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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

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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

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* 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).

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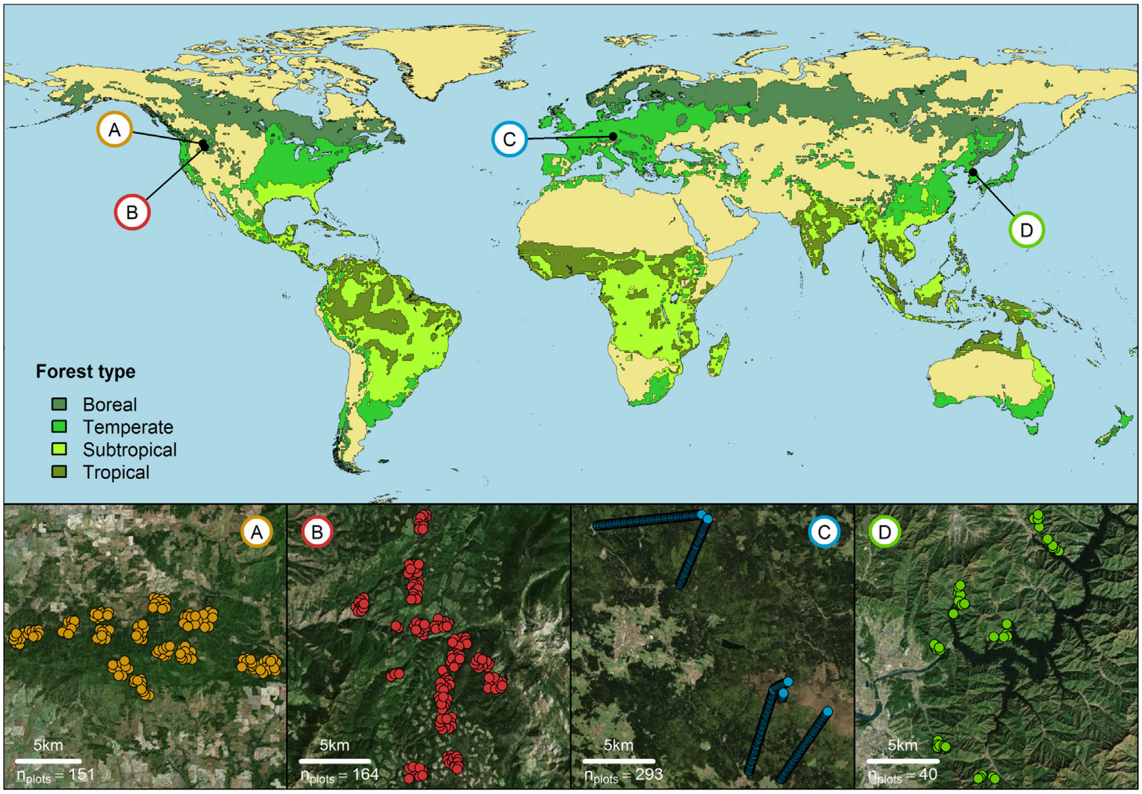

Fig. 1. Locations of four study areas in North America, Europe, and Asia (satellite image source: Bing map). Forest biomes according to the Holdridge Life Zone system (Holdridge, 1967) are indicated by different green shadings. (For interpretation of the references to color in this figure legend, the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