z (χ^2, p-value)	−0.04 (0.30, 0.58)	**0.25 (9.85, < 0.01)**	**0.34 (12.04, < 0.01)**	**−0.48 (19.55, < 0.01)**	**0.80 (643.90, < 0.01)**
Small mammals **($N_{Plots} = 71$)**	log C (random intercept)	−0.02 (0.19)	−0.02 (0.16)	−0.00 (0.10)	−0.01 (0.09)	−0.00 (0.01)
	Z (χ^2, p-value)	0.19 (2.72, 0.09)	−0.01 (0.01, 0.89)	0.21 (2.39, 0.12)	**−0.47 (11.9, 0.01)**	**0.89 (263.85, < 0.01)**
Beetles **($N_{Plots} = 195$)**	log C (random intercept)	−0.00 (0.10)	0.01 (0.15)	−0.00 (0.14)	0.00 (0.10)	0.00 (0.07)
	Z (χ^2, p-value)	**0.19 (7.02, < 0.01)**	**0.33 (21.76, < 0.01)**	−0.06 (0.70, 0.40)	**−0.29 (14.60, < 0.01)**	**0.70 (375.63, < 0.01)**

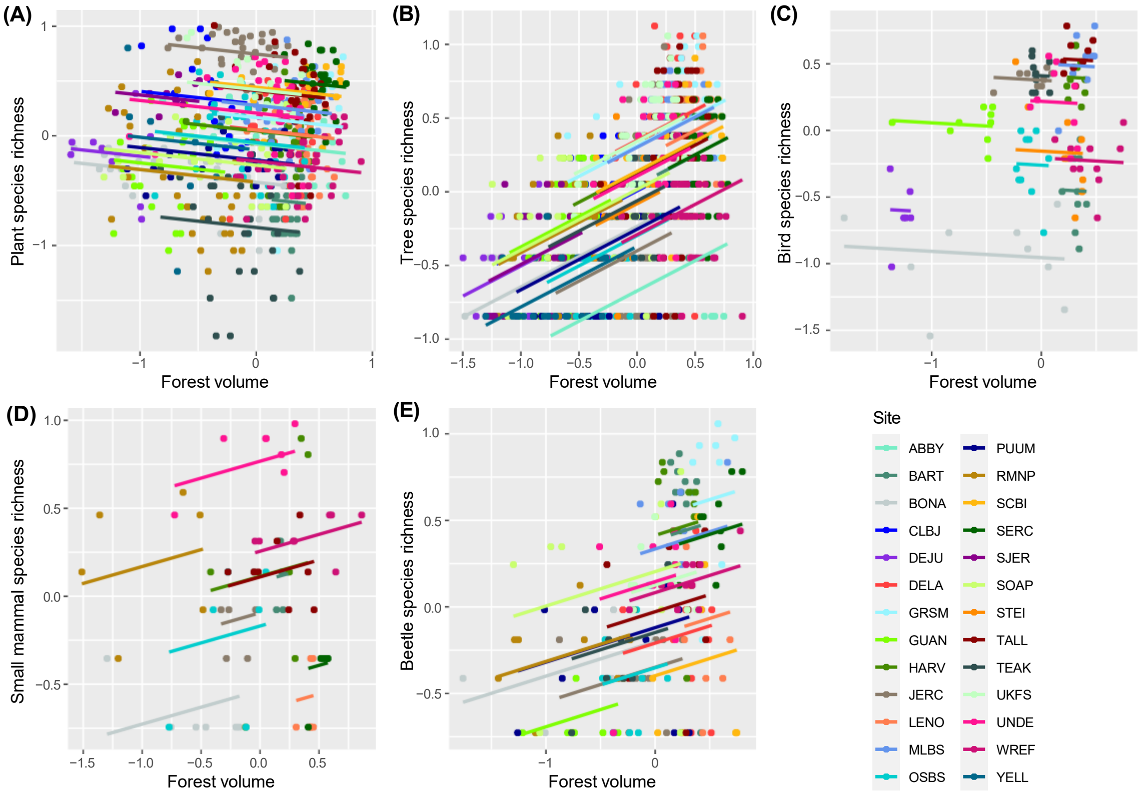

Figure 2. DVRs across the USA forest macrosystem shown for species richness – volume relationships for A) understory plants ($N_{Sites} = 25$), B) trees ($N_{Sites} = 26$), C) land breeding birds ($N_{Sites} = 13$), D) small mammals ($N_{Sites} = 11$), and E) ground beetles ($N_{Sites} = 20$). Plots and trend lines for each site are color coded as shown in the legend. All variables were $\log_{10}(1 + x)$ transformed and standardized to make variable effect sizes comparable. Trend lines are shown as the fixed slope (Z) and the random intercepts (C_{Site}) for each site from the linear model with forest volume as the independent and species richness as the response variable (see Table 2 for associated model results).

Direct relationships of volume with species richness and indirect via structural arrangement

Volume was directly related to species richness but also indirectly through several metrics of the structural arrangement of vegetation for four groups of organisms. First, the direct DVR relationship between volume and structural arrangement in piecewise SEMs models across the USA forest macrosystem (Table 3) was consistent with those described above in 'DVRs: Structural arrangement'. Second, the relationship between volume and species richness was always significant for plant taxa; the relationship was negative for understory plants and positive for trees (Table 3). The relationship between volume and beetle species richness was significantly positive for the beetles, except for the model with FHD (Table 3). The relationship between volume and species richness was insignificant for the other animal taxa, except for a negative relationship in the birds with FHD (Table 3). Third, volume was indirectly associated with species richness through structural arrangement metrics for understory plant and tree species richness, but the direction was opposite of that between volume and species richness in the piecewise SEM model (Table 3). Two metrics, rumple and CV(CV(ht)), were correlated with understory plant and tree species richness, but in different directions with understory plant (positive) and tree (negative) (Table 3). FHD was positively associated with understory plant richness and CV(ht) with tree richness (Table 3). For both plant groups, the direction of the relationship between structural arrangement and species richness was opposite of the relationship between volume and species richness (except for CV(ht) and tree richness) (Table 3). Volume was indirectly associated with bird and beetle species richness through two structural arrangement metrics: CV(CV(ht)) and FHD positively predicted bird species richness and rumple negatively predicted beetle species richness, whereas the remaining relationships were insignificant (Table 3). The direction of the relationship between structural arrangement and bird or beetle species richness was opposite of the relationship between volume and species richness, or only one of volume or structural arrange- ment was a significant predictor of animal species richness (when either were significant) (Table 3).

Discussion

We found that vegetation volume, as a 3D extension of area in the species area relationship, was a significant positive

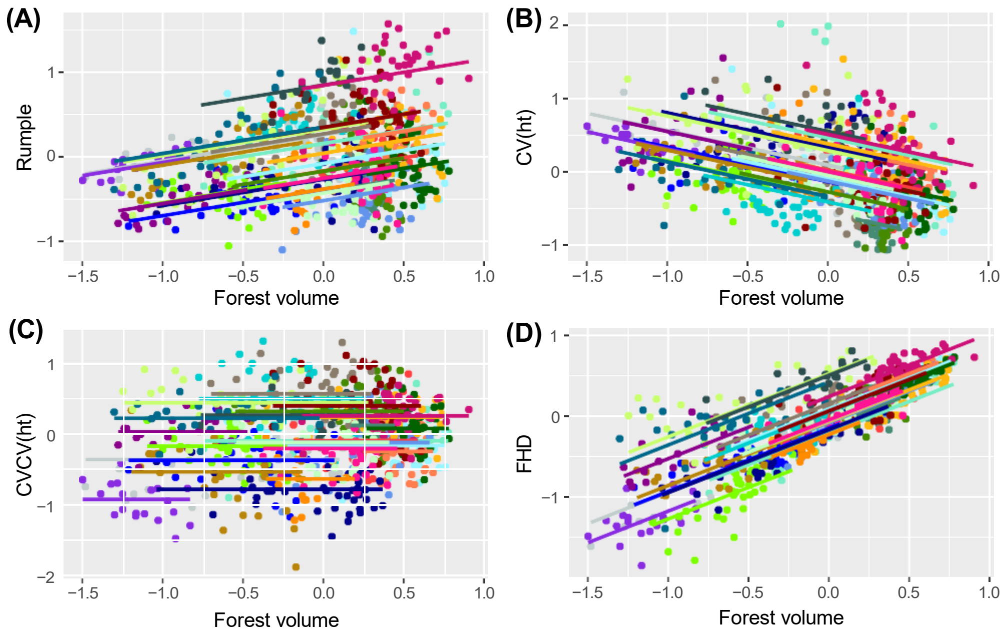

Figure 3. DVRs across the USA forest macrosystem shown for structural arrangement – volume relationships for A) rumple, B) CV of height (CV(ht)), C) horizontal CV of CV of height (CV(CV(ht)), and D) foliage height diversity (FHD). Data is shown for the tree organism group ($N_{\text{Sites}} = 26$). Plots and trend lines for each site are color coded as shown in the legend of Fig. 2. All variables were $\log_{10}(1 + x)$ transformed and standardized to make variable effect sizes comparable. Trend lines are shown as the fixed slope (Z) and the random intercepts (C_{Site}) for each site from the linear model with forest volume as the independent and structural arrangement as the response variable (Table 2 for associated model results).

predictor of tree and beetle species richness and negative predictor of understory plant species richness across the USA forest macrosystem. We did not find an overall relationship between volume and bird or small mammal species richness. However, there were several significant site-level relationships between volume and species richness, indicating that DVRs may vary at the local scale. Indeed, previous work has found that the Z coefficient strength varies by biome and landcover type (Gerstner et al. 2014), forest type or taxonomic group (He and Hubbell 2011). Furthermore,

Table 3. Direct and indirect relationships between volume, structural arrangement, and species richness modeled in a saturated piecewise structural equation model with a random intercept for sites. Significance of coefficients were assessed with a p-value of alpha < 0.05 (p-value shown in parentheses). Significant are bolded. Standardized coefficients from the SEM were used. All variables were $\log_{10}(1 + x)$ transformed and standardized to make variable effect sizes comparable.

Taxa	Coefficient	Volume ⟶ structural arrangement	Volume ⟶ taxonomic richness	Structural arrangement ⟶ taxonomic richness
Understory plants **($N_{\text{Plots}} = 636$)**	Rumple	**0.30 (< 0.01)**	**−0.15 (< 0.01)**	**0.11 (0.01)**
	CV(CV(ht)	0.07 (0.16)	**−0.13 (< 0.01)**	**0.21 (< 0.01)**
	CV(ht)	**−0.45 (< 0.01)**	**−0.12 (0.01)**	−0.01 (0.68)
	FHD	**0.79 (< 0.01)**	**−0.50 (< 0.01)**	**0.48 (< 0.01)**
Trees **($N_{\text{Plots}} = 812$)**	Rumple	**0.31 (< 0.01)**	**0.48 (< 0.01)**	**−0.21 (< 0.01)**
	CV(CV(ht)	0.00 (0.99)	**0.41 (< 0.01)**	**−0.23 (< 0.01)**
	CV(ht)	**−0.47 (< 0.01)**	**0.45 (< 0.01)**	**0.09 (0.01)**
	FHD	**0.78 (< 0.01)**	**0.33 (< 0.01)**	0.11 (0.13)
Birds **($N_{\text{Plots}} = 118$)**	Rumple	**0.26 (< 0.01)**	−0.08 (0.39)	0.12 (0.2)
	CV(CV(ht)	**0.35 (< 0.01)**	−0.10 (0.28)	**0.19 (0.01)**
	CV(ht)	**−0.49 (< 0.01)**	−0.04 (0.64)	0.01 (0.92)
	FHD	**0.80 (< 0.01)**	**−0.45 (0.04)**	**0.51 (0.04)**
Small mammals **($N_{\text{Plots}} = 71$)**	Rumple	−0.02 (0.89)	0.19 (0.11)	−0.17 (0.13)
	CV(CV(ht)	0.22 (0.13)	0.20 (0.10)	−0.05 (0.63)
	CV(ht)	**−0.47 (< 0.01)**	0.20 (0.12)	0.02 (0.82)
	FHD	**0.90 (< 0.01)**	0.38 (0.09)	−0.22 (0.31)
Beetles **($N_{\text{Plots}} = 195$)**	Rumple	**0.33 (< 0.01)**	**0.26 (< 0.01)**	**−0.18 (0.02)**
	CV(CV(ht)	−0.06 (0.40)	**0.19 (0.01)**	−0.09 (0.19)
	CV(ht)	**−0.29 (< 0.01)**	**0.18 (0.02)**	−0.08 (0.27)
	FHD	**0.70 (< 0.01)**	0.14 (0.28)	0.09 (0.55)

organisms that have a greater dispersal ability are expected to have low z coefficient values (Hovestadt and Poethke 2005), but we did not see significant z coefficients for the more mobile organism groups – birds and small mammals – in comparison to plants or beetles that are more spatially restricted. Additionally, volume was a significant predictor of four metrics that describe the structural arrangement of vegetation within the ecosystem across the USA forest macrosystem. Our study indicates that previous work that has focused on a 2D conceptualization of habitat abundance (physical area available to species to use for habitat) can be expanded to 3D habitat space across a macroscale for plant taxa, but that vertical heterogeneity is a critical consideration when examining these relationships at the landscape or macroscale. 3D metrics are conceptually complex as there are different ways to define 3D dimensions of habitat, such as volume or occupied vs unoccupied space, that may show different relationships with diversity. This requires further investigation into the different conceptualizations of 3D habitat space, including volume, in DVRs.

The different body size of trees versus understory plants may have contributed to the opposing direction of the macrosystem DVR patterns that we observed here. Plants make up the size and arrangement of the canopy through their vegetative growth and competition for resources, and thereby the volume of the ecosystem. Trees and shrubs would have made up the bulk of the vegetation volume measurement that our study used, because they make up most of the vertical portion of the canopy in forests. Whereas the understory plants (i.e. grasses, forbs, seedlings) can contribute to the forest volume indirectly through seedling recruitment (Dupuy and Chazdon 2008), but are more likely to be impacted by the volume of the canopy via competition for light or water differently than adult trees (Anderson et al. 1969, Anderegg et al. 2012). Understory plant richness was negatively correlated to vegeta- tion volume in the forest, indicating that across the USA for- est macrosystem, 3D habitat volume did not translate to the same expected positive relationship typically observed with species richness and area. Instead of volume indicating that there was greater niche space available to be filled by the sub- canopy plants, a greater volume likely means higher canopy cover and less light or water reaching the forest floor, and thereby limiting niche space (Niinemets 2007, 2010). This competition for light and water can influence plant species frequently found in the understory (Anderson et al. 1969, Hakkenberg and Goetz 2021). In contrast, tree species rich- ness was positively related to volume, which indicated that an increase in 3D habitat space has a similar relationship to the expected SAR patterns observed (MacArthur 1972, Matthews et al. 2021, Tjorve et al. 2021a). This positive relationship may be caused by the ability of large-bodied tree species to occupy different vertical niche spaces to compete for different resources such that different tree species vary in their functional traits or structural architecture (LaRue et al. 2023c). It is also possible that older forests have achieved a larger volume and simultaneously accumulated a greater number of tree species (Franklin 1981, van Pelt and Franklin 2000), however NEON does not have stand age data for their individual base plots to test this. Indeed, the SAR is not always a positive relationship and can depend upon stochastic and deterministic factors that shift the relationship shape (Condit et al. 1996, Tjorve et al. 2021b).

An increase in forest volume is hypothesized to enhance the habitat availability and potential for niche partitioning of animal species in the forest community (McCoy and Bell 1991, Loke and Chisholm 2022), but volume only predicted macrosystem patterns in one of the three animal groups (beetles). Different animal groups may vary in their vertical use of habitat (MacArthur and MacArthur 1961) due to in part to taxonomic differences in mobility or body size that result in different uses of vegetation as a resource (Sutherland et al. 2000, Makarieva et al. 2005, Barbaro and van Halder 2009). Indeed, vertical partitioning of species can be an evolutionary result of competitive exclusion (MacArthur 1958, Naikatini et al. 2022). The plot sizes here varied by the NEON sampling design for different taxonomic diversity surveys, however, future work could make 2D (SAR) and 3D (DVR) habitat comparisons using spatially nested sampling to help elucidate potential mechanisms underlying taxonomic specific relationships between habitat availability and diversity, including cross-scale (landscape – macrosystem) patterns of DVRs in animal taxa.

The strength and direction of the taxonomic DVRs tested here varied across the sites examined. We observed both sig- nificant and non-significant DVRs at the site-level for both the plant and animal organism groups studied. Past work has shown that relationships between habitat abundance and species diversity vary with environmental conditions or through underlying processes, such as dispersal, or environ- mental filtering, that influence regional diversity (Shen et al. 2009, Tjorve et al. 2021b, He et al. 2022). The impact of history, including climatic changes and biogeographic or evo- lutionary dynamics, may play an especially important role in constraining species pools in temperate habitats (Wiens and Donoghue 2004). However, it is yet unknown how local environment, regional species pools, and biogeographic and climatic histories may have contributed to site-level DVRs studied here. Finally, we were not able to investigate site-level relationships within the small mammals due to lower num- bers of plots per site in comparison to the other four groups of organisms.

We expanded our representation of species richness as the SAR diversity variable with metrics that describe the struc- tural arrangement of vegetation within the ecosystem. We expected that a higher volume available in a forest would allow for a greater number and complex arrangement of veg- etation layers in the canopy (Gough et al. 2020, Atkins et al. 2022). This was supported by a positive relationship between volume and the roughness of the canopy surface (rumple) and the diversity of the number of layers in the vertical canopy profile (foliage height diversity). Similarly, Atkins et al. (2022) found that the structural complexity of the canopy (number of layers or rugosity) increased with forest height, but that structural complexity did not scale equally with height. Our plot-level value of forest volume represents the occupied volume of vegetation in the forest stand, whereas Atkins et al. (2022) looked at average outer canopy height and maximum height which provide a proxy for the actual total volume of the outer canopy that we used here. Additionally, these relationships between volume and structural arrangement metrics were usually consistent across the taxa we looked at: positive (FHD, but one insignificant for rumple), negative (CV of height), or insignificant (CV(CV(ht)) except for positive in birds). At the macrosystem, even though the number of layers increased with volume, these layers may tend to occur in the upper or lower portion of the canopy as opposed to throughout that would be reflected with vertical heterogeneity of vegetation, therefore this may be why there is no significant relationship with CV(CV(ht)) and a negative relationship with CV(ht). Our measure of heterogeneity uses a coefficient of variation to remove effects of differences in the average mean of the points within the lidar dataset for forests that vary in their height (and volume).

We predicted that volume would indirectly influence species richness through structural arrangement, because plants that occupy different locations within the canopy will create niche spaces that other members of the forest community at different trophic levels may use (McCoy and Bell 1991, Davies and Asner 2014, Loke and Chisholm 2022). We did find that volume predicted understory plant and tree species richness directly and indirectly through structural arrangement, but that the direction of the relationship with species richness was opposite. Volume had a negative relationship with understory plant richness, but three structural arrangement metrics had a positive relationship with plant understory richness (rumple, CV(CV(ht)), FHD). Whereas volume had a positive relationship with tree species richness, two structural diversity metrics of three, rumple and CV(CV(ht)), had a negative association with tree species richness (but CV(ht) a positive relationship). This implies that volume and the structural arrangement of the forest canopy may represent different niche axes and thereby mechanisms for interacting with the species richness of understory plants and trees. Furthermore, we typically did not observe significant relationships between volume or structural arrangement and animal species richness across the USA forest macrosystem. The exceptions were a positive relationship between CV(CV(ht)) and FHD with bird richness and a negative relationship between rumple and beetle richness. It is possible that individual sites exhibited significant relationships among volume, structural arrangement, and species richness, but we did not have enough plots within each site across the entire macrosystem for all five plant and animal groups to comprehensively investigate individual site-level relationships. Therefore, future work that investigates how plant and animal taxa interact with different dimensions of habitat volume and structural arrangement would provide important insight into how 3D habitat representations of niche space influence community diversity across different ecosystem types.

Acknowledgements – We thank C. Tweedie for feedback on the idea.
Funding – Funding for this work was supported by NSF DEB no. 2212859 to EAL and SVZ, UTEP University Research Institute Award to EAL, NSF DEB no. 1954418 to VMS, and NSF DEB no. 2203216 to MGH. SVZ was supported by NSF OPP no. 1836861 and NASA ABoVE 80NSSC19M0110.

Author contributions

Elizabeth A. LaRue: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Anna G. Downing**: Formal analysis (supporting); Visualization (supporting); Writing – review and editing (supporting). **Sheila Saucedo**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Arturo Rocha**: Methodology (supporting); Writing – review and editing (supporting). **Sergio A. Vargas Zesati**: Conceptualization (supporting); Funding acquisition (supporting); Writing – review and editing (supporting). **Vicente Mata-Silva**: Supervision (supporting); Writing – review and editing (supporting). **Michael G. Harvey**: Methodology (supporting); Writing – review and editing (supporting).

Data availability statement

All data are available from the National Ecological Observatory Network (www.neonscience.org).

Data are available from Zenodo : https://doi.org/10.5281/ zenodo.8044405 (LaRue et al. 2023a), including provisional NEON data.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Adams, T. P., Purves, D. W. and Pacala, S. W. 2007. Understanding height-structured competition in forests: is there an R for light? – Proc. R. Soc. B 274: 3039–3047.

Anderegg, W. R. L., Anderegg, L. D. L., Sherman, C. and Karp, D. S. 2012. Effects of widespread drought-induced aspen mortality on understory plants. – Conserv. Biol. 26: 1082–1090.

Anderson, R. C., Loucks, O. L. and Swain, A. M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. – Ecology 50: 255–263.

Aponte, C., Kasel, S., Nitschke, C. R., Tanase, M. A., Vickers, H., Parker, L., Fedrigo, M., Kohout, M., Ruiz-Benito, P., Zavala, M. A. and Bennett, L. T. 2020. Structural diversity underpins carbon storage in Australian temperate forests. – Global Ecol. Biogeogr. 29: 789–802.

Atkins, J. W., Fahey, R. T., Hardiman, B. H. and Gough, C. M. 2018. Forest canopy structural complexity and light absorption relationships at the subcontinental scale. – J. Geophys. Res. Biogeosci. 123: 1387–1405.

Atkins, J. W., Walter, J. A., Stovall, A. E. L., Fahey, R. T. and Gough, C. M. 2022. Power law scaling relationships link canopy structural complexity and height across forest types. – Funct. Ecol. 36: 713–726.

Barbaro, L. and van Halder, I. 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. – Ecography 32: 321–333.

Barnett, D. T., Adler, P. B., Chemel, B. R., Duffy, P. A., Enquist, B. J., Grace, J. B., Harrison, S., Peet, R. K., Schimel, D. S., Stohlgren, T. J. and Vellend, M. 2019a. The plant diversity sampling design for the National Ecological Observatory Network. – Ecosphere 10: e02603.

Barnett, D. T., Duffy, P. A., Schimel, D. S., Krauss, R. E., Irvine, K. M., Davis, F. W., Gross, J. E., Azuaje, E. I., Thorpe, A. S., Gudex-Cross, D., Patterson, M., McKay, J. M., McCorkel, J. T. and Meier, C. L. 2019b. The terrestrial organism and biogeochemistry spatial sampling design for the National Ecological Observatory Network. – Ecosphere 10: e02540.

Bates, D., Mächler, M., Bolker, B., Walker, S. 2015. Fitting lin- ear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bergen, K. M., Goetz, S. J., Dubayah, R. O., Henebry, G. M., Hunsaker, C. T., Imhoff, M. L., Nelson, R.F., Parker, G. G., and Radeloff, V. C. 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: review and implications for LiDAR and radar spaceborne missions. – J. Geophys. Res. Biogeosci. 114: 1–13.

Boutaud, E., Nolte, D., Harry, I. Assmann, T., and Drees, C. 2022. Conservation value of semi-open habitats for ground beetles (Coleoptera: Carabidae, Cicindelidae) in Central Europe. – Biodivers. Conserv. 31: 1469–1489.

Condit, R., Hubbell, S. P., Lafrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B. and Ashton, P. S. 1996. Species–area and species–individual relationships for tropical trees: a comparison of three 50-ha plots. – J. Ecol. 84: 549.

Coverdale, T. C. and Davies, A. B. 2023. Unravelling the relationship between plant diversity and vegetation structural complexity: a review and theoretical framework. – J. Ecol., https://doi.org/10.1111/1365-2745.14068.

Davies, A. B. and Asner, G. P. 2014. Advances in animal ecology from 3D-LiDaR ecosystem mapping. – Trends Ecol. Evol. 29: 681–691.

Almeida, D. R. A., Stark, S. C., Chazdon, R., Nelson, B. W., Cesar, R. G., Meli, P., Gorgens, E. B., Duarte, M. M., Valbuena, R., Moreno, V. S., Mendes, A. F., Amazonas, N., Gonçalves, N. B., Silva, C. A., Schietti, J. and Brancalion, P. H. S. 2019. The effectiveness of LiDAR remote sensing for monitoring forest cover attributes and landscape restoration. – For. Ecol. Manage. 438: 34–43.

Dengler, J. 2009. Which function describes the species-area relationship best? A review and empirical evaluation. – J. Biogeogr. 36: 728–744.

Drag, L., Burner, R. C., Stephan, J. G., Birkemoe, T., Doerfler, I., Gossner, M. M., Magdon, P., Ovaskainen, O., Potterf, M., Schall, P., Snäll, T., Sverdrup-Thygeson, A., Weisser, W. and Müller, J. 2023. High-resolution 3D forest structure explains ecomorphological trait variation in assemblages of saproxylic beetles. – Funct. Ecol. 37: 150–161.

Dubayah, R., Blair, J. B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P., Marselis, S., Patterson, P. L., Qi, W. and Silva, C. 2020. The Global Ecosystem Dynamics Investigation: high-resolution laser ranging of the Earth's forests and topography. – Sci. Remote Sens. 1: 100002.

Dupuy, J. M. and Chazdon, R. L. 2008. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. – For. Ecol. Manage. 255: 3716–3725.

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H. J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S. L. and Ammer, C. 2021. Global patterns and climatic controls of forest structural complexity. – Nat. Commun. 12: 519.

Ehlers Smith, Y. C., Ehlers Smith, D. A., Ramesh, T. and Downs, C. T. 2017. The importance of microhabitat structure in maintaining forest mammal diversity in a mixed land-use mosaic. – Biodivers. Conserv. 26: 2361–2382.

Fahey, R. T., Alveshere, B. C., Burton, J. I., D'Amato, A. W., Dickinson, Y. L., Keeton, W. S., Kern, C. C., Larson, A. J., Palik, B. J., Puettmann, K. J., Saunders, M. R., Webster, C. R., Atkins, J. W., Gough, C. M. and Hardiman, B. S. 2018. Shifting conceptions of complexity in forest management and silviculture. – For. Ecol. Manage. 421: 59–71.

Fattorini, S., Ulrich, W. and Matthews, T. 2021. Using the species-area relationship to predict extinctions resulting from habitat loss. – In: Matthews, T., Triantis, K. and Whittaker, R. (eds), The species–area relationship: theory and application. Cambridge Univ. Press, pp. 345–367.

Forrester, D. I. and Bauhus, J. 2016. A review of processes behind diversity—productivity relationships in forests. – Curr. For. Rep. 2: 45–61.

Franklin, J. F. 1981. Ecological characteristics of old-growth Douglas-fir forests. – United States Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Gámez, S. and Harris, N. C. 2022. Conceptualizing the 3D niche and vertical space use. – Trends Ecol. Evol. 37: 953–962.

Gerstner, K., Dormann, C. F., Václavík, T., Kreft, H. and Seppelt, R. 2014. Accounting for geographical variation in species-area relationships improves the prediction of plant species richness at the global scale. – J. Biogeogr. 41: 261–273.

Goetz, S., Steinberg, D., Dubayah, R. and Blair, B. 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. – Remote Sens. Environ. 108: 254–263.

Gough, C. M., Atkins, J. W., Fahey, R. T., Hardiman, B. S. and LaRue, E. A. 2020. Community and structural constraints on the complexity of eastern North American forests. – Global Ecol. Biogeogr. 29: 2107–2118.

Hakkenberg, C. R. and Goetz, S. J. 2021. Climate mediates the relationship between plant biodiversity and forest structure across the United States. – Global Ecol. Biogeogr. 30: 2245–2258.

He, C., Fang, L., Xiong, X., Fan, F., Li, Y., He, L., Shen, X., Li, S., Ji, C. and Zhu, J. 2022. Environmental heterogeneity regulates species-area relationships through the spatial distribution of species. – For. Ecosyst. 9: 100033.

He, F. and Hubbell, S. P. 2011. Species–area relationships always overestimate extinction rates from habitat loss. – Nature 473: 368–371.

Helder, N. K., Burns, J. H. R. and Green, S. J. 2022. Intra-habitat structural complexity drives the distribution of fish trait groups on coral reefs. – Ecol. Indic. 142: 109266.

Hovestadt, T. and Poethke, H. J. 2005. Dispersal and establishment: spatial patterns and species-area relationships. – Divers. Distrib. 11: 333–340.

Jetz, W., McGeoch, M. A., Guralnick, R., Ferrier, S., Beck, J., Costello, M. J., Fernandez, M., Geller, G. N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F. E., Pereira, H. M., Regan, E. C., Schmeller, D. S. and Turak, E. 2019. Essential biodiversity variables for mapping and monitoring species populations. – Nat. Ecol. Evol. 3: 539–551.

Kampe, T. U. 2010. Neon: the first continental-scale ecological observatory with airborne remote sensing of vegetation canopy biochemistry and structure. – J. Appl. Remote Sens. 4: 043510.

Knuff, A., Staab, M., Frey, J., Dormann, C., Asbeck, T., Klein, A. 2020. Insect abundance in managed forests benefits from multilayered vegetation. – Basic Appl. Ecol. 48: 124–135.

Krause, K. and Goulden, T. 2015. NEON L0-to-L1 discrete return LiDAR algorithm theoretical basis document (ATBD), Neon.DOC.001292. https://data.neonscience.org/documents/10179/11204/NEON.DOC.001292vA/b0e5d4ae-84fa-4eae-8a90-d92f490d3d96?version=1.0

Kunstler, G. et al. 2016. Plant functional traits have globally consistent effects on competition. – Nature 529: 204–207.

LaRue, E. A., Hardiman, B. S., Elliott, J. M. and Fei, S. 2019. Structural diversity as a predictor of ecosystem function. – Envi- ron. Res. Lett. 14: 114011.

LaRue, E. A., Wagner, F. W., Fei, S., Atkins, J. W., Fahey, R. T., Gough, C. M. and Hardiman, B. S. 2020. Compatibility of aerial and terrestrial LiDAR for quantifying forest structural diversity. – Remote Sens. 12: 1407.

LaRue, E. A., Fahey, R., Fuson, T. L., Foster, J. R., Matthes, J. H., Krause, K. and Hardiman, B. S. 2022. Evaluating the sensitivity of forest structural diversity characterization to LiDAR point density. – Ecosphere 13: e4209.

LaRue, E. A., Downing, A. G., Saucedo, S., Rocha, A., Vargas Zesati, S. A., Mata-Silva, V. and Harvey, M. G. 2023a. Data from: Diversity – volume relationships: adding structural arrangement and volume to species – area relationships across forest macrosystems. – Zenodo, https://doi.org/10.5281/zenodo.8044405

LaRue, E. L., Fahey, R., Alveshere, B., Atkins, J. W., Buma, B., Chen, A., Cousins, S., Elmore, A., Hakkenberg, C., Hardiman, B., Johnson, J., Kashian, D., Koirala, A., Papes, M., St. Hilaire, J., Surasinghe, T., Zambrano, J., Zhai, L. and Fei, S. 2023b. A framework for the ecological role of structural diversity. – Front. Ecol. Environ. 21: 4–13.

LaRue, E. A., Knott, J. A., Domke, G. M., Chen, H. Y., Guo, Q., Hisano, M., Oswalt, C., Oswalt, S., Kong, N., Potter, K. M. and Fei, S. 2023c. Structural diversity as a reliable and novel predictor for ecosystem productivity. – Front. Ecol. Environ. 21: 33–39.

Lausch, A., Bannehr, L., Beckmann, M., Boehm, C., Feilhauer, H., Hacker, J. M., Heurich, M., Jung, A., Klenke, R., Neumann, C., Pause, M., Rocchini, D., Schaepman, M. E., Schmidtlein, S., Schulz, K., Selsam, P., Settele, J., Skidmore, A. K. and Cord, A. F. 2016. Linking Earth Observation and taxonomic, structural and functional biodiversity: local to ecosystem perspectives. – Ecol. Indic. 70: 317–339.

Lefcheck, J.S. 2016. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. – Methods Ecol. Evol. 7: 573–579.

Loke, L. H. L. and Chisholm, R. A. 2022. Measuring habitat complexity and spatial heterogeneity in ecology. – Ecol. Lett. 25: 2269–2288.

Luo, Y. H., Cadotte, M. W., Burgess, K. S., Liu, J., Tan, S. L., Zou, J. Y., Xu, K., Li, D. Z. and Gao, L. M. 2019. Greater than the sum of the parts: how the species composition in different forest strata influence ecosystem function. – Ecol. Lett. 22: 1449–1461.

MacArthur, R. H. 1958. Population ecology of some warblers of Northeastern coniferous forests. – Ecology 39: 599–619.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. – Princeton Univ. Press.

MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – Ecology 42: 594–598.

MacArthur, R., Recher, H. and Cody, M. 1966. On the relation between habitat selection and species diversity. – Am. Nat. 100: 319–332.

Makarieva, A. M., Gorshkov, V. G. and Li, B.-L. 2005. Why do population density and inverse home range scale differently with body size? implications for ecosystem stability. – Ecol. Complexity 2: 259–271.

Matthews, T., Triantis, K. and Whittaker, R. 2021. The species-area relationship: both general and protean? – In: Matthews, T., Triantis, K. and Whittaker, R. (eds), The species-area relationship: theory and application. Cambridge Univ. Press, pp. 1–19.

Mazel, F. and Thuiller, W. 2021. Functional and phylogenetic diversity – area relationships. – In: Matthews, T., Trianthis, K. and Whittaker, R. (eds), The species–area relationship: theory and application. Cambridge Univ. Press, pp. 107–132.

McCoy, E. D. and Bell, S. 1991. Ch. 1. Habitat structure: the evolution and diversification of a complex topic. In: Bell, S., McCoy, E. and Mushinsky, H. (eds), Habitat structure: the physical arrangement of objects in space. Chapman and Hall.

McElhinny, C., Gibbons, P., Brack, C. and Bauhus, J. 2005. Forest and woodland stand structural complexity: its definition and measurement. – For. Ecol. Manage. 218: 1–24.

Müller, J. and Brandl, R. 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. – J. Appl. Ecol. 46: 897–905.

Naikatini, A. N., Keppel, G., Brodie, G. and Kleindorfer, S. 2022. Interspecific competition and vertical niche partitioning in Fiji's forest birds. – Diversity 14: 223.

National Ecological Observatory Network 2020. neonUtilities: utilities for working with NEON data. R package, ver. 1.3.3. – https://CRAN.R-project.org/package=neonUtilities.

NEON[a] (National Ecological Observatory Network). Discrete return Lidar point cloud (DP1.30003.001). PROVISIONAL. – https://data.neonscience.org (accessed 24 January 2022).

NEON[b] (National Ecological Observatory Network). Discrete return Lidar point cloud (DP1.30003.001). RELEASE-2022. – https://doi.org/10.48443/ca22-1n03. Dataset accessed from https://data.neonscience.org on 24 January 2022.

NEON[c] (National Ecological Observatory Network). Plant presence and percent cover (DP1.10058.001). PROVISIONAL. – https://data.neonscience.org (accessed 15 February 2022).

NEON[d] (National Ecological Observatory Network). Plant presence and percent cover (DP1.10058.001). RELEASE-2022. – https://doi.org/10.48443/pr5e-1q60. Dataset accessed from https://data.neonscience.org on 15 February 2022.

NEON[e] (National Ecological Observatory Network). Vegetation structure (DP1.10098.001). PROVISIONAL. – https://data.neonscience.org (accessed 16 February 2022).

NEON[f] (National Ecological Observatory Network). Vegetation structure (DP1.10098.001). RELEASE-2022. – https://doi.org/10.48443/re8n-tn87. Dataset accessed from https://data.neonscience.org on 16 February 2022.

NEON[g] (National Ecological Observatory Network). Breeding landbird point counts (DP1.10003.001). PROVISIONAL. – https://data.neonscience.org (accessed 15 February 2022).

NEON[h] (National Ecological Observatory Network). Breeding landbird point counts (DP1.10003.001). RELEASE-2022. – https://doi.org/10.48443/88sy-ah40. Dataset accessed from https://data.neonscience.org on 15 February 2022.

NEON[i] (National Ecological Observatory Network). Small mammal box trapping (DP1.10072.001). PROVISIONAL. – https://data.neonscience.org (accessed 15 February 2022).

NEON[j] (National Ecological Observatory Network). Small mammal box trapping (DP1.10072.001). RELEASE-2022. – https://doi.org/10.48443/h3dk-3a71. Dataset accessed from https://data.neonscience.org on 15 February 2022.

NEON[k] (National Ecological Observatory Network). Ground beetles sampled from pitfall traps (DP1.10022.001). RELEASE-2022. – https://doi.org/10.48443/xgea-hw23. Dataset accessed from https://data.neonscience.org on 15 February 2022.

NEON[l] (National Ecological Observatory Network). Ground beetles sampled from pitfall traps (DP1.10022.001). PROVISIONAL. – https://data.neonscience.org (accessed 15 February 2022).

Niinemets, U. 2007. Photosynthesis and resource distribution through plant canopies. – Plant Cell Environ. 30: 1052–1071.

Niinemets, Ü. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. – Ecol. Res. 25: 693–714.

Pereira, H. M. *et al.* 2013. Ecology. Essential biodiversity variables. – Science 339: 277–278.

Redolfi De Zan, L., Battisti, C. and Carpaneto, G. 2014. Bird and beetle assemblages in relict beech forests of central Italy: a multi- taxa approach to assess the importance of dead wood in biodi- versity conservation. – Community Ecol. 15: 235–245.

Roussel, J.-R., Auty, D., Coops, N. C., Tompalski, P., Goodbody, T. R. H., Meador, A. S., Bourdon, J.-F., de Boissieu, F. and Achim, A. 2020. lidR: an R package for analysis of Airborne Laser Scanning ALS data. – Remote Sens. Environ. 251: 112061.

Russo, N., Davies, A., Blakey, R., Ordway, E. and Smith, T. 2022. Feedback loops between 3D vegetation structure and ecological functions of animals. – Authorea.

Schooler, S. L., and Zald, H.S.J. 2019. Lidar prediction of small mammal diversity in Wisconsin, USA. – Remote Sensing 11: 2222.

Shen, G., Yu, M., Hu, X. S., Mi, X., Ren, H., Sun, I. F. and Ma, K. 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. – Ecology 90: 3033–3041.

Sullivan, T. P., Sullivan, D. S. and Lindgren, P. M. F. 2001. Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. – Ecol. Appl. 11: 1151–1173.

Sutherland, G. D., Harestad, A. S., Price, K. and Lertzman, K. P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. – Conserv. Ecol. 4: 16.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. – J. Biogeogr. 31: 79–92.

Théry, M. 2001. Forest light and its influence on habitat selection. – Plant Ecol. 153: 251–261.

Thorpe, A. S., Barnett, D. T., Elmendorf, S. C., Hinckley, E. S., Hoekman, D., Jones, K. D., LeVan, K. E., Meier, C. L., Stanish, L. F. and Thibault, K. M. 2016. Introduction to the sampling designs of the National Ecological Observatory Network Terrestrial Observation System. – Ecosphere 7: e01627.

Tjorve, E., Matthews, T. and Whittaker, R. 2021a. The history of the species–area relationship. – In: Matthews, T., Triantis, K. and Whittaker, R. (eds), The species–area relationship: theory and application. Cambridge Univ. Press, pp. 20–48.

Tjorve, E., Tjorve, K., Sizlingova, E. and Sizling, A. 2021b. Determinants of the shape of species–area curves. – In: Matthews, T., Triantis, K. and Whittaker, R. (eds), The species–area relationship: theory and application. Cambridge Univ. Press, pp. 78–106.

Triantis, K. A., Guilhaumon, F. and Whittaker, R. J. 2012. The island species-area relationship: biology and statistics. – J. Biogeogr. 39: 215–231.

Valbuena, R., O'Connor, B., Zellweger, F., Simonson, W., Vihervaara, P., Maltamo, M., Silva, C. A., de Almeida, D. R. A., Danks, F., Morsdorf, F., Chirici, G., Lucas, R., Coomes, D. A. and Coops, N. C. 2020. Standardizing ecosystem morphological traits from 3D information sources. – Trends Ecol. Evol. 35: 656–667.

van der Gast, C. J., Jefferson, B., Reid, E., Robinson, T., Bailey, M. J., Judd, S. J. and Thompson, I. P. 2006. Bacterial diversity is determined by volume in membrane bioreactors. – Environ. Microbiol. 8: 1048–1055.

van Pelt, R. and Franklin, J. F. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. – Can. J. For. Res. 1245: 1231–1245.

Vieilledent, G., Courbaud, B., Kunstler, G., Dhôte, J. F. and Clark, J. S. 2010. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. – Oecologia 163: 759–773.

West, G. B., Enquist, B. J. and Brown, J. H. 2009. A general quantitative theory of forest structure and dynamics. – Proc. Natl Acad. Sci. USA 106: 7040–7045.

Westoby, M. 1998. A leaf-height-seed LHS plant ecology strategy scheme. – Plant Soil 199: 213–227.

Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – Trends Ecol. Evol. 19: 639–644.

Zheng, L. T., Chen, H. Y. H., Hautier, Y., Bao, D. F., Xu, M. S., Yang, B. Y., Zhao, Z., Zhang, L., and Yan, E. R. 2022. Functionally diverse tree stands reduce herbaceous diversity and productivity via canopy packing. – Funct. Ecol. 36: 950–961.