Remote Sensing of Environment 215 (2018) 145–156

Contents lists available at ScienceDirect

Remote Sensing of Environment

journal homepage: www.elsevier.com/locate/rse

# Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests

Soyeon Bae[a,b,c,*], Jörg Müller[a,d], Dowon Lee[c], Kerri T. Vierling[e], Jody C. Vogeler[f], Lee A. Vierling[g], Andrew T. Hudak[h], Hooman Latifi[i,j], Simon Thorn[a]

[a] Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashuettenstr. 5, 96181 Rauhenebrach, Germany
[b] Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, 07745 Jena, Germany
[c] Department of Environmental Planning, Graduate School of Environmental Studies, Seoul National University, 08826 Seoul, Republic of Korea
[d] Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[e] Fish and Wildlife Resources Department, University of Idaho, PO Box 441136, Moscow, ID 83844-1136, USA
[f] Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA
[g] Geospatial Laboratory for Environmental Dynamics, University of Idaho, PO Box 441133, Moscow, ID 83844-1133, USA
[h] Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, 1221 South Main Street, Moscow, ID 83843, USA
[i] Faculty of Geodesy and Geomatics Engineering, K.N. Toosi University of Technology, PO Box 15875-4416, Tehran, Iran
[j] Department of Remote Sensing in cooperation with German Aerospace center (DLR), University of Würzburg, Oswald-Kuelpe-Weg 86, 97074 Würzburg, Germany

ARTICLE INFO

*Keywords:*
Biodiversity
Productivity diversity hypothesis
Habitat heterogeneity hypothesis
Lidar
NDVI
Canopy density
Null model

ABSTRACT

Conserving multiple facets of biodiversity is important for sustaining ecosystems. However, understanding relationships between faunal diversity and measurable ecosystem quantities, such as heterogeneity and productivity, across continental scales can be complicated by disparate methods. We developed standardized approaches using lidar data and spectral greenness data (via NDVI; Normalized Difference Vegetation Index) from 637 sampling plots across four sites in North America, Europe, and Asia to test the local effects of habitat heterogeneity and productivity on taxonomic, functional, and phylogenetic diversity of breeding bird assemblages using boosted generalized additive models. Our results revealed the 3-D (three dimensional) vegetation structure (horizontal and vertical) to be of similar importance as NDVI in multiple biodiversity measures, and the importance of 3-D structure was higher for functional and phylogenetic biodiversity measures than for taxonomic measures. We found congruent responses between functional and phylogenetic diversity; however, patterns of taxonomic diversity differed from those of functional/phylogenetic diversity for most predictors. For example, NDVI had positive relationships with taxonomic diversity, but negative relationships with functional/phylogenetic diversity. The effect of canopy density on taxonomic diversity was generally bell-shaped, whereas the relationship was U-shaped for functional and phylogenetic diversity. As a result, this study supports a silviculture strategy with a high variety of canopy densities and vertical variabilities across forest stands to create maximum benefits for regional biodiversity. Here, early succession stands and closed stands sustain functionally-rich bird assemblages, while stands with a medium canopy density promote species-rich assemblages.

## 1. Introduction

Biodiversity plays a significant role in sustaining social-ecological systems (Chapin III et al., 2009; Díaz et al., 2013). In addition to taxonomic diversity, functional and phylogenetic diversity (measured as the combination of functional traits (or phylogenetic tribes) expressed in a local community) have become important for understanding links between biodiversity and ecosystem functioning (Cadotte et al., 2012). For example, functional diversity explains resource-use patterns better than species diversity (Petchey and Gaston, 2006), and it can provide more detailed insights of why and which spatial patterns of resource affect resource-use patterns. Phylogenetic diversity has been used as a proxy for functional diversity, since it can reflect the diversity of unknown traits (Webb et al., 2002). Therefore, the use of functional and phylogenetic diversity has been expanded to reassess biodiversity hotspots (Stuart-Smith et al., 2013; Winter et al., 2013), quantify the

* Corresponding author at: Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashuettenstr. 5, 96181 Rauhenebrach, Germany.
*E-mail address:* soyeon.bae@uni-wuerzburg.de (S. Bae).

https://doi.org/10.1016/j.rse.2018.05.031
Received 16 November 2017; Received in revised form 8 May 2018; Accepted 30 May 2018

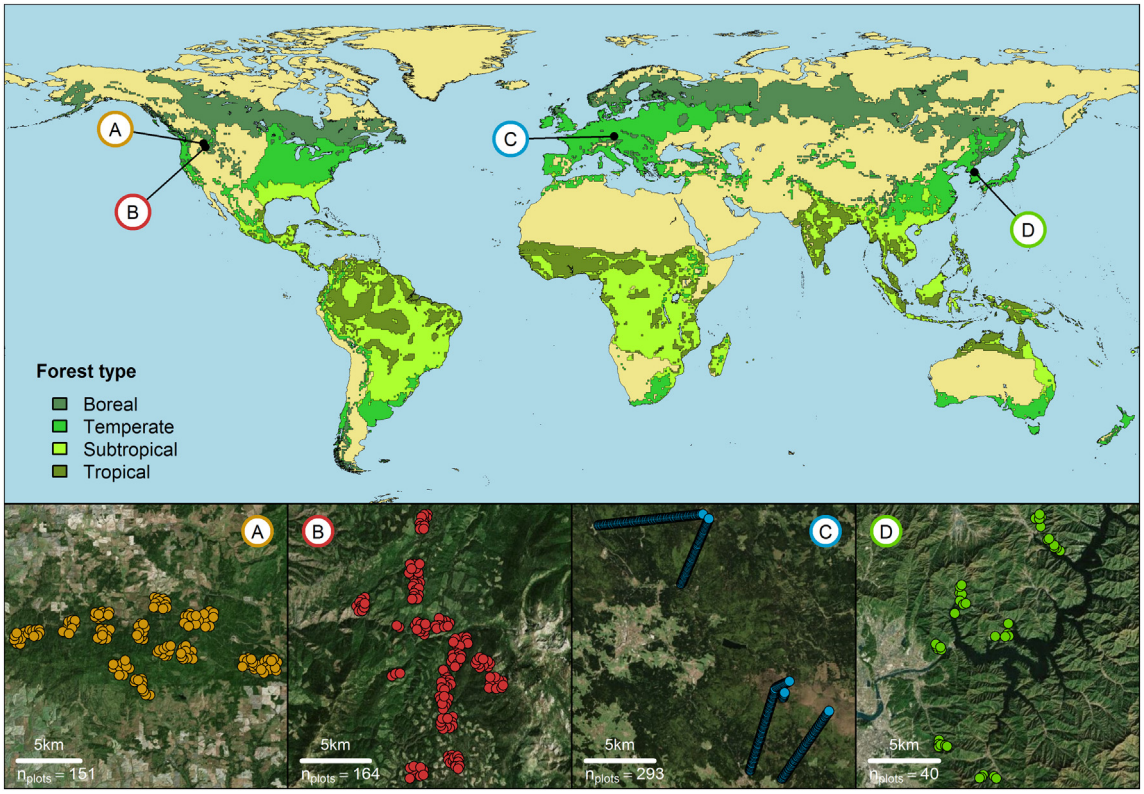


**Fig. 1.** Locations of four study areas in North America, Europe, and Asia (satellite image source: Bing map). Forest biomes according to the Holdridge Life Zone system (Holdridge, 1967) are indicated by different green shadings. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

impact of disturbances (Bässler et al., 2016b; Flynn et al., 2009), and understand overall drivers of biodiversity (Dehling et al., 2014; Gerisch et al., 2012).

Patterns of taxonomic, functional and phylogenetic diversity may not be spatially consistent (Bässler et al., 2016a; Devictor et al., 2010), and determinants of functional and phylogenetic diversity may differ from those of taxonomic diversity (Gerisch et al., 2012). Conserving various facets of biodiversity that might differ from each other hence requires a detailed scientific understanding of biodiversity drivers (Dehling et al., 2014; Grass et al., 2015). In addition, the different responses of functional diversity, phylogenetic diversity, and taxonomic diversity to environmental gradients have led to new insight into understanding of local community assembly mechanisms (Cadotte et al., 2013). Therefore, quantifying local taxonomic, functional, and phylogenetic diversity among large areas requires standardized measures of environmental conditions with sufficiently fine grain.

The most commonly used measures of taxonomic diversity include species richness or biodiversity incidences, such as the Shannon-Wiener index (Jost, 2006). According to the productivity-diversity relationship, species richness should be positively correlated to productivity (Wright, 1983). However, the form and the underlying mechanism of the productivity-diversity relationship is still under debate (Mittelbach et al., 2001; Rosenzweig, 1995; Whittaker and Heegaard, 2003). Another determinant of local taxonomic biodiversity is habitat heterogeneity, which assumes increasing species richness with increasing compositional or configurational habitat heterogeneity (Fahrig et al., 2011; Tews et al., 2004). The mechanisms which underlie these hypotheses include the increase of available niche space, which can increase functional diversity, with the increase of productivity and habitat heterogeneity (Evans et al., 2005; Stein and Kreft, 2015). As there are various underlying assumptions of the positive productivity-diversity relationships, the more specialization hypothesis assumes that a high level of productivity increases the abundance of rare resources which can be consumed by niche position specialists, and more niche position specialists increase total species richness. The more individuals hypothesis assumes higher number of species can be found at more productive sites supporting more individuals (Evans et al., 2005). In forest ecosystems, vegetation productivity has been frequently estimated using gross primary productivity (GPP) or remotely sensed proxies such as the Normalized Difference Vegetation Index (NDVI) (Evans et al., 2005; Verschuyl et al., 2008). More challenging is the use of standardized measures as proxies for structural heterogeneity in forests (i.e., configurational heterogeneity in three dimensions), even more than half a century after the seminal work by MacArthur and MacArthur (1961) using foliage height diversity as a proxy for avian niche diversity.

During the last two decades, the rise of airborne based lidar remote sensing has offered rapid and standardized quantifications of fine scale, 3-dimensional (3-D) forest structures (Lefsky et al., 2002; Vierling et al., 2008). In particular, canopy density and vertical variability in forests have been identified as important determinants for taxonomic diversity of birds, non-flying mammals, and insects (Davies and Asner, 2014; Goetz et al., 2014; Huang et al., 2014; Müller and Vierling, 2014). For example, Huang et al. (2014) demonstrated the importance of vegetation height-structured metrics (derived using the United States National Biomass and Carbon Dataset) in determining woodland bird species richness across the United States, while Goetz et al. (2014) used a comprehensive set of predictor variables (including structural metrics derived from spaceborne lidar) to assess the relative importance of vegetation structure in determining breeding bird species richness across the coterminous United States and southern Canada.

Despite the potential for broad scale, standardized measurement of 3-D forest structures, the determinants of taxonomic, functional, and phylogenetic diversity remain unclear (see Davies and Asner (2014)). Multiple studies have investigated determinants of these facets of diversity in short stature ecosystems such as grassland (Gerisch et al.,

2012; Grass et al., 2015; Sitters et al., 2016), but few studies have investigated determinants of functional and phylogenetic diversity in forests (Cisneros et al., 2015; Thorn et al., 2016). We investigated the effects of 3-D vegetation structure, measured via airborne scanning lidar, and Landsat-derived NDVI on taxonomic, functional, and phylogenetic diversity of breeding birds in temperate forests of the Northern Hemisphere. Our aim was to quantify whether these different facets of local diversity were consistently influenced by habitat heterogeneity and productivity. We hypothesized that taxonomic, functional, and phylogenetic diversity (i) increase with increasing productivity according to the productivity-diversity relationship and (ii) increase with increasing heterogeneity according to the habitat-heterogeneity hypothesis.

## 2. Methods

### 2.1. Bird data

Bird data were compiled from four temperate forests in North America, Europe, and Asia (Fig. 1). Two study areas in USA are located in north-central Idaho, Moscow Mountain (46°49′N, 116°50′W) and Slate Creek (45°38′N, 116°2′W), and both consist of mixed conifer forest stands. Moscow Mountain is dominated by Western Red Cedar (*Thuja plicata*) and Grand Fir (*Abies grandis*), whereas Slate Creek is dominated by Douglas Fir (*Pseudotsuga menziesii*) and Lodgepole Pine (*Pinus contorta*) (Vogeler et al., 2014). The study area in Germany is located in the Bavarian Forest National Park in southeast Germany (48°58′N, 13°23′E) and is dominated by mixed stands of Norway Spruce (*Picea abies*), European Beech (*Fagus sylvatica*), and Silver Fir (*Abies alba*) (Müller et al., 2009). The study area in Asia, Chuncheon, is located within the Soyang river watershed in the northeast of South Korea (37°55′N, 127°52′E). Here, mixed stands are dominated by Mongolian Oak (*Quercus mongolica*), Cork Oak (*Quercus variabilis*), Japanese Red Pine (*Pinus densiflora*), Pitch Pine (*Pinus rigida*), and Korean Pine (*Pinus koraiensis*). These forest types are representative for a wider range of forest biomes; e.g., the Bavarian Forest National Park represents a common mountainous forest ecosystems across central Europe and Scandinavia, and the forests in Chunchoen is composed of the typical forest type of the north and middle of South Korea. The two Idaho study areas are representative of temperate coniferous forests of the Northern Rocky Mountains, USA, with the Moscow Mountain study area representing actively managed forest with much recent harvesting, and the Slate Creek study area having undergone very little recent harvesting, prior to data collections.

Bird surveys in each study area were conducted using standardized point-counts during the breeding season (Bibby et al., 2012). Bird surveys were conducted in 2009 (Moscow Mountain, Idaho), 2010 (Slate Creek, Idaho), 2007 (Bavaria), and 2014 (Chuncheon) (Moning and Müller, 2008; Vogeler et al., 2014). Observers visited sampling sites within 5 h after sunrise during good weather conditions, without rain and limited wind. All species seen or heard within a standardized time period and within a fixed radius were recorded (Table 1). Because there were small differences in field sampling methodology, we used study area (i.e., Moscow Mountain, Slate Creek, Bavaria, and Chuncheon) as a random effect to account for different repeated measures and sampling years in these areas.

To quantify bird functional diversity, 13 ecological traits that reflect patterns of avian resource and habitat use were selected (Calba et al., 2014; Devictor et al., 2010). Traits were classified according to www.allaboutbirds.org (accessed 15 Nov. 2014, Glutz von Blotzheim and Bauer (1985)) and www.hbw.com (accessed 15 Oct. 2014). These traits included body mass and clutch size as continuous variables, and migration status, nest location (cavity, canopy, and ground), foraging substrates (air, trunk, vegetation, and ground), and diet (plant, invertebrate, and vertebrate) as binary variables (see Table S1).

To quantify bird phylogenetic diversity, we compiled phylogenetic

**Table 1**
Summary of bird surveys at four study areas.

| Study area | Plots [n] | Number of surveys per plot [n] | Period | Observers [n] | Duration [m] | Plot size | Minimum distance between points [m] | Details |
|---|---|---|---|---|---|---|---|---|
| Moscow Mountain | 151 | 2 | Late May–early Jul, 2009 | 1 | 8 | A circle with 75 m radius | 250 | - stratified random sampling across nine forest types<br>- see more details in Vogeler et al. (2014) |
| Slate Creek | 163 | 2 | Late May–early Jul, 2010 | 2 | 8 | A circle with 75 m radius | 250 | - stratified random sampling across nine forest types<br>- see more details in Vogeler et al. (2014) |
| Bavaria | 286 | 5 | Late Mar–early Jun, 2007 | 1 | 10 | 100 m × 100 m | 100 | - continuous square plots along four transects<br>- see more details in Moning and Müller (2008) |
| Chuncheon | 40 | 2 | Apr–May 2014 | 2 | 10 | A circle with 75 m radius | 200 | - deciduous and mixed forests only<br>- limited within the elevation below 400 m (asl)<br>- apart from road at least 100 m |

trees for each study area separately. We followed the phylogeny subset methodology from www.birdtree.org to mine 4000 bootstrap trees for each study area, based on the backbone provided by Hackett et al. (2008). Afterwards, those bootstrap replicates were condensed into one fully dated consensus tree using TreeAnnotator 1.8.2 (see Figs. S1–S4 for phylogenetic trees and Section 2.4 Data analysis for the calculation of diversity indices).

### 2.2. Quantification of 3-D vegetation structure

We used discrete return airborne scanning lidar data to estimate physiognomic characteristics of the forest stands. Data consisted of x, y, and z coordinates that were classified into ground and vegetation returns by respective algorithms. Classification of ground points in Chuncheon was conducted by iterative algorithms generating a triangulated surface model using TerraScan software (TerraSolid Ltd., Finland). Classification in USA and Bavaria was conducted using the Multiscale Curvature Classification (MCC) algorithm (Evans and Hudak, 2007) and the method by Axelsson (2000), respectively (Müller et al., 2010; Vogeler et al., 2014). Using the extracted ground points, spatially contiguous digital terrain models (DTMs) were generated with a grid cell size of 1 m × 1 m. The height of above ground lidar returns was calculated by subtracting the elevation of the underlying DTM from the elevation of each point. All bird surveys were conducted within six years of the lidar acquisitions (Table 2). On the Moscow Mountain site, Vierling et al. (2014) found no difference between mapped avian diversity patterns using concurrently acquired lidar data and 6 year old lidar data in areas that had not experienced harvest and disturbance (i.e. fire). Hill and Hinsley (2015) similarly found that time lags between lidar data acquisition and bird data were unlikely to influence mapped output of a variety of avian metrics when taken within a decade in a mature and undisturbed woodland. At Slate Creek and Chucheon, the time discrepancies were less (4 and 5 years, respectively), and little harvesting had occurred during those intervening years, hence the plots represented non-harvested conditions (Vogeler et al., 2014).

The effect of lidar point density on model performances of forest structural attributes is still under debate (Latifi et al., 2017; Ruiz et al., 2014). Therefore, we applied a point cloud thinning algorithm on the higher-density Bavarian dataset to homogenize point densities among the three lidar datasets. We used the routine implemented within FUSION version 3.60+ in a batch processing modus (McGaughey, 2016). In each case we initiated the thinning with 99 random number streams, and then used a 20 × 20 m cell size to calculate the return density. The procedure reduced the initial point density of 25 points per $m^2$ (in average) to uniform 4 points per $m^2$. Points were aggregated into 20 by 20 m grids, and values of two metrics describing different aspects of the stand structure were calculated for each grid cell (Table 3).

First the canopy density ($CD_{>2m}$) was calculated as the point ratio of vegetation returns higher than 2 m above ground. $CD_{>2m}$ is a measure of inverse light availability on the ground (Müller and Vierling, 2014), which reflects the main factor limiting the development of the understory (Brosofske et al., 2001) as well as the development of arboreal layers. It also reflects the horizontal variability in light regimes on the forest floor (Chen et al., 2004). If total area of the observation grid is open due to previous stand replacing disturbances (anthropogenic or natural), the horizontal heterogeneity is low, and if total area of the grid is completely shaded by shrubs and trees this kind of horizontal heterogeneity is low again, while a mixture of gaps and shaded areas provide a high horizontal heterogeneity. This kind of shading heterogeneity has been identified as the most important heterogeneity for taxonomic diversity of many taxa (Lehnert et al., 2013; Seibold et al., 2016).

Second, standard deviation of vegetation height ($H_{SD}$) was used as a proxy for vertical variability in vegetation structure. $H_{SD}$ is a common measure used for characterizing the variation or dispersion of vegetation height distribution for use in animal diversity studies (Davies and Asner, 2014). The vertical heterogeneity has been linked to stratification of species in a forest; the more different layers available the more different niches for ground, shrub and canopy breeding or foraging birds exists (MacArthur and MacArthur, 1961). However, not only in birds, but also for arthropod communities the vertical layers have been shown to determine different communities in temperate forests (see Floren and Schmidl (2008)).

$CD_{>2m}$ and $H_{SD}$ were calculated within a 75 m radius of each bird sampling point in the Idaho and Chuncheon sites, and a 100 × 100 m quadrat in Bavaria. Scale dependence is an important issue in ecology, as the associations between predictors and responses are dependent on spatial scale (Seavy et al., 2009; Weisberg et al., 2014). Here, we set the same spatial scale as bird surveys to describe the local 3-D structure of bird survey area. Lidar metrics were calculated using R version 3.1.1 (R Core Team, 2014) and R packages of 'sp', 'rgdal', 'raster', 'gdalUtils', 'data.table', and 'vegan.'. The correlation between the two structural heterogeneity indices were 0.36 (Spearman's rho), and the scatterplot of $H_{SD}$ versus $CD_{>2m}$ demonstrates a hump shaped relationship (Fig. S5).

**Table 3**
Predictor variables used to model taxonomic, functional, and phylogenetic diversity of breeding birds in four temperate forest across the Northern Hemisphere.

| Variables | Variable description | Source |
|---|---|---|
| Canopy density ($CD_{>2m}$) | Percentage of returns > 2 m above ground (%) | Lidar |
| Vegetation height variability ($H_{SD}$) | Standard deviation of vegetation heights (m) | Lidar |
| NDVI ($NDVI_{mean}$) | Mean Normalized Difference Vegetation Index | Landsat |
| NDVI variability ($NDVI_{SD}$) | Standard deviation of NDVI | Landsat |

### 2.3. NDVI from Landsat

NDVI responds to plant chlorophyll content and hence generally increases in response to plant productivity (e.g., Pettorelli et al. (2006)). NDVI data were derived from cloud-free Landsat imagery

**Table 2**
Summary of remote sensing data acquisitions at four study areas.

| Study area | Landsat collection date | Landsat image type | Lidar collection dates | Lidar scanner system | Point density (points/m²) | Vertical accuracy (cm) | Wavelength (nm) | Maximum echoes per pulse | More details |
|---|---|---|---|---|---|---|---|---|---|
| Moscow Mountain | 16 May 2009 | TM | June 2009 | Leica ALS50 | 4 | 4.3 | 1064 | 4 | Vogeler et al. (2014) |
| Slate Creek | 13 June 2010 | TM | Sep–Oct, 2006 | Leica ALS50 | 4 | 8.8 | 1064 | 4 | Vogeler et al. (2014) |
| Bavaria | 5 and 16 April 2007 | ETM+ | May 2007 | Riegl LMS-Q560 | 25 | 15 | 1550 | 11 | Moning and Müller (2008) |
| Chuncheon | 23 May 2014 | OLI | June–Oct, 2009 | Leica ALS60 and ALS50 | 4 | < 10 | 1064 | 4 | – |

acquired during the same spring sampling season (Table 2) as the bird surveys (Table 1). Top-of-atmosphere reflectance of each spectral band was calculated using band-specific gain and offset coefficients and based on solar elevation angle and earth-sun distance at the time of each acquisition. In Bavaria, data gaps caused by the failed scan line corrector (SLC) specific to Landsat 7 were conveniently offset, such that merging the two consecutive images served to fill in the data gaps. Preference was given to the later image values wherever pixel reflectance values from both images were available. NDVI was calculated as red band reflectance subtracted from the adjacent near infrared band reflectance, divided by their sum. As a proxy of mean productivity we calculated and extracted the average NDVI value within the 75-m radius around each plot center. Approximately, 13 whole and 12 partial pixels of the 30 m resolution NDVI map were included in metric calculations (Vogeler et al., 2014). As an additional proxy for horizontal heterogeneity we calculated the standard deviation of NDVI among the pixel of within the 75-m radius which displays variation in greenness among plot (Goetz et al., 2007).

### 2.4. Data analysis

Data were analyzed in the statistical software R version 3.1.1 (R Core Team, 2014). Three measures for taxonomic diversity were selected as target variables, namely (I) log-transformed *Species richness*, (II) *Shannon diversity,* and (III) *Evenness* were selected. Yet, a myriad of different measures based on species trait-based or phylogenetical differences exist (Cadotte and Davies, 2016). Here, we selected three distance-based measurements as proposed by Villéger et al. (2008) to represent functional and phylogenetic, namely (I) *Richness*, measured as the minimum convex hull, which covers all locally present species in a multi-dimensional functional/phylogenetic space, (II) *Entropy*, measured as mean pairwise distance between co-occurring in a multi-dimensional functional/phylogenetic space, and (III) *Evenness*, measured by comparing the observed abundance-weighted pairwise distance with the distance of perfect regularity of abundance distribution along a minimum spanning tree that covers all species in a multi-dimensional functional/phylogenetic space. Functional diversity indices were based on species-by-species distance matrices calculated by an abundance weighted Gower distance (Gower, 1971) using 'daisy' function in the R package 'cluster'. Phylogenetic diversity measures were based on patristic distances among species in a dated molecular phylogenetic tree, calculated by means of the function 'cophenetic' (see Table 4 for detailed R functions used and Fig. 2 and Mouillot et al. (2013) for a conceptual framework on different diversity measures).

However, functional and phylogenetic distance-based diversity indices, especially functional/phylogenetic richness or their variants, may not be independent from species richness (see Fig. S6), hence null-model approaches are widely advocated (Cadotte and Davies, 2016; Flynn et al., 2009; Petchey and Gaston, 2006). Hence, observed diversities per plot were compared with expected diversities of 999 artificial assemblages with the same species richness and evenness patterns. The 999 artificial assemblages were built of randomly selected species from each of our four regional species pools using tip shuffling null models (Cadotte and Davies, 2016). Thus, the null models removed species identities, but kept the species richness and evenness constant to provide a standardized effect size. The resultant standardized effect sizes thus represent functional and phylogenetic diversity, standardized by species richness (see more detail regarding the independence of diversity measures in Fig. S7).

Productivity and structural heterogeneity in forests can be correlated. For instance, increasing biomass is thought to increase structural heterogeneity via addition of structural elements such as stems, branches, and leaves as forests undergo succession (Dobson et al., 2015; Drever et al., 2009; Hurlbert, 2004; Winter and Brambach, 2011), and structurally complex mature forests contribute to high productivity (Hardiman et al., 2011; Ishii et al., 2004). Thus, we applied boosted generalized additive models (GAMS) to all data with Gaussian error distributions using the function *gamboost* in the package *mboost* in R 3.1.1. These models are particularly suitable to disentangle effects of variables with collinearity (Hothorn et al., 2010). We implemented component-wise boosting for optimizing parameter estimations and prediction accuracy including variable selection. GAMS are suitable for ecological modeling characterized by non-linearity, interaction between predictors, spatial autocorrelation, and non-stationarity (Hothorn et al., 2010). We checked the bivariate correlation of the four fixed factors with Spearman rank correlation test. We used study area (i.e., Moscow Mountain, Slate Creek, Bavaria, and Chuncheon) as a random effect to account for different repeated measures and sampling years in these areas (see Fig. S8). $H_{SD}$ and $CD_{>2m}$ derived from airborne lidar and $NDVI_{mean}$ and $NDVI_{SD}$ from Landsat were used as fixed factors. To mitigate overfitting, 25-fold bootstrap estimates of the empirical risks was used to determine the number of boosting iterations by

**Table 4**
The nine measures of bird diversity as response variables in this study with corresponding R-functions that were used to calculate observed diversities (note that observed diversities were subjected to a null-model procedure to standardize for the observed number of species).

| Variables | Variable description | R-function/package |
|---|---|---|
| Taxonomic diversity | | |
| Species richness | Log-transformed species richness | Specnumber/vegan |
| Species entropy (species diversity) | Shannon diversity index ($H' = -\sum_{i=1}^{S} p_i \ln p_i$, $p_i$ = the proportion of individuals belonging to the ith species, $S$ = species richness) | Diversity/vegan |
| Species evenness | Pielou's evenness index ($J' = H'/\ln S$, $H'$ = Shannon diversity index, $S$ = species richness) | Diversity/vegan, Specnumber/vegan |
| Functional diversity | | |
| Functional richness | The minimum convex hull, which covers all locally present species in a multi-dimensional functional space | dbFD/FD |
| Functional entropy | Mean abundance-weighted pairwise distance between co-occurring species in a multi-dimensional functional space | mpd/picante |
| Functional evenness | Measured by comparing the observed abundance-weighted pairwise distance with the distance of perfect regularity of abundance distribution along a minimum spanning tree that covers all species in a multi-dimensional functional space | dbFD/FD |
| Phylogenetic diversity | | |
| Phylogenetic richness | The minimum convex hull, which covers all locally present species in a multi-dimensional phylogenetic space | dbFD/FD |
| Phylogenetic entropy | Mean abundance-weighted pairwise distance between co-occurring species in a multi-dimensional phylogenetic space | mpd/picante |
| Phylogenetic evenness | Measured by comparing the observed abundance-weighted pairwise distance with the distance of perfect regularity of abundance distribution along a minimum spanning tree that covers all species in a multi-dimensional phylogenetic space | dbFD/FD |

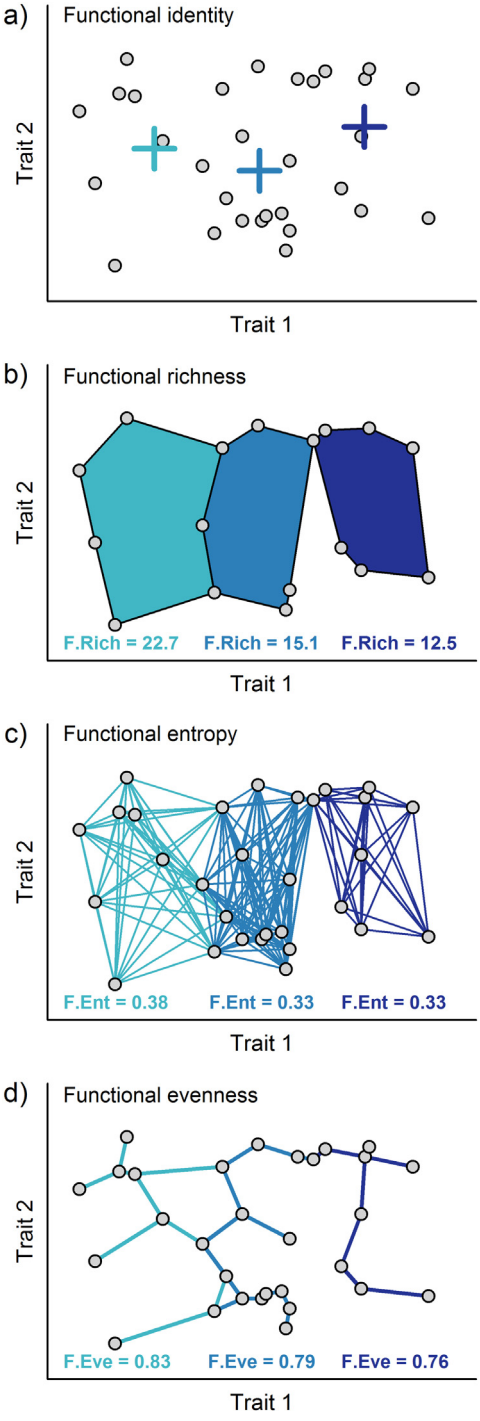


**Fig. 2.** Hypothetical examples of functional and phylogenetic diversities quantified via different distance-based measures, based on species differences in functional traits or phylogenetic ancestries. a) The functional (phylogenetic) structure of hypothetical bird community's change along three categories along a gradient of forest structures, indicated by different blue colors. Species (grey dots) are plotted in a two-dimensional functional space according to their trait values, whereas the mean trait values (i.e. functional identity of communities) along the gradient are marked by colored crosses (note that for simplification all species have abundance 1). b) Functional richness measured as minimum convex hull encompassing all species in a local community. Here, functional richness decreases along the environmental gradient. c) Functional entropy, measured as mean pairwise distance between co-occurring species. d) Functional evenness represents the distribution of species among the minimum-spanning tree in the functional space. Functional evenness will approach 1, when the distances between all nearest neighbor species pairs are identical and when all species have the same abundance. By contrast, functional evenness will approach 0, when species are clustered among the minimum-spanning tree. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

using the function *cvrisk*. To test for variability in effects, 25 bootstraps were applied for each model. We averaged the selection frequencies and explained risks of the 25 bootstraps to compare the importance of predictors. We did not use interaction terms, because in contrast to our main effects we lacked a-priori assumptions on ecological mechanisms of interactions.

## 3. Results

The bird data consisted of 15,142 individual observation records comprising 173 species in 637 plots across the four study areas. In our study plots, the bivariate correlation of the four environmental variables, the absolute values of Spearman rank correlation, were below 0.6 (Fig. S5), which revealed that each predictor related to a unique component of the environmental gradients in productivity and heterogeneity. However, $NDVI_{mean}$ was slightly correlated with $CD_{>2m}$ and $H_{SD}$ ($rho$ = 0.53 and 0.48, respectively). The average selection frequencies and explained empirical risks of 25 cross-validations were higher with $NDVI_{mean}$ and $CD_{>2m}$ for seven out of nine measures (Fig. 3). The effects of $NDVI_{mean}$ were consistently the strongest for taxonomic diversity measures, but the importance of $CD_{>2m}$, $H_{SD}$, and $NDVI_{SD}$ increased for functional/phylogenetic measures. In case of three taxonomic measures, the average selection frequencies were consistently the highest in $NDVI_{mean}$ (30.9%, 29.9%, and 37.7% for taxonomic richness, entropy, and evenness, respectively). On the other hand, in case of functional and phylogenetic measures, the most selected variables were $NDVI_{mean}$, $CD_{>2m}$, $H_{SD}$, and $NDVI_{SD}$ in turn; $NDVI_{mean}$ in functional evenness and phylogenetic richness (selection frequencies of 24.5% and 24.9%, respectively), $CD_{>2m}$ in functional and phylogenetic diversity (52.8% and 30.0%), and $H_{SD}$ in functional richness (28.7%), and $NDVI_{SD}$ for phylogenetic evenness (18.6%). The explained empirical risks showed similar relative importance of predictors on diversity measures as selection frequencies except functional richness and entropy (see more details in Table S2).

We found incongruent responses of taxonomic, functional, phylogenetic diversity to the four predictors tested, contrary to our hypotheses (Fig. 4). Functional and phylogenetic measures were compatible, while functional/phylogenetic measures showed contrary shapes to taxonomic measures, in particular richness and entropy indices. For instance, $NDVI_{mean}$ had positive-monotonic relationships with taxonomic richness/entropy concurring with our first hypothesis, but negative and fuzzy relationships with functional and phylogenetic richness/entropy, disagreeing with the hypothesis (Fig. 4c and g). The response of taxonomic richness/entropy on $CD_{>2m}$ and $NDVI_{SD}$ was bell-shaped, in contrast to functional and phylogenetic richness/entropy, which displayed a U-shaped response (Fig. 4a, d, e, and h). The taxonomic richness/entropy was highest at $CD_{>2m}$ about 40% and $NDVI_{SD}$ about 0.05, while functional and phylogenetic richness/entropy was lowest at $CD_{>2m}$ about 60% and $NDVI_{SD}$ about 0.05. Functional and phylogenetic richness/entropy was highest in very low or high levels of canopy density (i.e. widely open or densely closed canopy forest) where taxonomic richness/entropy was lowest. Taxonomic richness/entropy decreased with $H_{SD}$, while functional and phylogenetic richness increased (Fig. 4b and f). Such multiple diversity responses to heterogeneity were different from our second hypothesis.

While the richness and entropy revealed compatible responses to most predictors as described above, the evenness displayed incompatible responses, in particular to taxonomic measures. In low

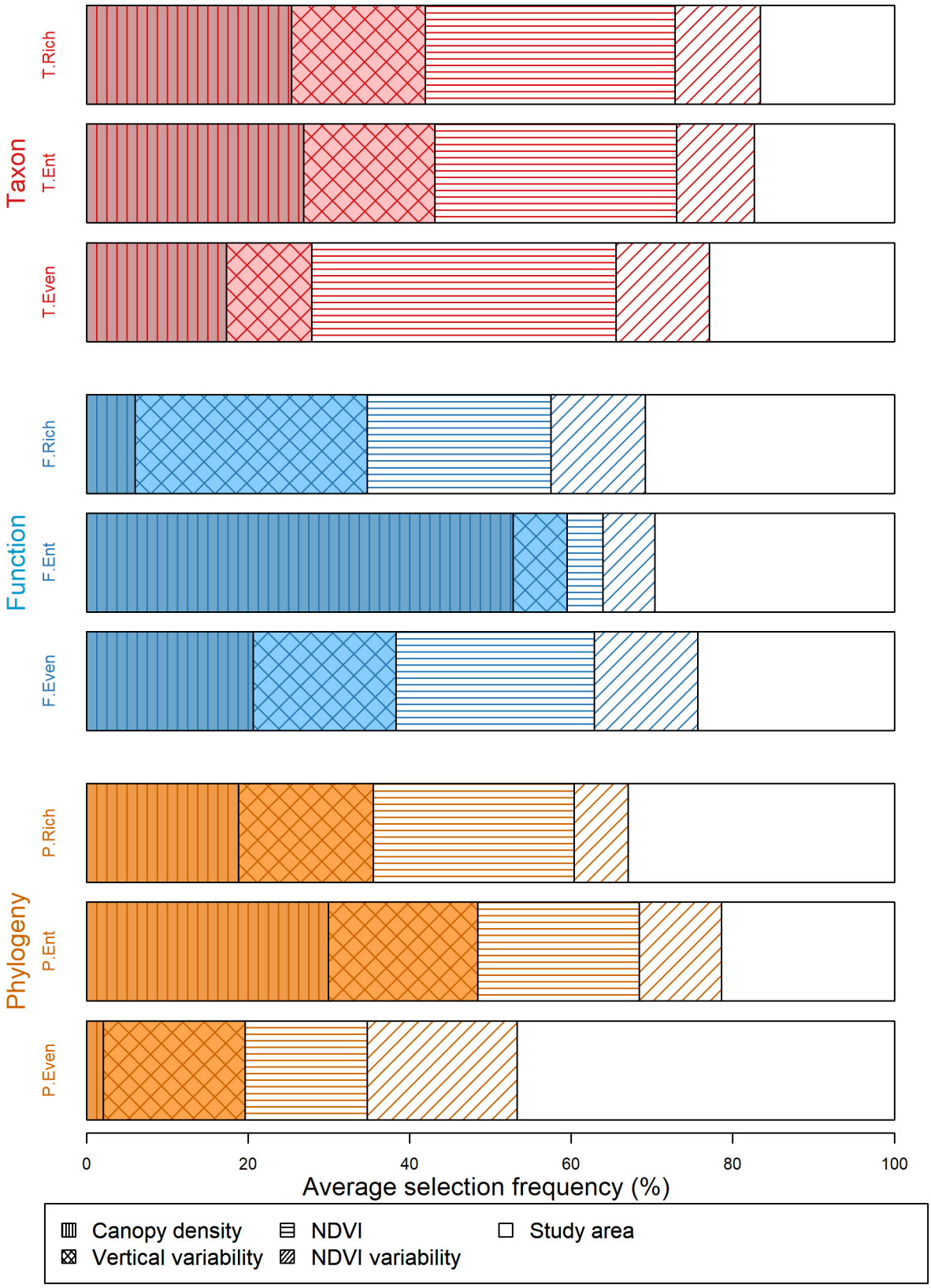


**Fig. 3.** Average selection frequencies (unit: %) of canopy density ($CD_{>2m}$), vertical variability ($H_{SD}$), mean NDVI (Normalized Vegetation Index) ($NDVI_{mean}$), and NDVI variability ($NDVI_{SD}$) as fixed factors and study area as a random factor in boosted generalized additive models for taxonomic, functional, and phylogenetic richness (T.Rich, F.Rich, P.Rich), entropy (T.Ent, F.Ent, P.Ent), and evenness (T.Even, F.Even, P.Even). The selection frequencies were averaged from 25 bootstrap models (see more details in Table S2).

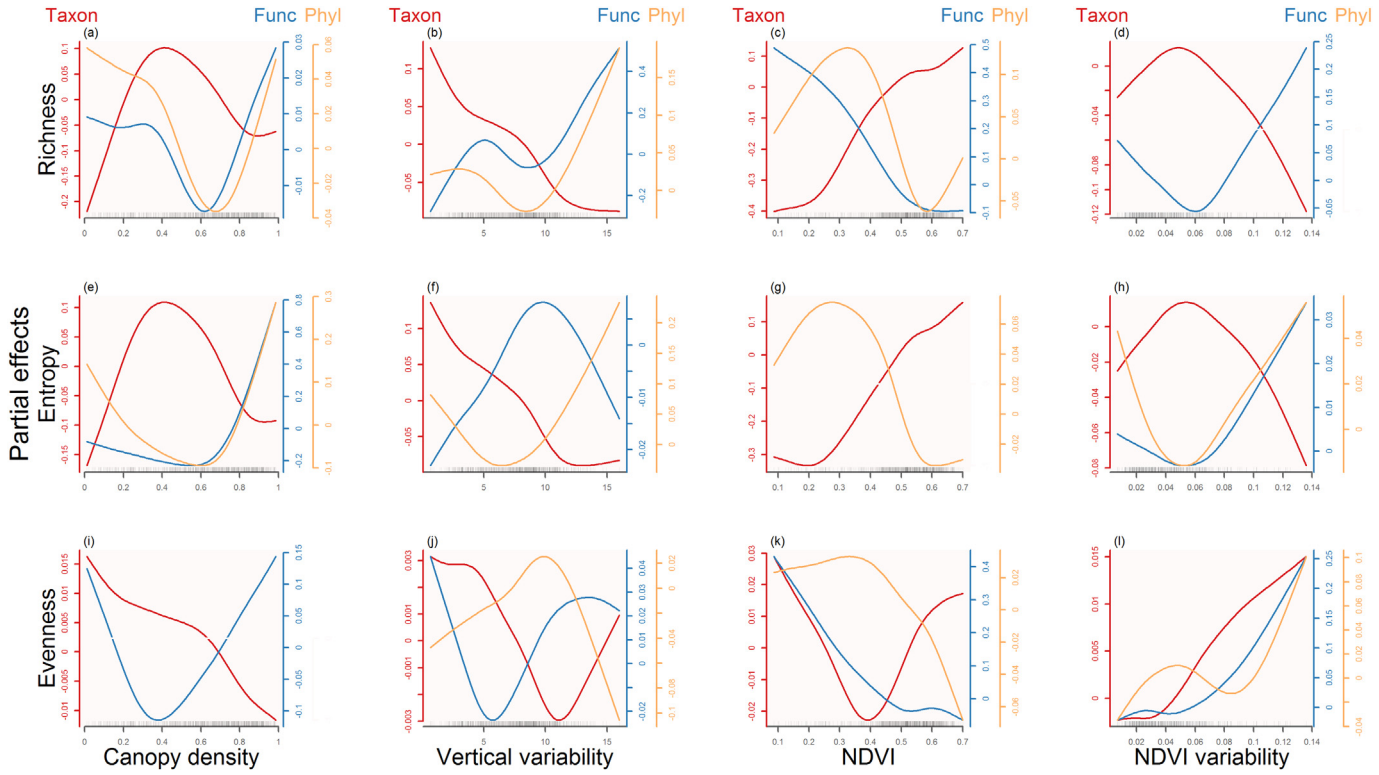


**Fig. 4.** Estimated partial effects of canopy density ($CD_{>2m}$), vertical variability ($H_{SD}$), mean NDVI ($NDVI_{mean}$), and NDVI variability ($NDVI_{SD}$) on taxonomic (Taxon), functional (Func), and phylogenetic (Phyl) diversity indices with red, blue, and orange lines, respectively; the response of taxonomic, functional, and phylogenetic richness on (a) $CD_{>2m}$, (b) $H_{SD}$, (c) $NDVI_{mean}$, and (d) $NDVI_{SD}$, the response of taxonomic, functional, and phylogenetic entropy on (e) $CD_{>2m}$, (f) $H_{SD}$, (g) $NDVI_{mean}$, and (h) $NDVI_{SD}$, and the response of taxonomic, functional, and phylogenetic evenness on (i) $CD_{>2m}$, (j) $H_{SD}$, (k) $NDVI_{mean}$, and (l) $NDVI_{SD}$. The ticks on the x-axis reflect the observed values. Only those variables selected by a boosted generalized additive model are displayed. Please refer to Appendices Figs. S10–S12 for detailed results. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

canopy density forests, both taxonomic and functional evenness were high, and taxonomic evenness decreased with increasing $CD_{>2m}$ (Fig. 4i). Taxonomic, functional, and phylogenetic evenness indices showed divergent peaks ranging from low to high $H_{SD}$ (Fig. 4j). They were high in forest with low $NDVI_{mean}$, and taxonomic evenness was high in forests with high $NDVI_{mean}$ as well (Fig. 4k). They increased with $NDVI_{SD}$ (Fig. 4l). Overall, bootstrap samples support the robustness of our effects (Figs. S9–S11).

## 4. Discussion

Our results demonstrate that measurement of the 3-D vegetation structure derived from airborne lidar provided similar independent and complementary explanatory power as NDVI variables extracted from Landsat measurements for multiple biodiversity measures at our local scale, and that 3-D vegetation structure tended to be more important for functional and phylogenetic diversity measures compared to taxonomic measures. This underlines the strength of relationship of remotely sampled forest structure to the functional/phylogenetical composition of breeding bird communities and generalizes recent findings of the importance of 3-D vegetation structure on bird diversity derived in single regions (Goetz et al., 2007; Goetz et al., 2014; Vogeler et al., 2014). Additionally, the effects of vegetation structure contrasted between taxonomic diversity and functional/phylogenetic diversity, which affirms the necessity to include functional and phylogenetic diversity measures beyond taxonomic diversities in local forest management for conservation objectives (Jetz et al., 2016).

It is important to acknowledge that our study only dealt with vegetation physiognomy and neglected the composition of tree species. We are aware that tree species composition might be another important predictor of bird diversity and is particularly critical for frugivores (Kissling et al., 2007). However, MacArthur and MacArthur (1961) noted that residuals of a bird diversity versus foliage height diversity model were not correlated with plant species diversity in temperate forests. The results from MacArthur and MacArthur (1961) initiated an ongoing debate about the relative importance of vegetation composition versus physiognomy for the diversity and composition of bird assemblages, but with equivocal results (Fleishman and Mac Nally, 2006; MacArthur and Pianka, 1966; Rotenberry, 1985). While plant composition might override the effects of physiognomy in more open forest types or savannas, the opposite has been found in temperate forests (Müller et al., 2010).

Our finding of the importance of mean NDVI is in line with studies using NDVI for estimating bird species richness (e.g. Pettorelli et al. (2006)), since it explains a large portion of spatial richness variation (for example, > 50% of avian species richness in North America (Hurlbert and Haskell, 2003; Seto et al., 2004) and could cover large spatial and temporal extents. Moreover, the positive relationships between NDVI and taxonomic richness and entropy are in agreement with results of previous studies on productivity-diversity relationships (Cusens et al., 2012; Rosenzweig, 1995; Waide et al., 1999). However, our positive productivity-diversity relationships were not explained by the more specialization hypothesis which assumes high levels of productivity increase rare resources and niche position specialists (Evans et al., 2005; Srivastava and Lawton, 1998). By contrast, our results showed that increased mean NDVI values are associated with a higher number of species, but highly productive forests support more species that are functionally similar (Fig. 4c). Although the phylogenetic richness did not show the same response to mean NDVI as functional richness, it indicated phylogenetically less rich communities despite more species in highly productive forests. Bird assemblages with taxonomically diverse but functionally and phylogenetically similar

species at highest levels of NDVI were presumably explained by the more individuals hypothesis, which assumes higher number of species is supported by more productive sites through low extinction risk because of higher population densities (Evans et al., 2005; Müller et al., 2017; Srivastava and Lawton, 1998).

Our study revealed that canopy density had the second highest explanatory power on diversity of temperate forest bird assemblages. The initial positive relationship of canopy density and avian taxonomic diversity confirms previous studies that employed traditional field survey measurements, such as the sum of coverage of multiple canopy layers (Karr and Roland, 1971; Willson, 1974), while to our knowledge the latter decrease of taxonomic diversity, i.e., bell-shaped pattern, has been rarely observed. However, Hanspach et al. (2012) found that both total bat activity and bat species richness in forests were highest at intermediate tree density, due to the fact that both species that prefer dense and sparse tree covers can co-occur in intermediate-density forests. Similarly, this finding might reflect the zone of overlap between (decreasing) shrub bird species and (increasing) forest species along the gradient of increasing canopy density (Goetz et al., 2007). This is in line with the findings that in temperate forest one of the major habitat variables is the variation in light near the floor. For instance, in an experiment where huge amounts of deadwood were exposed in canopy gaps and under closed canopy, the most important variable for determining the composition of deadwood dependent insects was the light availability near the ground (Seibold et al., 2016). Therefore a forest stand of intermediate canopy density with both sunny and shady conditions, more generally speaking the high horizontal heterogeneity of light on the forest floor, promotes very different species compositions and thereby a high total taxonomic diversity.

Likewise, canopy density was used as a metric of canopy gaps introducing shrubs and herbaceous vegetation in forests (Kane et al., 2010; Lesak et al., 2011) and hence intermediate canopy density might reflect the presence of different vertical layers such as herbs, shrubs, and trees. The unimodal peak might reflect the turning point of herb layer coverage (Fig. S12), thus the diversity of herbs, shrubs, and trees layer, generally speaking the vertical heterogeneity, is high at the middle canopy density. Canopy density was also highly correlated with the vertical distribution of canopy layers such as the vertical distribution ratio and the coefficient of variation of vegetation height (Spearman rank correlation = 0.85 and −0.87 respectively, $p < 0.001$, see Fig. S13), which were representative indices of vertical heterogeneity increasing bird diversity in previous studies (Davies and Asner, 2014). Therefore, such an effect of high structural heterogeneity in both horizontal and vertical axes on high taxonomic diversity at intermediate canopy density can be easily linked to the habitat heterogeneity hypothesis. Canopy density explained much variance which $H_{SD}$ (another vertical heterogeneity) and $NDVI_{SD}$ (horizontal heterogeneity) left in the boosted generalized additive models and the correlations between canopy density and $H_{SD}$ and $NDVI_{SD}$ were low ($rho = 0.36$ and $-0.25$, respectively, see Fig. S5). Hence, we inferred that canopy density might detect a unique component of the heterogeneity gradients different from $H_{SD}$ and $NDVI_{SD}$ in forest and could explain taxonomic diversity via both horizontal and vertical heterogeneity better than $H_{SD}$ and $NDVI_{SD}$.

To our knowledge, the U-shaped relationship between canopy density and functional/phylogenetic diversity, in contrast to the response patterns of taxonomic diversity have yet not been observed. Functional richness showed a slightly U-shaped pattern, which indicated more unique functions by relatively fewer species at very low or high levels of canopy density. In contrast, many species are functionally similar at intermediate levels of canopy density. Additionally, the U-shaped pattern of functional/phylogenetic entropy implied that functionally and phylogenetically distinct species were abundant, leading to high abundance weighted mean pairwise distances in very dense or very open forest. Moreover, the U-shaped response of functional evenness indicated that species assemblages at the extremes of the canopy density gradient were more evenly distributed in functional space than expected by chance. Taken together, at the extremes of canopy density, bird assemblages occupied slightly larger functional space, but with very regular distribution and high abundance of functionally distinct species.

Such differential responses of functional/phylogenetic diversity from taxonomic diversity to environmental gradients have led to new insights into understanding of community assembly mechanisms (Cadotte et al., 2013). These mechanisms can be theoretically assigned to two main assembly rules that act on species trait-based differences: environmental filtering and limiting similarity (Holdaway and Sparrow, 2006). Environmental filtering results in an aggregation of traits in local communities by selecting species that are more similar than expected by chance, to cope with given environmental conditions. By contrast, limiting similarity segregates traits present in a local community by interspecific competition, i.e., exclusion of ecologically similar species, and results in communities composed of species that are less similar than expected by chance (Calba et al., 2014; Holdaway and Sparrow, 2006). Increases in functional/phylogenetic diversity and decreases in taxonomic diversity in widely open or dense forests could be explained by competitive exclusion within same traits and lineages among species (Webb et al., 2002). Indeed, high interspecific competition can eliminate ecologically similar species, thereby segregating traits (i.e., limiting similarity in the traits held by multiple species) and increasing functional/phylogenetic diversity (Calba et al., 2014; Holdaway and Sparrow, 2006).

The lidar-derived vertical variability of vegetation ($H_{SD}$) negatively affected taxonomic richness and entropy, contrary to the habitat heterogeneity hypothesis. Previous studies occasionally revealed contrasting (both positive and negative) effects of vertical structural heterogeneity on bird species diversity, since the effects were dependent on other environmental factors such as productivity (Bar-Massada and Wood, 2014; Stirnemann et al., 2015; Verschuyl et al., 2008). For example, Bar-Massada and Wood (2014) and Verschuyl et al. (2008) demonstrated different responses of bird species richness (positive, negative, and unimodal relationship) among different habitat types (grasslands, savannas, or woodlands) and landscapes along a productivity gradient. Stirnemann et al. (2015) demonstrated that bird species richness revealed contrasting responses to shrub heterogeneity due to varying amounts of tall tree cover. A challenge with using structural heterogeneity and productivity in forests as determinants of biodiversity is the correlation between them (see Fig. S5). Such a correlation made studies about the relationship between vertical structural heterogeneity and species diversity difficult, regardless of long-held concerns since MacArthur and MacArthur (1961). However, by separating the effects of vertical variability on bird diversity using boosted generalized additive models (see details in Section 2.4. Data analyses), we showed negative effects of vertical structural heterogeneity when the effects of vegetation biomass or productivity (available energy for birds) were excluded.

Contrary to taxonomic diversity, the vertical variability of vegetation ($H_{SD}$) had a positive relationship with functional richness, phylogenetic richness, and phylogenetic entropy, which concurred with the habitat heterogeneity hypothesis. The result indicated that bird species having unique traits or phylogenetically distinct lineages may preferentially inhabit vertically variable forests. Consequently, fewer species could exist in vertically highly variable forest, but they cover a wider range of functional traits and phylogenetic lineages, since the functional traits and phylogenetic lineages of the few existing species can be very different from each other. On the contrary, more species could exist having similar function in ecosystem and could be phylogenetically closely related in vertically less variable forest.

We can find the mechanism of such results from the area-heterogeneity trade-off (Allouche et al., 2012). Allouche et al. (2012) suggested that the narrower the niche width of a species, the more rapidly the amount of effective niche area decreases with increasing habitat

heterogeneity. Hence, relationships between species richness and habitat heterogeneity vary from negative to positive, including bell-shaped relationships, promoted by stochastic extinction of narrow niche species in very heterogeneous habitats (Allouche et al., 2012). In our cases, high vertical variability may create high niche diversity with smaller niche size compared to the amount of suitable area for each species (see the T2_76 plot in Bavaria in Fig. S14), which results in increasing competition within similar functional groups (i.e. limiting similarity). Therefore, species at high values of the heterogeneity gradient may be more specialized (i.e., functionally unique), but fewer species can survive. For instance in multilayered stands even though there are shrubs, the area for a shrub species might be too small to cover the territory of songbird with 0.5–1.0 ha. Our study could give initial insights to answer the effects of vertical structural heterogeneity on local bird diversity of not only taxonomic, but also functional and phylogenetic aspects excluding the effects of productivity.

The NDVI variability ($NDVI_{SD}$) showed a bell-shaped relationship with taxonomic richness/entropy supporting the area-heterogeneity trade-off. The decrease in taxonomic diversity but increase in functional/phylogenetic diversity at higher values of $NDVI_{SD}$ (i.e., $NDVI_{SD} > 0.05$) can be caused by the shortage of sufficient niche area which promotes competition and limits similarity. From the increase of functional/phylogenetic diversity but decrease of taxonomic diversity in horizontally and vertically heterogeneous forest (i.e., very high $NDVI_{SD}$ and $H_{SD}$, respectively), we assumed that extinction in very heterogeneous habitat could be caused by competitive exclusions of functionally similar species, rather than stochastic extinctions.

Although our four productivity and heterogeneity predictors were associated with the multiple measures of bird diversity tested in this study, the distinct dependent variables (i.e. taxonomic, functional, and phylogenetic diversity) showed varying responses. Functional and phylogenetic measures were congruent, while functional/phylogenetic measures were dissimilar to taxonomic measures, in particular to richness and entropy. Previous studies found only the difference in the extent of effects of environmental factors on various measures of diversity (de Bello et al., 2013; Dehling et al., 2014; Grass et al., 2015; Sitters et al., 2016), while a few studies found contrasting response patterns between taxonomic diversity and functional diversity (Gerisch et al., 2012). Our results matched the results on ground beetle diversity of Gerisch et al. (2012), who reported that taxonomic and functional diversity were affected by environmental factors in contrasting ways. Our result suggests that functional and phylogenetic diversity of breeding birds may be fueled by very open and dense forest stands, in contrast to taxonomic diversity that may be fostered by medium density stands. Regarding the NDVI analysis, taxonomic richness and entropy were the highest in highly productive forests, while all three measures of functional diversity were highest in the least productive forests. The deviation between the different facets of biodiversity of birds in forests underlines the importance of considering a wide range of measures of biodiversity when exploring forest structure-biodiversity relationships. This finding is similar to recent findings that demonstrated that including goals for functional diversity led to the selection of a wider range of protected areas for coral fish species (Stuart-Smith et al., 2013).

Spatial grain size can influence the strength, shape, and underlying mechanism of productivity-diversity and habitat-heterogeneity relationships (Stein et al., 2014; Whittaker et al., 2001). Varying spatial grain might change the relative importance of independent variables, since the effect of environmental heterogeneity on species diversity could increase with the increase of spatial grain (Stein et al., 2014). In our study, we set the spatial grain of environmental variables equivalent to the resolution of the bird surveys (i.e., a radius of 75 m) to investigate effects of productivity and heterogeneity on multiple facets of bird diversity at a local scale. We used a spatial grain comparable to a forest management unit (i.e., a forest stand scale), rather than a landscape scale, to help address local forest management strategies aimed at conserving facets of biodiversity.

## 5. Conclusion

Combining standardized measures of taxonomic, functional, and phylogenetic diversity with derivatives from active and passive remote sensing provided new perspectives and tools for managing temperate forests for biodiversity conservation. Additionally, the contrary effects of environmental gradients on taxonomic, functional, and phylogenetic diversity affirm the necessity to consider multiple facets of biodiversity in local conservation management. The contrasting responses of different facets of biodiversity supports forest management that promotes a high variety of canopy densities and vertical variability across forest stands; for example, at very low or high levels of canopy density, bird assemblages displayed more functions despite being comprised of relatively fewer species, with very regular distributions and highly abundant, functionally distinct species. Such a strategy might mimic natural forests in which different successional stages co-exist alongside nearby disturbance-created open patches (Bormann and Likens, 1979). This strategy may be more important in areas such as the temperate deciduous forest in Europe and East Asia, where canopy density has become more homogeneous due to decreased levels of natural disturbance and increased growing stocks (Schelhaas et al., 2003). Our results only partly matched our expectations, based on the productivity-diversity and habitat-heterogeneity-hypotheses, but observed discrepancies could be explained by area-heterogeneity trade-offs and limiting similarity. Future research is needed to reveal whether these relationships hold in other temperate forest types and for other spatial grain and extent.

## Acknowledgement

This research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2013R1A1A2012874), the 4th National Ecosystem Survey by Ministry of Environment, and DFG (German Science Foundation) Priority Program 1374 “Biodiversity-Exploratories” (grant numbers LE 3316/2-1). National Geographic Information Institute of Korea, collaborations between the University of Idaho and the US Forest Service Rocky Mountain Research Station, and the Bavarian State Office for Land Survey and Geo-information provided the airborne lidar data for sites in Korea, Idaho, and Germany, respectively.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2018.05.031.

## References

Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., Kadmon, R., 2012. Area–heterogeneity tradeoff and the diversity of ecological communities. Proc. Natl. Acad. Sci. 109, 17495–17500.
Axelsson, P., 2000. DEM generation from laser scanner data using adaptive TIN-Models. Int. Arch. Photogramm. Remote. Sens. 33, 110–117.
Bar-Massada, A., Wood, E.M., 2014. The richness–heterogeneity relationship differs between heterogeneity measures within and among habitats. Ecography 37, 528–535.
Bässler, C., Cadotte, M.W., Beudert, B., Heibl, C., Blaschke, M., Bradtka, J.H., Langbehn, T., Werth, S., Müller, J., 2016a. Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. Ecography 39, 689–698.
Bässler, C., Müller, J., Cadotte, M.W., Heibl, C., Bradtka, J.H., Thorn, S., Halbwachs, H., 2016b. Functional response of lignicolous fungal guilds to bark beetle deforestation. Ecol. Indic. 65, 149–160.
de Bello, F., Lavorel, S., Lavergne, S., Albert, C.H., Boulangeat, I., Mazel, F., Thuiller, W., 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. Ecography 36, 393–402.
Bibby, C.J., Burgess, N.D., Hill, D.A., 2012. Bird Census Techniques. Academic Press, London.
Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady state in

northern hardwood forests: a new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. Am. Sci. 67, 660–669.
Brosofske, K.D., Chen, J., Crow, T.R., 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape. For. Ecol. Manag. 146, 75–87.
Cadotte, M.W., Davies, T.J., 2016. Phylogenies in Ecology A Guide to Concepts and Methods. Princeton University Press.
Cadotte, M.W., Dinnage, R., Tilman, D., 2012. Phylogenetic diversity promotes ecosystem stability. Ecology 93, S223–S233.
Cadotte, M., Albert, C.H., Walker, S.C., 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecol. Lett. 16, 1234–1244.
Calba, S., Maris, V., Devictor, V., 2014. Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices. Glob. Ecol. Biogeogr. 23, 669–678.
Chapin III, F.S., Kofinas, G.P., Folke, C., Chapin, M.C., 2009. Principles of Ecosystem Stewardship: Resilience-based Natural Resource Management in a Changing World. Springer.
Chen, X., Vierling, L., Rowell, E., Defelice, T., 2004. Using lidar and effective LAI data to evaluate IKONOS and Landsat 7 ETM+ vegetation cover estimates in a ponderosa pine forest. Remote Sens. Environ. 91, 14–26.
Cisneros, L.M., Fagan, M.E., Willig, M.R., 2015. Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. Divers. Distrib. 21, 523–533.
Cusens, J., Wright, S.D., McBride, P.D., Gillman, L.N., 2012. What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. Ecology 93, 2241–2252.
Davies, A.B., Asner, G.P., 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends Ecol. Evol. 29, 681–691.
Dehling, D.M., Fritz, S.A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., Schleuning, M., 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography 37, 1047–1055.
Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol. Lett. 13, 1030–1040.
Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P., Pearse, W.D., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecol. Evol. 3, 2958–2975.
Dobson, L.L., Sorte, F.A.L., Manne, L.L., Hawkins, B.A., 2015. The diversity and abundance of North American bird assemblages fail to track changing productivity. Ecology 96, 1105–1114.
Drever, M.C., Goheen, J.R., Martin, K., 2009. Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90, 1095–1105.
Evans, J.S., Hudak, A.T., 2007. A multiscale curvature algorithm for classifying discrete return LiDAR in forested environments. IEEE Trans. Geosci. Remote Sens. 45, 1029–1038.
Evans, K.L., Warren, P.H., Gaston, K.J., 2005. Species–energy relationships at the macroecological scale: a review of the mechanisms. Biol. Rev. 80, 1–25.
Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.
Fleishman, E., Mac Nally, R., 2006. Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy, and primary productivity in the central Great Basin, USA. Divers. Distrib. 12, 236–243.
Floren, A., Schmidl, J. (Eds.), 2008. Canopy Arthropod Research in Europe – Basic and Applied Studies From the High Frontier. Bioform Entomology, Nuremberg, Germany.
Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol. Lett. 12, 22–33.
Gerisch, M., Agostinelli, V., Henle, K., Dziock, F., 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos 121, 508–515.
Glutz von Blotzheim, U.N., Bauer, K.M., 1985. Handbuch der Vögel Mitteleuropas, 2nd ed. Aula-Verlag, Wiesbaden.
Goetz, S., Steinberg, D., Dubayah, R., Blair, B., 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sens. Environ. 108, 254–263.
Goetz, S.J., Sun, M., Zolkos, S., Hansen, A., Dubayah, R., 2014. The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness. Environ. Res. Lett. 9, 034013.
Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 27, 857–871.
Grass, I., Brandl, R., Botzat, A., Neuschulz, E.L., Farwig, N., 2015. Contrasting taxonomic and phylogenetic diversity responses to forest modifications: comparisons of taxa and successive plant life stages in south African scarp forest. PLoS One 10, e0118722.
Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768.
Hanspach, J., Fischer, J., Ikin, K., Stott, J., Law, B.S., 2012. Using trait-based filtering as a predictive framework for conservation: a case study of bats on farms in southeastern Australia. J. Appl. Ecol. 49, 842–850.
Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S., 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92, 1818–1827.
Hill, R., Hinsley, S., 2015. Airborne Lidar for woodland habitat quality monitoring: exploring the significance of Lidar data characteristics when modelling organism-habitat relationships. Remote Sens. 7, 3446.
Holdaway, R.J., Sparrow, A.D., 2006. Assembly rules operating along a primary riverbed–grassland successional sequence. J. Ecol. 94, 1092–1102.
Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San Jose.
Hothorn, T., Müller, J., Schröder, B., Kneib, T., Brandl, R., 2010. Decomposing environmental, spatial, and spatiotemporal components of species distributions. Ecol. Monogr. 81, 329–347.
Huang, Q., Swatantran, A., Dubayah, R., Goetz, S.J., 2014. The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. PLoS One 9, e103236.
Hurlbert, A.H., 2004. Species–energy relationships and habitat complexity in bird communities. Ecol. Lett. 7, 714–720.
Hurlbert, A.H., Haskell, J.P., 2003. The effect of energy and seasonality on avian species richness and community composition. Am. Nat. 161, 83–97.
Ishii, H.T., Tanabe, S.-i., Hiura, T., 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. For. Sci. 50, 342–355.
Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., Guralnick, R., Kattge, J., Latimer, A.M., Moorcroft, P., Schaepman, M.E., Schildhauer, M.P., Schneider, F.D., Schrodt, F., Stahl, U., Ustin, S.L., 2016. Monitoring plant functional diversity from space. Nat. Plants 2, 16024.
Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.
Kane, V.R., McGaughey, R.J., Bakker, J.D., Gersonde, R.F., Lutz, J.A., Franklin, J.F., 2010. Comparisons between field- and LiDAR-based measures of stand structural complexity. Can. J. For. Res. 40, 761–773.
Karr, J.R., Roland, R.R., 1971. Vegetation structure and avian diversity in several new world areas. Am. Nat. 105, 423–435.
Kissling, W.D., Rahbek, C., Böhning-Gaese, K., 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. Proc. R. Soc. B Biol. Sci. 274, 799–808.
Latifi, H., Hill, S., Schumann, B., Heurich, M., Dech, S., 2017. Multi-model estimation of understorey shrub, herb and moss cover in temperate forest stands by laser scanner data. Forestry 90, 496–514.
Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar remote sensing for ecosystem studies: lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists. Bioscience 52, 19–30.
Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J., Müller, J., 2013. Conservation value of forests attacked by bark beetles: highest number of indicator species is found in early successional stages. J. Nat. Conserv. 21, 97–104.
Lesak, A.A., Radeloff, V.C., Hawbaker, T.J., Pidgeon, A.M., Gobakken, T., Contrucci, K., 2011. Modeling forest songbird species richness using LiDAR-derived measures of forest structure. Remote Sens. Environ. 115, 2823–2835.
MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42, 594–598.
MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100, 603–609.
McGaughey, R.J., 2016. FUSION/LDV: Software for LIDAR Data Analysis and Visualization(Ver. 3.60+). (In P.N.R.S. USDA Forest Service (Ed.). Seattle, WA, USA).
Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82, 2381–2396.
Moning, C., Müller, J., 2008. Environmental key factors and their thresholds for the avifauna of temperate montane forests. For. Ecol. Manag. 256, 1198–1208.
Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.
Müller, J., Vierling, K., 2014. Assessing biodiversity by airborne laser scanning. In: Maltamo, M., Næsset, E., Vauhkonen, J. (Eds.), Forestry Applications of Airborne Laser Scanning. Springer, Netherlands, pp. 357–374.
Müller, J., Moning, C., Bässler, C., Heurich, M., Brandl, R., 2009. Using airborne laser scanning to model potential abundance and assemblages of forest passerines. Basic Appl. Ecol. 10, 671–681.
Müller, J., Stadler, J., Brandl, R., 2010. Composition versus physiognomy of vegetation as predictors of bird assemblages: the role of lidar. Remote Sens. Environ. 114, 490–495.
Müller, J., Brandl, R., Brändle, M., Förster, B., de Araujo, B.C., Gossner, M.M., Ladas, A., Wagner, M., Maraun, M., Schall, P., Schmidt, S., Heurich, M., Thorn, S., Seibold, S., 2017. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127, 814–824.
Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.
Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Chr. Stenseth, N., Delorme, D., Van Laere, G., Toïgo, C., Klein, F., 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112, 565–572.
R Core Tea, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.
Rotenberry, J., 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67, 213–217.
Ruiz, L., Hermosilla, T., Mauro, F., Godino, M., 2014. Analysis of the influence of plot size

and LiDAR density on Forest structure attribute estimates. Forests 5, 936.
Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Glob. Chang. Biol. 9, 1620–1633.
Seavy, N.E., Viers, J.H., Wood, J.K., 2009. Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. Ecol. Appl. 19, 1848–1857.
Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., Baraloto, C., 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. J. Appl. Ecol. 53, 934–943.
Seto, K.C., Fleishman, E., Fay, J.P., Betrus, C.J., 2004. Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. Int. J. Remote Sens. 25, 4309–4324.
Sitters, H., Di Stefano, J., Christie, F.J., Swan, M., York, A., 2016. Bird functional diversity decreases with time since disturbance: does patchy prescribed fire enhance ecosystem function? Ecol. Appl. 26, 115–127.
Srivastava, Diane S., Lawton, John H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am. Nat. 152, 510–529.
Stein, A., Kreft, H., 2015. Terminology and quantification of environmental heterogeneity in species-richness research. Biol. Rev. 90, 815–836.
Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17, 866–880.
Stirnemann, I., Ikin, K., Gibbons, P., Blanchard, W., Lindenmayer, D., 2015. Measuring habitat heterogeneity reveals new insights into bird community composition. Oecologia 177, 733–746.
Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501, 539–542.
Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.
Thorn, S., Bässler, C., Bernhardt-Römrmann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., Müller, J., 2016. Changes in the dominant assembly mechanism drives species loss caused by declining resources. Ecol. Lett. 19, 163–170.
Verschuyl, J.P., Hansen, A.J., Mcwethy, D.B., Sallabanks, R., Hutto, R.L., 2008. Is the effect of forest structure on bird diversity modified by forest productivity. Ecol. Appl. 18, 1155–1170.
Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S., Clawges, R.M., 2008. Lidar: shedding new light on habitat characterization and modeling. Front. Ecol. Environ. 6, 90–98.
Vierling, K.T., Swift, C.E., Hudak, A.T., Vogeler, J.C., Vierling, L.A., 2014. How much does the time lag between wildlife field-data collection and LiDAR-data acquisition matter for studies of animal distributions? A case study using bird communities. Remote Sens. Lett. 5, 185–193.
Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.
Vogeler, J.C., Hudak, A.T., Vierling, L.A., Evans, J., Green, P., Vierling, K.T., 2014. Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests. Remote Sens. Environ. 147, 13–22.
Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30, 257–300.
Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33, 475–505.
Weisberg, P.J., Dilts, T.E., Becker, M.E., Young, J.S., Wong-Kone, D.C., Newton, W.E., Ammon, E.M., 2014. Guild-specific responses of avian species richness to LiDAR-derived habitat heterogeneity. Acta Oecol. 59, 72–83.
Whittaker, R.J., Heegaard, E., 2003. What is the observed relationship between species richness and productivity? Comment. Ecology 84, 3384–3390.
Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28, 453–470.
Willson, M.F., 1974. Avian community organization and habitat structure. Ecology 55, 1017–1029.
Winter, S., Brambach, F., 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. For. Ecol. Manag. 262, 2120–2132.
Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: where are we? Trends Ecol. Evol. 28, 199–204.
Wright, D.H., 1983. Species-energy theory: an extension of species-area theory. Oikos 41, 496–506.