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Avian Functional Diversity Response to Changes in Forest Structure and Degradation in Northern New England

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DEDICATION

To my incredible wife Jackie Thompson who has been supporting me in every way since the start of this journey, and to my beautiful, bright, silly, and all-around wonderful son Ephraim who was born at the start of this, and I am so excited to see grow and learn.

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ABSTRACT

Exploitative forest harvesting has led to widespread economic degradation of forests across the northeastern United States. Tree species composition and structure vary across degradation categories, which may lead to differences in wildlife communities and the ecosystem functions wildlife provide. Avian communities in particular respond quickly to changes in habitat, are easy to survey, and contribute to a variety of important ecosystem functions. Here, we investigated the relationship between economic degradation and avian functional diversity focusing on the ecosystem functions of seed dispersal, nutrient cycling, and pest control. We found that avian functional diversity responded to degradation in a unimodal manner with stands of moderate economic value supporting the highest functional diversity. Further, the response of functional diversity to degradation varied depending on the specific metric used (i.e., functional dispersion, functional divergence, and functional evenness) and ecosystem function assessed (i.e., seed dispersal, nutrient cycling, and pest control). Differences in functional diversity among degradation categories were primarily driven by softwood composition and canopy structure and how those factors interact with several avian behavioral traits. Our work illustrates the importance of integrating both economic and ecological values when making management decisions and provides insight into ways land managers may support vital ecosystem functions.

INTRODUCTION

Forests provide a diverse array of ecosystem services including clean water (e.g., T. C. Brown & Binkley, 1994; Edwards & Stuart, 2002; Stuart & Edwards, 2006), carbon sequestration and storage (e.g., Birdsey et al., 2006; Gunn & Buchholz, 2018; Nunery & Keeton, 2010), and timber (e.g., Ashton & Kelty, 2018; Clary, 1986; Nyland, 2016). Timber and other wood products are also an integral part of the economy, supporting infrastructure and livelihoods across northern New England (e.g., Public Sector Consultants & Fast, 2020) and worldwide (e.g., Babulo et al., 2009; Crabtree & Consulting, 2015; Jolley et al., 2020). Land managers often work to balance the sometimes competing interests of economic and ecological value (e.g., DeGraaf et al., 2006; Gustafsson et al., 2012; Sinacore & Howard, 2015). This is particularly true in New England where much of the forests are privately owned (Bulter et al., 2021), and competing objectives of private landowners need to be balanced (e.g., Butler et al., 2007; Butler & Leatherberry, 2004; Rickenbach & Kittredge, 2009). Adding to this challenge, exploitative harvesting practices, such as commercial clear-cutting and high-grading, have resulted in forests with reduced economic value in New England (Belair & Ducey, 2018; Gunn et al., 2019). The current condition of New England forests provides an opportunity for management to improve timber yields with consideration for ecosystem functions that will feedback to help sustain timber production and other ecosystem services.

In the 1980's, much of New England forests experienced an increase of exploitative harvesting methods that prioritized short-term economic gain resulting in a reduction of high quality large diameter timber (Nyland, 1992). In response to this short-term mindset, foresters were urged to push back more strongly against these exploitative cuts and strive for more sustainable management that would allow quality timber to grow and protect wildlife habitats (Nyland, 1992; Salwasser, 1990; Seymour & Hunter, 1992). However, recent work has shown that exploitative forestry practices are still used and influence the current economic value of northeastern forests (Belair & Ducey, 2018). Building on the work done by Belair and Ducey (2018), Gunn et al. (2019) developed criteria for determining whether a forest stand may be considered economically degraded. This framework uses the relative density (Ducey & Knapp, 2010) of trees to define multiple categories of productivity potential and scores stands as economically degraded if, (following an improvement thinning) they would require more than 10 years to return to a closed canopy. Using this framework, Gunn et al. (2019) showed nearly 40% of New England forests are economically degraded.

Wildlife are an integral part of forest ecosystems, providing an array of ecological functions and feedbacks that enhance forest health, resiliency, and support ecosystem services (e.g., Daily, 1999; Lacher et al., 2019; Wenny et al., 2011). Birds are a useful taxon to examine ecological response to changes in the environment because they are diverse, easy to survey, and provide important ecosystem functions such as seed dispersal, pest control, and nutrient cycling (Whelan et al., 2008). These functions have been shown to support ecosystem services by increasing the volume and quality of timber (e.g., Bello et al., 2015; Jonard et al., 2015; Norby et al., 2010), as well as preventing significant growth loss caused by herbivorous insects (MacLean, 1990; Marini et al., 2022). For example, northeast neotropical migrants such as Bay-breasted Warbler (*Setophaga castanea*), and Cape May Warbler (*Setophaga tigrina*) can dampen the severity of spruce budworm (*Choristoneura fumiferana*) outbreaks by helping maintain low population levels (Venier & Holmes, 2010). Birds also play a unique role as seed dispersers due to their ability to move seeds long distances (Vittoz & Engler, 2007) and facilitate seed germination when gut passage breaks seed dormancy (Traveset & Verdú, 2002). In addition, seasonal changes in bird density, due to the influx of neotropical migrants, have been shown to increase nutrient biomass in northern hardwood forests during the breeding season (Sturges et al., 1974).

Biodiversity plays a key role in shaping ecosystem function (Magurran & McGill, 2011). Traditionally, biodiversity is measured using taxonomic diversity based on the presence and abundance of species (Magurran & McGill, 2011). While taxonomic diversity is important, it does not incorporate ecological differences between species and thus cannot inform on ecosystem functions and services. In contrast, functional diversity measures the type and commonality of species traits in a community and thus links patterns of biodiversity to ecological processes (Cadotte et al., 2011; Mouillot et al., 2013; Petchey & Gaston, 2007). Functional traits can be morphological (e.g., bill length or mass), behavioral (e.g., diet or nest location), or physiological (e.g., metabolic rate) and reflect the niche requirements of a species (Grinnell, 1917; Petchey & Gaston, 2007; Sutherland et al., 2000). Functional diversity can inform on the differences between species assemblages and the ecosystem functions they provide, including in response to disturbance (Barzan et al., 2023; Mouillot et al., 2013; Villéger et al., 2010).

It is crucial to understand the relationship between the economic value of timber, the ecological functions a forest may provide, as well as the influence of past management on both. Here, we specifically, sought to: (1) Asses the relationship between the overall functional diversity of bird communities and economically degraded forests, (2) compare functional diversity response to degradation among three specific ecosystem functions of seed dispersal, pest control, and nutrient cycling and (3) examine how forest composition and structural components may influence these ecosystem functions. This work aims to understand how specific ecosystem functions may differ in the response to forest composition, structure, and value, which can provide useful insights to land managers working to balance economic and ecological values in a forest.

METHODS

Study system

Our study occurred in temperate forest at two sites in northern New England: Nulhegan Basin Division of the United States Fish and Wildlife Service Silvio Conte National Wildlife Refuge (hereafter Nulhegan), and Bartlett Experimental Forest in the White Mountain National Forest (hereafter Bartlett). The climate is humid continental and characterized by warm summers (mean July temperature, Nulhegan = 18 °C, Barlett = 19 °C,) and cold winters (mean January temperature, Nulhegan = -10 °C, Bartlett = -9 °C) with 115 cm of precipitation at Nulhegan and 127 cm of precipitation at Bartlett distributed throughout the year (National Weather Service, 2023; Richardson et al., 2007). Both sites host a wide range of temperate and boreal passerines and have a long history of timber harvest (commercial, experimental, or ecological) which provides a suitable context for comparing economic forest degradation and avian functional diversity.

Nulhegan consists of 10,767 hectares, in northeastern Vermont (44° 50' N, 71° 44' W) (Fig. 1) (USFWS, 2018). Nulhegan has changed ownership several times with its earliest purchase in the mid 1800s by the Connecticut Valley Logging Company followed by the New Hampshire Stave and Heading Company in the early 1900s (USFWS, 2018). In 1984, the property was sold to Champion International along with 178,062 surrounding hectares for logging that was predominantly used for paper and pulp production (VT Fish and Wildlife, 2014). In 1998, Nulhegan was purchased by the US Fish and Wildlife Service (USFWS) who still owns it to this day. The extensive history of logging over the last century has left much of the forested landscape with depleted growing stock, visible ruts from logging equipment, and low market value tree species. In 2018, the USFWS created a Habitat Management Plan to facilitate the rehabilitation of Nulhegan for both wildlife and forestry (USFWS, 2018). In its current state, Nulhegan is predominantly a mix of spruce-fir (*Picea* spp.-*Abies* spp.) (31%), red spruce (*Picea rubens*)-hardwood (27%), and northern hardwood (25%) with over 1,600 hectares of multi-cohort forest (USFWS, 2018). At Nulhegan, we selected 12 stands based on landcover data and preliminary site visits to target conditions across a range of degradation categories. These stands varied in elevation from 365 m to 609 m.

Bartlett encompasses 2,343 hectares in north central New Hampshire (44° 03' N, 71°17' W) (Fig. 2) (King et al., 2011). The experimental forest was established by the USDA Forest Service in 1932 (Leak & Yamasaki, 2010). Prior to its establishment, the region was subject to substantial harvesting between 1870 and 1910 (Leak & Yamasaki, 2010). Current forest cover consists of a mosaic of secondary successional deciduous and coniferous forest types. Dominant species are, American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and eastern hemlock (*Tsuga canadensis*) with less dominant species including yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*) and red spruce (*Picea rubens*) (Ducey et al., 2023). At Bartlett, we selected 17 stands using cruise plot data (Ducey et al., 2023) to target conditions across a range of degradation categories. These stands varied in elevation from 263 m to 537 m.

Field surveys

Avian point counts

We conducted avian point count surveys during the breeding season in 2021 and 2022 to assess community composition and abundance. Stands ranged in size from 4 ha to 6 ha and contained either four or six points depending on the stand size. Within a stand, two transects were established 200 m apart with point count locations spaced 100 m apart along each transect. In larger stands, transects were 200 m in length with three points per transect and in smaller stands, transects were 100 m in length with two points per transect (Fig. 3). This orientation was used to align with pre-established permanent vegetation plots at Bartlett (Ducey et al., 2023). We surveyed each point three times in the first season and four times in the second season between June 1st and July 30th. All surveys were conducted by a trained technician between 5 am and 10 am. After arriving at the point, the technician waited two minutes to allow birds to settle. Counts lasted for 10 minutes wherein all individual birds seen or heard were identified to species and tallied inside a 50 m radius to avoid double counting distant individuals. Point counts were not conducted during days of heavy rain or wind which would hinder detection (Ralph et al., 1995).

Forest inventory

We measured the forest composition and structure of each stand using variable radius plot sampling (Kershaw et al., 2017). Sampling was conducted at 15 or 21 plots per stand (depending on size) with seven plots spaced every 50 m along three 300 m transects in large stands and five plots spaced every 50 m along three 200 m transects in small stands (Fig. 3). All transects were spaced 100 m apart. Transects ran the length of the stands and crossed through avian point count locations. For each plot, a 4.59 (m^2/ha) basal area factor prism was used to count trees wherein all tallied trees were identified to species, the diameter at breast height (DBH) was measured, and each tree was classified as either acceptable growing stock (AGS) or unacceptable growing stock (UGS). We defined AGS as trees with the potential to produce a 2.4 m (8 ft) sawlog with at least one face reasonably free from defect (USDA Forest Service, 2015). UGS were therefore trees that lacked a potential saw log which could be due to either structural irregularities (e.g., increased branching or forking), presence of cavities, or fungal growth (Nyland, 2016). American beech trees were given a beech bark disease severity score (BBD) between 0 (no disease detected) and 3 (severely infected) (Latty et al., 2003); trees with a BBD ≥ 2 were classified as UGS. The decay class of all standing dead trees were classified from 1 (freshly dead) to 5 (most of the tree has fallen) (Province of British Columbia, 2009). In addition, all trees were classified along the growth form scale (F Scale, 1-8) and health risk scale (R Scale,1-4) developed by Pelletier et al. (2016). Tree height and canopy height were measured using a hypsometer on a randomly sampled quadrant in each plot. To assess canopy cover, a hemispherical photo was taken at each plot (Nikon D700) from which percent canopy coverage and foliage coverage were calculated using the R package *coveR* (Chianucci et al., 2022). Downed woody material (DWM) was measured using line intersect sampling along a 40 m transect that was centered on our plot and oriented along a randomly generated bearing to account for potential non-random orientation of fallen logs (Kershaw et al., 2017). Logs that intersected our transect were counted, the diameter at the point of intersection was measured, the decay class (1 to 5) was determined, and they were classified as hardwood, softwood, or unknown (Pyle & Brown, 1998). Lastly, the percent cover of woody understory was surveyed at each plot at two height classes, below 1.3 m and from 1.3 m to 3 m.

Statistical analysis

Calculating degradation

All analyses were conducted using the R statistical computing language (R Core Team, 2022). The degradation category for each stand was calculated using the Ducey & Knapp (2010) relative density index (RD), growing stock group (AGS/UGS), and commercial desirability (primary, secondary, and tertiary) (Belair & Ducey, 2018; Gunn et al., 2019). RD was determined using the following equation:

$$RD_i = TF_i * (a + b * SG_i) * \left(\frac{DBH_i}{25}\right)^2 \qquad (1)$$

Where *TF* is the expansion factor for the i^{th} tree, *SG* is the specific gravity of the i^{th} tree species, *DBH* is the diameter at breast height for the i^{th} and both *a* and *b* are constants. The RDs were then grouped by commercial desirability: primary (preferred commercial species), secondary (consistent commercial markets but lower sawlog prices), and tertiary (low or no market value species) as well as growing stock (AGS/UGS). The sum of RD_i within each desirability and growing stock group was then determined across the entire stand:

$$RD_{jk} = \sum_{i \in jk} RD_i \qquad (2)$$

Where *j* is a given stand, *k* is the desirability and growing stock group. Once RD for each desirability group was determined in each stand, we evaluated the degradation category of the entire stand:

$$f(g) = \begin{cases} 1: & P \geq 0.4; \\ 2: & P + S \geq 0.4 \quad P < 0.4; \\ 3: & P + S + T \geq 0.4 \quad P + S < 0.4; \\ 4: & P + S + T + U \geq 0.4 \quad P + S + T < 0.4; \\ 5: & P + S + T + U < 0.4; \end{cases} \qquad (3)$$

Where P is the RD of the most desirable (primary) species that were AGS, S is the RD of the second most desirable (secondary) species that were AGS, T is the RD of the third most desirable (tertiary) species that were AGS, and U is the RD any species that was UGS. A stand in which primary species have an RD ≥ 0.4 has a degradation category of 1 while stands that require all trees (P, S, T, and U) to reach an RD ≥ 0.4 have a degradation category of 4 (see Eq. 3). Categories 1 and 2 were considered non-degraded and would have the potential for quality timber currently or in the future, while stands with a degradation category greater than 2 were considered degraded and may require management to improve timber quality and composition of valuable species (Gunn et al., 2019). During preliminary field studies, three stands were identified as Category 5. However, according to Gunn et al (2019), Category 5 forests lack enough open habitat to be suitable for early successional songbirds. The Category 5 stands we identified in the field were actively managed specifically as early successional shrubland habitat. Thus, these stands were not representative of the degraded forests defined in Gunn et al (2019) and were subsequently excluded from analysis.

Forest composition and structure

Using the vegetation data collected in the field, we calculated 13 structural or compositional variables that might both be influenced by degradation and impact avian composition. Variables included: total RD (using Eq. 1), RD of standing dead trees (using Eq. 1), fraction of softwood RD (using Eq. 1, hereafter softwood fraction), average R scale (Pelletier, Landry, & Giouard, 2016), quadratic mean diameter (QMD), basal area weighted diameter (Dg) (Ducey & Kershaw, 2023), coefficient of variation (CV) of canopy height, coefficient of variation (CV) of total height, structural complexity index (SCI) (Looney et al., 2021), average crown cover, average foliage cover (Chianucci et al., 2022), total understory cover, and Shannon's diversity index of DWM. For understory cover, we used the combined total of low understory cover and high understory cover which resulted in a range from 0 to 2. DWM quality and type have been shown to impact bird populations more so than volume (Kalies & Rosenstock, 2013; Utschick, 1991). Thus, we calculated Shannon's diversity of DWM across wood types (hardwood, softwood, unknown) and decay classes (1-5), treating each group as a "species" and the volume as "abundance".

The total number of forest structure and composition variables was reduced from 13 to 7 after assessing collinearity using variance inflation factors (VIF) in the *car* package in R (Fox & Weisberg, 2019). We used a VIF of 5 (which corresponds to an R^2 of 0.8) as our cutoff. The final variable set included: RD of standing dead trees, percent understory cover, Shannon's diversity of DWM, average R scale, basal area weighted mean DBH (Dg), softwood fraction, and the coefficient of variation (CV) of canopy height. We used an ANOVA and post-hoc Tukey test to assess changes in composition and structure between each degradation category.

Bird Abundance

Abundance of each bird species was calculated by first determining the maximum number of individuals at a given point across all surveys within a given year:

$$\alpha_i = \max(s_1 \ldots s_n) \tag{4}$$

Where s_n is the survey and α is the maximum count at a point for species *i*. Then the mean α_i of all points in a given stand across both years was calculated:

$$m_{ij} = \frac{\sum \alpha_i}{N_{ij}} \tag{5}$$

where *m* is the mean value of α_i for all points across both years in stand *j* and *N* is the total number of points across both years in stand *j* (e.g., in a 4-point stand N = 4 * 2 = 8). Finally, abundance was converted from birds per 50 m circle area to birds per hectare (Ralph et al., 1995).

Functional diversity

We built a matrix (All-Traits) of 27 traits for the 73 bird species found at our two sites. Traits were collated from the online databases Birds of the World (Birds of the World, 2022) and Animal Diversity Web (*Animal Diversity Web*, 2023) as well as the trait databases of AVONET (Tobias et al., 2022) and Elton Traits (Wilman et al., 2014) (Table 1). From the All-Traits matrix, we subset three additional matrices using traits associated with three specific ecosystem functions: Seed Dispersal, Nutrient Cycling, and insect Pest Control (Table 2). Only one trait, sociality, was shared between all three ecosystem functions and caching behavior was shared between Seed Dispersal and Nutrient Cycling.

For each of the four trait matrices, we calculated Gower's dissimilarity matrices (Gower, 1971) using the *gawdis* package in R (de Bello et al., 2021). The *gawdis* package allowed us to appropriately weight each trait such that categorical or binary traits were not over contributing to the dissimilarity between species. Once dissimilarity matrices were calculated, a principal coordinate analysis (PCoA) was run for each stand to reduce dimensionality and plot species in 'trait space' before calculating the desired functional diversity metric using the *mFD* package in R (Magneville et al., 2021).

We calculated three functional diversity metrics, each of which was weighted by abundance. Functional dispersion (FDis) is the average distance in trait space from all points (species) to the center of the group and represents the breadth of available niches within a community (Fig. 4a) (Lalibert & Legendre, 2010; Mouillot et al., 2013). To measure how functionally distinct a stand was, we used functional divergence (FDiv) which is the proportion of species in trait space, that fall outside the average distance to the center of the group (Fig. 4c) (Villéger et al., 2008). Assemblages with high FDiv have a higher proportion of functionally distinct species and reflect high niche differentiation and low functional redundancy. Functional evenness (FEve) measures the degree to which species are regularly distributed in trait space (Fig. 4e). We interpret high FEve as a measure of resiliency (Goswami et al., 2017). All degradation categories were not present at both sites, so to compare functional diversity and degradation both sites were aggregated prior to analysis. We used ANOVA and post-hoc Tukey tests to compare each of the three functional diversity metrics (FDiv, FDis, FEve) among forest stands using degradation category as the predictor variable. All metrics (FDis, FDiv, FEve) were calculated separately for each trait matrix (All-Traits, Seed Dispersal, Nutrient Cycling, and Pest Control) resulting in 12 total analyses.

Taxonomic diversity and functional diversity

It is important to compare taxonomic and functional diversity because it is often assumed to have a positive correlation, however, the relationship between the two metrics can vary depending on the study system (Morelli et al., 2018). To assess the relationship between taxonomic diversity and functional diversity in our study system, we calculated Shannon's diversity index using the *vegan* package in R (Oksanen et al., 2022) and compared it against FDis using linear regression. We use FDis because it measures the overall spread of species in trait space rather than how those species are distributed like FEve or FDiv (Lalibert & Legendre, 2010).

Forest structure and avian functional diversity

To test how forest composition and structure may influence functional diversity for each ecosystem function we used multiple linear regression. Separate models were built for each ecosystem function (Seed Dispersal, Nutrient Cycling, Pest Control), and each functional diversity metric (FDis, FDiv, FEve) as the response variable resulting in nine different linear models. For each model, we included the seven forest structure and composition variables as predictors. In addition, for each ecosystem function, we applied a fourth-corner analysis using the package *mvabund* in R (Wang et al., 2012) to better understand what structural or compositional variables may be influencing specific traits. Fourth-corner analysis integrates three matrices, species x traits (Q), species x sites (L), and structural variables x sites (R), to estimate coefficients of the fourth corner covariates which reflect trait-structure relationships (A. M. Brown et al., 2014). Larger coefficient values reflect a greater influence on positive or negative interactions. Fourth-corner analysis uses a Poisson distribution to predict the abundance for a given site and species. Poisson distributions require whole integers, however, because our values were averaged across points within a stand and thus contained decimals, they could not be used directly in our fourth-corner analysis. To account for this, we first simulated 1000 Poisson distributions for each stand using our estimated abundances as the means for each species. We then ran the fourth-corner analysis with a LASSO penalty to help correct for misleading trait-structure correlations due to species interactions (Hastie et al., 2009) and averaged the results over the 1,000 simulations.

RESULTS

Species composition and structure

Vegetation composition and structure

Of the 29 stands surveyed, five stands were Degradation Category 1 and Category 3, six stands were Category 4, and 13 stands were Category 2 (all of which were at Bartlett). Tree species composition and richness varied across the four degradation categories (Fig 5). Category 1 stands were all hardwood forests (median softwood fraction = 0.07) dominated by sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) with a relatively low proportion of UGS (Fig. 5a). Category 2 stands were often mixed forests (median softwood fraction = 0.42) dominated by eastern hemlock (*Tsuga canadensis*) and red maple (*Acer rubrum*) (Fig. 5b). Category 3 stands were nearly all softwood forests (median softwood fraction = 0.85) where the most abundant species were balsam fir (*Abies balsamea*), eastern hemlock, and tamarack (*Larix laricina*) (Fig. 5c). Category 4 stands were primarily hardwood (median softwood fraction = 0.1) dominated by American beech (*Fagus grandifolia*) and had the highest proportion of UGS (Fig. 5d).

Five of the seven forest structure variables differed significantly across the degradation categories (Table 3; Fig 6). The low average R scale, Dg, and standing dead RD in the Category 3 stands are likely a reflection of the high proportion softwood balsam fir (*Abies balsamea*) within this category. These stands were primarily single-cohort spruce-fir (mostly balsam fir) forests which tended to have a small average diameter and possess traits (e.g., minimal forking and few defects) that would preclude them from being high risk (R scale). In addition, these stands were comparatively denser than the hardwood stands in Categories 1,2 and 4 with few trees that were disproportionally taller than their surroundings. These characteristics have been shown to lower the probability of wind damaging trees (e.g., Foster, 1988; Peltola, 2006), which may lead to fewer standing dead trees.

Avian composition

We detected a total of 73 avian species, 60% were shared between the two study sites, Bartlett (spp. = 53) and Nulhegan (spp. = 64). The most abundant species at Bartlett were Red-eyed Vireo (*Vireo olivaceus*) (1.48 birds/ha), Black-throated Green Warbler (*Setophaga virens*) (1.03 birds/ha), and Ovenbird *(Seiurus aurocapilla*) (0.99 birds/ha), which accounted for 32.9% of the 2,705 detections inside 50 m. At Nulhegan, our most abundant species were Red-eyed Vireo (1.39 birds/ha), Ovenbird (1.04 birds/ha), and Black-throated Blue Warbler (*Setophaga caerulescens*) (0.88 birds/ha), which accounted for 27.7% of the 2,990 detections inside 50 m. Across degradation categories, species richness varied from 38 to 54; Category 3 stands had the highest avian species richness and Category 1 stands the lowest (Fig 7).

Functional diversity across degradation

Taxonomic and functional diversity comparisons

Taxonomic diversity (Shannon's diversity index) and functional diversity (FDis) were positively correlated (R^2= 0.56, $p < 0.001$, Fig. 8).

Functional diversity and degradation

Overall, we found differences in how functional diversity varied between degradation categories depending on the metric used and the ecosystem function that was examined (Fig. 9). Of the 12 comparisons (three functional diversity metrics across the four trait matrices), significant differences between degradation categories were detected in six (Fig. 9). Most significant comparisons yielded a similar unimodal trend where Categories 1 and 4 had the lowest functional diversity and Category 3 the highest. Pest Control FDis was the only significant comparison that did not show a unimodal trend and instead, increased to Category 2 and plateaued (Fig. 9).

For the All-Traits dataset, we found only one functional diversity metric, FDis, was significantly different among degradation categories ($F = 4.3_{(3,25)}$, $p = 0.014$). The post-hoc Tukey test revealed significant differences between categories 1-2, and categories 1-3 (Table 4b). For Seed Dispersal, all three functional diversity metrics differed significantly across degradation categories: FDis ($F = 8.75_{(3,25)}$, $p < 0.001$), FDiv ($F = 21.65_{(3,25)}$, $p <0.001$), and FEve ($F = 3.68_{(3,25)}$, $p = 0.025$). FDis and FDiv were significantly different between categories 3-1 categories 2-1, and categories 4-3, with FDiv additionally showing significance between categories 3-2 (Table 4b). Pairwise differences in FEve were only significant between categories 1 and 3 (Table 4b). In contrast to Seed Dispersal, only FDis was significantly different across degradation categories for Nutrient Cycling ($F = 4.09_{(3,25)}$, $p = 0.017$) and Pest Control ($F = 3.45_{(3,25)}$, $p = 0.032$). For Nutrient Cycling, FDis was significantly different between categories 1-3, while Pest control FDis was significantly different between categories 1-2 (Table 4b).

Forest structure and degradation

Forest composition and structure was a significant predictor in three of our linear regression models (FDis and FDiv in Seed Dispersal and FDis in Nutrient Cycling; Table 5). In these three models, only two predictor variables were significant, softwood fraction and CV of canopy height, both of which had a positive linear relationship with functional diversity (Table 5; Seed Dispersal FDis and FDiv, Nutrient Cycling FDis). While mean R scale and percent understory cover also had a significant positive correlation in two different models, the overall F-statistic was not significant for either of these models (Table 5, Nutrient Cycling FDiv, Pest Control FDiv).

The fourth-corner analysis revealed several structural variables that were significantly correlated with multiple avian traits ($p < 0.05$, Fig. 10). Here we limit our discussion to softwood fraction and CV of canopy height because they were the only significant structures in models where the overall linear model was also significant. Although the effect sizes of these variables are small, this is common with a LASSO penalty (A. M. Brown et al., 2014; Friedman et al., 2010) and is exacerbated by variation introduced in our abundance simulations, and shouldn't be interpreted as weak effects. Across all three ecosystem functions, softwood fraction was positively correlated with sociality. In Seed Dispersal and Nutrient Cycling, softwood fraction was also negatively correlated with birds that exhibit caching behavior. In Pest Control, softwood fraction was negatively correlated with birds that are resident, birds that exhibit bark and aerial foraging behavior, and moderate caterpillar predation (med lepid pred). CV of canopy height was positively correlated with neotropical migrants in Pest Control and Nutrient Cycling as well as high invertebrate diet and fruit diet in Pest Control and Seed Dispersal, respectively.

DISCUSSION

Our research examined the relationship between the economic value and ecological value of forest stands. Specifically, we explored how past timber management may influence avian functional diversity. Our results suggest the relationship between avian functional diversity and economic degradation is unimodal with the highest functional diversity in stands in Category 2 and 3. The response of functional diversity to degradation was dependent on which ecosystem function was measured, Seed Dispersal, Nutrient Cycling, or Pest Control, and which functional diversity metric was used. Our findings illustrate the importance of using separate trait matrices that reflect discrete ecosystem functions because forest composition and structure may mediate these responses in different ways. Past work has shown varying relationships between taxonomic and functional diversity dependent on the study system and land use (e.g., Jacoboski & Hartz, 2020; Morelli et al., 2018; Tinoco et al., 2018). Here, we found a positive correlation between taxonomic and overall functional diversity, which suggests that efforts that increase taxonomic diversity in these ecosystems may also increase overall functional diversity.

Among the significant models comparing functional diversity and degradation in All-Traits, Nutrient Cycling, and Seed Dispersal, we detected a unimodal trend where functional diversity increases between Category 1 and 3 before decreasing in Category 4. However, we found differences in the magnitude of response dependent on which trait matrix was considered (i.e., All-Traits, Seed Dispersal, Nutrient Cycling, Pest Control). Under All-Traits, FD differed between Category 1 and 2 as well as between Category 1 and 3. However, the All-Traits matrix cannot inform on how specific ecosystem functions may be influenced. For example, Pest Control only captures significant differences between Category 1 and 2, and Nutrient Cycling only differed significantly between Category 1 and 3. These differences underscore the importance of selecting traits that answer specific questions when using functional diversity (Petchey & Gaston, 2007; Philpott et al., 2009).

Differences in tree quality, composition, and structure contribute to the variation in avian functional diversity observed among degradation categories. In Gunn et al. (2019) degradation categories are differentiated based on tree quality and species composition. However, the differences between non-degraded stands (Categories 1 and 2), and degraded stands in Category 3 are driven primarily by species composition because Categories 1,2, and 3 only includes the RD of trees that are good quality (AGS). In contrast, the RD of trees of all quality (AGS or UGS) are included when calculating Category 4, so this category may be driven by both tree species as well as UGS. While UGS are present in the first three categories, they make up a much larger percentage in Category 4 (Fig. 5). Trees can be classified as UGS due to a variety of features, such as increased branching or forking, presence of cavities, or fungal growth (Nyland, 2016). These features may also provide important avian habitat for perches (branching), nesting locations (cavities), or nest building material (fungal growth) (DeGraaf et al., 2006; Hunter, 1990; Kahler & Anderson, 2006). Because UGS can provide key habitat features we might expect an increase in habitat diversity and thus broader niche requirements and greater functional diversity as the proportion of UGS increased in Category 4. Instead, functional diversity decreased in Category 4. This result could be a function of beech bark disease (BBD) on American beech which was the dominant tree species in Category 4. In addition to structure, a tree may also be classified as UGS due to a disease that would not provide additional avian habitat (Evans et al., 2005; Witter et al., 2005). Poor harvesting practices in the northeast have left many stands dominated by American Beech, a low value timber species, as beech saplings are shade tolerant and outcompete other hardwood species post-harvest (Bose et al., 2017; Hane, 2003). BBD has been widespread in the region since the 1950s leaving most American Beech infected (Evans et al., 2005) and is known to decrease canopy density used by foliage gleaning birds (Witter et al., 2005) and infected trees are less preferred by bark foraging birds (Adamík & Korňan, 2004). The majority of American Beech at our sites were classified as UGS due to BBD and not because of increased habitat features. Because these diseased beeches were the most dominant species in Category 4, these stands had a higher proportion of UGS without providing additional avian habitat features.

Increases in tree species richness found in mixed conifer-broadleaf stands have been shown to increase structural trait variability in a forest (Benavides et al., 2019) as well as avian species diversity (e.g., Felton et al., 2021; Jansson & Andrén, 2003). Niche-based community assembly dictates that species within a given location will have similar traits that reflect their shared environmental tolerances, while diverging in traits to partition resources (Chesson et al., 2001; Weiher et al., 2011). Thus, as the habitat becomes more diverse, traits will diverge, and both avian species richness and functional traits within that community will increase, allowing a larger area in trait space to be occupied (FDis) (Duflot et al., 2022). In addition, greater tree species diversity may increase the likelihood of functionally distinct species resulting in more separation between species in trait space and thus higher niche differentiation (FDiv) (Benavides et al., 2019; Schuldt et al., 2014). Lastly, as more unique niche requirements are met due to increased structure, FEve increases as species abundances can more evenly spread out in trait space (e.g., Coddington et al., 2023; Melo et al., 2020; Sitters et al., 2016). This increase in FEve indicates the avian community is better utilizing available resources in niche space (Mason et al., 2005; Villéger et al., 2008). The increase in tree species from Category 1 to 2 provides an increase in environmental heterogeneity and thus a significant increase in FDis in all but Nutrient Cycling (Fig. 9). However, in our study region Category 3 shifts back towards a more homogeneous composition as it is softwood dominated. Therefore, the continued rise of functional diversity present in Category 3 cannot be attributed to an increase in tree species richness alone and may reflect interactions between forest structure and avian traits.

Softwood fraction and CV of canopy height were significant predictors of functional diversity metrics (Table 5) and strongly correlated with a suite of avian traits (Fig. 10). Across all three ecosystem functions, softwood fraction was positively associated with sociality. In softwood dominant stands, the three most common species present were Golden-crowned Kinglet (*Regulus satrapa*), Myrtle Warbler (*Setophaga coronata*), and Magnolia warbler (*Setophaga magnolia*), all of which are gregarious and engage in mixed foraging flocks (Mangini et al., 2023; Morse, 1970). In contrast, the most abundant species in hardwood dominated stands, were Red-eyed Vireo (*Vireo olivaceus*), and Ovenbird (*Seiurus aurocapilla*) which tend to be more territorial and less likely to gather in large flocks (Mazerolle & Hobson, 2004; Robinson, 1981). For Nutrient Cycling and Seed Dispersal, softwood fraction was negatively correlated with caching behavior which may be attributed to the preference of some species to cache in loose or shaggy bark present in many hardwood trees (Woodrey, 1991). For Pest Control, softwood fraction appears to divide species along migratory behavior. Resident bark foraging species and generalist insectivores (i.e., med lepid pred) were negatively correlated with softwood fraction. In contrast, foliage gleaning specialists, which tend to be neotropical migrants, were positively correlated with softwood fraction, as they rely on high invertebrate abundance which would not be present during the winter (Finch & Stangel, 1992; Sherry & Holmes, 1985).

CV of canopy height was positively correlated with neotropical migrants in the Pest Control dataset and may be associated with the positive correlation between CV of canopy height and percent invertebrate diet. Increasing variation in canopy height allows for a greater diversity of insects and insectivorous predators (Willson, 1974) and thus, a greater number of neotropical species to occupy the forest (Finch & Stangel, 1992). Neotropical migrants are typically invertebrate consumers and may also be driving the positive correlation between neotropical migrants and CV of canopy height present in Nutrient Cycling. In Seed Dispersal, the negative relationship between higher seed diet and CV of canopy height may be a function of increased tree species diversity. As the diversity of tree species increases, growth rates between those species differ, resulting in greater variation in canopy height (Oliver & Larson, 1996). Because of this, the relationship with CV canopy height is likely a function of increased tree species diversity. As tree species diversity increases, and subsequently variation in canopy height, the forest could provide a broader diversity of food resources, decreasing the proportion of species that specialize on seeds (MacArthur & MacArthur, 1961). The positive correlation between CV canopy height and fruit diet is unexpected as our stands with lower CV canopy height tended to be hardwood dominant and have a greater number of frugivorous species. However, a few common species like Swainson's Thrush (*Catharus ustulatus*), and Veery (*Catharus fuscescens*) may be driving the positive correlation as these species consume a high fruit diet (40%) and were more abundant in stands with higher variation in canopy height compared to those with lower canopy height variation.

Much work has been done to quantify economic degradation across northern New England (Belair & Ducey, 2018; Ducey & Knapp, 2010; Gunn et al., 2019). These efforts have allowed foresters and managers the opportunity to quickly assess forest degradation in their region and inform forest management (S. Roberge, personal communication, March 15th, 2023). Because of this, it is important to link economic degradation to wildlife and the ecosystem functions they can provide. Our findings illustrate that changes in the species composition and structural variation among degradation categories are the primary drivers for changes in avian functional diversity. This has implications in terms of how we manage horizontal and vertical complexity. In concert with these drivers, the continued impact of BBD on species richness (e.g., Cale et al., 2013; Hane, 2003; McNulty & Masters, 2005) and poor vertical structure (e.g., Garnas et al., 2011; Latty, 2005; McNulty & Masters, 2005) may be further impacting ecosystem functions and the services they support. However, further work is needed to quantify the interaction between BBD and low functional diversity. While our aim was not to directly link specific silvicultural methods to avian functional diversity, there has been much work linking different silvicultural methods to taxonomic diversity (e.g., Akresh et al., 2023; Costello et al., 2000; Pohlman et al., 2023; Rolek et al., 2018). The relationship between functional and taxonomic diversity discussed here may allow land managers to indirectly improve functional diversity when managing forests for taxonomic diversity. Our findings highlight the importance of not viewing ecology and economics separately, but rather, by integrating them, we can grow functionally diverse and economically valuable forests that support human well-being.

TABLES

Table 1: The 27 functional traits used in the full trait matrix with variable class type and source. Average clutch size, hand-wing Index (HWI), and mass were natural log transformed to account for skewed distribution.

Functional Trait	**Variable Class**	**Source**
Migrant	Categorical	(Costello et al., 2000)
Percent diet invertebrate	Continuous	(Wilman et al., 2014)
Percent diet vertebrate	Continuous	
Percent diet fruit	Continuous	
Percent diet nectar	Continuous	
Percent diet seed	Continuous	
Percent diet plant	Continuous	
Percent foraging-water	Continuous	
Percent foraging-ground	Continuous	
Percent foraging-understory	Continuous	
Percent foraging-midstory	Continuous	
Percent foraging-canopy	Continuous	
Percent foraging-aerial	Continuous	
Mass (g)	Continuous	
Geo-affinity[1]	Categorical	(Terry et al., 2011)
Nest location	Categorical	(Cornell Lab of Ornithology, 2019)
Habitat	Categorical	
Foraging strategy	Categorical	(Birds of the World, 2022)
Cavity dependence	Binary	
Caching	Binary	
Lepid larval predation	Categorical	
Fungal disperser	Binary	
Sociality	Binary	
Average clutch size	Continuous	
Maximum annual clutches	Continuous	
Hand-wing index (HWI)	Continuous	(Tobias et al., 2022)
Temperature range	Continuous	(Sheard et al., 2020)

[1] Geo-affinity was categorized as north, south or none, and reflects where the majority of the species geographic range falls in relation to our study sites. We followed the methods in Terry et al. (2011) to calculate geo-affinity using QGIS v.3.8.

Table 2: Selected traits associated with each ecosystem function.

Functional Trait	Variable Type
Seed Dispersal	
Hand-wing index (HWI)	Continuous
Mass (g)	Continuous
Percent diet fruit	Continuous
Percent diet seed	Continuous
Caches	Binary
Sociality	Binary
Pest Control	
Hand-wing index (HWI)	Continuous
Mass (g)	Continuous
Percent foraging in midstory	Continuous
Percent foraging in canopy	Continuous
Percent diet invertebrate	Continuous
Migrant type	Categorical
Foraging strategy	Categorical
Degree of lepidopteran larval specialist	Categorical
Sociality	Binary
Nutrient Cycling	
Hand-wing index (HWI)	Continuous
Mass (g)	Continuous
Percent foraging on ground	Continuous
Migrant type	Categorical
Nest location	Categorical
Caches	Binary
Sociality	Binary
Fungal disperser	Binary

Table 3: Results from ANOVA comparing forest structure across degradation categories (a), where columns indicate degrees of freedom (DF), sum of squares (SS), mean sum of squares (MS), F-statistic (F), and p-value (p). Significant comparisons (p<0.05) are in bold. Only significant results are shown from Tukey tests (b) where columns indicate pairwise category comparisons (Groups), the mean difference between the groups (diff), the lower end point of the interval (lwr), the upper end point of the interval (upr) and the p-value after adjustment for multiple comparisons (adj p).

(a)

Variable	**DF**	**SS**	**MS**	**F**	**p**
Average DBH	3	621.844	207.281	7.835	**0.007**
Average R scale	3	1.570	0.523	9.807	**0.002**
CV of canopy height	3	77.387	25.796	2.141	0.120
Diversity DWM	3	2.042	0.681	19.659	**<0.001**
Percent understory cover	3	0.180	0.060	1.355	0.279
RD snags	3	0.014	0.005	2.915	0.054
Softwood fraction	3	1.659	0.553	21.848	**<0.001**

(b)

Variable	**Groups**	**diff**	**lwr**	**upr**	**adj p**
Diversity DWM	3-1	-0.568	-0.892	-0.244	<0.001
Fraction softwood RD	3-2	0.397	0.167	0.628	<0.001
Average DBH	3-2	-12.701	-20.146	-5.255	<0.001
Average R scale	3-1	-0.671	-1.073	-0.269	<0.001
Diversity DWM	4-3	0.501	0.191	0.811	<0.001
Average R scale	4-3	0.621	0.236	1.005	<0.001
Fraction softwood RD	2-1	0.343	0.113	0.574	0.002
Average R scale	2-1	-0.368	-0.703	-0.034	0.027
Fraction softwood RD	4-2	-0.232	-0.448	-0.016	0.032
Standing dead RD	3-2	-0.060	-0.117	-0.002	0.042
Average R scale	4-2	0.318	0.005	0.632	0.046
Diversity DWM	3-2	-0.750	-1.019	-0.480	<0.001
Fraction softwood RD	3-1	0.741	0.464	1.018	<0.001
Fraction softwood RD	4-3	-0.630	-0.895	-0.365	<0.001

Table 4: Results from ANOVA comparing functional diversity across degradation categories for All Traits and each ecosystem function (a), where columns indicate the functional diversity metric used (FD), degrees of freedom (DF), sum of squares (SS), mean sum of squares (MS), F-statistic (F) and p-value (p). Significant comparisons ($p<0.05$) are in bold. Only significant results are shown from Tukey tests (b) where columns indicate pairwise category comparisons (Groups), the mean difference between the groups (diff), the lower end point of the interval (lwr), the upper end point of the interval (upr) and the p-value after adjustment for multiple comparisons (adj p).

(a)

Ecosystem Function	FD	DF	SS	MS	F	p
All Traits	FDis	3	0.01	0.00	4.30	**0.014**
All Traits	FDiv	3	0.00	0.00	0.75	0.532
All Traits	FEve	3	0.01	0.00	1.82	0.170
Nutrient Cycling	FDis	3	0.02	0.01	4.09	**0.017**
Nutrient Cycling	FDiv	3	0.01	0.00	1.63	0.208
Nutrient Cycling	FEve	3	0.02	0.01	1.63	0.208
Pest Control	FDis	3	0.00	0.00	3.45	**0.032**
Pest Control	FDiv	3	0.00	0.00	1.79	0.176
Pest Control	FEve	3	0.02	0.01	2.51	0.082
Seed Dispersal	FDis	3	0.04	0.01	8.75	**<0.001**
Seed Dispersal	FDiv	3	0.13	0.04	21.65	**<0.001**
Seed Dispersal	FEve	3	0.02	0.01	3.68	**0.025**

(b)

Ecosystem Function	FD	Group	diff	lwr	upr	Adj p
All Traits	FDis	2-1	0.04	0.00	0.07	0.022
All Traits	FDis	3-1	0.05	0.00	0.09	0.024
Nutrient Cycling	FDis	3-1	0.08	0.01	0.15	0.015
Pest Control	FDis	2-1	0.03	0.00	0.06	0.024
Seed Dispersal	FDis	3-1	0.13	0.06	0.20	<0.001
Seed Dispersal	FDis	2-1	0.07	0.02	0.13	0.009
Seed Dispersal	FDis	4-3	-0.07	-0.14	0.00	0.033
Seed Dispersal	FDiv	3-1	0.20	0.12	0.28	<0.001
Seed Dispersal	FDiv	4-3	-0.18	-0.26	-0.11	<0.001
Seed Dispersal	FDiv	3-2	0.13	0.07	0.19	<0.001
Seed Dispersal	FDiv	2-1	0.07	0.01	0.14	0.025
Seed Dispersal	FEve	3-1	0.09	0.01	0.17	0.019

Table 5: Forest composition and structure variables that were significant within linear models. Columns summarize model results for each functional diversity metric (FDis, FDiv, FEve) for each ecosystem function. Overall model significance was evaluated using the F-Statistic and significant models are denoted with asterisks. The degree of significance is shown with asterisks (**.** $P < 0.1$, *$p<0.05$,** $p<0.01$).

composition and structure coefficients	**Seed Dispersal**			**Nutrient Cycling**			**Pest Control**		
	FDis	FDiv	FEve	FDis	FDiv	FEve	FDis	FDiv	FEve
Standing dead RD									
Percent cover understory	.							*	
DWM diversity									
Mean R scale					*				
Mean DBH (Dg)								.	
Softwood fraction	*	*					.		
CV of canopy height	*			.			*		
Adjusted R^2	0.457	0.708	0.270	0.337	0.102	-0.043	0.187	0.179	0.070
Residual Std. Error (7,21)	0.040	0.043	0.043	0.036	0.038	0.062	0.0189	0.025	0.047
F Statistic (7,21)	4.362**	10.702**	2.477	3.035*	1.456	0.835	1.921	1.872	1.3

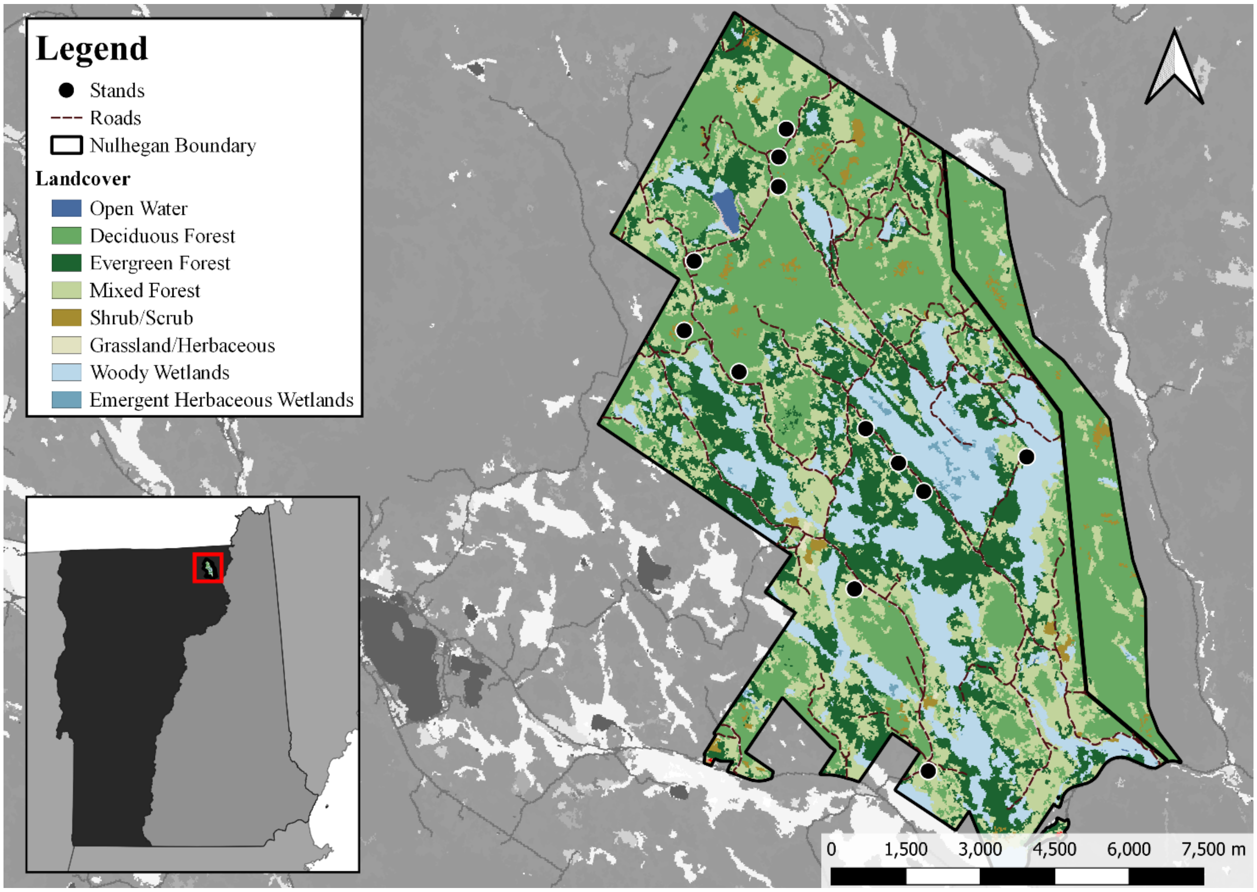

Figure 1: Map of the Nulhegan Basin Division of the USFWS Silvio Conte National Wildlife Refuge. Black dots show the location of stands where field surveys took place. The lower left inset shows the location of Nulhegan in VT.

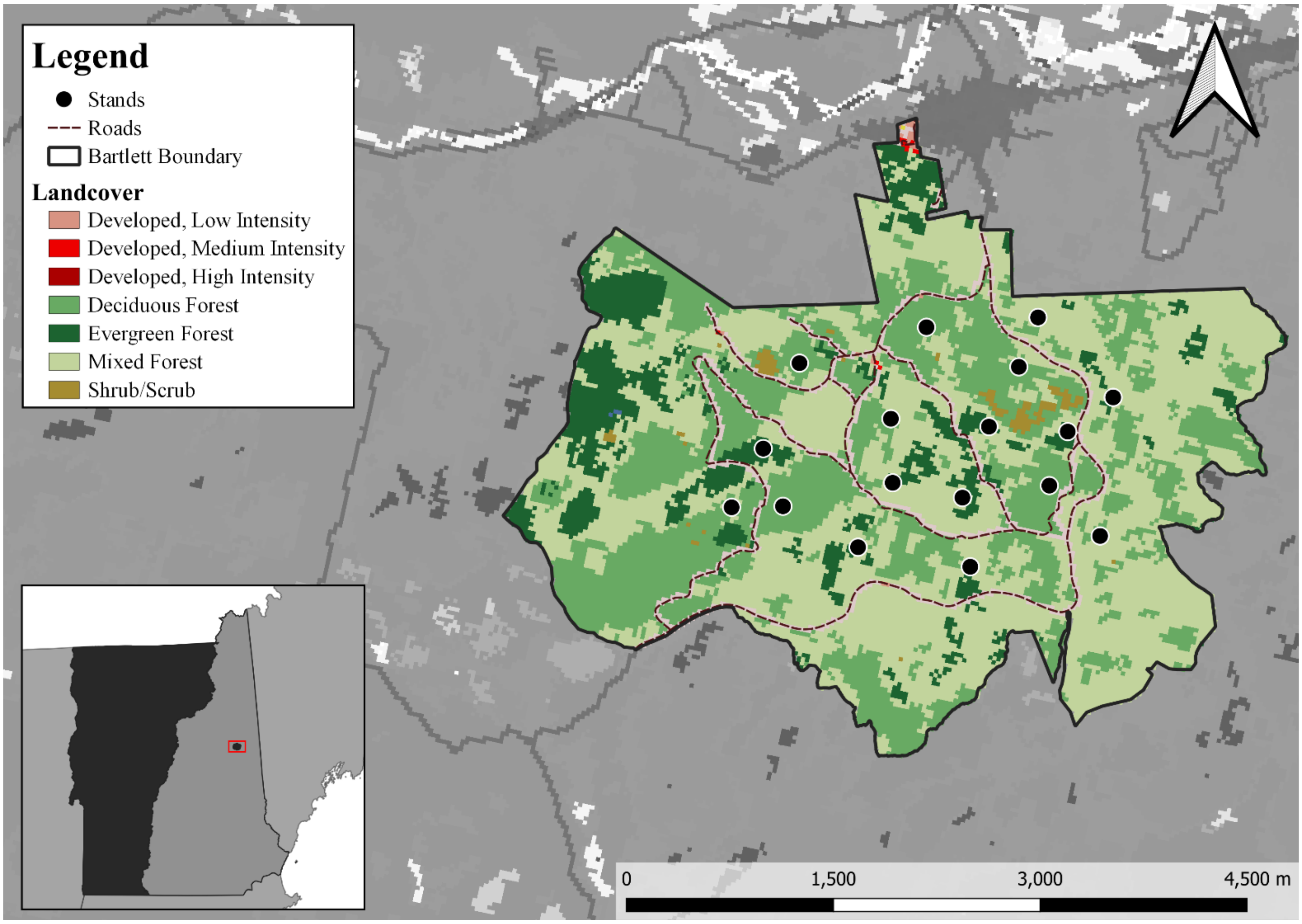

Figure 2: Map of Bartlett Experimental Forest, White Mountain National Forest, NH. Black dots show the location of stands where field surveys took place. The lower left inset shows the location of the Bartlett Experimental Forest in NH

(a) (b)

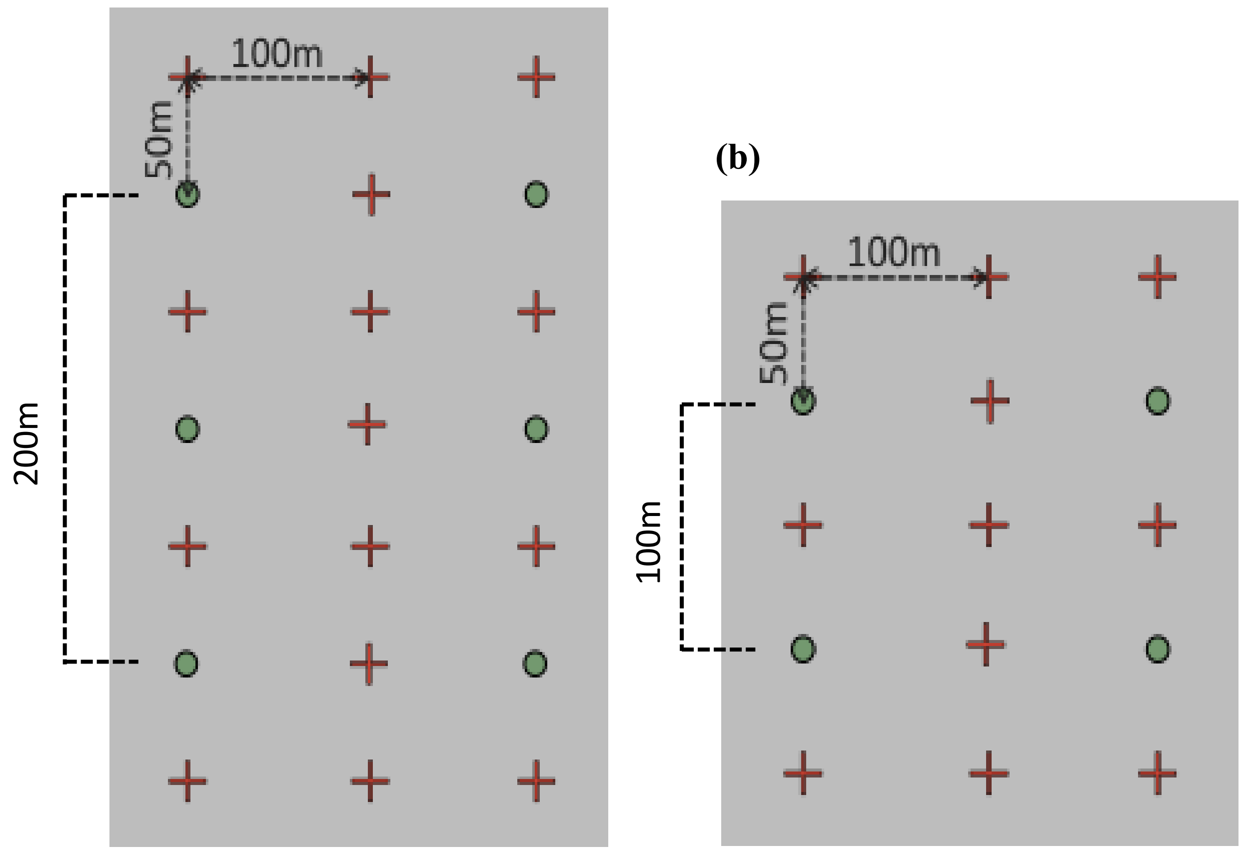

Figure 3: Diagram illustrating the orientation of avian point counts and vegetation transects in each stand. In six-point stands (a), point count locations (green dots) were set along two 200m transects spaced every 100m and variable radius plots were set along three 300m transects spaced every 50m. In four-point stands (b) point count locations were set along two 100m transects spaced every 100m and variable radius plots were set along three 200m transects spaced every 50m.

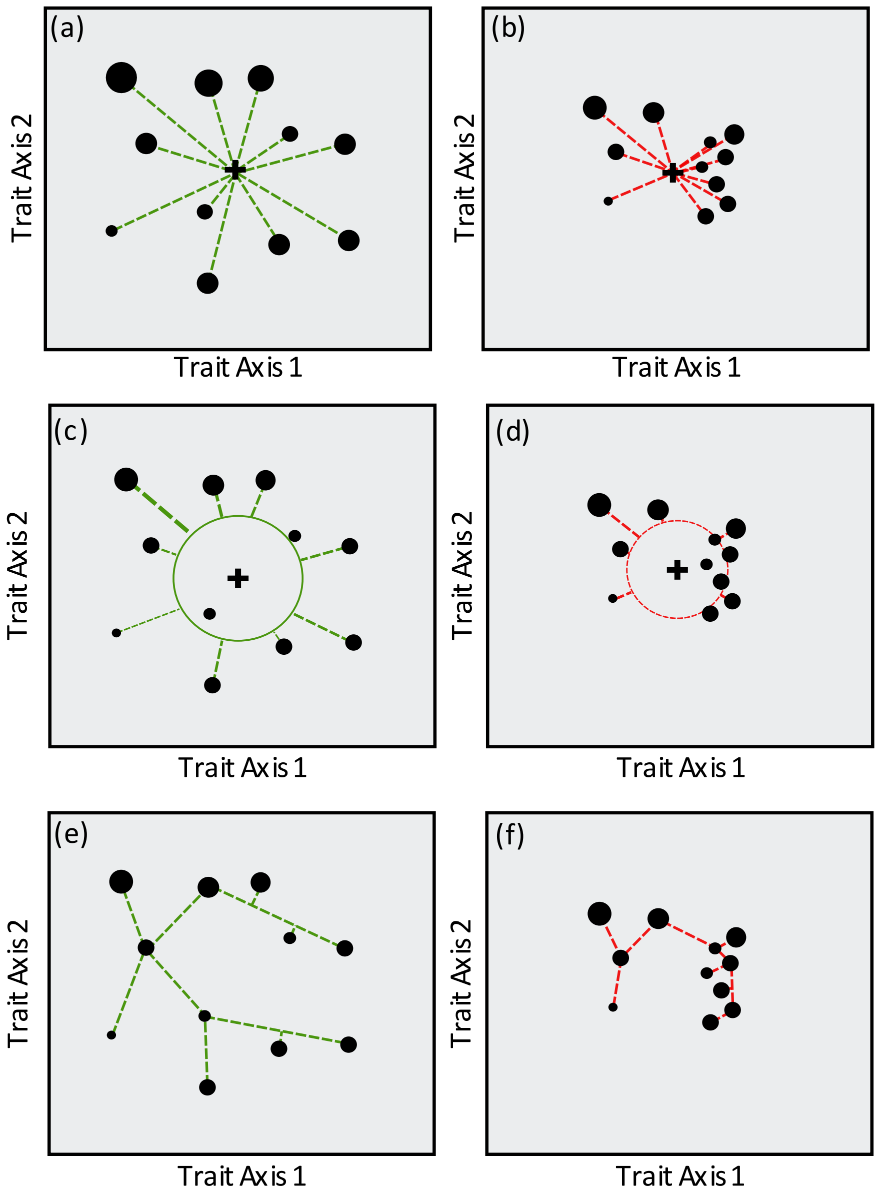

Figure 4: Theoretical examples of each functional diversity metric. Dots represent species in trait space, with larger dots illustrating more abundant species, and dotted lines represent Euclidean distance. Examples of high functional diversity are in green and low functional diversity in red. A stand will have high functional dispersion (a) when species are spread out and have a large mean distance to the center of the group (cross), and low functional dispersion (b), when species are clustered together and have a low average distance to the center of the group (cross). A stand will have high functional divergence (c) when a high proportion of species are outside the average distance to the center (green circle) and low functional divergence (d) when a low proportion of species fall outside the average distance to the center (red circle). A stand will have high functional evenness (e) when species are evenly distributed along the shortest branching tree (green dotted line) and low functional evenness (f) when species are clumped along the shortest branching tree (red dotted line).

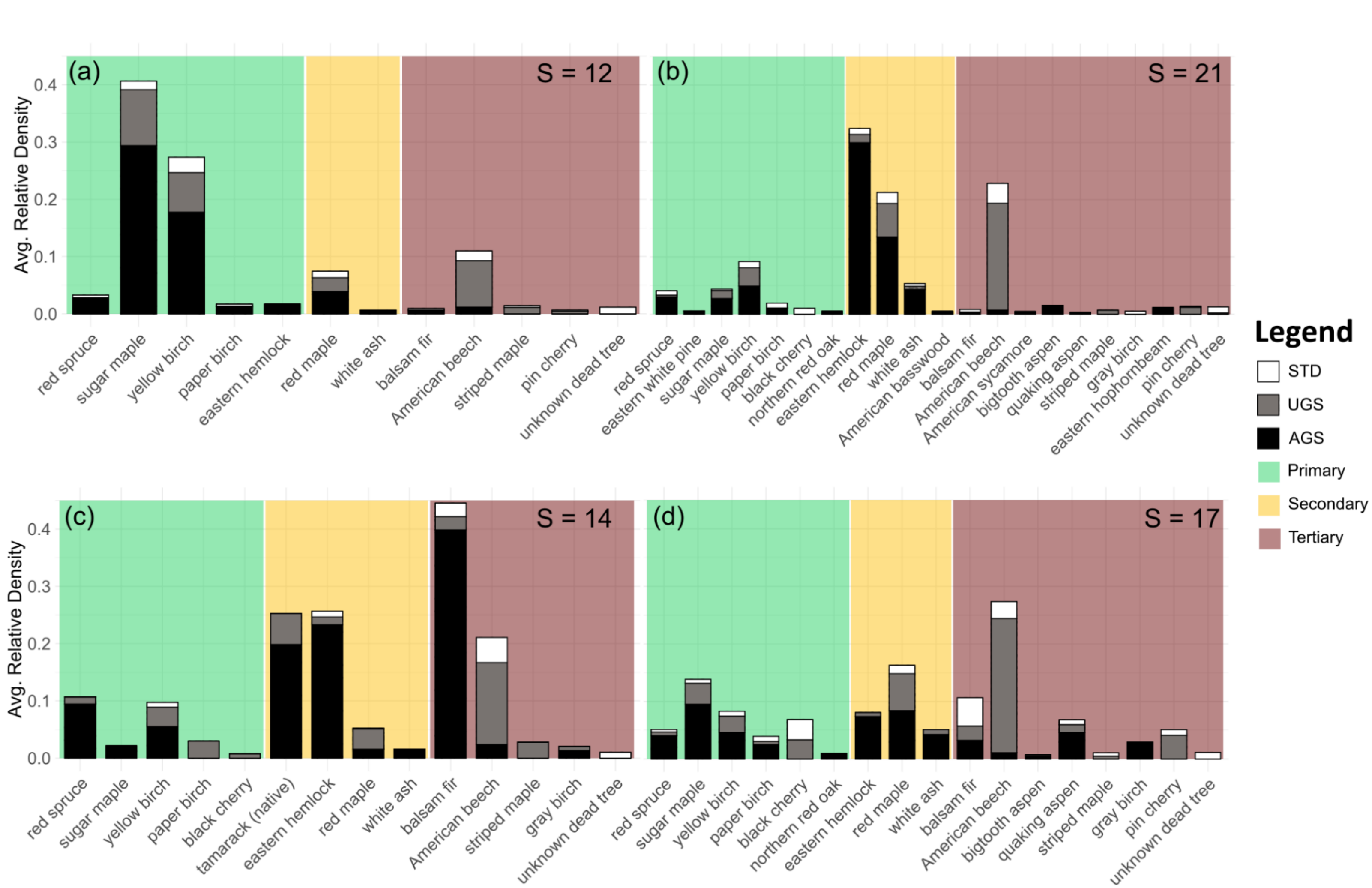

Figure 5: Average RD of tree species within stands grouped by degradation Category: 1 (a), 2 (b), 3 (c), and 4 (d). Species are separated by market value into primary (green box), secondary (yellow box), and tertiary (red box). Average RD within a species is separated into the proportion of standing dead trees (STD, white), unacceptable growing stock (UGS, grey), and acceptable growing stock (AGS, black). Tree species richness (S) is provided for each category in the upper right corner of each plot.

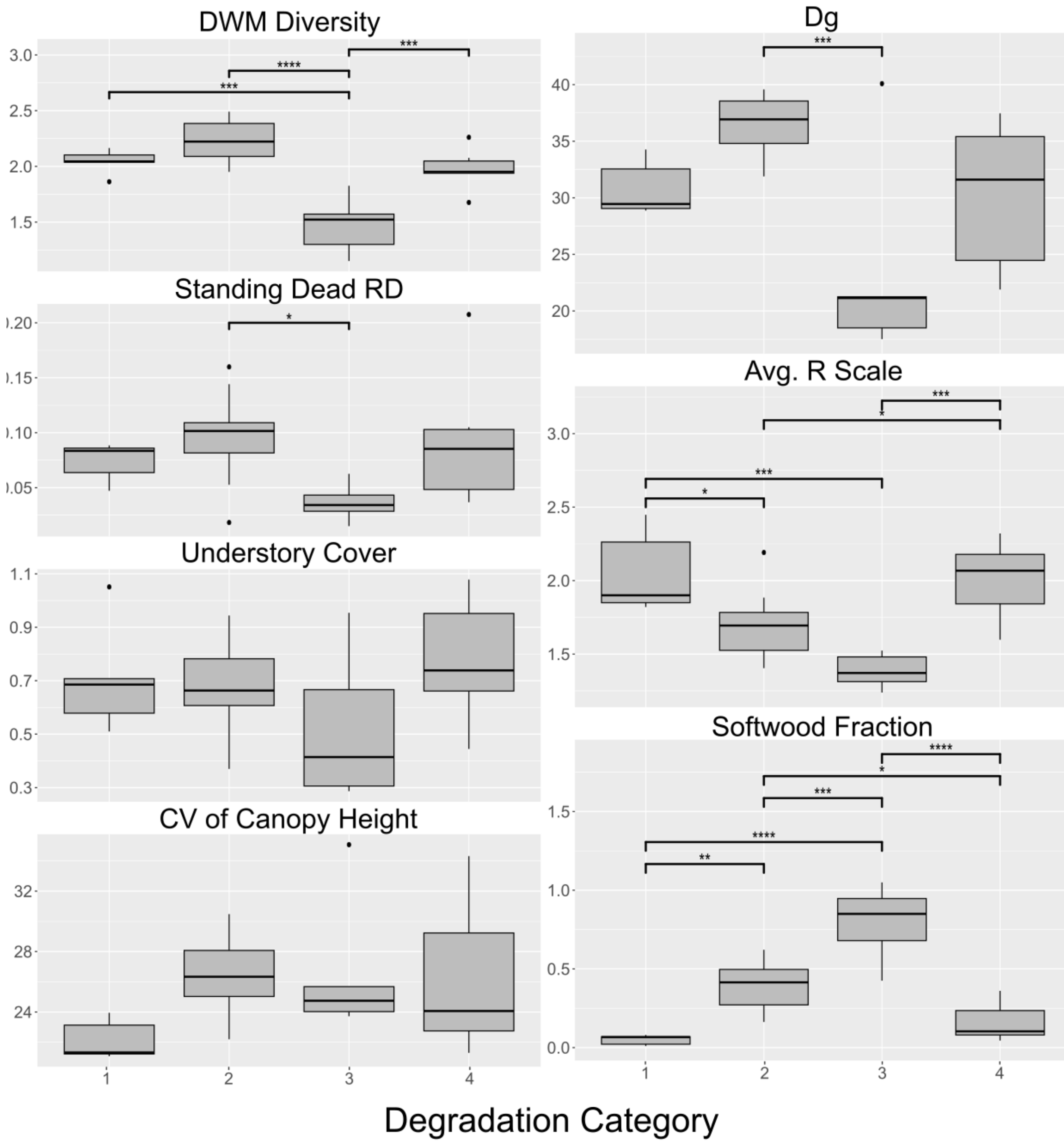

Figure 6: Boxplots for each forest structure and composition variable across degradation categories. Box limits are the first and third distributional quartiles, the center black bar is the median, and whiskers extend to the most extreme data point within 1.5 times the interquartile range. Dots beyond the whiskers are outliers. Brackets indicate significance between groups with the number of asterisks equal to the degree of significance (* p<0.05, ** p < 0.01, ***p < 0.001, **** p <0.0001).

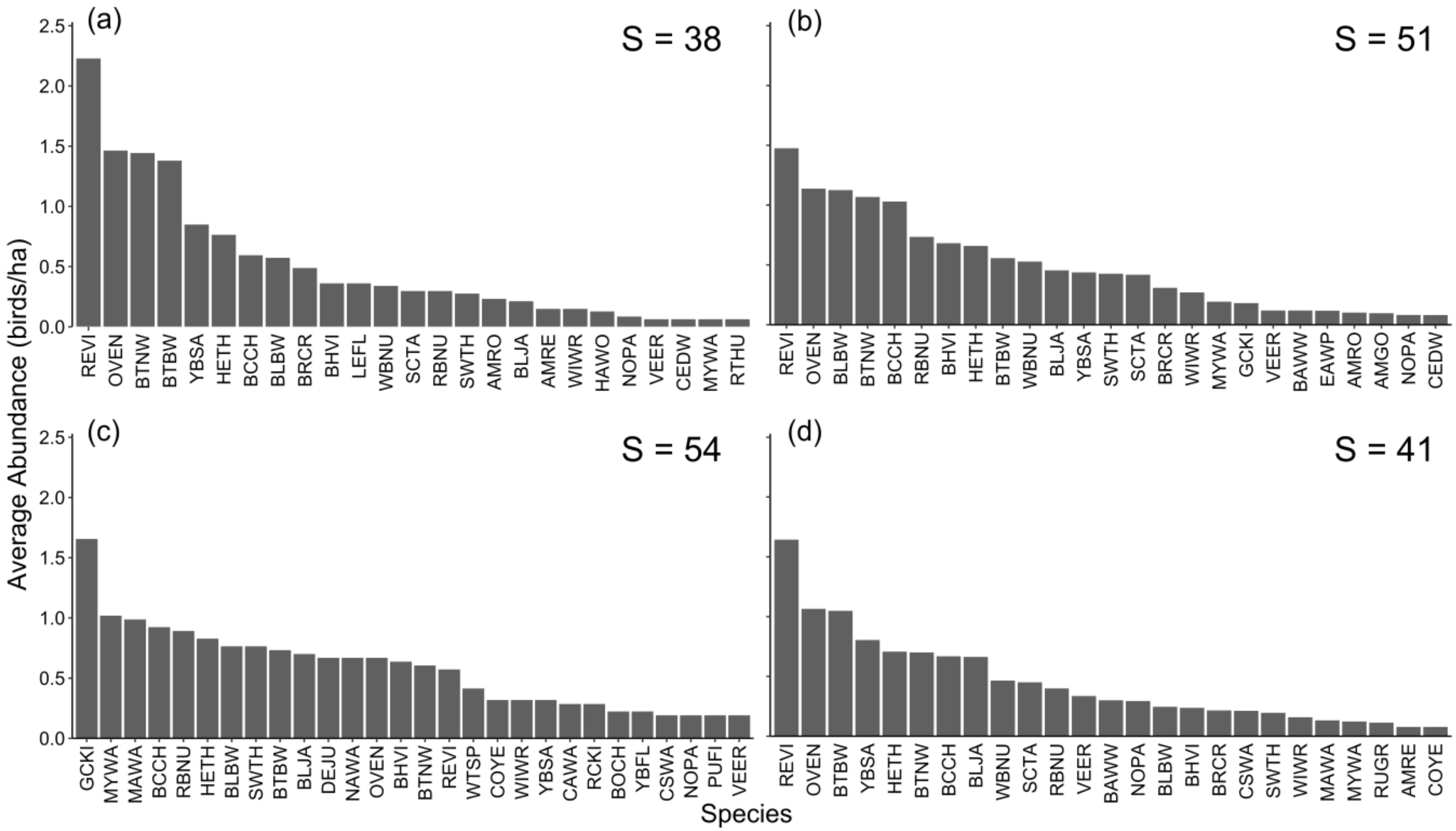

Figure 7: Average abundance (birds/ha) across stands for the top 25 most common species for degradation categories 1 (a), 2 (b), 3 (c), and 4 (d). Total species richness (S) within a degradation category is given in the top right corner of each plot. See Table 1 in the Appendix for the common name associated with each species code.

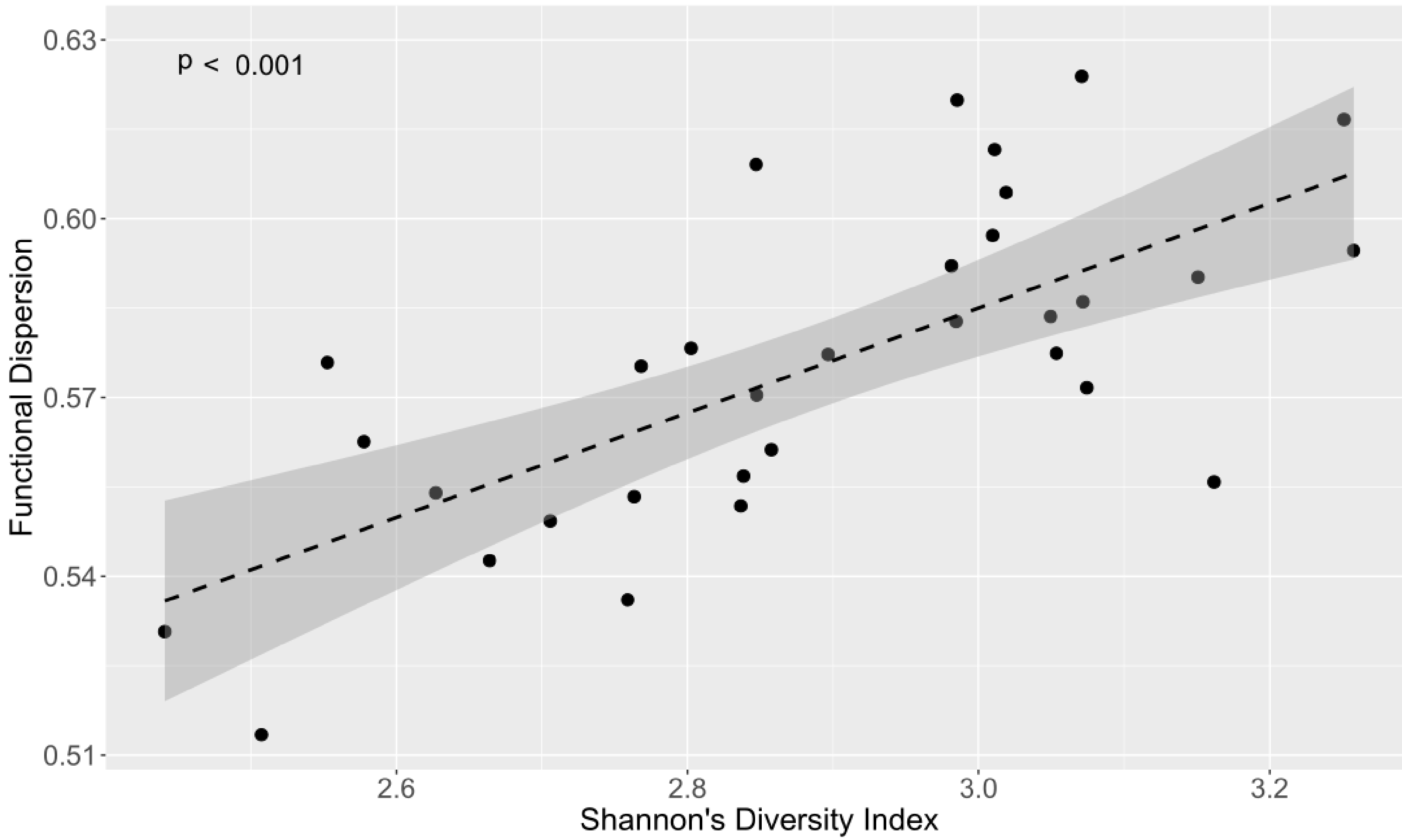

Figure 8: Relationship between taxonomic (Shannon's diversity index) and functional diversity (FDis) of avian species in each stand. Dotted line indicates regression line ($R^2 = 0.57$) and shaded area indicates standard error (SE = 0.02).

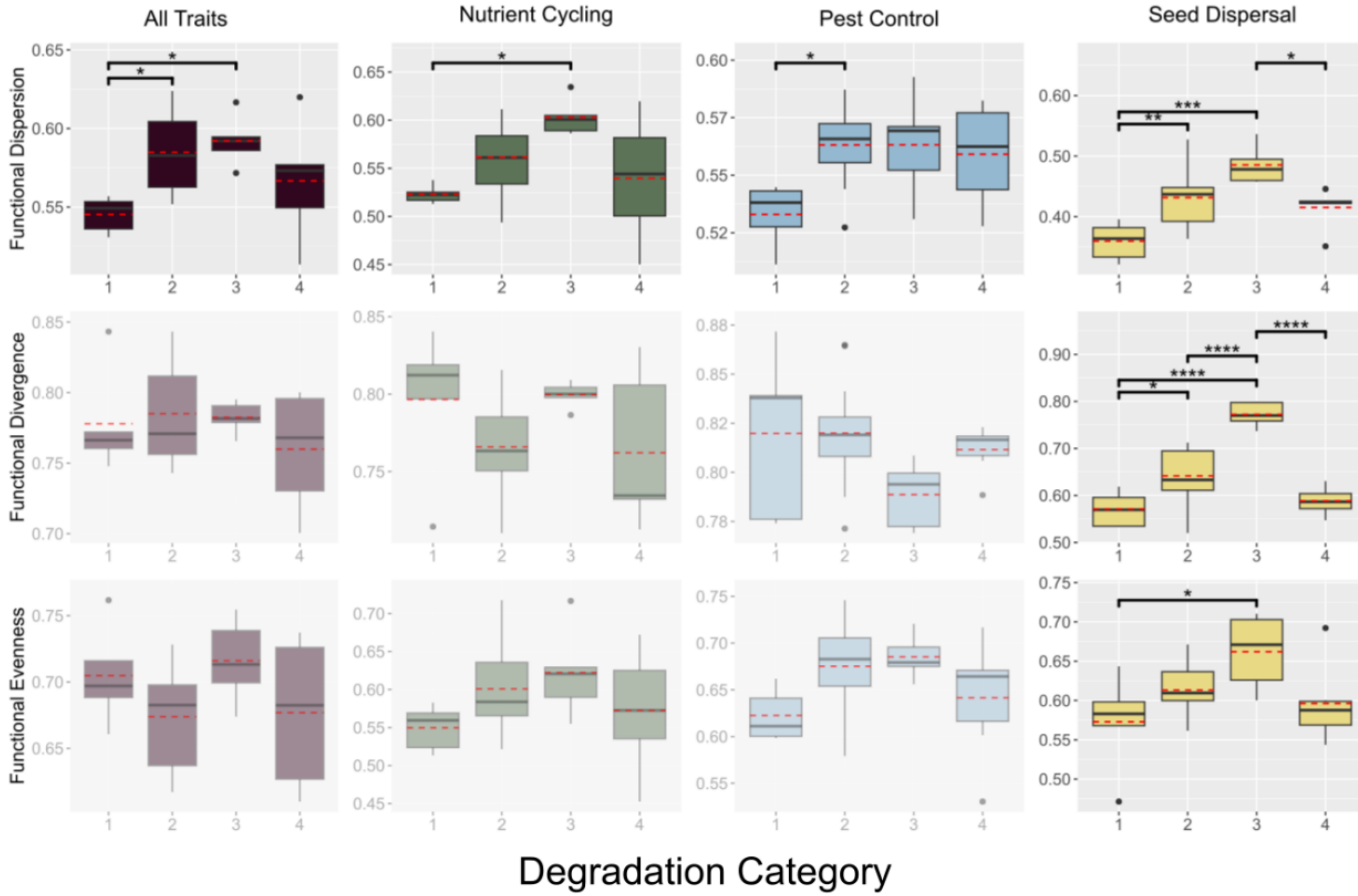

Figure 9: Boxplots comparing functional diversity across degradation categories for the All-Traits matrix and separately for each ecosystem function. Box limits are the first and third distributional quartiles, the center black bar is the median, and whiskers extend to the most extreme data point within 1.5 times the interquartile range. Dots beyond the whiskers are outliers. Brackets indicate significance between groups with the number of asterisks equal to the degree of significance (* $p<0.05$, ** $p < 0.01$, ***$p < 0.001$, **** $p <0.0001$). Functional diversity metrics that did not significantly differ among categories are greyed out.

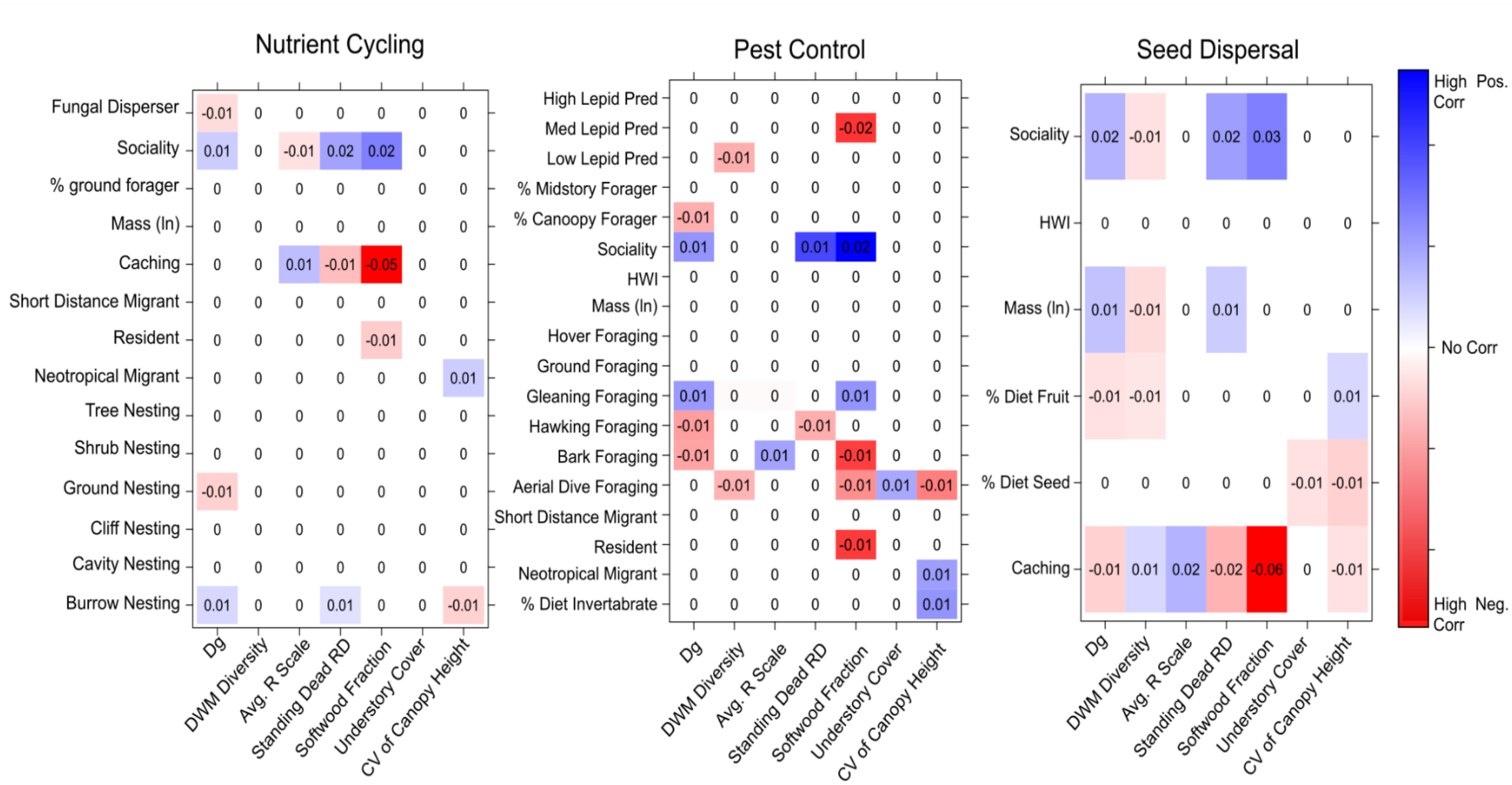

Figure 10: Results of fourth-corner analysis showing the relationship between forest variables and functional traits for each ecosystem function. Zeros represent correlations that were not significant. Red boxes represent strong negative correlations and blue boxes represent strong positive correlations. Values are rounded to the nearest tenth. Categorical traits (e.g., foraging strategy) are separated out to show correlations within each category.

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APPENDIX

Table 1: Species common names and four-letter species codes for all species detected at both Bartlett and Nulhegan.

Common Name	**Species Code**
Alder Flycatcher	ALFL
American Goldfinch	AMGO
American Redstart	AMRE
American Robin	AMRO
Baltimore Oriole	BAOR
Barred Owl	BDOW
Bay-breasted Warbler	BBWA
Belted Kingfisher	BEKI
Black-and-white Warbler	BAWW
Black-billed Cuckoo	BBCU
Black-capped Chickadee	BCCH
Black-throated Blue Warbler	BTBW
Black-throated Green Warbler	BTNW
Blackburnian Warbler	BLBW
Blackpoll Warbler	BLPW
Blue Jay	BLJA
Blue-headed Vireo	BHVI
Boreal Chickadee	BOCH
Broad-winged Hawk	BWHA
Brown Creeper	BRCR
Canada Jay	CAJA
Canada Warbler	CAWA
Cape May Warbler	CMWA
Cedar Waxwing	CEDW
Chestnut-sided Warbler	CSWA
Chipping Sparrow	CHSP
Common Grackle	COGR
Common Raven	CORA
Common Yellowthroat	COYE
Dark-eyed Junco	DEJU
Downy Woodpecker	DOWO
Eastern Wood-pewee	EAWP
Golden-crowned Kinglet	GCKI
Great Crested Flycatcher	GCFL
Hairy Woodpecker	HAWO
Hermit Thrush	HETH
Indigo Bunting	INBU

Least Flycatcher	LEFL
Lincoln's Sparrow	LISP
Magnolia Warbler	MAWA
Mourning Warbler	MOWA
Nashville Warbler	NAWA
Northern Flicker	NOFL
Northern Parula	NOPA
Northern Waterthrush	NOWA
Olive-sided Flycatcher	OSFL
Ovenbird	OVEN
Palm Warbler	PAWA
Philadelphia Vireo	PHVI
Pileated Woodpecker	PIWO
Purple Finch	PUFI
Red Crossbill	RECR
Red-breasted Nuthatch	RBNU
Red-eyed Vireo	REVI
Rose-breasted Grosbeak	RBGR
Ruby-crowned Kinglet	RCKI
Ruby-throated Hummingbird	RTHU
Ruffed Grouse	RUGR
Scarlet Tanager	SCTA
Song Sparrow	SOSP
Swainson's Thrush	SWTH
Swamp Sparrow	SWSP
Tufted Titmouse	TUTI
Veery	VEER
White-breasted Nuthatch	WBNU
White-throated Sparrow	WTSP
White-winged Crossbill	WWCR
Winter Wren	WIWR
Wood Thrush	WOTH
Yellow-bellied Flycatcher	YBFL
Yellow-bellied Sapsucker	YBSA
Yellow-billed Cuckoo	YBCU
Yellow-rumped Warbler	MYWA