# EVALUIERUNG INTRINSISCHER UND EXTRINSISCHER GEFÄHRDUNGSURSACHEN HEIMISCHER LIBELLENARTEN AUF UNTERSCHIEDLICHEN RÄUMLICHEN SKALEN

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## Content

# 1 Introduction

Biodiversity can be divided in the three facets: taxonomic, functional, and phylogenetic diversity. The loss of biodiversity as well as its drivers and the organisms most affected by these processes are intensely recognized and discussed in recent decades (Butchart et al., 2010; Newbold et al., 2015; Sala et al., 2000). Insects are an important part of the world's terrestrial and freshwater biodiversity (Mora, Tittensor, Adl, Simpson, & Worm, 2011; Stork, 2018). Insects provide crucial ecosystem services, such as decomposition and pollination (Cardoso et al., 2020; Macadam & Stockan, 2015; Santos et al., 2020). Especially in densely populated areas of the northern hemisphere insect declines are well documented (Montgomery et al., 2020). Insect extinctions and declines do not solely mean the loss of species but e.g. biomass, unique ecological functions, and fundamental parts of extensive networks of biotic interactions (Cardoso et al., 2020). The concept of ecosystem services raised the awareness of human beings for the importance of insects in our surroundings (Ari, Hortal, Azcárate & Berg, 2018; Reilly et al., 2020), but insects are still underrepresented in the scientific literature. As a consequence, the development and implementation of conservation measures is still hampered (Basset & Lamarre, 2019).

In recent years, many strategies were developed to halt the global decline of biodiversity (Butchart et al., 2010). Essential tools are for instance international or national red lists, the Habitats Directive or long-term monitoring programs, which try to assess all kind of threats to species (Gruber et al., 2012; Lindenmayer, Piggott & Wintle, 2013). Knowing these threats potentials helps to develop approaches and methods for the species´ protection (Primack, 2014).

The causes of species threats can be separated into extrinsic and intrinsic factors. Extrinsic factors in terrestrial habitats include agricultural intensification, habitat loss, reduced connectivity, and nitrogen influx (Jan C. Habel et al., 2019; Seibold et al., 2019). Intrinsic factors refer to functional traits, meaning any morphological, physiological, behavioural, and phenological feature measurable at the individual level of species determining their interaction with the environment (McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007; Wong, Guénard, & Lewis, 2019).

Conservation strategies mainly focus on the protection of biotopes (e.g. Special Protection Areas) and processes (e.g. natural forest development). Due to the availability of range-size data for species these strategies are taxonomically shaped and evaluated, mainly by the number of species (Mammides, 2019; Miller, Jolley-Rogers, Mishler, & Thornhill, 2018; Zupan et al., 2014). These strategies ignore functional or phylogenetic aspects of biodiversity

(Vane-Wright, Humphries, & Williams, 1991; Veron, Davies, Cadotte, Clergeau, & Pavoine, 2015). But these differences or variability between the species are essential for future adaptations to changing environments (Faith, 1992; Vane-Wright et al., 1991). One obvious example is the high taxonomic diversity found in urban areas, but the respective assemblages are composed of closely related species and thus represent a reduced phylogenetic diversity (Knapp, Kühn, Schweiger, & Klotz, 2008; Riedinger, Müller, Stadler, Ulrich, & Brandl, 2013). 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). Thuiller et al. (2015b) demonstrated that a random choice of protected areas would have been more expedient in protecting the functional and phylogenetic diversity for many mammals, birds, amphibians, and reptiles than the existing Natura 2000 network. The discipline of phylogenetical and functional studies is steadily developing and improving. During the last decades the availability of e.g. phylogenetic data as well as standardized trait data increased in availability for different taxa as well as in their quality. A similar link exists for trait data or trait-based approaches (Wong et al., 2019). Their availability for and comparability between different taxa is still improving, which is in line with the growing demand for comparative studies e.g. in the relation of traits and extinction risk (Chichorro, Juslén, & Cardoso, 2019). The basis for comparative studies is a standardized measurement of e.g. traits (Moretti et al., 2017) and a comparable level of the respective phylogenetic tree data.

Odonates and butterflies are well-studied insect orders. Consequently, a huge amount of available species data and complete phylogenetic trees exist. Odonates have a highly specialized lifecycle. Their larval stages solely develop in lentic (e.g. lakes) or lotic (e.g. streams) water (Corbet, 1999). Their flying imagos depend on waterbodies for e.g. egg laying and terrestrial habitats for hunting (Corbet, 1999). Freshwater habitats cover just 2.4% of the earth’s terrestrial surface (Allan et al., 2015; Lehner & Döll, 2004), underlining the vulnerability of this habitat. The demand for freshwater is still growing for example due to an increased anthropogenic requirement for drinking water or artificial irrigation. Simultaneously, studies show a fast recovery of populations after an improvement of water conditions due to environmental regulations and restoration measures (Termaat, Van Grunsven, Plate, & Van Strien, 2015) as well as general increase of the abundance of freshwater insects in comparison to terrestrial insects (van Klink et al., 2020).

We evaluated intrinsic and extrinsic causes of threat on different spatial scales. The core species for this consideration were odonates. Using surrogate taxa for prioritising conservation measures is a common approach in conservation biology (Larsen, Bladt, & Rahbek, 2009; Margules & Pressey, 2000). Advantages are that e.g. costly and time-expansive species surveys can be avoided (Yong et al., 2018). Different species and their e.g. responses to a certain environment are correlated, but the strength of cross-taxa congruence varies greatly and the responses are complex (Aubin, Venier, Pearce, & Moretti, 2013). This taxon-specific patterns of diversity underpin the necessity of multi-taxa approaches for a successful conversation in the interest of nature and preserving biodiversity. Further, we argue that instead of using species as a surrogate for others, information on different species groups should be combined to guide effective nature protection measures. Therefore, we extended the species spectrum for the paper "Predicting regional hotspots of phylogenetic diversity across multiple species groups" by birds, bats, butterflies, and locust and for the paper "Modelling the extinction risk of European butterflies and odonates" by butterflies. At the county level we analysed the number of species in relation to local habitat parameters and its changes over time expressed by the time passed since excavation of these artificial ponds. At the federal state level, we analysed the standardized phylogenetic diversity of the several species depending on local habitat and climatic variables. Throughout Europe we conducted a comparative, phylogenetic-controlled trait-based study for butterflies and odonates to analyse causes of extinction risk.

## 2 Zusammenfassung

Biodiversität beinhaltet drei Teilbereiche: taxonomische, phylogenetische und funktionale Diversität. In den letzten Jahrzehnten wurden der allgemeine Verlust der Biodiversität, meistens gleichgesetzt mit einem Verlust der Artenvielfalt, seine Ursachen und die am meisten gefährdeten Organismen viel diskutiert (Butchart et al., 2010; Newbold et al., 2015; Sala et al., 2000). Insekten bilden einen wichtigen Teilbereich der weltweiten Land- und Süßwasserbiodiversität (Mora, Tittensor, Adl, Simpson, & Worm, 2011; Stork, 2018). Sie leisten essentielle Ökosystemdienstleistungen wie Zersetzungsprozesse und Bestäubung (Cardoso et al., 2020; Macadam & Stockan, 2015; Santos et al., 2020). Vor allem in den dicht besiedelten Gebieten der nördlichen Erdhalbkugel sind Insektenrückgänge gut dokumentiert (Montgomery et al., 2020). Insektensterben und -rückgänge bedeuten nicht alleinig den Verlust einer Art, sondern eben auch den Verlust von Biomasse, einzigartigen ökologischen Funktionen und grundlegenden Bestandteilen extensiver Netzwerke biotischer Interaktionen (Cardoso et al., 2020). Das Konzept von Ökosystemdienstleistungen weckte das Bewusstsein der Menschheit für die Wichtigkeit von Insekten in ihrem Lebensumfeld (Ari, Hortal, Azcárate & Berg, 2018; Reilly et al., 2020), aber dennoch sind Insekten unterrepräsentiert in der Forschungsliteratur. Daraus resultierend verläuft sowohl die Umsetzung als auch die Entwicklung von insektenbezogenen Schutzmaßnahmen schleppend (Basset & Lamarre, 2019).

In den vergangenen Jahren wurden viele Strategien entwickelt um den weltweiten Rückgang der Biodiversität aufzuhalten (Butchart et al., 2010). Wichtige Werkzeuge dafür sind zum Beispiel internationale und nationale Rote Listen, die Flora-Fauna-Habitat Richtlinie oder Langzeit-Monitoringprogramme, die versuchen sämtliche Gefährdungen von Arten abzuschätzen (Gruber et al., 2012; Lindenmayer, Piggott & Wintle, 2013). Kenntnis der Gefährdungspotentiale hilft Ansätze und Methoden für den Schutz von Arten zu entwickeln (Primack, 2014).

Die Gefährdungsursachen von Arten lassen sich in extrinsische und intrinsische Faktoren unterteilen. Extrinsische Faktoren terrestrischer Habitate umfassen beispielsweise landwirtschaftliche Intensivierung, Habitatverluste, verminderte Verbindung zwischen Habitaten sowie Stickstoffeinträge (Jan C. Habel et al., 2019; Seibold et al., 2019). Intrinsische Faktoren beziehen sich auf funktionelle Merkmale wie morphologische, physiologische, verhaltensbezogene oder phänologische Eigenschaften, die auf Individuumsebene messbar sind und deren Interaktion mit ihrer Umwelt beeinflussen

(McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007; Wong, Guénard, & Lewis, 2019).

Naturschutzstrategien konzentrieren sich vor allem auf den Schutz von Biotopen (z.B. besondere Schutzgebiete) und Prozessen (z.B. natürliche Waldentwicklung).

Aufgrund der nahezu flächendeckenden Verfügbarkeit von Verbreitungsdaten für Arten basieren solche Strategien zumeist auf taxonomischen Grundlagen, hauptsächlich auf der Anzahl der Arten (Mammides, 2019; Miller, Jolley-Rogers, Mishler, & Thornhill, 2018; Zupan et al., 2014). Diese Strategien ignorieren folglich jedoch funktionale und phylogenetische Komponenten der Diversität (Vane-Wright, Humphries, & Williams, 1991; Veron, Davies, Cadotte, Clergeau, & Pavoine, 2015). Dabei sind es genau diese Unterschiede, beziehungsweise die Variabilität zwischen den Arten, die entscheidend für zukünftige Anpassungen an sich ändernde Umweltbedingungen sind (Faith, 1992; Vane-Wright et al., 1991). Ein augenscheinliches Beispiel ist die hohe taxonomische Diversität in urbanen Gebieten, deren Artzusammensetzung jedoch aus eng verwandten Arten besteht und somit nur eine reduzierte phylogenetische Diversität aufweist (Knapp, Kühn, Schweiger, & Klotz, 2008; Riedinger, Müller, Stadler, Ulrich, & Brandl, 2013). Die Bedeutung solcher Orte für den Schutz der Biodiversität hängt daher maßgeblich vom phylogenetischen Kontext der vorkommenden Arten ab (Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017). Thuiller et al. (2015b) zeigten, dass eine zufällige Auswahl von Schutzgebieten zweckmäßiger für den Schutz funktioneller und phylogenetischer Diversität von Säugetieren, Vögeln, Amphibien und Reptilien gewesen wäre als das bestehende Natura-2000-Gebietsnetz.

Die wissenschaftliche Disziplin funktionaler und phylogenetischer Untersuchungen entwickelt und verbessert sich stetig. In den letzten Jahrzehnten nahm die Verfügbarkeit und Qualität beispielsweise von Stammbaumdaten sowie standardisierten Artmerkmalsdaten für verschiedene Taxa zu. Ein ähnlicher Zusammenhang besteht für Artmerkmalsdaten und merkmalsbasierte Untersuchungen (Wong et al., 2019). Die Verfügbarkeit dieser Daten und die sich daraus ergebende Möglichkeit zwischen verschiedenen Arten Vergleiche ziehen zu können, wächst kontinuierlich und kommt so der steigenden Nachfrage nach Vergleichsstudien, die z.B. die Beziehung von Merkmalen und dem Aussterberisiko untersuchen, entgegen (Chichorro, Juslén, & Cardoso, 2019). Die Basis für vergleichende Studien sind standardisierte Messmethoden, beispielsweise für die Erhebung von Artmerkmalen (Moretti et al., 2017) und eine vergleichbare Güte der jeweiligen Stammbäume.

Libellen und Schmetterlinge sind gut untersuchte Insektenordnungen. Daher existiert eine Vielzahl von Artdaten und kompletten Stammbäumen. Libellen haben einen hoch spezialisierten Lebenszyklus. Ihre Larvenstadien entwickeln sich ausschließlich in stehenden (z.B. Seen) oder fließenden Gewässern (z.B. Bächen) (Corbet, 1999). Ihre fliegenden Imagos benötigen sowohl Gewässer, zum Beispiel zur Eiablage, als auch terrestrische Habitate zum Jagen (Corbet, 1999).

Süßwasserhabitate bedecken lediglich 2,4% der Landmasse der Erde (Allan et al., 2015; Lehner & Döll, 2004), wodurch sie zu anfälligen Habitaten werden. Die Nachfrage nach Frischwasser erhöht sich ständig, beispielsweise durch einen erhöhten anthropogenen Bedarf an Trinkwasser oder künstlicher Bewässerung. Zeitgleich zeigen Studienergebnisse am Beispiel von Libellen, dass sich Populationen in ihren Habitaten schnell wieder erholen können, wenn sich die Gegebenheiten aufgrund von Umweltauflagen und Renaturierungsmaßnahmen verbessern (Termaat, Van Grunsven, Plate, & Van Strien, 2015). Zudem belegen sie in solchen Fällen eine generelle Zunahme der Häufigkeit von Süßwasserinsekten im Vergleich zu terrestrischen Insekten (van Klink et al., 2020).

Wir untersuchten intrinsische und extrinsische Gefährdungsursachen auf unterschiedlichen räumlichen Skalen. Die Hauptart unserer Analysen waren Libellen. Mit surrogaten Arten zu Arbeiten um Priorisierungen im Naturschutz vorzunehmen, ist eine gebräuchliche Methode im Naturschutz (Larsen, Bladt, & Rahbek, 2009; Margules & Pressey, 2000). Vorteile davon sind beispielsweise das Wegfallen kosten- oder zeitintensiver Arterfassungen (Yong et al., 2018). Die Reaktion unterschiedlicher Arten auf bestimmte Umwelteinflüsse korrelieren, aber die Stärke dieser Kongruenz über Arten hinweg variiert stark und die Antworten sind komplex (Aubin, Venier, Pearce, & Moretti, 2013). Diese artspezifischen Muster von Diversität unterstreichen die Wichtigkeit von Multitaxa-Analysen für einen gelungenen Naturschutz im Sinne der Natur und des Erhalts der Biodiversität. Wir sind außerdem davon überzeugt, dass Anstelle eines Rückgriffs auf surrogate Arten, Informationen vieler verschiedener Artengruppen kombiniert werden sollten, um einen effektiven Naturschutz gestalten zu können. Deswegen haben wir unser Standard-Artspektrum für das Manuskript “Predicting regional hotspots of phylogenetic diversity across multiple species groups” um Vögel, Fledermäuse, Schmetterlinge und Heuschrecken erweitert. Das Manuskript “Modelling the extinction risk of European butterflies and odonates” wurde um Schmetterlinge erweitert. Auf Landkreisebene haben wir die Abhängigkeit der Artanzahl von lokalen Habitatparametern untersucht sowie deren Veränderung im Laufe der Zeit, gemessen in Jahren, die seit dem Ausbaggern der untersuchten Teiche vergangen sind. Auf Bundeslandebene untersuchten wir den Zusammenhang zwischen der standardisierten phylogenetischen Diversität verschiedener Arten und lokalen Habitat- und Klimavariablen. Europaweit machten wir eine vergleichende, phylogenetisch-kontrollierte merkmalsbasierte Studie mit Schmetterlingen und Libellen um deren Aussterberisiko zu analysieren.

# 3 Manuscripts of this thesis

## 3.1 List of manuscripts

All listed publications are part of this cumulative dissertation.

| | | |
|---|---|---|
| I | Title: | Predicting regional hotspots of phylogenetic diversity across multiple species groups |
| | Authors: | **Sophia Franke**, Roland Brandl, Christoph Heibl, Angelina Mattivi, Jörg Müller, Stefan Pinkert, Simon Thorn |
| | Status: | Published. *Diversity and Distributions* (26): 1305-1314 (2020) |
| | Contribution: | data analyses and figures: 60 %; writing and revising: 70 %, concept: 40 %. |

| | | |
|---|---|---|
| II | Title: | Modelling the extinction risk of European butterflies and odonates |
| | Authors: | **Sophia Franke**, Stefan Pinkert, Roland Brandl, Simon Thorn |
| | Status: | Accepted. Ecology and Evolution. |
| | Contribution: | data analyses and figures: 60 %; writing and revising: 80 %, concept: 50 %. |

| | | |
|---|---|---|
| III | Title: | Ponds in Bavaria |
| | Authors: | **Sophia Franke,** Simon Thorn |
| | Status: | In preparation. (see appendix) |
| | Contribution: | data analyses and figures: 70 %; writing and revising: 70 %, concept: 50 %. |

The above-mentioned publications are not part of any further scientific qualification work.

Sophia Franke Roland Brandl

## 3.2 Manuscripts

### 3.2.1 Predicting regional hotspots of phylogenetic diversity across multiple species groups

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

Published in *Diversity and Distributions* | *DOI: 10.1111/ddi.13125*

### Abstract

**Aim:** The protection of phylogenetic diversity has become a priority in conservation biology, but its achievement requires a detailed understanding of i) hotspots of phylogenetic diversity on a management-relevant scale and ii) 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 programs 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, landuse was more important than climate in determining phylogenetic diversity. Our study highlights the importance of involving land users into strategies for protecting phylogenetic diversity.

KEYWORDS: Cross-taxon congruence, insects, landuse, phylogenetic diversity, regional scale, terrestrial ecosystems

# 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, Martín-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 et al., 2018; Zupan et al., 2014). However, it is increasingly recognized that these strategies ignore functional or phylogenetic aspects of biodiversity (Vane-Wright et al., 1991; Veron et al., 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, & Mirotchnick, 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, & Mirotchnick, 2011; Cadotte, Dinnage, & Tilman, 2012; Cadotte & Davies, 2010), 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, & 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

### *Study area*

The study was conducted in the federal state of Bavaria (see Appendix S1a in the Supporting Information for major natural regions), located in south-eastern Germany (47°16'N, 8°58'E) that covers an area of 70,550 $km^2$ and broad environmental gradients. The elevation ranges from 100 m a.s.l. (Main River) to 2962 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%.

### *Biodiversity data*

The dragonfly distribution data used in this study originated from “Libellen in Bayern” (see also Kuhn and Burbach, 1998), the grasshopper records from the “Mapping of Species Protection” (ASK database; Bavarian Environment Agency; Schlumprecht & Waeber, 2003), the bat data from “Fledermäuse in Bayern” (see also Meschede and Rudolph, 2004), data on breeding birds from “Atlas der Brutvögel in Bayern” (see also Rödl et al., 2012) and data on butterflies from “Tagfalter in Bayern” (see als Bräu et al., 2013). In addition, available data from the database of the Bavarian Environment Authority (Landesamt für Umwelt, 5 km × 5 km resolution) were used. The grid cells were adopted from the topographic map (TK) 1:25,000 of Bavaria and had an average area of $\approx 33.9\ km^2$ (TK ¼ grids) (see Appendix S6).

Only grid cells whose area was entirely within Bavaria and which contained more than two species were included (Pfeifer, Müller, Stadler, & Brandl, 2009).

### *Environmental data*

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). 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 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 km$^2$). All land use and climate variables were aggregated to our grid using R package *raster* (Robert J. Hijmans, 2018).

### *Phylogenetic trees*

The phylogeny of birds (see Appendix S2.1) was based on a Bayesian phylogenetic analysis (Hackett et al., 2008; Jetz, Thomas, Joy, Hartmann & Mooers, 2012) available on www.birdtree.org. One thousand samples (bias corrected according to Roff 2006) were downloaded from the posterior distribution of topologies and branch lengths and applied to create a consensus tree using TreeAnnotator 1.8.2 in the software bundle BEAST (Drummond, Suchard, Xie, & Rambaut, 2012). The phylogeny of European dragonflies (Appendix S2.3) was taken from Pinkert et al. (2018).

The phylogenies of bats (Appendix S2.2), grasshoppers (Appendix S2.4), and butterflies (Appendix S2.5) were based on cox1 sequence alignments prepared with the R package megaptera (available on https://github.com/heibl/megaptera). Sequences were downloaded from GenBank® (https://www.ncbi.nlm.nih.gov/genbank/), filtered and aligned with MAFFT (Katoh, Rozewicki, & Yamada, 2017). Topology and branch length were estimated in a likelihood framework using RAxML (Stamatakis, 2014). Sequence evolution was modeled according to a GTR model of substitution rates with rate heterogeneity following a discretized Gamma distribution (Stamatakis, 2006). Node support was assessed using non-parametric bootstrapping (Stamatakis, Hoover, & Rougemont, 2008). Ultrametric branch lengths were estimated with a penalized likelihood approach based on a relaxed clock model of substitution rate variation among branches and a smoothing parameter $\lambda = 1.0$ using ape::chronos (Paradis, 2013), using a relaxed clock model of rate evolution and a smoothing parameter λ = 1.0.

### *Data analysis*

All analyses were performed using R version 3.5.1 (R Core Team, 2020). 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 non-parametric 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 non-linear 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).

### *Patterns of phylogenetic diversity*

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

For birds, the hotspots in central Bavaria were distributed between 48° and 49.5° (Fig. 1, a). 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 (Fig. 1, b/d). By contrast, phylogenetic diversity of birds, dragonflies and butterflies, there was lower in the Alpine region (Fig. 1, a/c/e), although one hotspot for butterflies was located here (Fig. 1, e). 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 (Fig. 1, c–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 (Fig. 2). Established protected areas covered only approximately 9.6% of these hotspots.

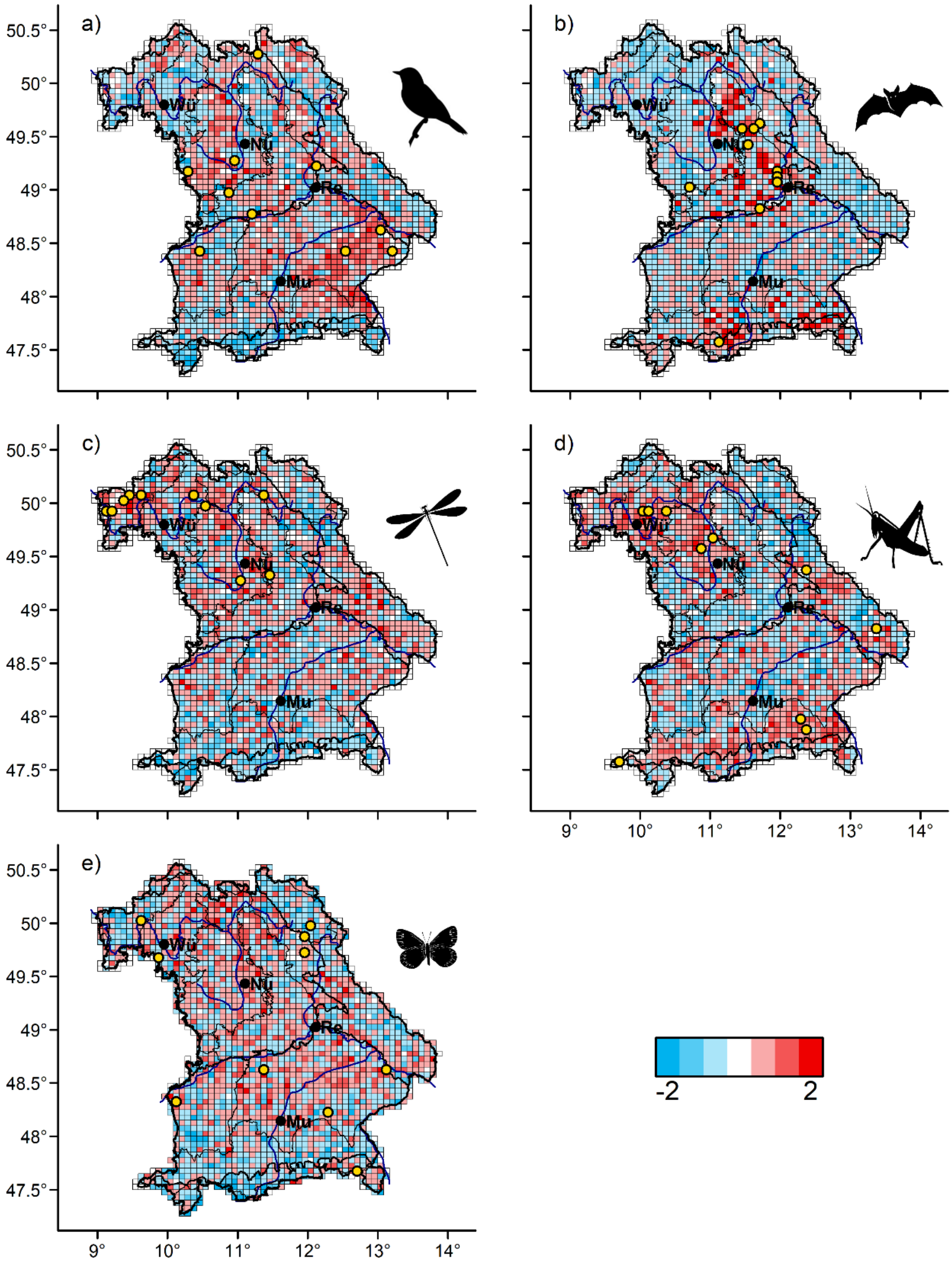

*Figure 1: Standardized phylogenetic diversity for a) birds, b) bats, c) dragonflies, d) grasshoppers and e) butterflies. Color intervals range from blue (low) to red (high). Yellow dots indicate those 10 grids hosting highest standardized phylogenetic diversity for each species group, and black dots 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.*

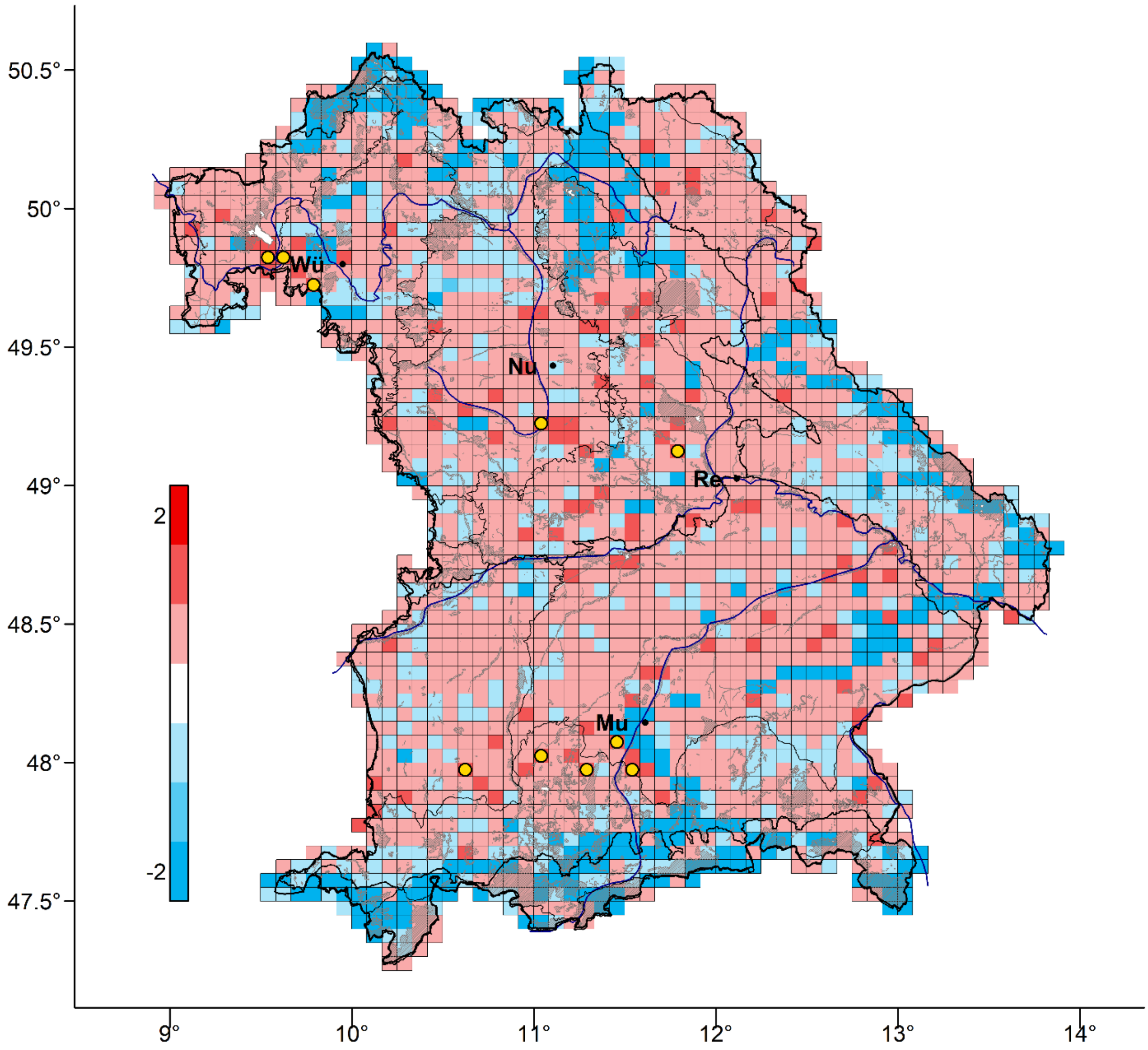

*Figure 2: Standardized phylogenetic diversity of all five studied species groups combined. Color intervals range from blue (low) to red (high). Yellow dots indicate those 10 grids hosting highest standardized phylogenetic diversity of all five studies species groups and grey hachured areas the protected areas in Bavaria, including national parks, natural reserves and Flora-Fauna-Habitat Directive areas. Black dots mark 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.*

### *Influence of environmental factors*

Landuse significantly determined the phylogenetic diversity of bats, birds, grasshoppers and butterflies but not that of dragonflies (Fig. 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 (Fig. 3, a). Sealed areas and the standardized phylogenetic diversity of bats (Fig. 3, b) and standing water and the standardized phylogenetic diversity of grasshoppers (Fig. 3, c) 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 (Fig. 3, b). Annual mean temperature (p-value: 0.68) and annual precipitation (p-value: 0.81) had no influence on the standardized phylogenetic diversity of any of the investigated species groups (see Appendix S3).

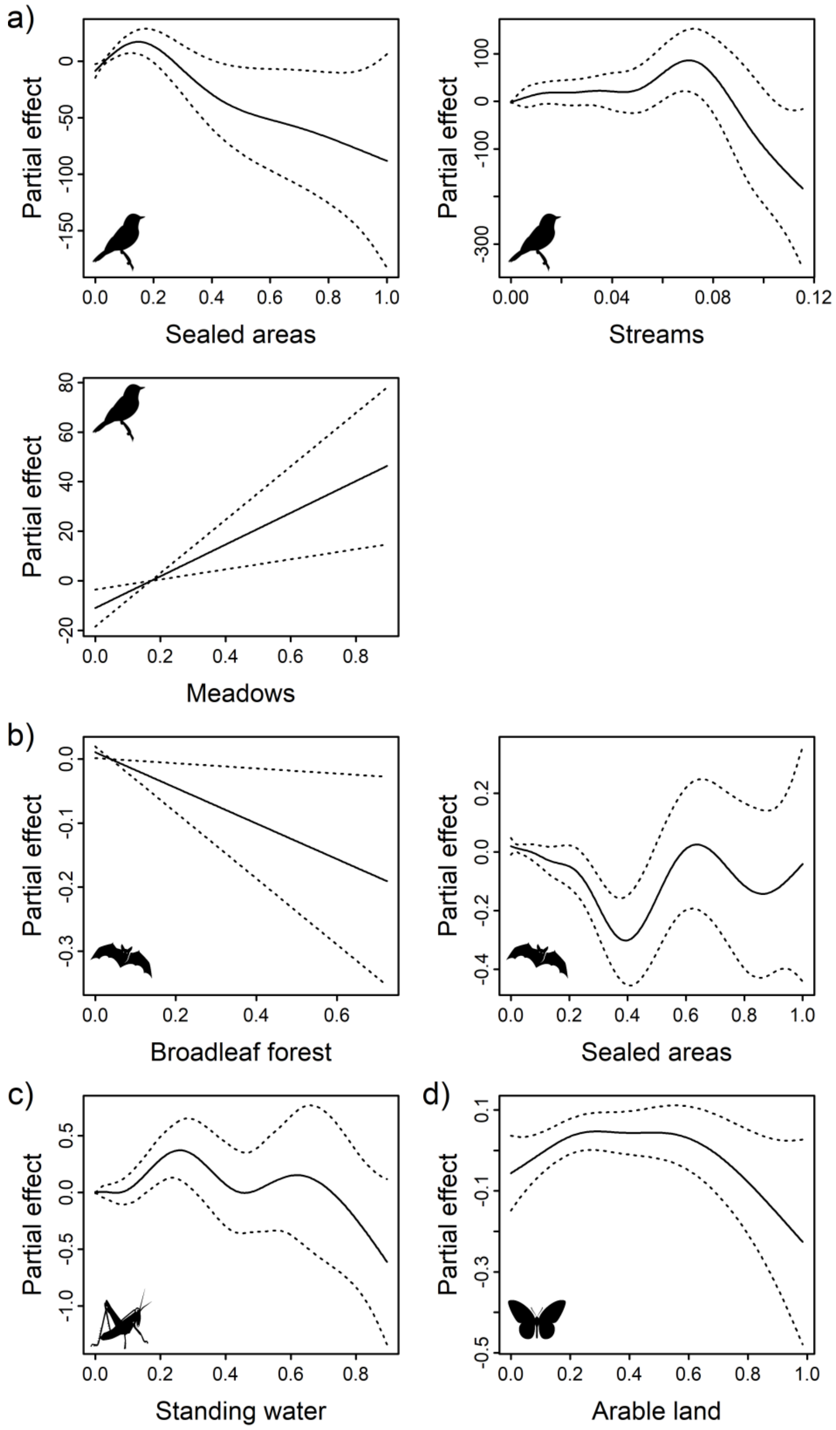

*Figure 3: Significant results of generalized additive models of the standardized phylogenetic diversity of a) birds, b) bats, c) grasshoppers and d) butterflies as dependent variable and landuse cover (%/100) as predictor variables. Dotted lines indicate 95% confidence intervals.*

## 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 landuse. 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 et al., 2017), mammals (Dalerum, 2013) and amphibians (Fritz & Rahbek, 2012). In all of those studies, large-scale patterns of single taxa were analyzed 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 e.g. bats (Mehr et al., 2011) but the respective assemblages are composed of closely related species (Knapp et al., 2008; La Sorte et al., 2018), resulting in reduced phylogenetic diversity (Riedinger et al., 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 et al. 2017). The importance of such places for the protection of biodiversity therefore depends on the phylogenetic context of the resident species (Ibáñez-Álamo et al., 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 (*Numenius arquata*), bee-eater (*Merops apiaster*), patridge *(Perdix perdix*), Common quail (*Coturnix coturnix*) and European lapwing (*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, 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 et al., 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 (WallisDeVries & van Swaay, 2006). Furthermore, landuse intensification as well as abandonment of grasslands destroys formerly valuable breeding areas and habitats for butterflies (C. A. M. Van Swaay et al., 2019). A higher species richness of bats, but lower standardized phylogenetic diversity was found with increasing amount of broadleaf forests (Fig. 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 bechsteinii*). 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 landuse 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 et al., 2013; Voskamp et al., 2017). At a global scale, phylogenetic diversity has been explained by macroevolutionary processes such as biogeographic barriers as well as landuse 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-Mayaet al., 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 Platts et al. (2019) studied the effects of climate change and habitat fragmentation/availability on a regional scale and stated that restoring semi-natural areas and reducing fragmentation will mitigate species loss due to climate change. Mehr et al. (2011) concluded that landuse 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 landuse 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*). WallisDeVries, Baxter & 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 landuse on the preservation of butterfly diversity (Oliver et al., 2015; Thomas, 2016).

## 5 CONCLUSIONS

We demonstrated that landuse is of higher importance than macro-climate 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.

## 3.2.2 Modelling the extinction risk of European butterflies and odonates

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### Abstract

Insect populations have become increasingly threatened during the last decades due to climate change and landuse intensification. Species characteristics driving these threats remain poorly understood. Trait- based analyses provide a straight- forward approach to gain a mechanistic understanding of species' extinction risk, guiding the development of conservation strategies. We combined morphological traits and phylogenetic relationship for 332 European species of butterflies and 115 species of odonates (dragon and damselflies) to model their red list status via phylogenetically controlled ordered logistic regression. We hypothesized that extinction risk increases with increasing body volume and wing area, decreasing range size, and is larger for brighter species. All investigated traits exhibited a strong phylogenetic signal. When controlling for phylogenetic relationship, we found that extinction risk of butterflies increased with decreasing range size. The extinction risk of odonates showed no relationship with the selected traits. Our results show that there is no universal trait defining the extinction risk of our investigated insect taxa. Furthermore, evolutionary history, measured as the phylogenetically predicted part of our analyzed traits, poorly predicted extinction risk. Our study confirms the focus of conservation measures on European butterfly species with small range sizes.

# 1 INTRODUCTION

Insects are an important part of the world’s terrestrial and freshwater biodiversity (Mora et al., 2011). They provide crucial ecosystem services, such as decomposition and pollination (Cardoso et al., 2020; Macadam & Stockan, 2015; Santos et al., 2020). During the last decades, a lot of insect populations became threatened due to pollution, climate change, and land-use intensification (Clausnitzer et al., 2009; Warren et al., 2021). This has resulted in declining abundances, local extinctions, and reduction of overall insect biomass (Basset & Lamarre, 2019; Seibold et al., 2019). These effects are particularly strong in landscapes dominated by agriculture, whereas they are less pronounced in freshwater ecosystems (van Klink et al., 2020). In some regions, odonates even rapidly recover under favourable environmental conditions (Termaat et al., 2015). Both habitat loss and the loss of connectivity between the remaining habitats contribute to insect decline (Habel, Samways, & Schmitt, 2019; Habel et al., 2019). Another important threat is climate change, especially its consequences on freshwater biodiversity due to e.g. an increasing anthropogenic water demand (Koutroulis et al., 2018; Vörösmarty et al., 2010).

The threat of species can broadly be divided into extrinsic and intrinsic factors. Former are defined as factors describing the environment in which a species lives, including but not limited to habitat change, land-use, and climate change. The latter factors refer to traits of species that determine their interaction with the environment, such as physiological adaptations as well as traits involved in resource use or dispersal (Seibold et al., 2015). For instance, body size is correlated with resource use (Savage et al., 2004; Pinkert et al., 2020), metabolism (Gillooly, Brown, West, Savage, & Charnov, 2001), development rates (Gillooly et al., 2002), and population densities (Pinkert et al., 2020). Large species require more energy and are therefore characterized by smaller populations within a given habitat. Hence, species with larger body sizes are more likely to be threatened due to demographic stochasticity (Lande, Engen, & Saether, 2003; Melbourne & Hastings, 2008) than their smaller relatives (Fritz et al., 2009; Gaston & Blackburn, 1995; Suárez-Tovar et al., 2019). Wing size is a proxy for the dispersal ability and in a wider context for predicting the range size, being therefore crucial for the extinction risk since mobile species are less endangered than less mobile ones (Outomuro & Johansson, 2019; Pöyry, Luoto, Heikkinen, Kuussaari, & Saarinen, 2009; Sekar, 2012). Colouration also corresponds to several aspects of environmental interaction such as fitness and distribution range (Clusella Trullas et al., 2007; Pinkert et al., 2020).

Butterflies and odonates (damselflies and dragonflies) are charismatic insect groups that are among the most intensively studied insect lineages (Kalkman et al., 2018; Lewis & Senior, 2011). Both groups are easy to identify, a fact that predestines these two groups as indicators for biodiversity changes in terrestrial (Thomas, 2005) and freshwater ecosystems (Dolný, Harabiš, Bártaa, Lhota, & Drozd, 2013; Miguel, Oliveira-Junior, Ligeiro, & Juen, 2017). Yet, extrinsic extinction factors such as habitat fragmentation and water scarcity have been repeatedly studied for these groups (Kalkman et al., 2018; Thomas, 2016), mainly in Central and Northern Europe (Tang & Visconti, 2021). However, much less is known for traits increasing the  extinction risk of species and whether trait-threat relationships are similar across taxa (Nylin & Bergström, 2009).

We used data on European butterflies and odonates as representatives of terrestrial and freshwater insects. We tested (i) whether larger species are more endangered than smaller ones using body size, (ii) whether widely distributed species are less endangered than locally distributed ones (using wing area or the gridded distribution across Europe), whether (iii) darker coloured species are less endangered than lighter coloured ones and (iv) to what extent the results are influenced by evolutionary relationships.

## 2 MATERIAL AND METHODS

### *Species data*

The taxonomy and nomenclature of European butterflies were taken from Wiemers et al. (2018). To estimate extinction risk, we used the European Red List of Butterflies from 2010 (van Swaay et al., 2010).451 species were assessed within this list. Our analyses relate to the EU 27 countries. About 7 % of butterflies occurring within the EU 27 countries are threatened (9 % for Europe) and an additional 10 % are considered as near threatened (van Swaay et al., 2010). The recent European Red List of odonates from 2010 contains 137 assessed species. Of these, 15 % are listed in one of the three IUCN threat categories (Kalkman et al., 2010). We excluded species endemic to small islands and species that reach Europe with their distributional edges (e.g., distributed mainly in Asia). In general, we restricted our analysis to species with retrievable red-list status, phylogeny, and traits. This resulted in complete data sets for 332 butterflies and 115 odonates.

To assess the relationship between species' traits and their extinction risk as estimated by the red list status, we selected four different morphological and biogeographical traits, namely body volume in $cm^3$ as a measure of body size, colour lightness via the additive colour mixing with the basic colours red-green-blue (mean RGB value), wing area in $cm^2$ and the geographical range size. These traits were available for both butterflies and odonates. We followed Pinkert et al. (2018) and Zeuss et al. (2014) using drawings of European butterflies (Tolman & Lewington 2009) and of European odonates (Dijkstra & Lewington 2006) to estimate body size and colour lightness. To prepare images for the analysis, the body (head, abdomen, and thorax) in scanned drawings of species' dorsal body surfaces (24-bits, sRGB, 1,200 dpi resolution) was cropped out and saved to separate files using functions of Adobe Photoshop CS2.

Based on these images, we calculated the body volume in cm3 (π × [½ length of pixel row]2 × pixel edge length) as an estimate of the body size of a species based on the assumption that bodies of butterflies and odonates generally have a cylindrical form. The calculations were performed using functions of the R-package png (Urbanek, 2013). Body volume instead of linear size measures, such as wing length, head width, and body length, was used because it allows for a more realistic estimate of the body mass as a three-dimensional measure of a body size (Kühsel et al., 2017). Note that previous studies have shown that the colour lightness and body volume estimates are correlated between drawings from different sources and between males and females (Pinkert, Brandl, & Zeuss, 2017; Zeuss, Brunzel, & Brandl, 2017).

In addition, we calculated the average colour of pixels of an image across the red, green, and blue channels (RGB) as an estimate of the colour lightness of a species (8-bit grey values ranging from 0: absolute black to 255: pure white). For estimating the colour lightness of butterfly species, we focused on the body and 1/3 of the wing area closest to the body because this area is probably the most important for thermoregulation (Tsai et al., 2020; Wasserthal, 1975). For example, in the Pieridae family most species have white wings, but with a dark wing base, which is linked to the V-wing position basking behaviour. Some butterfly species use lateral basking for thermoregulation (e.g. Satyrinae), whereas dorsal and ventral colour estimates are correlated (Zeuss et al., 2014). Differences between clades are considered regarding phylogeny.

The wing area was calculated as the number of pixels of the four wings × pixel area in cm2. To obtain a measure of species' dispersal abilities, wing area estimates were corrected for body size considering only the residual variation in wing area from a linear regression between the log-transformed (natural logarithm) wing area and the log-transformed (natural logarithm) body volume (Outomuro, Golab, Johansson, & Sniegula, 2021).

Gridded distribution data on European butterflies was taken from Schweiger et al. (2014). For odonates, we intersected vector distribution maps (Dijkstra & Lewington (2006)) with a grid of equal area cells (~50 km × 50 km). As an estimate of range sizes, range occupancies were calculated as the number of grids occupied by a species relative to the total number of grid cells covering Europe. Furthermore, we compiled the flight period length (i.e. the sum of months when the imago is active) and the annual mean temperature of occupied grid cells (Karger et al., 2017), but excluded them from the final modelling due to multi-collinearity. Multicollinearity was assessed using the function vifcor of the R-package usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014).

### *Statistical analyses*

All statistical analyses were performed in R version 4.0.2 (R Core Team, 2020). The phylogenetic relationship of species violates the statistical requirement of independent observations (Felsenstein, 1985). Hence, we corrected species traits by their respective phylogenetic relationship among each other. To do so, we used the phylogeny of European odonates from Pinkert et al. (2018) and the phylogeny of European butterflies from Wiemers et al. (2019). Both phylogenies were constructed using a Bayesian framework that integrated morphological as well as phylogenetic data and they are fully resolved to the species-level.

Given these and other similarities, the quality of the two phylogenies is comparable. First, we tested the selected traits for their phylogenetic signal using Pagel’s lambda, a value between zero (no signal) and one, using the function phylosig of the R-package phytools (Revell, 2012). We controlled traits if they had a significant phylogenetic signal. Subsequently, we decomposed each trait into its phylogenetically predicted part (ancestral component of the trait, hereafter P-component; Lynch’s A + u) and the residual deviation (species-specific variance of the trait, hereafter S-component; Lynch’s E) using Lynch's comparative method (Lynch, 1991).

To relate the species traits to their extinction risks, we used threat categories of the European Red List. These were converted into an ordinal scale of extinction risk ranging from 0 (Least Concern) to 4 (Critically Endangered). Ordinal scaled data require ordinal regression models (Seibold et al., 2015; Verde Arregoitia, Blomberg, & Fisher, 2013). We tested for relationships between species’ traits and their extinction risk using an ordered logistic regression with the function polr of the R- package MASS (Agresti, 2010) with the red list status as ordered factor response variable and the traits body volume, wing area, and colour lightness, as predictors. The assessment of the red-list status is in part based on the species range size. Hence, we included the geographical range size as a predictor to statistically account for this effect. This modelling approach estimates the relative strength of predictors in determining a species’ extinction risk, controlled by range size.

## 4 Results

All traits had a significant phylogenetic signal (Table 1). For butterflies, the strength of the phylogenetic signal decreased from body volume to wing area, to colour lightness, to range size. Body volume and range size of odonates had the highest phylogenetic signal and colour lightness the lowest. A significant phylogenetic signal necessitates a control for the phylogeny in the further statistical modelling.

Table 1: Phylogenetic signal lambda of all four traits for 332 butterflies and 115 odonates calculated via the phylosig function (phytools). In all cases $p < 0.001$.

| | **Butterflies** | **Odonates** |
|---|---|---|
| | Phylogenetic signal λ | Phylogenetic signal λ |
| Body volume | 0.99 | 1.00 |
| Wing area | 0.93 | 0.94 |
| Colour lightness | 0.89 | 0.76 |

| | | |
|---|---|---|
| Range size | 0.27 | 1.00 |

The phylogenetic component of the selected traits did not influence the extinction risk of our studied groups (Table.2, P - component). The same applies for the species-specific component and the extinction risk of odonates. However, analysing the S-component, the extinction risk of butterflies decreased with increasing range size. Body volume and wing area had no significant influence on the extinction risk of both groups (Table 2).

*Table 2: Effects of body volume, wing area, colour lightness and range size on the extinction risk of 332 European butterflies and 115 odonates modelled by ordered logistic regression. The P-component represents the phylogenetically predicted part of the respective trait, and the S-component represents the respective deviation of the average trait from the P-component. The raw data represent the trait values without phylogenetic control. Significant relationships (p < .05) are given in bold.*

| **Traits** | **Butterflies** | | | | **Odonates** | | | |
|---|---|---|---|---|---|---|---|---|
| ***S - component*** | *Estimate* | *Std.error* | *z-value* | *p-value* | *Estimate* | *Std. error* | *z-value* | *p-value* |
| Body volume | –17.06 | 27.51 | –0.62 | 0.54 | 6.59 | 58.39 | 0.11 | 0.91 |
| Wing area | –1.08 | 2.82 | –0.38 | 0.70 | 10.51 | 8.88 | 1.18 | 0.24 |
| Colour lightness | –0.01 | 0.23 | –0.42 | 0.67 | 0.08 | 0.04 | 1.79 | 0.07 |
| Range size | –0.71 | 0.22 | –3.09 | **0.01** | 9.47 | 44.26 | 0.21 | 0.83 |
| ***P – component*** | *Estimate* | *Std.error* | *z-value* | *p-value* | *Estimate* | *Std. error* | *z-value* | *p-value* |
| Body volume | 1.20 | 2.01 | –0.60 | 0.55 | –3.48 | 4.07 | –0.86 | 0.39 |
| Wing area | 0.36 | 0.49 | 0.73 | 0.46 | –1.96 | 1.44 | –1.36 | 0.17 |
| Colour lightness | 0.003 | $4.64 \times 10^{-3}$ | 0.61 | 0.54 | 0.01 | 0.02 | 0.32 | 0.75 |
| Range size | –0.28 | 0.49 | –0.57 | 0.57 | 1.92 | 1.92 | 1.00 | 0.32 |
| **Raw data** | *Estimate* | *Std.error* | *z-value* | *p-value* | *Estimate* | *Std. error* | *z-value* | *p-value* |
| Body volume | 1.19 | 1.77 | 0.67 | 0.50 | –1.33 | 2.93 | –0.45 | 0.65 |
| Wing area | 0.42 | 0.47 | 0.91 | 0.36 | –0.92 | 1.19 | –0.78 | 0.44 |
| Colour lightness | $2.16 \times 10^{-4}$ | $4.04 \times 10^{-3}$ | 0.54 | 0.59 | 0.02 | 0.02 | 1.30 | 0.20 |
| Range size | –0.52 | 0.19 | –2.73 | **0.01** | 0.96 | 1.39 | 0.70 | 0.49 |

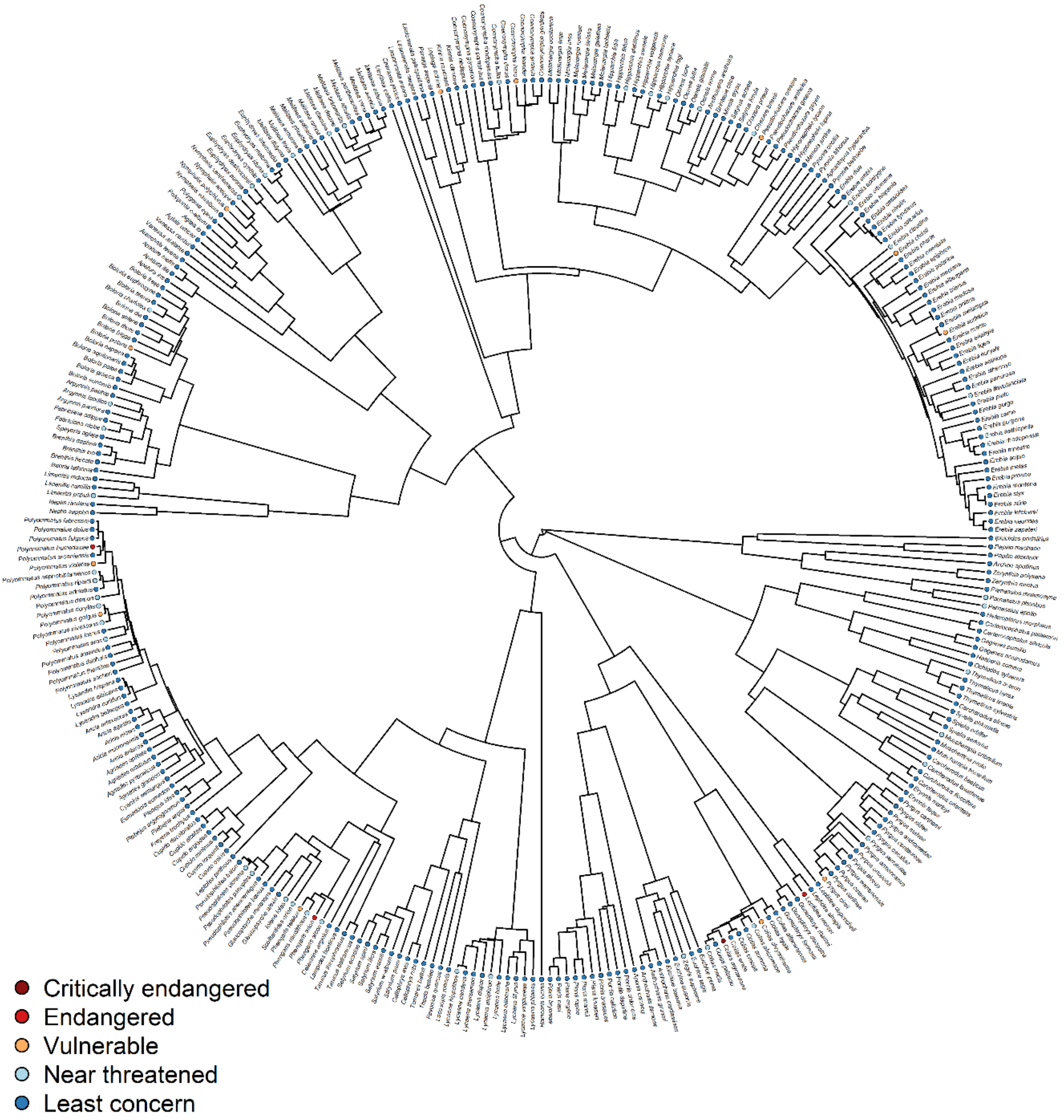

Figure 4: Phylogenetic tree of 332 European butterfly species and their IUCN red list status.

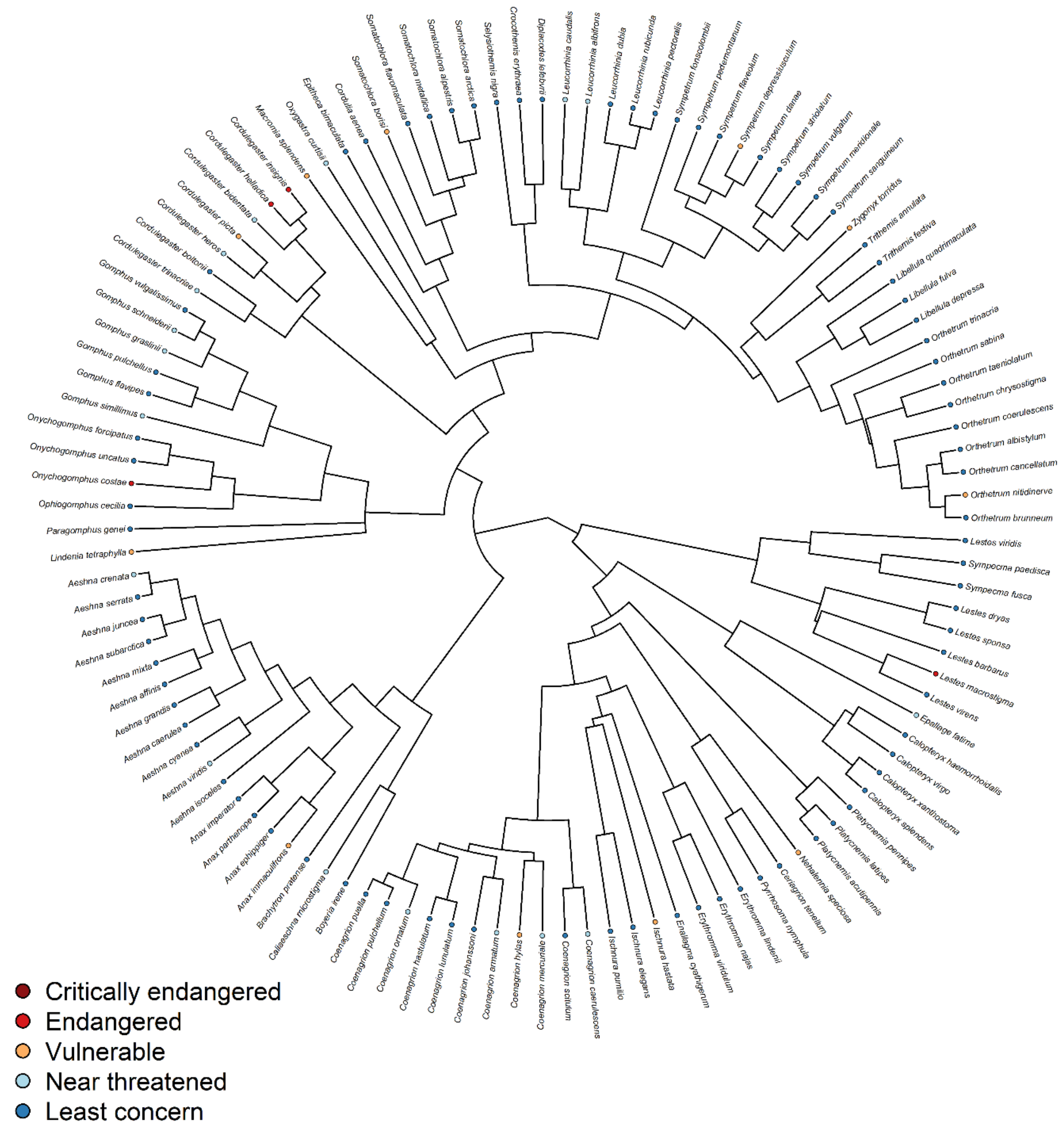

Figure 5: Phylogenetic tree of 115 European odonates and their IUCN red list status.

## 4 DISCUSSION

Our study showed that the extinction risk of butterflies increased with decreasing range size ( Table *2*). Thereby the extinction risk of butterflies only depends on the species-specific variation of range size and not on the phylogenetically predicted part of this trait. The extinction risk of European odonates showed no relationship with the selected traits ( Table *2*).

In our study, all traits exhibited a strong phylogenetic signal (Table 1). The phylogenetic signal quantifies the tendency of related species to resemble each other more than species randomly drawn from the same phylogenetic tree (Blomberg, Garland, & Ives, 2003) (Fig.1, Fig.2). Despite this fundamental fact, Chichorro et al. (2019) found that only half of the 24 evaluated studies on insects were phylogenetically controlled. We split the variance in our morphological traits into phylogenetic and species-specific components to determine the influence of the respective component on our analyses. In this case, the phylogenetic component showed no influence, but the species-specific component, which is thought to represent recent adaptations to climatic conditions (Pinkert et al., 2017), niche conservatism and dispersal limitations (Pinkert et al. 2018), did.

Studies investigating moths commonly do not control species traits in a consistent manner for evolutionary ancestry, often caused by the absence of valid molecular phylogenies (Nieminen, Rita, & Uuvana, 1999; Slade et al., 2013). Coulthard et al. (2019) found, via a genetic distance matrix, no significant relationship between phylogenetic relatedness and population trends, but traits in general as reliable predictors of population changes in moths. Further, they highlight that the relationships of life-history traits are not always in line with conclusions drawn from literature (Coulthard et al., 2019). Two further measures to evaluate the phylogenetic signal are Blomberg's K and Pagel's λ. All studies that calculated these measures determined a high and significant phylogenetic signal in the studied insect traits (Arbetman et al., 2017; Arnan, Cerdá, & Retana, 2017; Pinkert et al., 2020; Suárez-Tovar et al., 2019). We used Pagel's λ to quantify the strength of the phylogenetic signal in our investigated traits (Diniz-Filho et al., 2012; Freckleton, Harvey, & Pagel, 2002; Pagel, 1999).

Our result, that wider distributed butterfly species were less prone to extinction ( Table *2*) is in line with other studies that analysed the role of species distribution for extinction risk (Arbetman et al., 2017; Korkeamäki & Suhonen, 2002; Mattila, Kotiaho, Kaitala, & Komonen, 2008; Pöyry et al., 2009). Butterflies with narrow distribution ranges, are more prone to extinction, such as e.g. *Pseudochazara orestes* and *Polyommatus* *humedasae* (Habel, Gossner, & Schmitt, 2020; Maes et al., 2019). Additionally, forest macro moth species can be threatened by decreasing forest connectivity, despite their high dispersal capability (Slade et al., 2013). However, we did not analyse traits connected to habitat use, which would enable a more direct link to anthropogenically altered habitats and resources (Seibold et al., 2015). In contrast to the butterfly model, for odonates the influence of range size on the extinction risk was not significant. This result is remarkable, because the correlation of range size and extinction risk seems trivial and was found in several insect groups (Mattila, Kaitala, Komonen, Kotiaho, & Päivinen, 2006; Terzopoulou, Rigal, Whittaker, Borges, & Triantis, 2015). However, odonates are able to use small habitat patches to overcome adverse conditions, show rapid responses to changing environment and some species are highly mobile. For example, Kortello and Ham (2010) studied *Argia vivida* in fuel management areas and found that maintaining unmodified stands of dense trees in association with cleared patches of appropriate dimension is a valuable conservation measure for this species. Flenner and Sahlén (2008) studied community reorganisation of odonates in boreal forest lakes under climate change. They found rapid reactions of the population with an equal number of species but a reduction of diversity within 10 years. Suhling et al. (2017) studied long-distance dispersal events of odonates in arid Namibia, where individuals covered distances of several hundred kilometers without any possible reproduction habitat in between. This enables some odonates to strongly recover (Termaat et al., 2015) and might in general lead to a reduced impact of range size on the extinction risk.

Body size did not significantly influence the extinction risk of our study taxa (

Table *2*). Nonetheless, many studies, mainly for mammals or birds, found this correlation and one explanation is that larger species have higher viability costs, which makes them more prone to extinction (Fritz et al., 2009; Gaston & Blackburn, 1995). This general link was also found for butterflies, with body size measured as the median of male and female forewing length corrected by their phylogenetic relationship (García-Barros, 2000). Although body size is often an appropriate surrogate for extinction risk, it also correlates with other traits and is, therefore, often difficult to interpret (Bennett & Owens, 1997; Chichorro et al., 2019). Suárez-Tovar et al. (2019) studied the relation of body size and extinction risk in damselflies (Zygoptera) by measuring four components of body size (body length/ head width/ length of fore and hind right wings) and modelled them with a super-tree of Zygoptera species. They found an increased risk of extinction with increasing body size for most size estimators, but not for body length, which we also found after controlling for phylogeny (

Table *2*). Further, it is essential which measure was taken as proxy for the body size. We selected body volume to study the influence of body size on the extinction risk and used the wing area as proxy for the dispersal ability. Wingspan is an easily accessible species-specific trait among different taxa and can, carefully interpreted, indicate dispersal ability, but it might not be the best for trait analysis (Sekar, 2012). Bowden et al. (2015) found decreasing wing lengths as a response to warmer summers during a period of 18 years in high arctic butterflies. This in turn influences dispersal capacity and fecundity and might predispose these species to a higher extinction risk (Bowden et al., 2015). In line with our findings, Koh et al. (2004) found for males and females that body size did not affect extinction risk of tropical butterfly species (
Table *2*). Kuussaari et al. (2014) studied the influence of body size of butterflies, measured as the average female wingspan, on their mobility and found that, after correcting for phylogeny, the effect was not significant anymore, which is also in line with our findings (
Table *2*). Both studies explain this by the small variation in relative body size compared to other taxa.

## 5 CONCLUSION

In summary, our results show that intrinsic traits alone are poor predictors of the extinction risk of odonates and butterflies, despite well-known mechanistic links of these traits to the environment and species’ population dynamics. In addition, European butterfly species with smaller ranges are more vulnerable, while range size did not affect the extinction risk of European odonates. Thereby our results underline the previous finding that improvements of the water and habitat quality have generally led to the recovery of many freshwater insects, whereas land use continues to threaten terrestrial insect diversity (Engelhardt et al., 2022). Our analyses do not support trait - extinctions risk relationships documented for well-studied taxa such as birds and mammals, but rather suggest idiosyncratic responses of insect species to pollution, land use and climate change. Hence, both the relative importance of major threats and the mechanisms linking intrinsic traits to environmental factors need to be assessed to understand extinction of insects. Without such species-specific information, it will be difficult to mitigate their threat.

# 5 Synthesis and outlook

*Synthesis*

In the following chapter I primarily focus on the two research projects I conducted in the context of my thesis, both of which led to published articles. On the federal state scale, we identified regions in Bavaria where measures of taxonomic diversity fail to protect the phylogenetic diversity. We therefore assessed i) the extent to which patterns in phylogenetic diversity are congruent with patterns of taxonomic diversity and ii) the environmental drivers of these patterns. Throughout Europe we iii) analysed the influence of intrinsic traits, synonymously to functional diversity as another important and deserving protection facet of biodiversity, on the extinction risk of insects. We did this due to well-known mechanistic links of our selected traits to the environment and species' population dynamics for e.g. mammals and birds. Further, we iv) evaluated to what extent the results are influenced by evolutionary relationships. Primarily we used data on European odonates as representatives of terrestrial and freshwater insects.

It needs to be kept in mind that iconic insects represent just a very small fraction of the insect species described worldwide (Basset & Lamarre, 2019). For example, in the IUCN database 67% of vertebrates have been assessed versus 0.8% of insects, but 63% of cycads are assessed as threatened versus 'only' about 13% of bird species (Cardoso, 2012; Chichorro et al., 2019). Another point of criticism can be found in the generalizations of recent scientific findings on insect decline that are based on restricted species sets or geographical scope (Jan Christian Habel, Samways, et al., 2019). Most data are available for charismatic insect groups e.g. due to citizen science projects, and conservation measures are most likely practicable for these groups as the public gain is easier to comprehend (Basset & Lamarre, 2019).

Climate change and biodiversity loss are seen as twin crisis (Corlett, 2020). Our evaluation of extrinsic causes of threat at federal state level revealed that landuse is of higher importance than climate in determining local standardized phylogenetic diversity of different species groups. This confirms the findings of e.g. Habel et al. (2019) that all factors related to agricultural intensification are of much higher relevance or these of Termaat et al. (2015) that found strong recoveries of odonates as a result of an improved water quality. This highlights the responsibility of land users to protect the diversity of the tree of life (Lowe, Threlfall, Wilder, & Hochuli, 2018).

Related species tend to resemble each other more than species randomly drawn from the same phylogenetic tree (Blomberg et al., 2003). Therefore, we tested the phylogenetic signal using Pagel’s lambda, a value between zero (no signal) and one. All traits had a strong signal. This shows the necessity to control for the phylogeny in the further statistical modelling. Despite this obvious methodological circumstance a lot of studies on insects were not phylogenetically controlled (Chichorro et al., 2019). In our Europe-wide study we decomposed each trait into its phylogenetically predicted part (ancestral component of the trait, hereafter P-component) and the residual deviation (species-specific variance of the trait, hereafter S-component) using Lynch's comparative method (Lynch, 1991). We assumed an influence of the P-component. Nonetheless our model results showed no influence of the phylogenetic component, but at least for butterflies the species-specific component did. For our multi-taxa species approach at federal state level we selected another measure of phylogeny, namely the most common measure of phylogenetic diversity Faith PD (Faith, 1992). This ensures a comparability between previous and future studies. This measure is calculated as the sum of branch lengths of the minimal spanning tree among co-occurring species (Faith, 1992). The regional hotspots of standardized phylogenetic diversity differ considerably among the studied taxonomic groups. In a further step we mapped the 10 grids with the highest standardized phylogenetic diversity of all five studies species groups. These hotspots can guide the prioritization of land areas for the conservation of the respective species groups. Altogether we argue rather than using one species as a surrogate for others, information on different species groups should be combined to guide effective nature protection measures. Therefore, we demand to consider this facet of biodiversity stronger. In Bavaria, established protected areas (national parks, natural reserves and areas of the Habitats Directive) were intersected with the 10 hotspots of cross-taxon phylogenetic diversity and the overlap was only approximately 9.6%. This is in line with the results of Mazel et al. (2018) that conservation strategies prioritizing phylogenetic diversity do not necessarily protect functional diversity. Therefore, only focusing on the first is risky in terms of conserving general diversity (Mazel et al., 2018).

The informative value of comparative modelling approaches naturally depends on the quality of the raw data. For our Europe-wide comparison we selected easily available and commonly used traits as well as data on iconic insect species to detect patterns behind the threat status of butterflies and odonates via a trait-based analyses. We would have appreciated to have more comparable traits, ideally such that are more clearly to discuss and not interlinked as for example body size. Generally, we missed the availability of more standardized data. We are aware that the more specific the traits, the less comparability is given, and the more traits, the more correlation occurs. Available traits for both butterflies and odonates were morphological traits, namely body volume in cm³, colour lightness, wing area in cm². We also selected the biogeographical trait geographical range size. The range size status is already incorporated in red-list assessments. That's why findings regarding this topic might seem somewhat redundant at first glance. In order to have consistent models leading to valid conclusions about potential threats, we included it. Otherwise our analyses would have been statistically skewed. Hence, we kept the range size as a control variable in our analyses to statistically remove the effect of range size. Also available were the flight period length (i.e. the sum of months when the imago is active), but we excluded it from the final modelling due to multi-collinearity.

In his MacArthur Award lecture Levin (1992) once said so aptly: "When we observe the environment, we necessarily do so on only a limited range of scales; therefore, our perception of events provides us with only a low-dimensional slice through a high-dimensional cake." Everything in ecology is scale dependent and the influence processes occurring on small spatial scales have on the large scale of e.g. an entire country is astonishing (Gotelli, Graves, & Rahbek, 2010; McGill, 2010). A similar effect can be seen with the consideration of the extinction risk of species. This can partly, in our case only poorly, be explained by the influence of functional traits, but simultaneously e.g. stochastic processes are contributing (Melbourne & Hastings, 2008) or the knowledge of species-specific information is necessary to mitigate their threat. Likewise it is on a nature conservation scale, when linking findings of global and local scales with scales of management relevance (Cash & Moser, 2000).

### *Outlook*

Multi taxa approaches as well as working with phylogenetic data is no new method in ecology but still there is a lot potential.

For multi-taxa studies comparable raw data is necessary. During the last ten years there was increasing effort in establishing protocols for standardized measurement of terrestrial invertebrate functional traits (e.g. Moretti et al., 2017) as well as establishing databases for various species (e.g. Bouget, Brustel, & Zagatti, 2008; Homburg, Homburg, Schäfer, Schuldt, & Assmann, 2014; Kattge et al., 2011). Knowing full well that comparability of different species ignores the species particular nature, e.g. butterflies and their connection to specific host plants, the opportunity to compare species and finding a common ground is a promising way nonetheless. We argue a better one than working with surrogate species. Thus, it would be good to have comparable trait data for more species and to repeat our study for example additionally with small mammals or beetle species. Another aspect that still develops further for future research is the quality of phylogenetic data. For example, studies on moth still use the family level for their phylogenetic input (Slade et al., 2013). These results should be refined as soon as more detailed knowledge on the phylogenetic tree is available. In our case we started with the assumption that the phylogenetic component would have a strong impact on the threat status of our studied species, which could not be confirmed. Furthermore, we are convinced that the application of phylogenetic data in practical nature conservation is essential. It is one main facet of biodiversity and in general the consideration of this topic is still underrepresented in conservation science.

On a final note, while the public perception of biodiversity as an important aspect is constantly growing, it is still important to gather and spread information about the topic. Garden owners, farmers as well as consumers need to be aware of their responsibility for nature conservation.

## 6 Acknowledgements

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# 7 Appendix

The appendix contains the current work progress of my third manuscript.

Working title: Size matters but what else? Optimizing ponds on a management relevant scale.

by Sophia Franke and Simon Thorn

In preparation

## Introduction

Insects are an integral part of terrestrial and freshwater biodiversity (Stork, 2018). Especially in human populated areas of the northern hemisphere insect declines are well documented (Montgomery et al., 2020). Simultaneously for terrestrial habitats extrinsic factors such as agricultural intensification, habitat loss, reduced connectivity, nitrogen influx and much more are well known (Jan Christian Habel, Samways, et al., 2019). One problem might be the lack of implementation of nature-friendly land-use practices on a large scale (Jan Christian Habel, Samways, et al., 2019; Sayer & Greaves, 2020). Another problem is the biased view on insects (Basset & Lamarre, 2019).

The crux of insect extinctions and declines is that not just species but e.g. biomass, unique ecological functions, and fundamental parts of extensive networks of biotic interactions are lost (Cardoso et al., 2020). It is therefore even more gratifying, that van Klink et al. (2020) showed with their meta-analysis that the abundance of freshwater insects in comparison to terrestrial insects increases. In Europe the water quality improved since the 1980s due to environmental regulations and restoration measures, which leads partially to positive trend changes of dragonflies (Termaat et al., 2015). However, fresh water represents only 2.4% of the earth’s terrestrial surface (Allan et al., 2015; Lehner & Döll, 2004), which underlies the vulnerability of this habitat. On the one hand a positive trend of freshwater insect indices cannot compensate the worldwide insect decline (van Klink et al., 2020). On the other hand due to e.g. climate change and the attendant increase in anthropogenic water demand this habitat is under ongoing pressure (Koutroulis et al., 2018; Vörösmarty et al., 2010).

Small waterbodies of both natural and human origin occur in nearly all biogeographic regions (Céréghino, Boix, Cauchie, Martens, & Oertli, 2014; Oertli, 2018). Moreover in an unexpected, but for years seriously undervalued areal extend (J. A. Downing et al., 2006), which underlies their importance in global cycles (John A. Downing, 2010). As freshwater in general, natural ponds, also underlie a strong anthropogenic pressure (Dudgeon et al., 2006; Vörösmarty et al., 2010). Land use changes led to high loss of natural ponds, but simultaneously by these changes many types of artificial water bodies occur (Oertli, 2018). This shift from natural to artificial water bodies is a global trend (Oertli, 2018). Often, these artificial ponds are or at least can be managed in a way that they are ecological quite similar to natural ones (De Marco et al., 2014; Maynou, Martín, & Aranda, 2017; Vad et al., 2017), even though their conservation value might be lower than that of natural systems (Oertli, 2018). Besides, it is not the single waterbody as such, but the network of ponds in a region, which develops its potential as very important freshwater habitat (Hill et al., 2018). These pond rich regions can be e.g. seen as stepping stones for the observed northward and/or upward movements of species due to climate change (Céréghino et al., 2014), underlying their enormous values for future conservation measures (Oertli, 2018). However, little attention is paid to these habitats in the context of conservation of water environments (J. Biggs, von Fumetti, & Kelly-Quinn, 2017; Boix et al., 2012). The management and conservation of ponds offers the opportunity to protect nature even in human dominated landscapes, where the establishment of larger conservation areas is not implementable (Hill et al., 2018; Sayer & Greaves, 2020).

Dragonflies (Odonata: Anisoptera and Zygoptera) are established indicators to evaluate e.g. the ecological value of a pond or the effectiveness of restoration measures (Janssen, Hunger, Konold, Pufal, & Staab, 2018). Their larval stages strictly depend on freshwater, the imagos, on which we focussed, inhabit terrestrial and freshwater habitats (Corbet, 1999). Odonates species richness is influenced by the pond size (Kadoya, Suda, & Washitani, 2004; Oertli et al., 2002) since larger ponds are more stable due to buffering effects (De Marco et al., 2014). Many odonate species are adapted to mediate or even low pH values (Buczyńska & Buczyński, 2019) and their richness increases with increasing pH values (Kietzka, Pryke, & Samways, 2017; Pollard & Berrill, 1992).

Most important for the occurrence of odonates is the vegetation and its biological functions (Buczyńska & Buczyński, 2019; Corbet, 1999; Le Gall, Fournier, Chaput-Bardy, & Husté, 2018). For adult odonates macrophytes are important for the egg laying whereas the terrestrial vegetation at the pond edges is essential during the aerial adult stages for foraging, as refuges from predators, and for distribution (Raebel *et al.*, 2012; Le Gall *et al.*, 2018). The vegetation in and around ponds is in steady development, hence the species richness depends indirectly on the pond age (Kadoya et al., 2004).

To mitigate the insect decline it is essential to urgently establish or extend local strategies that favour insect habitats and at best have a reasonable price. We studied 41 ponds that were created between 1999 and 2019 and after excavation left to natural succession. We assumed that excavating is the most expensive work and the larger and/or deeper the pond the higher the excavation cost. Physio-chemical processes within as well as succession in the surrounding changes the pond quality associated with changes in the number of species or their general composition (Biggs, Williams, Whitfield, Nicolet, & Weatherby, 2005). For example low pH- values affect the survival and emergence of aquatic organisms (Bell, 1971) and vegetation on the water surface, along the shoreline and in the surrounding of the pond influences the number of species by e.g. shading or higher prey offer due to highly structured water bodies (Nagy et al., 2019; Remsburg, Olson, & Samways, 2008). Ponds that are left to natural succession offer different habitat conditions at the process of time and thus, might fail to comply at some succession stages with the species requirements.

In this study, we examined the influence of (i) the pond size, (ii) the pH-value, (iii) the bankside cover and (iv) the time since excavation on the number of dragonflies at different ponds on county level in Bavaria.

## Material and Methods

### *Study area*

The study was conducted in south-eastern Germany, in the administrative district Haßberge, Bavaria, covering an area of about 950km². The Haßberge district is located between the cities Schweinfurt, Coburg, and Bamberg. It is divided by the River Main and the Main valley. Furthermore, the study area is characterized by low mountain ranges up to 500 m a.s.l., extensively managed meadows, river valleys, and dry meadows.

The study ponds were created by the local conservation agency in close collaboration with local forestry enterprises between 1999 and 2019 (Fig. 1). In total we studied 41 ponds out of 15 different years. All ponds were left to natural succession after their creation.

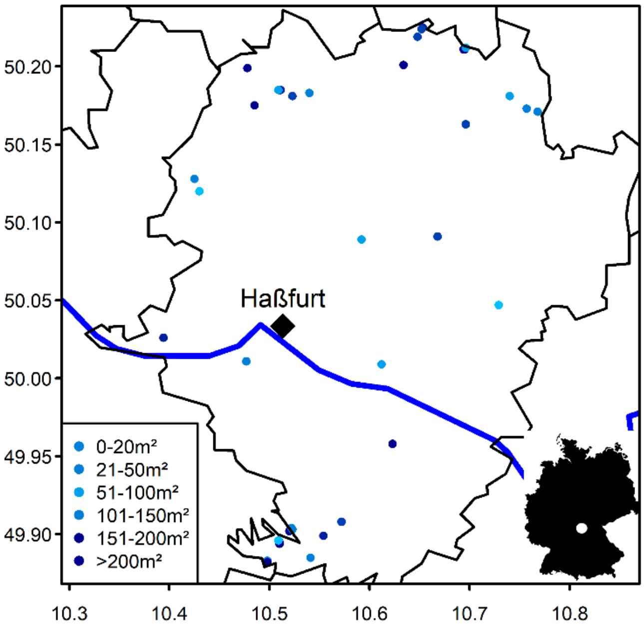


Fig. 1: Administrative district Haßberge and its position in Germany (white dot on black inset map). Blue dots represent the studied ponds according to their size; blue line is the river Main.

### *Sampling design*

The study was conducted during the growing season between May to the beginning of September 2020. Every pond was investigated once in the end of May, mid-July and in the end of August. This was done to detect both early species e.g. *Pyrrhosoma nymphula* and late species e.g. *Aeshna mixta*.

For each pond, we recorded following local parameters: depth (m), surface area (m²), bankside cover with trees/bushes/herbs (%) and pH- value. In the beginning, we considered to analyze the volume of the ponds (depth times surface area) in relation to the species number. In the final analyses we selected the surface area

To overcome sampling bias and underestimation we used both, adult and exuviae sampling during each visit (Bried, D'Amico, & Samways, 2012; Raebel, Merckx, Riordan, Macdonald, & Thompson, 2010). We recorded Odonata only in the daytime from 10 am to 6 pm and under favorable weather conditions meaning sunny, windless, and a minimum air temperature ≥ 15 °C (Dijkstra & Lewington, 2006). In case, a determination was not possible by direct visual observation, individuals were caught with a hand net, identified, and released immediately. All visible exuviae were collected and determined by using a microscope. For the determination of the Anisoptera exuviae we used the key of Bellmann (2013) and for the Zygoptera exuviae the key of  Brochard, Groenendijk, Van der Ploeg, & Termaat (2016).

*Statistical analyses*

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020). The species observations of all three visits were summed up for each pond. The pond size was log transformed for further analysis. We tested for relationships between pond characteristics and land use on species numbers by fitting a general linear model (GLM) (Agresti, 2010) with the species number as response variable and pond size, pH-value, bankside cover, and the year of excavation as predictors. The residual variance of the GLM was explained by the number of species by fitting a linear model (LM).

To verify the variation of the species composition in relation to the ponds and the environmental variable we used Non-metric Multidimensional Scaling with Bray-Curtis dissimilarity index on two axis using *metaNMDS* function and analysed the influence of environmental variables using *envfit* function of the R package vegan (Oksanen et al., 2019).

## Results

The 41 observed ponds were between 10 to 140 cm deep (mean: 66 cm) and their size varied between 6 and 440 cm² (mean: 135 cm²). We classified the surrounding of the ponds in four categories, according to their vegetation- the percentage distribution is open land (0%), more meadow as forest (24%), light forest (34%) and forest (41%). The measured pH- value differed between 5 to 9; acid (37%), neutral (46%) and alkaline (17%). 34 % of the ponds were without water surface vegetation, 13 ponds were covered with at least 30 % vegetation, another 4 ponds were covered with at least 31 - 60% surface vegetation and further 10 ponds were covered with 61 to 100% water surface vegetation.

A total of 1735 dragon- and damselflies belonging to 18 species were recorded (s. Appendix S1). This corresponds to 24% of odonates listed for Bavaria (Winterholler et al., 2018). Further, we recorded two species listed in the red-list of Odonata in Bavaria. *Lestes dryas* is categorized as threaten (category 3) and *Aeshna cyanea* is classified as near threaten (Winterholler et al., 2018). The two most common species were *Coenagrion puella* (515 individuals including exuviae) and *Aeshna cyanea* (459 individuals including exuviae). Species that we observed in total with less than 10 individuals during the three observation were: *Calopteryx virgo* (8), *Platycnemis pennipes* (3), *Aeshna mixta* (3), *Sympetrum vulgatum* (1), *Somatochlora metallica* (1) and *Anax imperator* (1). The maximum number of species was nine at two ponds, the mean was 4.8 species per pond.

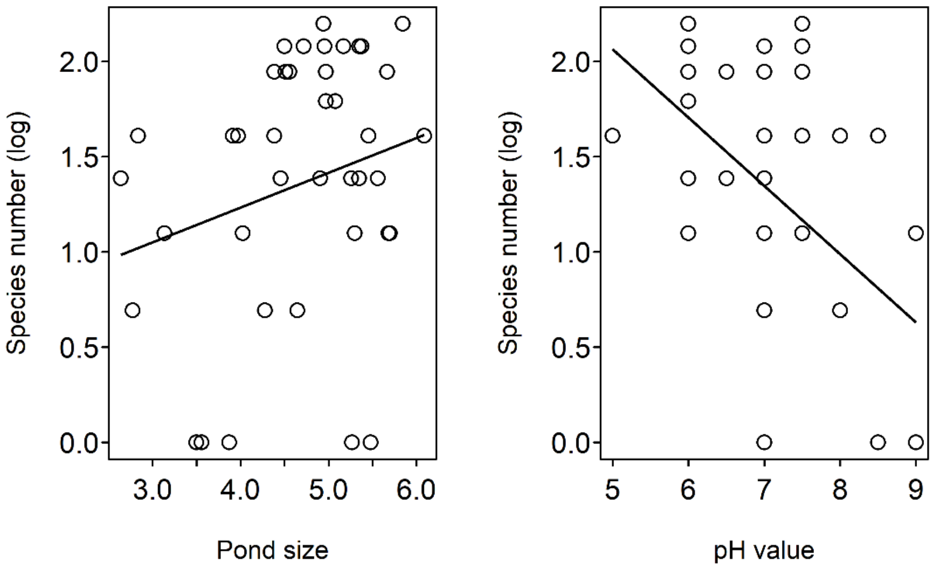


Fig. 2: Scatterplots

The number of species increases with an increasing pond size, decreasing pH-value and decreasing bankside cover (s. table 1). The effect sizes of the variables are nearly similar, thus they are of equal importance. The year of excavation has no significant effect on the number of species.

Table 3: Results of the generalized linear model of the number of species as dependant variable and pond size, vegetation along the shoreline, year and pH-value as predictor variable.

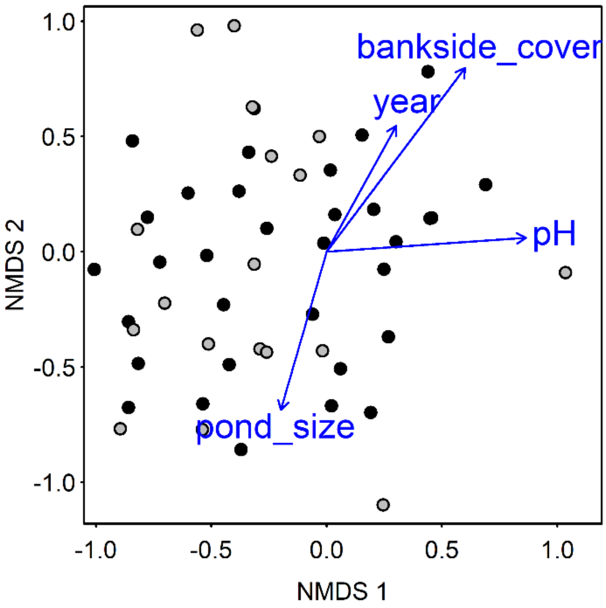
| | Estimate | Std. Error | z value | p value |
|---|---|---|---|---|
| **Pond size (log)** | 0.226 | 0.094 | 2.405 | **0.016** |
| **pH- value** | -0.217 | 0.098 | -2.222 | **0.026** |
| **bankside cover** | -0.630 | 0.246 | -2.565 | **0.010** |
| year | 0.016 | 0.013 | 1.312 | 0.189 |

The residual variance of the generalized linear model could be explained by the number of species (Tab.2).

Table 4: Result of the linear model of the residuals of the model results (glm) as dependent variable and number of species (natural logarithm) as predictor variable.

| | Estimate | Std. Error | z value | p value |
|---|---|---|---|---|
| number of species | 1.014 | 0.130 | 7.823 | **0.000** |

The species composition of the studied ponds is significantly driven by the pH- values (Fig. 2).



**stress = 0.208**

Fig. 3: Result of the Non-metric Multidimensional Scaling (NMDS). Black dots represent the ponds and grey dots represent the species. Blue arrows represent the environmental variables.

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## 9 Erklärung

Ich versichere, dass ich meine Dissertation

**Evaluierung intrinsischer und extrinsischer Gefährdungsursachen heimischer Libellenarten auf unterschiedlichen räumlichen Skalen**

selbstständig ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Horb, den 31.01.2023

Sophia Franke