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# Forest Ecology and Management

# Divergent response to forest structure of two mobile vertebrate groups

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## ARTICLE INFO

## ABSTRACT

Taxonomic and functional diversity of animals respond to habitat heterogeneity. However, how structural heterogeneity at the stand level of differently managed forests drives species richness across taxa is not clear. Here we analyze how birds and bats, sharing the ability to fly, respond to the structural composition of the vegetation layers in differently managed forests. We combined datasets of birds and bats and compared their response as taxonomic vs. functional richness towards forest structure. Overall our results revealed that bird and bat species richness were positively correlated and species richness of both taxa peaked within the same forest stands. In contrast to our prediction that richness of mobile vertebrates with similar ecological traits (the ability to fly) should respond alike to forest stand characteristics, our results showed almost no congruence. Using Generalized Linear Mixed Effects Modeling (GLMM) with model selection based on AICc and model averaging, we found that taxonomic richness of birds and bats as well as functional richness (based on main diet and foraging mode) responded to forest structure in very different ways. While the taxonomic richness of birds was mainly associated with the structural parameters contrast and forest height, representing tall trees and a relatively closed canopy, richness of bat species increased with vertical and horizontal heterogeneity within forest stands. Our findings indicate that functional richness is more useful to understand responses of bird and bats species richness to land use, forest structure and forest management, rather than focusing solely on taxonomic groups.

## 1. Introduction

Intensification of forest management practices has modified natural vegetation dynamics in human-dominated landscapes in Central Europe (Ellenberg, 2009) and changed the underlying 'natural' patterns determining species richness and diversity (Lund and Rahbek, 2002; Renner et al., 2014). Understanding and identifying drivers of species richness and diversity in human-dominated landscapes has captivated ecologists for some time (Terborgh et al., 1990; Myers et al., 2000; Orme et al., 2005), but most studies limit their approaches to a single taxonomic group. In addition to land cover type, terrestrial species richness and diversity are influenced by habitat heterogeneity (Tews et al., 2004; Goetz et al., 2010), species-specific ecological and functional traits (Elith and Leathwick, 2009; Flynn et al., 2009), land use change (Sala et al., 2000), and also by chance (Gotelli and Ulrich, 2012; Renner et al., 2014). These factors may drive species richness across different taxa at the same localities in similar ways. However, the

direction, strength and significance of correlation between taxonomic groups across a set of localities and habitats have not yet been linked to functional groups. An improved understanding of whether taxa with similar ecological traits respond in similar or different ways to land use intensity would facilitate the setting of conservation priorities (Schulze et al., 2004). In addition, a comparison of the association of taxonomic groups and functional traits with the same suite of habitat descriptors would improve understanding of general rules related to local community assembly (sensu Martin and Proulx, 2016).

Most forests in Central Europe have been replaced by managed forest stands with modified tree species composition, age structure, and tree densities resulting in significant changes in microclimatic conditions and forest structure (Lindenmayer et al., 2000; McElhinny et al., 2005). Past and current silvicultural practices in Central Europe shaped over time a patchwork landscape of differently managed and structured forest stands, which in turn have resulted in increased suitable habitats and available resources for birds or bats. Forest structure has been

identified as a major driver of species richness through its influence on habitat quality for individual species (Bradbury et al., 2005). Forest structure is especially important for flying animals such as birds and bats that navigate and forage within the three-dimensional arrangements of trees (Jung et al., 2012). So far, both groups have been shown to respond to structural forest parameters by changes in species composition, species richness, and spatiotemporal habitat use (Bradbury et al., 2005; Flynn et al., 2009; Goetz et al., 2010; Müller et al., 2010; Ricklefs, 2011; Jung et al., 2012). However, whether taxonomic and functional richness of birds and bats within differently managed forest stands are associated with the same structural parameters remains unresolved.

*Li*ght *D*etection *A*nd *Ra*nging (LiDAR) methods have been shown to provide near continuous and quantitative forest structure variables that are impossible to assess using ground-based forest inventories (Lefsky et al., 2002; Vierling et al., 2008). Structural parameters derived from LiDAR provide a high spatial resolution of the three-dimensional arrangement of vegetation (Nieschulze et al., 2012) and have been used successfully as independent variables in studies with bird and bat species richness (Bradbury et al., 2005; Goetz et al., 2010).

Most importantly, several studies have shown that forest structure, particularly parameters describing forest height and vertical forest structure, can explain the increase or variation in species richness, species diversity, habitat use of birds or bats (e.g., Goetz et al., 2010; Vogeler et al., 2014; Froidevaux et al., 2016). Here we analyzed whether and how taxonomic and functional richness of two phylogenetically distinct vertebrate taxa, birds and bats, which share the ability to fly, respond to structural forest stand characteristics of differently managed forest stands in Central Europe. As both taxa navigate and forage in a three-dimensional space, we predicted that the same structural characteristics of the forest stands would be associated with species richness of birds and bats in managed forests, with particularly forest height driving species richness of both birds and bats.

## 2. Methods and study area

### 2.1. Study area

The study was conducted in the Biosphere Reserve Schorfheide-Chorin in north-east Germany, which harbors one of the three broadscale and long-term research platforms of the "Biodiversity Exploratories" (Fischer et al., 2010). We focused on 50 permanently marked forest sites (100 m × 100 m) representing characteristic forest stands of the study region, but differing in forest management history, tree species composition and vegetation structure. The 50 sites, each surrounded by a buffer zone of at least 30 m of the same management type, were classified according to the dominant tree species (forest inventory resulted in over 70% of canopy trees belonging to one species) into pine (*Pinus sylvestris*; 15 sites), beech (*Fagus sylvatica*; 20), oak (*Quercus rubor*; 7), oak/beech (1), and pine/beech (7) stands. The age of canopy trees on stand level varied from 23 years to 180 years (Pine: 23–100 years; Beech: 86–180; Oak: 95–130; Oak/Beech: 173; Pine/Beech: 88–135). A detailed description of the study area, selection of the 50 sites, and classification procedures is given in Fischer et al. (2010).

### 2.2. Bird and bat surveys

We surveyed birds on each of the 50 forest sites using standardized five minute point-counts located at the center of a site and recorded all birds seen and heard during this period on each site. Each forest site was visited five times between 15 March and 15 June 2009, resulting in a total observation time of 25 min per site. Five to 15 forest sites per day were surveyed by one observer from sunrise to 11:00 AM. The sequence of visited sites was randomized to avoid surveying sites always at the same time during the day. We considered a species to be present at a site if it was recorded at least once during all five surveys (assigned 1 for present and 0 for not observed). For all analyses, we used as response variable the accumulated number of species observed on each site during the survey period, i.e. species richness.

Birds were classified into functional groups based on their predominant food preference during the breeding season (about end of March to mid-June in Central Europe), which corresponded to our surveyed period. Functional groups included insectivores, omnivores, and granivores, based on Renner and van Hoesel (2017).

Bats were surveyed using standardized acoustic monitoring between June and September 2009. Surveys started after sunset and continued until 01:00 AM to cover the first peak in bat activity during the night (Rydell et al., 1996). Acoustic recordings were conducted for a total of 48 min along a 400 m transect following the site perimeter. Three to five forest sites were sampled each night and a total of two visits were made to each site during the season. Recordings were made using a Petterson-D1000x bat detector (Petterson Electronic AG, Uppsala, Sweden) at a sample rate of 384 kHz and manual triggering with a pre-trigger time of 10 s and a post trigger time of 50 s. We identified bat species and determined their presence (assigning 1 for present and 0 for not observed) per forest site using the software Avisoft SAS Lab Pro, Version 5.0.24 (Raimund Specht, Avisoft Bioacoustics, Berlin, Germany; spectrogram settings: Hamming window, 1024 FFT and 96% overlap). Some bat species, however, are difficult to identify with acoustics as they overlap in frequencies and call structure; we therefore grouped them into three sonotypes: *Plecotus*, *Myotis*, and 'Nyctaloid' to avoid overestimation of species richness (Jung et al., 2012).

Bats were classified according to their preferred foraging space into open space, edge space, and gleaning foragers (Schnitzler and Kalko, 2001). Within each of these functional groups, bat species share similar morphological and sensory traits, which directly affect species mobility, agility and prey perception.

To adjust for potential issues of detectability in birds and bats we used a species based approach and not abundance or activity (cf. Jung et al., 2012; Renner et al., 2014).

### 2.3. Forest structure

We used Light Detection and Ranging (LiDAR) to obtain continuous structural parameters of vegetation on all forest sites during leaf-on season in September 2009. LiDAR largely outperform traditional (i.e., discrete) forest type classifications (Bradbury et al., 2005; Goetz et al., 2010). Laser scanning was conducted using a Riegl LMS-Q 560 mounted on a helicopter. The scanner operated at a pulse repetition rate of 240 kHz and recorded up to seven peaks in the intensity of laser pulse returns. Because local point density varied up to $1159\,m^{-2}$ depending on flight velocity, altitude, and reflectivity, we down-sampled the local point density to a maximum of $500\,m^{-2}$. This resulted in a horizontal sampling accuracy of 50 cm and a vertical sampling accuracy of 15 cm. We mathematically derived 85 parameters for the forest structure of each forest site based on normalized raw data and the canopy height model (refer to Jung et al. (2012) and Nieschulze et al. (2012) for more details – variables are explained in Table 1).

### 2.4. Statistical analysis

We used Spearman rank-order correlation to assess whether bird and bat species richness were correlated and peaked at the same forest