**Title**: 3D habitat structure drives avian functional and trait diversity across North America

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**Abstract**:

Understanding how three-dimensional (3D) habitat structure drives biodiversity patterns is key to predicting how habitat alteration and loss will affect species and community-level patterns in the future. To date, few studies have contrasted the effects of 3D habitat composition with those of 3D habitat configuration on biodiversity, with existing investigations often limited to measures of taxonomic diversity (i.e., species richness). Here, we examined the influence of Light Detecting and Ranging (LiDAR)-derived 3D habitat structure–both its composition and configuration–on multiple facets of bird diversity. Specifically, we used data from the National Ecological Observatory Network (NEON) to test the associations between eleven measures of 3D habitat structure and avian species richness, functional and trait diversity, and phylogenetic diversity. We found that 3D habitat structure was the most consistent predictor of avian functional and trait diversity, with little to no effect on species richness or phylogenetic diversity. Functional diversity and individual trait characteristics were strongly associated with both 3D habitat composition and configuration, but the magnitude and the direction of the effects varied across the canopy, subcanopy, midstory, and understory vertical strata. Our findings suggest that 3D habitat structure influences avian diversity through its effects on traits. By examining the effects of multiple aspects of habitat structure on multiple facets of avian diversity, we provide a broader framework for future investigations on habitat structure.

**Keywords**: 3D habitat structure, avian diversity, functional diversity, habitat composition, habitat configuration, LiDAR

**Introduction**:

Habitat loss is the leading cause of terrestrial biodiversity declines globally (Pereira et al. 2010, 2012, Jaureguiberry et al. 2022), yet it remains unclear how habitat structure shapes biodiversity (Fletcher et al. 2018, Fahrig et al. 2019). Habitat structure is an umbrella term that encompasses two main concepts: (1) habitat composition, measured as the number or amount of different habitat types and often considered a proxy for niche space, and (2) habitat configuration, the spatial arrangement of those habitat types and encompassing multiple axes of spatial heterogeneity (Ben-Hur and Kadmon 2020, LaRue et al. 2023, Moudrý et al. 2023). Though the number of habitat types typically has a positive and linear (Kerr et al. 2001) or hump-shaped (Fahrig et al. 2011, Ben-Hur and Kadmon 2020) relationship with species richness, the effects of habitat configuration on biodiversity remain more ambiguous. Negative, positive, or neutral associations of habitat configuration with biodiversity have all been demonstrated (Valente et al. 2023), variation that might be a result of contextual dependencies of individual studies (Betts et al. 2019, Mimet et al. 2019, Santos et al. 2021, Banks-Leite et al. 2022) or disparities in the methods used to measure habitat configuration (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019, Valente et al. 2023). Furthermore, though habitat composition and configuration are hypothesized to exert disparate effects on biodiversity (Fischer and Lindenmayer 2007, Villard and Metzger 2014), their impacts are rarely disentangled in practice, potentially leading to inconclusive findings. Finally, and perhaps crucially, habitat structure is predominantly assessed in a two-dimensional (2D) realm (Ewers and Didham 2008, Haddad et al. 2015), even though the vertical nature of habitat structure has long been recognized to play a crucial role in the assembly and maintenance of communities (MacArthur and MacArthur 1961).

Three-dimensional (3D) habitat structure incorporates the vertical dimension of habitats alongside the typical horizontal (or 2D measures) of habitat structure. Vertical height strata, such as canopy, subcanopy, midstory, and understory, can be considered different habitat types or niche spaces (Gámez and Harris 2022, Coddington et al. 2023), analogous to different landcover types in a 2D realm. Thus, 3D habitat composition measures the volume of such height strata, analogous to total habitat amount in a 2D context. 3D habitat configuration, on the other hand, considers the horizontal arrangement of vegetation, similar to 2D habitat configuration, but also incorporates the vertical arrangement of vegetation, both within and between different height strata.

Though 3D habitat structure is a relatively new term, it has long been thought to be particularly important for volant taxonomic groups such as birds (MacArthur and MacArthur 1961, Robinson and Holmes 1982, Davies and Asner 2014), likely influencing large scale patterns of avian diversity. While positive associations between avian species richness and vegetation at various height strata have been previously reported (Lesak et al. 2011, Vogeler et al. 2014, Zellweger et al. 2017, Feng et al. 2020, Burns et al. 2020), many ascribe this relationship to an increase in available niche space, without explicitly examining the effects of 3D composition versus 3D configuration (Richardson and Moskal 2011). The few studies that have investigated both 3D habitat composition and configuration present conflicting findings. While some studies find a greater effect of 3D habitat composition on avian richness compared to habitat configuration (Lesak et al. 2011, Vogeler et al. 2014), others find 3D habitat configuration to be a more important driver of bird richness, with both positive (Goetz et al. 2007) and negative (Carrasco et al. 2019) effects reported. These inconsistencies suggest that our understanding of the effects of 3D habitat structure on avian diversity is incomplete, ultimately hampering any attempts to elucidate the mechanisms underlying vegetation structure-biodiversity associations.

Inconsistencies in the reported effects of 3D habitat structure on biodiversity may in part stem from the exclusion of relevant dimensions of biodiversity from studies of vegetation-biodiversity associations. For example, while habitat composition consistently emerges as the primary predictor of avian diversity, the effects of 3D habitat configuration varies across different functional groups (Davison et al. 2023). This pattern suggests that the link between habitat structure and biodiversity is likely mediated by species traits (Valente and Betts 2019, Jones et al. 2023), which is further supported by the documented associations between habitat heterogeneity and traits such as foraging stratum, diet, body mass, beak shape, and hand-wing index (HWI) (Weisberg et al. 2014, Stirnemann et al. 2015, Coddington et al. 2023). 3D habitat structure might thus directly influence trait composition of an assemblage. Biodiversity measures such as functional diversity (FD) measure the range of functional trait values within a community (Petchey and Gaston 2002), and might thus exhibit stronger correlations with habitat structure than trait-agnostic measures like species richness. Likewise, phylogenetic diversity (PD), i.e., the diversity of evolutionary histories within an assemblage, has also been shown to correlate with some measures of habitat structure (Rurangwa et al. 2022), possibly reflecting a degree of phylogenetic conservatism for traits relevant to habitat structure (but see E-Vojtkó et al. 2023). More research is needed, however, to understand the relationship between avian PD and 3D habitat structure.

Here, we leverage high-resolution Light Detecting and Ranging (LiDAR) (Bergen et al. 2009) and avian survey data from the National Ecological Observatory Network (NEON) (Hargrove and Hoffman 1999), paired with trait and phylogenetic information to investigate the associations of 3D habitat structure with avian species richness, trait and functional diversity, and phylogenetic diversity across North America. We test the effects of a comprehensive suite of measures of 3D habitat composition and 3D habitat configuration, allowing us to gain deeper insights into the mechanisms of avian community assembly along vegetation gradients. We hypothesize that 3D habitat composition will show more consistent relationships with avian diversity across all diversity dimensions compared to 3D habitat configuration, owing to its association with available niche space. We also hypothesize that functional diversity and individual traits will respond more strongly to 3D habitat structure compared to either species richness or phylogenetic diversity.

**Methods**:

Data

*Avian Plots.* To conduct our study, we used National Ecological Observatory Network data from 2017, as it was the year with the greatest number of plots used for avian point counts available. NEON collects multiple point count surveys for breeding landbirds at each of its 47 terrestrial sites, with sites located across 20 North American ecological “Domains”. At each plot, observers record the total number of birds seen or heard within a 6-minute time period, making note of the distance to each individual bird and plot-level environmental metrics. Surveys are timed to coincide with the breeding season at each NEON site, to best capture the abundance of resident breeding birds. Avian plots are usually arranged in a 3x3 grid, with each plot centroid being spaced 250m apart. At smaller sites, single plots are used in lieu of a grid (Kampe 2010, Kao et al. 2012, Weiskopf et al. 2020). To allow for both single plots and gridded plots to be used in the analysis, we retained only the central plot at NEON sites with grids and the first sample period at NEON sites with single plots. We further retained only those plots that overlapped with NEON Airborne Observation Platform (AOP) LiDAR data (see below) collected in 2017. In total, we used 385 avian plots from 38 NEON terrestrial sites across 17 of the 20 NEON Domains (Figure 1a), with vegetation ranging from scrubland to forest in terms of height. As avian sampling occurred during the daytime, we removed all nocturnal species from all avian plot counts, which resulted in a total of 260 species being included in the analysis.

*Biodiversity data*. To calculate FD and PD, we took advantage of a number of existing datasets. We collected trait data from the AVONET (Tobias et al. 2022) and EltonTraits 1.0 databases (Wilman et al. 2014). We used five trait categories: diet, foraging stratum, and body mass from Wilman et al. (2014) and beak measurements and hand-wing index (HWI) from Tobias et al. (2022). The diet category included ten axes: proportion of diet that is insects, amphibians and reptiles, mammals and birds, fish, unknown vertebrates, carrion, nectar, fruit, seeds, and other plant matter. The foraging stratum category included seven axes: proportional use of aerial, canopy, mid-height, understory, ground, water above surface, and water below surface. The beak category included three axes: beak width, beak depth, and beak length. The categories of body mass and HWI both had a single trait axis. To calculate PD, we obtained a random sampling of 100 phylogenetic trees from the Bird Tree database, using the Ericson backbone (Jetz et al. 2012).

*LiDAR data*. To quantify 3D habitat structure, we used NEON’s AOP LiDAR data, which are flown above NEON sites during peak vegetation greenness and have a minimum density of 4 LiDAR shots per square meter (data product: DP1.30003.001) (Kampe 2010). We downloaded all LiDAR point cloud data that overlapped with each of the 385 plots from the NEON repository from 2007 using the R package “neonUtilities” (Lunch et al. 2024).

*Environmental data.* We also collected environmental data to control for variables known to drive avian diversity. Elevation and latitude of each plot were taken directly from the NEON database while climatic data were obtained from Daymet, which produces interpolated estimates of daily weather at a 1km x 1km gridded spatial resolution (Thornton et al. 2022). We selected temperature range (i.e., min-max) of the NEON avian survey period (May-June) as our sole climatic variable after first testing multiple candidate climatic variables and removing those highly correlated with elevation/latitude. Temperature range was taken at the centroid of each plot using the R package “daymetr” (Hufkens et al. 2018).

Species abundance

We corrected for imperfect detection in avian count data using a Bayesian Hierarchical Distance Sampling (BHDS) model (Buckland et al. 2001, Oedekoven et al. 2014). The BHDS model consisted of a hierarchically linked detection model and an ecological process model (see Supporting information for formulation). The ecological process model related environmental covariates (elevation and latitude) to species abundance via a Poisson model. The detection model was used to correct for distance-dependent observation bias by modeling the observation probability as a function of cloud cover, air temperature, windspeed, and observer identity. More specifically, we used a half normal detection function in the BHDS model to model declining rates of detection with increasing distance from the observer (Buckland et al. 2001). We used both species-level parameters and community-level hyper parameters, which allowed us to better estimate abundances () for rare species for a given area (here, a circular plot of 250 m radius) (Sollmann et al. 2016). All BHDS model calculations were run using the R package “jagsUI” (Plummer 2003, Kellner 2015) following model formulation similar to those outlined in Kéry and Royle (2016) and Sollman et al (2016). To avoid instances where the BHDS model estimated for species that are unlikely to be present given their ecological constraints, we *post hoc* filtered detection corrected species abundance estimates so that only species whose geographic ranges overlapped a NEON Domain within which a given plot was embedded could have at that plot. Expert range maps used for filtering were obtained from BirdLife International (BirdLife International 2022). Lastly, species whose at a given plot were considered to be absent at that location, i.e., their was fixed to 0, while those whose were considered to be probable presences and retained for further analysis. The threshold of 0.95 rather than 1 was used to ensure inclusion of species with highly likely presences. The resulting species were used as inputs for quantification of avian species richness, functional and trait, and phylogenetic diversity.

Avian diversity

Avian species richness (SpRich) was calculated for each plot as the sum of all species whose abundance estimates , again using = 0.95 as the threshold to ensure the inclusion of probable presences.

We calculated functional diversity using three complimentary but independent functional components: Functional richness (FRich), functional evenness (FEven), and functional divergence (FDiv) (Villéger et al. 2008). FRich measures the breadth of the trait space occupied by a given assemblage, FEven is a measure of regularity of the distribution of species abundances in trait space, and FDiv measures the proportion of the trait space represented by extreme trait values (Villéger et al. 2008, Mouillot et al. 2013). To obtain these metrics, we first calculated multivariate trait dissimilarity among all species found in all plots using a corrected Gower’s distance (Gower 1971, de Bello et al. 2021). A corrected Gower’s distance better balances the contribution of trait categories and axes to overall dissimilarity (de Bello et al. 2021) and can handle quantitative, semi-quantitative, and qualitative traits (Botta-Dukát 2005). We designated diet, foraging niche, body mass, beak measurements, and hand-wing index as distinct trait categories, and optimized traits weights for each category and their axes using 300 iterations of the optimization algorithm from the “gawdis” package (de Bello et al. 2021). The resulting multivariate trait dissimilarity matrix was then fed into the function “dbFD” in the R package “FD”, along with a plot-level abundance matrix, to quantify FRich, FEven, and FDiv (Laliberté et al. 2023). FRich was quantified as a minimum convex polygon, FEven was quantified as the minimum spanning distance between all species in the trait space, and FDiv was quantified as the average distance of all species to the centroid of the trait space.

FRich is closely correlated with species richness (Cornwell et al. 2006). To correct for this association, we generated a null model expectation for each NEON plot. We first reshuffled (100 times) species abundance estimates using random independent swaps between plots within each NEON Domain, while keeping plot-level species richness constant. For each NEON plot, only species whose range boundaries overlapped with the NEON Domain of that plot were allowed to “appear” in that assemblage. For each of the 100 null communities, we calculated the resulting null expectation of FRich. Finally, we calculated the standardized effect sizes (SES) of the deviation of the observed values of FRich from those expected given species richness as , with representing mean values and representing standard deviation. SES were considered species richness-corrected values of FRich (FRichSES) and used in all subsequent analyses. FEven and FDiv are abundance-weighted and not related to species richness, and thus not requiring a correction (Laliberte and Legendre 2010).

We additionally quantified the prevalence of different trait characteristics in each assemblage. First, using the Gower’s distance matrix for each pairwise combination of species, we ran a Principal Coordinate Analysis (PCoA) using the “cmdscale” function in the “stats” R package. Diagnostic plots were run using the “mFD” package’s “quality.fspaces.plot” function (Magneville et al. 2022), which found improved fit at the fourth principal coordinate (PC) axis (see Supporting information); we thus retained the first four principal coordinates (PC) axes for further analysis. PC scores associated with each species, weighted by their plot-level abundance estimates , were then averaged at the plot level to obtain assemblage-level estimates for each PC axis. To determine how individual traits were correlated with each PC axis, trait vectors were fit to the PCoA ordination using the “vegan” package’s “envfit” function (Oksanen et al. 2022).

Finally, for each NEON plot, we quantified phylogenetic diversity using two indices, Mean Pairwise Distance (MPD) and Faith’s Phylogenetic Diversity (FPD) using the R package “picante” (Kembel et al. 2010). MPD and FPD were based on the distribution of 100 phylogenetic trees from Bird Tree (Jetz et al. 2012). MPD quantifies the average phylogenetic tree branch length between the closest pairs of relatives in a given assemblage. FPD is the sum of all phylogenetic branch lengths for a given assemblage (Tucker et al. 2017). As both MPD and FPD are correlated with species richness, we then corrected both indices by comparing each index against a null distribution of values, which we generated using the same 100 null communities used to generate FRichSES and the same randomization procedure. We created null estimates for each of the 100 phylogenetic trees, resulting in 10,000 total “null” trees. We then quantified SES, which we considered species richness-corrected values of MPD (MPDSES) and FPD (FPDSES).

3D Habitat Structure

We pre-processed LiDAR data by first clipping NEON pointcloud data using a 250 m radius circle measured from the centroid of each of the 385 selected avian plots. Raw pointcloud data was then height normalized to eliminate height differences due to topographic variation using the function “normalize\_height” from the “lidR” package (Roussel et al. 2020) and a digital terrain model (DTM) generated with a k-nearest neighbor approach with an inverse-distance weighting using the function “knnidw” and default settings. To eliminate outlier values, LiDAR points that fell below zero height after height normalization or those high above the vegetation were removed using function “filter\_poi” from “lidR” package.

We derived a suite of 3D habitat compositional and configurational metrics using 0.5 m x 0.5 m x 0.5 m voxels (3D-rasters), which were obtained by converting pointclouds into voxels using the function “voxelize\_points” from package “lidR” (Roussel et al. 2020). To obtain strata-specific measures of habitat structure, voxels were split into four vertical height bins: understory (0-5 m), Und; midstory (5-15m) Mid; subcanopy (15-25 m) Sub; and canopy (>25 m) Can (Figure 1b). Note that while we used nomenclature for the four height strata that is consistent with nomenclature in forest-related disciplines, the selection of strata thresholds were based on those commonly used in ecological studies (Whitehurst et al. 2013, Coddington et al. 2023).

We calculated ten measures of 3D habitat structure (five measures of 3D habitat composition and five measures of 3D habitat configuration) and one measure of 2D habitat structure for comparison. 3D habitat composition was quantified as total habitat amount (TotalA) and as habitat amount within each of the four vertical strata. TotalA was calculated by summing the total number of voxels found along the entire vegetation profile within the 250m radius (Figure 1d). Habitat amounts of each vertical stratum (understory, UndA; midstory, MidA; subcanopy, SubA; canopy, CanA) were calculated as the sum of all voxels within each stratum for each 250m radius plot (Figure 1d). We quantified 3D habitat configuration as vertical habitat configuration along the entire vegetation profile and as habitat configuration at each of the four vertical strata. To quantify vertical habitat configuration, we first assigned each voxel into one of seventy 1 m vertical height bins and summed the total number of voxels in each bin. We then quantified vertical habitat configuration of the resulting array as the variance of that array (VertV) (Figure 1g). Note that though Shannon’s Diversity Index (SDI) is often used to quantify vertical habitat configuration (Carrasco et al. 2019), we opted to not use SDI in our analysis because of its high correlation with total habitat amount in our study system (see Supporting information). To obtain strata-specific measures of habitat configuration (UndC, MidC, SubC, CanC), we used voxels associated with each vertical stratum and converted them into 2D raster layers (Petras et al. 2017) (Figure 1e). For each strata-specific raster layer, we then calculated habitat configuration as the number of patches (NP) (Fahrig 2003), using the R package “landscapemetrics” (Hesselbarth et al. 2019). Finally, we quantified a total 2D habitat configuration (TotalC) by converting TotalA into a single 2D raster and calculating NP (Figure 1e).

Bayesian Mixed Effect Models

To understand the influence of 3D and 2D habitat structure on avian diversity, we fitted 12 hierarchical Bayesian mixed effect models to each metric of avian diversity: SpRich, FD (FRichSES, FEven, FDiv), traits (PC1, PC2, PC3, PC4), and PD (FPDSES, MPDSES). All models followed the same general formulation (equation 1), where is the response variable, is the intercept, and terms are slope (coefficient) estimates for each covariate. To control for random site effects, we fitted NEON site IDs as random intercepts. Models were fitted with a Poisson (SpRich), Beta (FEven), or Gaussian (all others) distributions.

*Equation 1).* ; = link function

We chose to apply a model selection approach, wherein each of the 12 models represented a different hypothesis and thus comprised different combinations of habitat and environmental covariates (Table 1). Note that TotalA was highly correlated with CanA so we ran two versions of the full model, with and without TotalA, and opted to use only the full model without TotalA for all further statistical inferences due to the poor fit of the full model with TotalA.

We ran all models using the R package “brms” (Bürkner 2017). All covariates were centered and scaled prior to the analysis. Prior and posterior predictive checks were conducted and we evaluated models for MCMC convergence (Kruschke 2021). We used leave-one-out (LOO) comparisons from the “loo” R package (Vehtari et al. 2017, Kruschke 2021) to compare the relative fit of all models. Following existing practice (Sivula et al. 2022), models were considered significantly different from one another when the pairwise difference in expected log pointwise predictive density was at least three times the standard error. In cases where no one model was chosen as top performing, all equally top performing models were used to inform overall covariates’ coefficient estimates and their effect sizes.

**Results**:

Trait space

The first four PCs from the PCoA together captured a total of 28% of the variability in trait composition of birds. PC1 captured 11.44% of the variability in trait space, with water-surface foraging, piscivorous diet, body mass, and beak length loading positively on PC1 and insectivorous diet and mid-canopy foragers loading negatively (Supporting information). PC2 accounted for 7.55% of the variability in trait space, with aerial and below-water foraging and HWI loading positively on PC2 and granivore diet and ground foraging loading negatively. PC3 accounted for 4.34 % of the variability in trait space, with herbivorous diet loading positively and nectarivorous diet loading negatively. Lastly, PC4 accounted for 3.45% of the variability in trait space, with canopy foraging, ectotherm diet, endotherm diet, scavenger diet, frugivorous diet, beak depth, and beak width loading positively and understory foraging loading negatively (Figure 2, Supporting information).

We found a shift in trait space along the vertical profile of the vegetation (Figure 3). Bird assemblages in plots with vegetation up to the canopy height stratum and, to a lesser extent, up to subcanopy height stratum occupied larger trait volumes than assemblages in plots with vegetation up to only midstory or understory height stratum (Figure 3). Trait space also shifted along the PC axes from low to high vertical height strata, reflecting a shift from predominantly understory and ground foraging birds (negative PC2 and PC4) to canopy and midstory foraging birds (positive PC2 and PC4). Additionally, plots with only understory vegetation tended to harbor communities comprised of species with on average larger bodies and aquatic lifestyles (positive PC1), in contrast to plots with vegetation reaching higher height strata, which promoted small-bodied communities with largely insectivorous diets (negative PC1).

Avian diversity-vegetation structure associations

3D habitat structure overall had no or a minor effect on species richness and phylogenetic diversity, with only MPDSES showing a positive association with MidC. In contrast, functional diversity showed strong associations with 3D habitat structure. Specifically, FRichSES increased with TotalA and CanA and decreased with SubC (Figure 4), indicative of strong influences of habitat amount and configuration at higher vegetation strata on the breadth of the functional space of avian communities. FDiv increased with TotalA, MidA, and UndA, and decreased with CanC, indicating that increased habitat amount at lower vegetation strata and more spatially homogeneous canopies lead to more functionally dispersed communities. However, FEven only increased with SubC, suggesting that a discontinuous subcanopy leads to communities where species’ abundances are more regularly distributed within the functional space (Figure 4).

PC trait axes showed strong associations with 3D habitat structure. In terms of 3D habitat composition, PC1 decreased with TotalA, SubA, MidA, and UndA (Figure 4), suggesting that high 3D habitat amount leads to assemblages with on average smaller body mass and beak size and an increased prevalence of traits such as insectivorous diet and mid-height foraging, but decreased prevalence of traits associated with aquatic foraging and piscivorous diets. PC2 increased with TotalA, SubA, and MidA (Figure 4), suggesting that greater 3D habitat amount supports on average larger HWI and increased prevalence of aerial and below water foraging, but leads to decreased prevalence of ground foraging and granivorous diets. PC3 increased with TotalA and MidA (Figure 4), suggesting that more 3D habitat amount leads to increased prevalence of herbivore diets and decreased prevalence of nectarivore diets. TotalA, CanA, SubA, and MidA were all positively related to PC4, with more 3D habitat amount leading to increased prevalence of canopy foraging, frugivore diets, scavenger diets, endotherm diets, ectotherm diets, wider and taller beaks, as well as decreased prevalence of understory foraging. However, PC4 decreased with UndA, indicating that understory amount supported the opposite traits than CanA, SubA, and MidA (Figure 4).

In terms of habitat configuration, TotalC and strata-specific configuration indices showed opposite relationships with PC axes. PC1 increased with TotalC (Figure 4), suggesting that increased 2D habitat heterogeneity leads to assemblages with on average larger body mass and beak dimensions, increases the prevalence of water surface foraging and piscivorous diets, but decreases the prevalence of insectivore diets and mid-height foraging. In contrast, PC1 decreased with CanC and UndC. PC2 decreased with TotalC (Figure 4), indicating that 2D habitat heterogeneity leads to increased prevalence of ground foraging and granivore diets and decreased prevalence of aerial and below-water foraging. PC2 decreased with UndC, MidC, and CanC. PC3 showed no relationships with either 2D or 3D habitat configuration. PC4 decreased with TotalC (Figure 4), indicating that 2D habitat heterogeneity leads to increased prevalence of understory foraging but decreased prevalence of canopy foraging, frugivore, scavenger, endotherm, and ectotherm diets, as well as narrower and shallower beaks. In contrast, PC4 increased with SubC (Figure 4).

**Discussion**:

Our study is one of the first to evaluate the associations of a comprehensive suite of 3D habitat composition and configuration metrics with measures of avian species richness, and their phylogenetic, trait, and functional diversity, and to contrast the effects of 3D habitat configuration with those of 2D habitat configuration. Our findings illustrate that although total 3D habitat amount emerged as the most consistent predictor of avian functional and trait-based diversity, it did not have a strong effect on species richness and phylogenetic diversity, thus offering only partial support to our first hypothesis. Functional and trait-based diversity, however, showed the strongest relationships with 3D habitat structure, supporting our second hypothesis.

Effects of 3D habitat composition on avian diversity

Increases in 3D habitat amount correspond to an expansion of functional space, which is consistent with studies that have demonstrated a strong relationship between canopy height and functional space (MacArthur and MacArthur 1961, Feng et al. 2020, Remeš et al. 2021). This expansion of functional space along the gradient of 3D habitat amount is likely driven by the addition of more species that exhibit extreme trait values that are positioned farther away from the functional space centroid, as suggested by the positive relationship between habitat amount and avian functional divergence. Interestingly, despite the expansion of functional space with increasing habitat amount, functional evenness remains stable, suggesting that abundances are added to functional space in a regular manner as vegetation amount increases.

Increased vegetation amount led to communities that, on average, foraged at higher vertical levels and had broader spectrum of dietary characteristics, which supports the notion that increases in 3D habitat amount lead to increases in available niche space. On the other hand, communities in locations with lower habitat amount were composed of more ground foraging species that consumed a higher proportion of seeds and nectar in their diet. Intuitively, this result aligns well with the notion that grasslands and other types of open habitats support greater proportions of seed and flower-producing flora such as grasses and forbs. In partial contrast, increasing amount of understory habitat was associated with increased understory foraging but reduced canopy foraging. However, this result is in line with previous findings that show that, while understory vegetation provides cover to low foraging birds (Tallei et al. 2021), closed canopies suppress the growth of understory plants (Svenning 2000, Van Pelt and Franklin 2000), indicating that increased canopy amount limits species foraging in understory.

Increases in 3D habitat composition were also associated with communities composed of, on average, smaller and more migratory species. This observation makes sense given that smaller species often require denser vegetative cover to hide from predators (Stirnemann et al. 2015) and are perhaps able to maneuver more easily in dense vegetation than larger birds (Provini and Höfling 2020). Furthermore, higher habitat amount also supported communities with on average larger hand-wing index, which is closely correlated with migration ability (Sheard et al. 2020). Migratory birds tend to be smaller (Soriano-Redondo et al. 2020), have a larger portion of their diet comprised of seasonally available foods such as fruit and insects, and are more likely to forage in the canopy compared to resident bird species (Levey and Stiles 1992, Boyle et al. 2011). Through the creation of more seasonally available foods and suitable habitats, increased 3D habitat amount might thus attract species characterized by increased migration ability and smaller body size.

Effects of 2D and 3D habitat configuration on avian diversity

Increased heterogeneity of the subcanopy level decreases the breadth of the functional space but increases the regularity of species abundances in that space. More heterogenous canopies also tend to support higher prevalence of more extreme trait values within the functional space compared to less heterogenous canopies. This finding suggests that as higher vertical strata become more heterogenous, low-abundant species that fall at the periphery of the functional space disappear from the assemblage, leaving the remaining species evenly distributed within that space. While abiotic edge effects, such as more extreme microclimates (Fischer and Lindenmayer 2007), play a role, the absence of changes in functional space across lower height strata suggests unique pressures at higher vertical strata.

Higher 3D habitat heterogeneity was associated with foraging in higher strata, higher proportions of species with carnivorous diets, and larger HWI. Increased openness of the vegetation profile, especially at higher height strata, thus appears to facilitate predatory species and increased flying ability. Previous research indeed suggests that open spaces at high strata support raptors (Swolgaard et al. 2008), perhaps by providing greater foraging opportunities facilitated by increased maneuverability or improved habitat for prey species. This observation is further supported by research on 2D habitat configuration that shows greater predation rates from raptors and other predators in more heterogenous habitats compared to more homogenous ones (Preston 1990, Batary and Baldi 2004). Moreover, species with larger HWI tend to have a greater gap-crossing ability (Claramunt et al. 2022), perhaps allowing them to easily maneuver and persist in patchy habitats (but see Jones et al. 2023). Indeed, larger HWI has been found to be more prevalent in areas with increased disturbance (Claramunt et al. 2022, Naka et al. 2022, Weeks et al. 2023). However, an alternative explanation for the increase in HWI could be an increase in the presence of migratory insectivorous species, which are known to increase along forest edges (Terraube et al. 2016).

Interestingly, 2D habitat configuration had largely the opposite effect on individual trait characteristics compared to 3D habitat configuration. Increases in 2D habitat heterogeneity led to assemblages comprised of proportionally more ground and understory foraging species, higher prevalence of granivore diets, aquatic-associated traits, and on average larger body mass. Granivores and ground foraging species are shown to be less sensitive to 2D habitat heterogeneity, with changes in resource availability between disturbed and non-disturbed habitats being a key driver of the observed differences in trait responses (Kennedy et al. 2010). Therefore, species foraging at higher strata and in dietary guilds other than granivorous might be more sensitive to disturbance and less represented in areas of high 2D habitat heterogeneity.

The differing effects of 2D and 3D habitat configuration on bird assemblages might stem from the fact that 3D configuration captures gaps in vegetation at a particular height stratum that may still have vegetation above or below, whereas 2D configuration only captures gaps when there is no vegetation left at any of the vertical strata. Metrics of 2D configuration are thus much more likely to capture hard edges, an abrupt boundary between habitat types (Malt and Lank 2007), which often includes open habitats, such as grasslands, that favor lower foraging and granivore diets (Wiens and Rotenberry 1979). We suggest that measures of 2D configuration lack the capacity to capture internal structural heterogeneity in a manner comparable to measures of 3D habitat configuration. While 3D configuration more accurately measures the effects of habitat arrangement and the effects of open space at different height strata, 2D configuration inherently captures aspects of habitat mosaicism.

In contrast to previous studies (MacArthur and MacArthur 1961, Huang et al. 2014, Carrasco et al. 2019, Moudrý et al. 2021, 2023), we did not find any associations between avian diversity and habitat configuration along the entire vertical profile. Our chosen metric, variance of the number of voxels across the vegetation profile, was largely independent of 3D habitat composition and demonstrated no discernible relationships with avian diversity. Our finding suggests that vertical configuration might not be important for birds when measured independent of habitat amount, perhaps because most bird movement is not entirely vertical, instead occurring both horizontally and vertically.

Conclusions: Among various facets of avian diversity, functional and trait diversity are most reliably influenced by 3D habitat structure, implying that the relationship between avian diversity and vegetation structure is mediated through species traits. Total 3D habitat amount emerged as the most reliable predictor of functional and trait-based diversity, suggesting that 3D habitat composition plays an outsized role in shaping avian community diversity, likely through an increase in niche space. Importantly, both habitat composition and habitat configuration had negative, positive, and neutral effects on avian diversity across different height strata and between 2D and 3D measures of habitat configuration. These mixed findings reveal that: 1) different processes can operate along different height strata, and 2) the findings of studies on habitat structure are sensitive to how structural indices are defined. By carefully considering relationships between multi-faceted avian diversity and both compositional and configurational 3D habitat structure, our work provides a framework for addressing the inconsistencies that have historically troubled studies on the interplay between biodiversity and vegetation structure.

**Author Contributions**:

**Colin P. Sweeney**: Conceptualization (equal); Data curation (lead); Software (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **William Peterman**: Conceptualization (supporting); Software (supporting); Methodology (supporting); Writing – review and editing (supporting). **Kaiguang Zhao**: Conceptualization (supporting); Software (supporting); Methodology (supporting); Writing – review and editing (supporting). **Karen Goodell**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Benjamin Zuckerberg**: Writing – review and editing (supporting). **Marta A. Jarzyna**: Conceptualization (equal); Data curation (supporting); Software (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

**Acknowledgements**:

We thank Michael Broe, Corey Ash, Juan Pablo Quimbayo, Brooks Kohli, and Collin VanBuren for various computational, logistical, and general assistance throughout this project. This work was supported by the US National Science Foundation awards DEB-2307188 to MAJ and KZ and DEB-2307189 to BZ.

**Data Availability Statement**:

All derived data used to create this publication have been made publicly available on <https://doi.org/10.5061/dryad.t76hdr87q> with links to all other public data repositories already in use. Annotated code used in these analyses is also available on GitHub at the following link <https://github.com/ColinPSweeney/3D-habitat-structure-drives-avian-functional-and-trait-diversity-across-North-America.git>

**Conflict of Interest Statement**:

The authors declare no conflicts of interest.

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**TABLES AND FIGURES**

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| --- | --- | --- |
| **Table 1.** Model specification for the 12 Bayesian mixed effect models relating avian diversity to habitat structure and environment covariates. All 12 models were used to model the 10 biodiversity indices. Models contained different combinations of compositional habitat structure (TotalA, CanA, SubA, MidA, UndA), configurational habitat structure (TotalC, CanC, SubC, MidC, UndC, VertV), and environmental variables (TempRange, Elevation, Latitude). Color designates parameters in broad categories of environmental (pink), habitat composition (blue), and habitat configuration (orange). | | |
| **Model Name** | **Model Description** | **Independent Variables** |
| 1). Full | Contains all structural and environmental variables | TempRange+ Elevation + Latitude + TotalA + CanA + SubA + MidA + UndA + TotalC + CanC + SubC + MidC + UndC + VertV |
| 2). Full\_minusTotVol | Contains all structural and environmental variables except TotalA | TempRange+ Elevation + Latitude + CanA + SubA + MidA + UndA + TotalC + CanC + SubC + MidC + UndC + VertV |
| 3). Structure | Contains all structural variables but not environmental variables | CanA + SubA + MidA + UndA + TotalC + CanC + SubC + MidC + UndC + VertV |
| 4). Configuration | Contains only configurational variables | TotalC + CanC + SubC + MidC + UndC + Variance |
| 5). Configuration\_env | Contains configurational variables and environmental variables | TempRange+ Elevation + Latitude + TotalC + CanC + SubC + MidC + UndC + VertV |
| 6). Composition | Contains only compositional variables | CanA + SubA + MidA + UndA |
| 7). Composition\_env | Contains compositional variables and environmental variables | TempRange+ Elevation + Latitude + CanA + SubA + MidA + UndA |
| 8). Horizontal | Contains all structural variables except for vertical variance | CanA + SubA + MidA + UndA + CanC + SubC + MidC + UndC |
| 9). Horizontal\_env | Contains all structural variables except for vertical variance and environmental variables | TempRange+ Elevation + Latitude + CanA + SubA + MidA + UndA + CanC + SubC + MidC + UndC |
| 10). Amount | Contains only TotalA and environmental variables | TempRange+ Elevation + Latitude + TotalA |
| 11). Vertical | Contains TotalA and vertical variance and environmental variables | TempRange+ Elevation + Latitude + TotalA + VertV |
| 12). Climate | Environmental variables only | TempRange+ Elevation + Latitude |

**A diagram of a multicolored cylinder

Description automatically generated with medium confidence**

**Figure 1.** Conceptual Diagram of 3D habitat structure calculations. For each of the 385 NEON plots we studied (a), LiDAR data were split into 1m bins (b, left) and discretized into four height strata (understory, Und, 0-5m; midstory, Mid, 5-15m; subcanopy, Sub, 15-25m; canopy, Can, >25m; b, right). Vertical habitat configuration was quantified as the variance of number of voxels found in each 1m height bin (VertV; c). 3D habitat composition was quantified as the number of voxels at each height bin (UndA, MidA, SubA, CanA) and the sum of all voxels (TotalA; d). 3D habitat configuration at each height stratum (UndC, MidC, SubC, CanC) was quantified by converting the voxels in each height stratum into rasters before quantifying the number of habitat patches in the raster and 2D habitat configuration (TotalC) was quantified by converting all voxels in the plot into a raster and then quantifying the number of habitat patches (e).

A screenshot of a graph

Description automatically generated

**Figure 2.** Vectors from Principal Coordinate Analysis (PCoA) for the first four Principal Coordinates (PCs) for foraging (a), dietary (b), and morphological (c) traits. The numbers associated with each trait loading specify the PC axis upon which the respective trait exhibits the strongest loading. Vectors are shaded in grey for traits that do not display the strongest loading on the given PC axis. Unknown vertebrate was left off of dietary trait plots because no species in our analysis had this trait axis.

A collage of graphs showing different colored dots

Description automatically generated

**Figure 3.** Principal Coordinate (PC) trait space for all avian plots (grey) and avian plots subsetted based on the maximum height strata occupied by vegetation (color): Canopy (a), Subcanopy (b), Midstory (c), and Understory (d). Color indicates plots with vegetation that reaches but does not exceed the four height strata. Points indicate NEON plots; values for PC1 – PC4 for each NEON plot represent average PC scores for all species occurring at that plot, weighted by their abundance estimates. All density plots are generated with contour lines up to the 100% percentile.

A screenshot of a graph

Description automatically generated

**Figure 4.** Parameter estimates from each model (excluding full model) for all ten biodiversity response variables (SpRich=species richness, PD=Faith’s Phylogenetic Diversity, MPD=mean pairwise distance, FRich=Functional Richness, FEven=Functional Evenness, FDiv=Functional Divergence, PC1= Principal Coordinate 1, PC2=Principal Coordinate 2, PC3=Principal Coordinate 3, PC4=Principal Coordinate 4). Boxes and tails around parameter estimates designate 80% and 95% credible intervals (CIs), respectively. Positive and negative parameter estimates whose 95% CIs do not overlap zero are shown in green and red, respectively. Parameter estimates whose 95% CIs overlap zero are shown in grey. Colored outlines designate parameters in broad categories of environmental (pink), habitat composition (blue), and habitat configuration (orange).