Predicting regional hotspots of phylogenetic diversity across multiple species groups

Sophia Franke | Roland Brandl | Christoph Heibl | Angelina Mattivi | Jörg Müller | Stefan Pinkert | Simon Thorn

Abstract
Aim: The protection of phylogenetic diversity has become a priority in conservation biology, but its achievement requires a detailed understanding of (a) hotspots of phylogenetic diversity on a management-relevant scale and (b) the land use and climate factors determining local phylogenetic diversity. In this study, we identified spatial patterns of taxonomic and phylogenetic diversity and their environmental drivers.

Location: Bavaria, Germany.

Methods: To map the cross-taxon phylogenetic diversity, we combined species distribution data obtained from country-wide monitoring programmes and phylogenetic trees of birds, bats, dragonflies, grasshoppers and butterflies and calculated the phylogenetic diversity standardized by species richness. Generalized additive models were used to test the effects of land use and climate on phylogenetic diversity. We identified hotspots of phylogenetic diversity and assessed the extent to which established protected areas in Bavaria cover these hotspots.

Results: High coverage by urban areas, arable land and water bodies negatively affected the phylogenetic diversity of most species groups. The phylogenetic diversity of birds increased with increasing meadow cover. Climate did not influence the phylogenetic diversity of the studied groups. We identified 10 regional hotspots that contained the highest standardized phylogenetic diversity across the examined species groups. There was a strong mismatch between hotspots of phylogenetic diversity among the species groups. Protected areas (national parks, natural reserves and areas of the Flora-Fauna-Habitat Directive) overlapped only to ~9.6% with these hotspots of standardized phylogenetic diversity.

Main conclusions: Cross-taxon approaches are required to identify hotspots of phylogenetic diversity at a management-relevant scale. At regional scales, land use was more important than climate in determining phylogenetic diversity. Our study highlights the importance of involving land users into strategies for protecting phylogenetic diversity.
1 | INTRODUCTION

Human population growth has led to an intensification of land use that often resulted in dramatic changes in species’ distributions and abundances (Habel, Samways, & Schmitt, 2019; Hooke, Martin-Duque, & Pedraza, 2012; Pimm & Raven, 2000). To slow down the rate of species loss, numerous conservation strategies have been developed (Gruber et al., 2012; Samways et al., 2020). Because range-size data for species are generally readily available, the focus of many of these strategies is the occurrence of enigmatic species or estimates of taxonomic diversity (Mammides, 2019; Miller, Jolley-Rogers, Mishler, & Thornhill, 2018; Zupan et al., 2014). However, it is increasingly recognized that these strategies ignore functional or phylogenetic aspects of biodiversity (Vane-Wright, Humphries, & Williams, 1991; Veron, Davies, Cadotte, Clergeau, & Pavoine, 2015).

Phylogenetic diversity has recently gained increasing attention as a surrogate for the diversity of functional traits of species that support the maintenance of ecological processes (Forest et al., 2007; Srivastava, Cadotte, MacDonald, Marushia, & Mirochnick, 2012). As such, it represents the ability of biological communities to respond to environmental changes (Winter, Devictor, & Schweiger, 2013). The recognition of phylogenetic diversity patterns is key to protecting both the unique features of biodiversity and the evolutionary history of local communities (Faith, 2013).

Measures of taxonomic and phylogenetic diversity are often strongly correlated (Devictor et al., 2010; Tucker & Cadotte, 2013). However, regions with comparatively high phylogenetic diversity can host biogeographically and phylogenetically unique species (Pouget et al., 2016). Phylogenetic diversity is also a surrogate for the historical factors underlying diversity patterns (Pinkert et al., 2018). By contrast, communities with disproportionally closely related species typically cluster in regions where environmental factors filter particular clades (Devictor et al., 2010; Faith, 1992; Tucker & Cadotte, 2013). Furthermore, patterns of phylogenetic diversity might differ considerably between taxonomic groups in the same area (Zupan et al., 2014), suggesting that single taxa are rather poor surrogates for the overall biodiversity. Nevertheless, the extent to which different species groups depict similar patterns of phylogenetic diversity in space remains largely unexplored, especially at scales relevant for conservation management.

Despite significant research effort on patterns and drivers of phylogenetic diversity during the last decade (Cadotte, Carscadden, & Mirochnick, 2011; Cadotte & Davies, 2010; Cadotte, Dinnage, & Tilman, 2012), the results of those studies have seldom been integrated into conservation practices (Veron et al., 2015; Winter et al., 2013). This is in part due to the fact that decision-making in conservation practice is carried out by small and arbitrarily defined political entities (Schwartz, 1999), whereas most phylogenetic diversity studies focus on countries (Devictor et al., 2010; Graham, Parra, Rahbek, & McGuire, 2009) or continents (Thuiller et al., 2015; Zupan et al., 2014). Furthermore, these studies are based on large grain sizes, which makes it difficult to define local conservation priorities and can lead to strong biases in prioritizing conservation actions (Pouget et al., 2016). For example, Huang, Davies, and Gittleman (2012) found that estimates of the loss of phylogenetic diversity at a global scale underestimate the actual loss of local phylogenetic diversity. Here, we investigated the phylogenetic diversity of birds, bats, dragonflies, grasshoppers and butterflies, important species groups in conservation planning and decision-making, across Bavaria, a federal state in Germany. Our main objective was to identify regions in Bavaria where measures of taxonomic diversity fail to protect the phylogenetic diversity of the considered species groups. We therefore assessed the extent to which patterns in phylogenetic diversity are congruent with patterns of taxonomic diversity. Further, we assessed the environmental drivers of these patterns. In addition, we mapped hotspots of phylogenetic diversity of the five species groups.

2 | METHODS

2.1 | Study area

The study was conducted in the federal state of Bavaria (see Appendix S1a for major natural regions), located in south-eastern Germany (47°16′N, 8°58′E) that covers an area of 70,550 km² and broad environmental gradients. The elevation ranges from 100 m a.s.l. (Main River) to 2,962 m a.s.l. (at the Zugspitze, the highest peak in the Wetterstein Mountains). The annual mean temperature ranges from −5°C in the south (at the Zugspitze) to 10°C in the north (Lower Franconia), and annual mean precipitation ranges from around 500 mm in the north to 2000 mm in the south (the Alps). Agriculture accounts for 47% of the land use in Bavaria (see Appendix S1b), whereby meadows occur largely in the south and crop land in the north. Cities, infrastructure and industry (i.e. urban areas) cover 12% and forests 36% (24% coniferous forests, 12% broadleaf and mixed forests), with broadleaf forests dominating at lower elevations and coniferous forests at higher elevations. Only 2% of Bavaria is covered by wetlands, lakes or rivers (Bavarian State Office for Statistics, 2014). National parks, natural reserves and areas of the Flora-Fauna-Habitat Directive (FFH) account for 12%.

KEYWORDS

cross-taxon congruence, insects, land use, phylogenetic diversity, regional scale, terrestrial ecosystems
2.2 | Biodiversity data

The dragonfly distribution data used in this study originated from "Libellen in Bayern" (see also Kuhn & Burbach, 1998), the grasshopper records from the "Mapping of Species Protection" (ASK database; Bavarian Environment Agency; Schlumprecht & Waebler, 2003), the bat data from "Fledermäuse in Bayern" (see also Meschede & Rudolph, 2004), data on breeding birds from "Atlas der Brutvögel in Bayern" (see also Rödl, Rudolph, Geiersberger, Weixler, & Görgen, 2012) and data on butterflies from "Tagfalter in Bayern" (see also Rödl, Rudolph, Geiersberger, Weixler, & Görgen, 2012) and data on butterflies from "Tagfalter in Bayern" (see also Rödl, Rudolph, Geiersberger, Weixler, & Görgen, 2012). Referring to the CORINE Environment. These data are based on a European-wide land cover as extracted from CORINE (Coordinated Information of the European Environment). These data are based on a European-wide land cover mapping using LANDSAT-7 satellite images during the year 2000 (https://land.copernicus.eu/pan-european/corine-land-cover/clc-2000). This year was selected since most species data, including standardized surveys, were collected around the year 2000. Referring to the CORINE land cover classes we defined the following categories: conifer forest, broadleaf forest, mixed forest, sealed areas (including urbanization, industry, and traffic), meadows, arable land, streams and standing water.

The importance of land use in patterns of phylogenetic diversity was investigated using the percentage of cover of eight land use categories as extracted from CORINE (Coordinated Information of the European Environment). The role of climate was tested using the annual mean temperature and annual precipitation data downloaded from WorldClim.org (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The data have a resolution of 30 arc seconds (0.93 km × 0.93 km = 0.86 km²). All land use and climate variables were aggregated to our grid using R package raster (Hijmans et al., 2018).

2.3 | Environmental data

All analyses were performed using R version 3.5.1 (R Core Team, 2014). The species richness of assemblages within grids, as the sum of all co-occurring species, was calculated based on the distribution data of the species groups. To facilitate comparison with previous studies, the most common measure of phylogenetic diversity (i.e. Faiths PD; Faith, 1992) was calculated as the sum of branch lengths of the minimal spanning tree among co-occurring species using the pd function of the R package picante (Faith, 1992; Kembel et al., 2010). Because Faiths PD is inherently correlated with species richness (Pavoine & Bonsall, 2011), the observed phylogenetic diversity was controlled for species richness by calculating the residuals of a nonparametric regression of this relationship using the function loess (package stats with default settings) (Cleveland, Grosse, & Shyu, 1992). In addition, the 10 grids with the highest standardized phylogenetic diversity of all five studies species groups were mapped as hotspots. To visualize these common, regional hotspots, the residuals of each model for each species group were scaled by subtracting the mean from each value and dividing it by the standard deviation (function scale from the R package base).

2.4 | Phylogenetic trees

All analyses were performed using R version 3.5.1 (R Core Team, 2014). The species richness of assemblages within grids, as the sum of all co-occurring species, was calculated based on the distribution data of the species groups. To facilitate comparison with previous studies, the most common measure of phylogenetic diversity (i.e. Faiths PD; Faith, 1992) was calculated as the sum of branch lengths of the minimal spanning tree among co-occurring species using the pd function of the R package picante (Faith, 1992; Kembel et al., 2010). Because Faiths PD is inherently correlated with species richness (Pavoine & Bonsall, 2011), the observed phylogenetic diversity was controlled for species richness by calculating the residuals of a nonparametric regression of this relationship using the function loess (package stats with default settings) (Cleveland, Grosse, & Shyu, 1992). In addition, the 10 grids with the highest standardized phylogenetic diversity of all five studies species groups were mapped as hotspots. To visualize these common, regional hotspots, the residuals of each model for each species group were scaled by subtracting the mean from each value and dividing it by the standard deviation (function scale from the R package base).

The influence of land use and climate on phylogenetic diversities was assessed by fitting a spline-based smoothed regression in general additive models (GAMs), using the gam function of the R package mgcv to account for nonlinear trends. A distance-weighted auto-covariate (function autocov_dist from the R package spdep, (Bivand, Pebesma, & Gomez-Rubio, 2013)) was included to account for potential spatial autocorrelation (Augustin, Mugglestone, & Buckland, 1996).

We correlated species richness and phylogenetic diversity (Appendix S4), and a principal component analysis (PCA) was conducted to visualize the spatial congruence of the phylogenetic diversity across the species groups. The PCA revealed congruence between the phylogenetic diversity of bats and grasshoppers and between that of birds and dragonflies (Appendix S5). Finally, established protected areas (national parks, natural reserves and areas of the FFH Directive) were intersected with the
10 hotspots of cross-taxon phylogenetic diversity to calculate the extent of their potential overlap.

3 | RESULTS

The final dataset consisted of 179 bird, 21 bat, 73 dragonfly, 66 grasshopper and 163 butterfly species recorded in Bavaria (see Appendix S2.1–5).

3.1 | Patterns of phylogenetic diversity

Regional hotspots of standardized phylogenetic diversity differed remarkably between the studied species groups (Figure 1 and Appendix S6).

For birds, the hotspots in central Bavaria were distributed between 48° and 49.5° (Figure 1a). For bats and grasshoppers, both large areas of disproportionately higher standardized phylogenetic diversity but only few hotspots clustered in southern Bavaria, in the Alps and in the Alpine foothills (Figure 1b, c, d). By contrast, phylogenetic diversity of birds, dragonflies and butterflies, there was lower in the Alpine region (Figure 1a, c, e), although one hotspot for butterflies was located here (Figure 1e). For dragonflies, grasshoppers and to a lower extent butterflies, regional hotspots of standardized phylogenetic diversity were in north-western Bavaria, in the area of Würzburg (Figure 1c–e).

The 10 hotspots of cross-taxon phylogenetic diversity were located in northern Bavaria, west of Würzburg; in the Alpine foothills and in eastern Bavaria (Figure 2). Established protected areas covered only approximately 9.6% of these hotspots.

FIGURE 1  Standardized phylogenetic diversity for (a) birds, (b) bats, (c) dragonflies, (d) grasshoppers and (e) butterflies. Colour intervals range from blue (low) to red (high). Yellow dots indicate those 10 grids hosting highest standardized phylogenetic diversity for each species group, and black dots larger Bavarian cities (Wue, Würzburg, Nu, Nuremberg, Re, Regensburg, Mu, Munich). Bold black lines inside the Bavarian border correspond to geomorphic units and thin lines to landscape units.
3.2 | Influence of environmental factors

Land use significantly determined the phylogenetic diversity of bats, birds, grasshoppers and butterflies but not that of dragonflies (Figure 3, for statistical results see Appendix S3).

The standardized phylogenetic diversity of birds increased with increasing percentage of meadows, whereas increases in sealed areas and streams resulted in a bell-shaped pattern (Figure 3a). Sealed areas and the standardized phylogenetic diversity of bats (Figure 3b) and standing water and the standardized phylogenetic diversity of grasshoppers (Figure 3c) displayed a wave-like relationship, although the general trend was positive for bats and negative for grasshoppers. Broadleaf forests negatively influenced the standardized phylogenetic diversity of bats (Figure 3b). Annual mean temperature \((p\)-value: .68) and annual precipitation \((p\)-value: .81) had no influence on the standardized phylogenetic diversity of any of the investigated species groups (see Appendix S3).

4 | DISCUSSION

Our study showed that climate is a poor predictor of the standardized phylogenetic diversity of multiple species groups; instead, the standardized phylogenetic diversity of several species groups is influenced by land use. It is therefore the responsibility of land users to maintain the diversity of the tree of life while being aware that regional hotspots of standardized phylogenetic diversity differ considerably among taxonomic groups.

Previous studies have investigated the phylogenetic diversity of plants (Chun & Lee, 2018) and vertebrates, mainly birds (Voskamp, Baker, Stephens, Valdes, & Willis, 2017), mammals (Dalerum, 2013) and amphibians (Fritz & Rahbek, 2012). In all of those studies, large-scale patterns of single taxa were analysed whereas the congruence across multiple taxa, especially across groups with very different ecologies, has received little attention (e.g. Hawkins et al., 2012). Our study contributes to closing this gap by considering the spatial variation of standardized phylogenetic diversity across five different species groups.

Previous studies determined that urban areas can contain high taxonomic diversity of, for example bats (Mehr et al., 2011) but the respective assemblages are composed of closely related species (Knapp, Kühn, Schweiger, & Klotz, 2008; La Sorte et al., 2018), resulting in reduced phylogenetic diversity (Riedinger, Müller, Stadler, Ulrich, & Brandl, 2013). Birds are an exception, in which a few species contribute to high levels of phylogenetic diversity in urban settings (Pfeifer et al., 2009; Sol, Bartomeus, González-Lagos, & Pavoine, 2017). The importance of such places for the protection of biodiversity therefore depends on the phylogenetic context of the resident species (Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017). We determined a similar pattern for agricultural landscapes, with their mixture of meadows, vineyards and orchards. These habitats hosted both common and rare bird species, such as Eurasian curlew \((\textit{Numenius arquata})\), bee-eater \((\textit{Merops apiaster})\), patridge \((\textit{Perdix perdix})\), Common quail \((\textit{Coturnix coturnix})\) and European lapwing \((\textit{Vanellus vanellus})\), recruited from distantly related clades of the phylogenetic tree. One of these areas, where we found high standardized
phylogenetic diversity, was around the city of Würzburg along the river Main (see also Appendix S1a). This area has a comparably high diversity of different land use types (e.g. riparian landscapes and vineyards), representing suitable habitats for dragonflies, grasshoppers and butterflies. For butterflies, the bell-shaped effect of arable land on diversity confirmed earlier findings of a strongly decreasing diversity in landscapes largely consisting of arable land (Habel, Ulrich, Biburger, Seibold, & Schmitt, 2019). There are several, intertwined reasons for this loss. For example, atmospheric nitrogen influxes from traffic, industry and agriculture, which reduces the quality of seminatural grasslands for butterflies (Wallis DeVries & van Swaay, 2006). Furthermore, land use intensification as well as abandonment of grasslands destroys formerly valuable breeding areas and habitats for butterflies (Van et al., 2019). A higher species
richness of bats, but lower standardized phylogenetic diversity was found with increasing amount of broadleaf forests (Figure 3b). This finding might be caused due to the co-occurring of closely related species from the genus Myotis, such as Natterer’s bat (Myotis nattereri), greater mouse-eared bat (Myotis myotis), Bechstein’s bat (Myotis bechsteini). Those species typically occur together in large closed forests.

The Alps and the Alpine foothills host high numbers of butterfly species, but those species were most likely recruited from the same lineages. For example, of the 18 Erebia species in our dataset, 15 were restricted to the Alps (see also Pellissier et al., 2013). This results in high taxonomic diversity but low standardized phylogenetic diversity. In our study, certain land use variables influenced the standardized phylogenetic diversity of at least four of the five species groups, but most of the effects contrasted with those reported by studies at larger spatial scales (Safi, Armour-Marshall, Baillie, & Isaac, 2013; Voskamp et al., 2017). At a global scale, phylogenetic diversity has been explained by macroevolutionary processes such as biogeographic barriers as well as land use and climate (Fritz & Rahbek, 2012; Voskamp et al., 2017) or extinction and migration events (Davies & Buckley, 2011). At smaller scales, slope as topographic variable (González-Maya, Viquez-R, Arias-Alzate, Belant, & Ceballos, 2016) and elevation for birds (Dehling et al., 2014), ants (Machac, Janda, Dunn, & Sanders, 2011) and butterflies (Pellissier et al., 2013) influenced the phylogenetic diversity. A possible explanation is environmental filtering, and specifically the associated low temperatures on high ground. For invertebrates, Oliver et al. (2015) and Plattts et al. (2019) studied the effects of climate change and habitat fragmentation/availability on a regional scale and stated that restoring seminatural areas and reducing fragmentation will mitigate species loss due to climate change. Mehr et al. (2011) concluded that land use is more important than climate for species richness of bats in Bavaria. Our result extends this finding to standardized phylogenetic diversity. Four climate-sensitive bat species, namely Myotis emarginatus, Pipistrellus kuhlii, Rhinolophus ferrumequinum and R. hipposideros, have been identified for Bavaria by Mehr et al. (2011). Temperature and precipitation have for example an influence on the food availability, development of juveniles or the spread of diseases (Sherwin, Montgomery, & Lundy, 2013). However, the climate-sensitive species in our dataset are extremely rare in Bavaria. In comparison to annual mean temperature and precipitation, land use is more important for the standardized phylogenetic diversity of bats.

Most grasshoppers (Voith et al., 2016) and dragonflies (Winterholler et al., 2018) benefit from warming, whereas only a few depend on colder climate (e.g. Somatochlora alpestris). Wallis DeVries, Baxter, and van Vliet (2011) stated that butterflies are susceptible to weather conditions in different life stages. Further, smaller species might rely more on microclimate (Habel, Teucher, Ulrich, Bauer, & Rödder, 2016). Hence, climate sensitivity of butterflies might act on smaller spatial scales or might be related to extreme temperatures instead of mean temperatures than investigated in our study. Nevertheless, recent studies also highlight the importance of land use on the preservation of butterfly diversity (Oliver et al., 2015; Thomas, 2016).

5 | CONCLUSIONS

We demonstrated that land use is of higher importance than macroclimate in determining local standardized phylogenetic diversity of different species groups. This finding highlights the responsibility of land users to protect the diversity of the tree of life. The hotspots of standardized phylogenetic diversity identified in our study can guide the prioritization of land areas for the conservation of the respective species groups. However, our results also demonstrate that, rather than using one species as a surrogate for others, information on different species groups should be combined to guide effective nature protection measures.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the Bavarian environment authority.

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BIOSKETCH
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Author contribution: SF, ST and RB designed the study; SF and ST performed the analyses; SF drafted the manuscript; RB, CH, JM and SP contributed data; all authors contributed significantly to the writing and revisions of the manuscript.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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