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by

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Abstract

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Understanding the impacts of anthropogenic change on the world's biodiversity is a fundamental goal of ecology. Assessing broad-scale patterns in biodiversity is especially critical for appropriately allocating limited conservation resources amid the ongoing biodiversity crisis. Recent advances in data availability and computational tools have made synthesis an increasingly powerful approach for exploring these patterns, allowing us to assess previously intractable continental and global scale questions. However, controversy over the use of synthesis methods is ongoing due to limitations in data and tools. Further, synthesis largely focuses on species-based approaches, leaving unaddressed other critical dimensions of biodiversity.

Over three chapters, I discuss the powerful opportunity synthesis represents and address the critical need for improved methodology for understanding biodiversity change. In chapter 1, I lay out a road map for overcoming limitations of biodiversity synthesis. I advocate for improved metadata for constituent studies to facilitate better inclusion of ecological context in synthesis work, adoption of best practices in code development and sharing, and more explicit statements of inference grounded in data scope. In chapter 2, I present my contribution to synthesis software, the R package `taxadb`, a tool for reconciling taxonomic discrepancies. `taxadb` uses a local database to interface with taxonomic data providers allowing quick resolution of species names to taxonomic ID's. In chapter 3, I perform the first broad-scale synthesis of temporal functional diversity trends. Bridging 1000's of assemblage time series and functional trait data, I assess general patterns of functional change. I find evidence of maintenance of functional structure across communities, regardless of taxon, climate, or realm.

To August, who always brought me back to solid ground.

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Introduction

Earth is in the midst of what is being described as the Sixth Mass Extinction (Barnosky et al. 2011). As a result of anthropogenic impacts such as habitat destruction, land use intensification, pollution, and climate change, we are losing species at rates far exceeding past extinction rates (Pimm et al. 2014). In addition to increasing extinctions, human influence is also causing profound and fundamental changes to where species are found and how they coexist in communities (Cardinale et al. 2012, Bartley et al. 2019). Understanding how biodiversity is changing is critical for assessing ongoing anthropogenic impacts on the ecological process that support ecosystems and human life. However, spatial and temporal patterns of biodiversity change are challenging to assess, as biodiversity is inclusive of many dimensions of life on earth including variation in genomes, species, traits, evolutionary history, and ecosystems, many aspects of which are profoundly data limited (Magurran and McGill 2011, Hughes et al. 2021).

Recent advances in data availability and computational tools have facilitated a wave of biodiversity synthesis work assessing broad-scale biodiversity patterns using existing data. Already, synthesis analyses have led to significant advances in our understanding of where biodiversity is (Norman 2003, Jenkins et al. 2015), how it is changing through time (Vellend et al. 2013, Dornelas et al. 2014), and how it is responding to disturbance (Supp and Ernest 2014, Li et al. 2020). Still, adoption of synthesis approaches is relatively nascent and many challenges relating to best practices, software tools, and inference from biased data, remain unaddressed (Cardinale et al. 2018). Synthesis is further limited by the prevalence of a species-based lens for assessing biodiversity, reflecting both the ubiquity of species approaches in biodiversity work and the kinds of data that until recently have been available. My dissertation focuses on the utility of synthesis approaches for understanding biodiversity change, looking at methodological process, tools, and application.

The first chapter discusses the current state of synthesis work and outlines a path forward for shoring up some serious limitations. Concern about the role of synthesis in ecology has been ongoing since its adoption (Lindenmayer and Likens 2011), playing out recently in a few high-profile discussions of synthesis-based studies of broad-scale biodiversity patterns (e.g. Dornelas et al. 2014, Gonzalez et al. 2016, Vellend et al. 2017, Cardinale et al. 2018, Primack et al. 2018). Critiques of synthesis cite data biases, poor incorporation of site-specific characteristics, and overreach in scope of inference as seriously undermining their efficacy (Desquilbet et al. 2020). Still, many broad-scale questions are simply intractable with any other approach. I give my perspective on reconciling urgency in understanding broad-scale patterns with methodological limitations.

The second chapter outlines an R package developed to fix taxonomic discrepancies in biodiversity data synthesis. One of the fundamental and often hidden challenges of combining biodiversity data from multiple sources is differences in the taxonomy used to distinguish species (Dayrat 2005, Remsen 2016). Discrepancies arise from several sources including splitting and merging of species, synonyms, common names, and misspellings. Multiple sources of taxonomic data exist which provide a consistent taxonomic concept for resolving these discrepancies, by translating scientific names to taxonomic ID's (e.g. Roskov Y. 2018, Biotechnology Information 2019, ITIS 2019). However, the tools for accessing those providers in a traditional data processing workflow are computationally limited. I develop a new approach for accessing taxonomic data from multiple providers using a local database, allowing resolution of millions of names to taxonomic ID's in seconds.

The third chapter presents an analysis of broad-scale functional diversity change through time. Multiple recent assessments of biodiversity change have found that the net trend in local species diversity across many communities is not significantly different from zero, despite increasing turnover in species identity (Vellend et al. 2013, Dornelas et al. 2014, Supp and Ernest 2014). These results seemingly stand in opposition to expectations for anthropogenic stress on ecological communities. While community structure is clearly changing, species diversity metrics are unable to capture the nature of that change. Functional diversity provides an alternative approach to measuring community structure, by describing species in term of the traits which determine their ecological role (Mcgill et al. 2006). Shifts in functional diversity are more tightly linked to ecosystem function, resilience, and stability than species-based metrics and therefore give us an operational measure for understanding how communities are changing (Hooper et al. 2002). I pair thousands of existing community time series with functional trait data to assess broad patterns in functional structure change through time.

The overall contribution of this dissertation is to general synthesis approaches, tools, and applications. Chapter 1 develops the conversation around how synthesis can be appropriately applied even in situations of limited or biased data. Chapter 2 describes an R package that automates a significant logistical challenge in biodiversity synthesis, taxonomic inconsistencies. Chapter 3 uses the best practices described in Chapter 1 and the tool presented in Chapter 2 to perform the first broad-scale analysis of functional diversity change through time. Together, these chapters push forward further development of synthesis approaches and demonstrate how synthesis can address previously inaccessible biodiversity questions.

Chapter 1

Power and limitations of synthesis approaches for understanding biodiversity change

Kari E. A. Norman   Carl Boettiger

Abstract

Assessing broad-scale patterns of biodiversity distribution and change is a fundamental goal of ecology and conservation. Recent advances in data availability and computational tools have made biodiversity synthesis an increasingly powerful approach for exploring these patterns, allowing us to assess previously intractable questions. However, concerns about the efficacy of synthesis, particularly with limited and biased data, have called to questions the role synthesis should play in addressing biodiversity change. Here, we survey the current state of broad-scale biodiversity knowledge across species, functional, phylogenetic, and interaction diversity, discuss the current state of the tension about synthesis approaches, and lay out our perspective for best steps in moving synthesis work forward. We advocate for improved metadata to incorporate ecological context into synthesis work, higher standards of code reproducibility and transparency, and greater nuance in how results from biased data are presented.

Introduction

Assessing the state of the globe's biodiversity and how it is being impacted by human pressures is a fundamental goal of ecology. From the formation of Conservation Biology as a field focused on biodiversity's protection over 30 years ago (Soulé 1985), a monumental effort has been poured into describing biodiversity and how it relates to ecological processes. While we have a better understanding now than we ever have before of how biodiversity is distributed across the globe and which areas are of greatest concern (Norman 2003, IPBES 2019, Bradshaw 2020), fundamental gaps remain in our understanding of biodiversity and how it is changing (McGill et al. 2015). Recent advances in data availability and computational tools have facilitated a new wave of "big data" biodiversity work, which seeks to address some of these gaps by establishing general biodiversity patterns from syntheses of existing data (Farley et al. 2018, Runting et al. 2020). This approach stands in contrast to a long history of place-based ecology, raising concerns about inference based on data removed from its ecological context (Lindenmayer and Likens 2011, Hampton et al. 2013).

Debate about the role of synthesis work in ecology has been ongoing since the beginning of its use, with some skeptics going so far as to cite it as endangering the "culture of ecology" (Lindenmayer and Likens 2018). Recently, the debate has further crystallized in a few high profile and highly-polarized exchanges in the literature surrounding meta-analyses of broad-scale biodiversity trends (Dornelas et al. 2014, Cardinale et al. 2018, Primack et al. 2018, van Klink et al. 2020, Desquilbet et al. 2020). These studies found no net change in species diversity across studies, and increases in abundance of some taxa, two results that seemingly run counter to prevailing beliefs about how biodiversity is changing. While no one disagrees about the importance of understanding these patterns and that we should use best available tools to address them, there is profound disagreement about whether or not synthesis is an appropriate or even trustworthy approach. Entrenchment of the two perspectives has made charting a course forward for synthesis approaches to broad-scale questions difficult. Here, we discuss the nature of the debate and offer our perspective on how to reconcile criticisms of synthesis approaches with the urgent need to better understand general biodiversity trends.

Comprehensively describing biodiversity is fundamentally challenging not just because of the sheer scope of the world's biota, but because biodiversity is inclusive of variation across ecosystems, species, functional traits, phylogenies, interactions, and genetic composition (Magurran and McGill 2011, Miraldo et al. 2016). Recent work, such as the Essential Biodiversity Variables framework, has made significant strides in defining key variables representative of the many biodiversity dimensions (Pereira et al. 2013). However, while biodiversity is conceptually inclusive of variation across biological scales, in practice it is most often summarized by community-level metrics of a few facets of biodiversity. Species-based metrics are by far the most common method of quantifying biodiversity, as species are a ubiquitous unit of ecology and often the first thing measured in an ecological system.

Both functional diversity and phylogenetic diversity have increasingly been incorporated alongside species measures in comprehensive assessments of biodiversity and conservation priorities (Albouy et al. 2017, Brum et al. 2017, Robuchon et al. 2021). Functional diversity describes the span and structure of the functional space of a group of species, where the functional space is constructed from the traits of constituent individuals. By directly measuring the traits that determine an organism's role in ecological process, functional diversity provides a more mechanistic summary of community structure (Petchey and Gaston 2006). Phylogenetic diversity describes the length and span of the underlying phylogenetic tree of a group of species (Faith 2018). Measuring the evolutionary history represented by species provides an estimate of evolutionary capacity and therefore potential capacity of a community to adapt to environmental change (Véron et al. 2019). Most recently, species interactions have been recognized as a critical fourth dimension of biodiversity, reflecting their role as a fundamental building block of ecological processes (Tylianakis et al. 2010). Summaries of interaction diversity are often stated in terms of the larger network of interactions in a community.

Synthesis methods are a potentially powerful bridge between increasing volumes of heterogeneous ecological data and gaps in biodiversity knowledge (Koricheva et al. 2013, Heberling et al. 2021). Biodiversity data come from a variety of sources collected for different purposes, including experiments testing specific hypotheses, individual observations from community scientists, specimens from museum collections, and long-term monitoring programs (Farley et al. 2018). We have seen huge steps forward in making these data available for synthesis, with an explosion in databases for different forms of biodiversity data, many of which are accessible through existing analysis tools such as R. This data allows us to assess for the first time similar patterns across many taxa and systems. Still, many legitimate concerns have been raised about how to do synthesis in a robust way, particularly when data may be fundamentally biased (Bayraktarov et al. 2018, Yen et al. 2019, Hughes et al. 2021).

Biodiversity science is at a critical time, with increasing urgency to provide a comprehensive scientific foundation for conservation action alongside increasing availability of computational and data resources. Synthesis approaches are uniquely suited to address the intersection of need and data availability, however concerns about their efficacy undermine their integration into the biodiversity toolbox. We advocate for a more nuanced conversation surrounding the applications of synthesis methods for biodiversity work. We start with a brief summary of the major threads of agreement in our understanding of biodiversity, outline some steps forward for reconciling the synthesis debate, and discuss what that may look like for some of the outstanding questions of the field.

Agreement and knowledge gaps in biodiversity understanding

While tension over the nature of broad-scale biodiversity trends has been prevalent over recent years, there is significant agreement about many aspects of both the state of biodiversity and existing knowledge gaps. It is therefore first helpful to take a step back and outline what we do and don't know about biodiversity from a natural science perspective. We structure our summary loosely following the framework of McGill et al.

(2015) looking at diversity across global, regional, and local scales, but expand beyond species diversity to include functional diversity, phylogenetic diversity, and species interactions. These four components represent the most commonly studied community-level dimensions of biodiversity. We focus on macroscopic organisms, as they are largely the systems within which the synthesis debate has played out. We assess the current known state, temporal trends, and relevant data available for synthesis. Rather than replicating existing comprehensive reviews of biodiversity (see for example Hortal et al. 2015, IPBES 2019), this section outlines understanding and questions at the forefront of large-scale biodiversity science, and the resources available to assess them.

Species Diversity

Species are by far the most commonly studied unit of diversity (Chiarucci et al. 2011). Species richness and species diversity are ubiquitous in assessments of the temporal and spatial state of biodiversity and in work linking diversity to ecosystem function, resilience, and stability. Multiple recent overviews of the state of species diversity illustrate that while it may be the best understood facet of biodiversity, there are still clear fundamental gaps in our current understanding (Cardinale et al. 2012, McGill et al. 2015).

An estimated 8.7 million eukaryotic species live on earth, with less than 15% of those species currently described (Mora et al. 2011). Global trends in species diversity are some of the best established patterns of biodiversity science. Of known species, extinction rates are estimated to be up to 1000-fold higher than background rates (Pimm et al. 2014), indicating magnitudes of loss consistent with the sixth mass extinction (Barnosky et al. 2011). Since recently described species are more likely to be critically endangered, this rate is likely an underestimate of true loss. And while trends in global species diversity are also a function of the speciation rate, no clade-level estimate of diversification outpaces estimated levels of extinction, even in taxa with a relatively high speciation rate like vascular plants (Pimm et al. 2014). There is no doubt that global species diversity is decreasing at an accelerating rate.

Assessing biodiversity patterns at smaller geographic and temporal scales, our view changes from evolutionary time to the last century of global change. At the regional scale, trends in species diversity are quite different from global trends. Net regional species diversity is being maintained or increasing even in areas of high impact for many taxa, particularly plants, mammals, reptiles, and freshwater fish (Sax and Gaines 2003, Winter et al. 2009, McGill et al. 2015). While extinctions are clearly occurring at regional levels, they are compensated for by introductions of non-native species and ongoing biotic homogenization. Still, net increases are not necessarily an indication of no conservation concern, as losses of specialist species and decreases in the regional species pool will likely impact landscape resilience and result in a growing extinction debt (Sax and Gaines 2003).

Local species diversity change has been the topic of substantial debate in recent years. A series of high-profile papers estimated trends in local species diversity and found no net loss of species diversity for plant communities (Vellend et al. 2013), disturbed communities (Supp and Ernest 2014), or thousands of community time series spanning climate, realm, and taxon (Dornelas et al. 2014). A series of critiques raised concerns about a lack of data from areas expected to have high biodiversity impact, analyses with no historical baselines, and extrapolation of trends from relatively short time windows (Cardinale 2014, Gonzalez et al. 2016, but for a defense see Vellend et al. 2017). Still, despite clear limitations in these studies, a generous body of work has amassed finding similar patterns using a variety of datasets in many systems (Elahi et al. 2015, Jones et al. 2017, Gotelli et al. 2017, Dunic et al. 2017, Barnagaud et al. 2017). There is now strong evidence that particularly in communities not experiencing direct human impact (Sax and Gaines 2003), and even in some communities that experience significant land use change (Finderup Nielsen et al. 2019, but see Li et al. 2020 for losses along land use gradients), richness is maintained or increasing (Li et al. 2020, Trindade-Santos et al. 2020). Such a consistent finding across studies suggests that in the absence of catastrophic disturbance species richness is a strongly regulated quality of an ecosystem (Brown et al. 2001, Gotelli et al. 2017).

As species diversity trends seem unable to capture the kind of change happening in many communities, recent work focuses on potential alternative approaches for understanding community change. Identifying elevated rates of turnover and what changes in species identity mean for community structure is one potentially promising avenue (Magurran et al. 2010, Hillebrand et al. 2017, Magurran et al. 2019, Blowes et al. 2019, Rishworth et al. 2020). However it presents a number of challenges, including difficulty in determining background rates of turnover (Dornelas et al. 2019), especially in communities with no baseline. It also presents a significant departure from usual approaches in conservation where the goal is to maintain as many species as possible. Conservation based on turnover rates means identifying which communities are desirable when there are differences only in species composition rather than number. Some have suggested that turnover should be minimized as much as possible (Hillebrand et al. 2017), however higher levels of turnover may actually be desirable, as they are evidence of communities adapting to environmental shifts such as climate change.

Still another option for understanding biodiversity change is to move beyond simplistic species-based metrics to capture shifts in different dimensions of biodiversity. Efforts to understand trends in biodiversity change through functional, phylogenetic, and network lenses will be discussed in greater detail in later sections.

Data

Accessibility of species data has increased rapidly over the last decade with multiple efforts spanning a wide range of goals and included data types and quality. Databases such as GBIF cast the widest net by collating biodiversity data of any form, ranging from point observations from community scientists to data from rigorous long term monitoring programs ("GBIF" 2021). It subsumes other more targeted efforts, such as iNaturalist which focuses on community science data and eBird, which collects bird lists from birders of a wide range of skill levels (Sullivan et al. 2009). Other databases collate only high-quality data from studies with consistent sampling protocols and detailed metadata. For example, bioTIME collates occurrence and abundance time series of communities following rigorous data quality standards (Dornelas et al. 2018). PREDICTS collects data from studies looking at the impacts of human disturbance on biodiversity (Hudson et al. 2017). Long term ecological research networks (LTER's) like the National Ecological Observation Network are another source of high quality replicated biodiversity data. Many LTER's release data continuously as it is collected, constructing high quality biodiversity time series with many geographic and temporal replicates.

Despite the wealth of biodiversity data now available, it does exhibit some systematic biases in taxonomic and geographic coverage. Data largely reflect legacies of colonialism, discrepancies in funding availability for different countries, and historical taxonomic preference (Nuñez et al. 2021). Only an estimated <7% of the globe is represented by the largest sources of biodiversity data (Hughes et al. 2021). The majority of well sampled areas are in the global North and severely mismatched to areas of highest conservation concern (Cardinale 2014).

We examined GBIF data to identify general data distribution across taxa. For all non-fossil occurrence records in the most recent version of the database (accessed 11/01/2021) we found that for vertebrate species, birds have by far the most samples, especially relative to the number of species in the Aves class (Fig 1.1). Percentage of observations were much more balanced for vascular plant classes, where percentage of observations follows percentage of species relatively closely. Still, the vast majority of species are sample-poor. We found almost half a million species only have a single recorded observation in the database and approximately 1.2 million species have less than 10 observations. With 1.8 million total species represented in the database, only 0.6% of species represent 90% of the observations. These patterns are in line with findings from other databases, where for example open data of tree species have 20 high quality records for only 26% of species (Serra-Diaz et al. 2018). Data gaps are especially profound for microbial species, for which data only skims the surface of the number of species (Thaler 2021).

Functional Diversity

Functional diversity as a way of describing communities has become a fundamental approach over the last 15 years, building on a rich history of trait-based ecology (Mcgill et al. 2006). Functional diversity work can be categorized in two main veins, 1) functional diversity as a descriptor of community structure, often measuring response to a perturbation and 2) functional diversity as a link between biodiversity and ecosystem function,

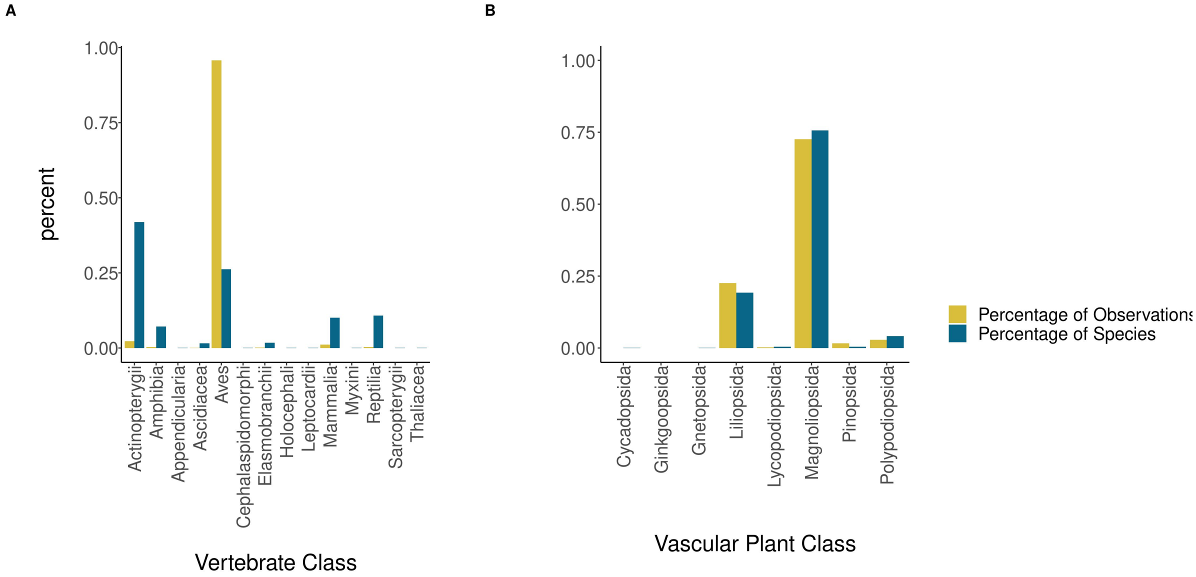

Figure 1.1: Comparison of percentage of the total number of observations (in blue) to percentage of total number of species (in red) for A) vertebrate classes and B) vascular plant classes.

where functional traits provide a mechanistic representation of community structure. Despite a substantial body of observational and experimental work in both veins, synthesis across studies is often hindered by methodological differences in the traits measured for different taxa, trait selection, and metric calculation (Palacio et al. 2021), making formal meta-analyses from existing studies difficult. Recent efforts to collate functional trait data from existing data sets and museum specimens has facilitated a new wave of functional diversity assessments starting from primary data (Villéger et al. 2014, Wong et al. 2018, e.g. Newbold et al. 2020, Trindade-Santos et al. 2020). This work has further allowed us to examine general functional diversity patterns across scale.

On a global scale we have an in-depth understanding of some commonly studied traits and broad descriptions of the global trait space as a whole. Ecologists have been studying traits long before the concept of a trait was fully articulated, with examples going back as far as the beaks of Darwin's finches, or Raup's study of coiled shells (Raup 1966, Gerber 2017). More recent comprehensive assessments of multiple traits build on that foundation while taking a more holistic approach. For example, work in vascular plants indicates that the trait space can be described by two major axes of variation in size and features of the leaf economic spectrum (Wright et al. 2004, Díaz et al. 2016). First assessments of the global trait space based on species-level means give evidence that the distribution of traits for multicellular organisms is uneven and characterized by a high degree of functional redundancy, with non-redundant species also being mostly functionally unique (Mouillot et al. 2021, Carmona et al. 2021). Many trait combinations are not realized by existing species (Cooke et al. 2019b). Studies in birds and mammals also suggest that the global trait space is geographically structured, with higher redundancy in the tropics (Cooke et al. 2019a).

Because the species-level trait means available for large-scale analysis are static identifying how global functional diversity has changed through recent time is difficult. However, we have some projections as to how it may continue to be impacted by anthropogenic activity. Species losses are predicted to reduce both functional richness and functional redundancy (Carmona et al. 2021, Toussaint et al. 2021). While initial losses may be buffered by existing redundancy, disproportionate losses on the boundaries of the trait space will likely have an erosive effect on overall functional diversity (Pimiento et al. 2020a, Carmona et al. 2021). Generally, higher loss is expected to occur in large, long-lived, and slow-reproducing species (Pimiento et al. 2020b).

Studies looking at functional diversity at a regional scale are rare, particularly those looking at temporal trends (Rossi et al. 2020). Unlike species diversity, which has a well established species-area relationship (SAR), the relationship between functional diversity metrics and area is mixed particularly for metrics that incorporate abundances (Karadimou et al. 2016). While we have no comprehensive assessments of temporal change in regional functional diversity, we do know that it may not necessarily follow species trends. The relative impact of species losses and gains on functional diversity is a function of the uniqueness of those species. We would expect that the processes of homogenization and invasion would also shift functional composition, however even when biological homogenization is occurring for species there is not necessarily homogenization of the functional space (White et al. 2018). Describing general trends in regional functional change will be critical for understanding how ecosystem functions may be maintained at the landscape level.

Local assessments of functional diversity are similarly limited and largely look at the response of functional diversity to disturbance rather than trends in communities at a relative equilibrium (Mouillot et al. 2013). We know the most about bird and plant groups, reflecting trait and species data availability. For birds, local functional diversity generally increased over the last fifty year, with declines at the continental scale beginning around the year 2000 (Jarzyna and Jetz 2016, Barnagaud et al. 2017). In plants, local functional diversity shows complex responses to disturbance, fragmentation, and succession processes, with generally significant functional turnover, but not necessarily functional gains or losses (Purschke et al. 2013, Chun and Lee 2019, Zambrano et al. 2019). Functional diversity response to disturbance for other taxa is also varied and a function of disturbance type and intensity (Flynn et al. 2009).

The resolution of trait data is another critical dimension of functional diversity assessment. Almost all work mentioned previously in this section is performed using species-level means, which do not account for individual variation in traits. Intraspecific variation has been estimated to account for ~25% of the overall variation in communities (Siefert et al. 2015) and is critical for maintaining demographic resilience and evolutionary potential (Violle et al. 2012). It is also particularly prone to human impact (Des Roches et al. 2018). Due to the significant costs associated with collecting individual-level traits we don't know much beyond these basic outlines of intraspecific variation, particularly the degree of variation for different traits and how it may be changing.

Data

Access to functional trait data has greatly increased over the past decade with multiple taxa-specific databases compiling species trait means or intraspecific observations. Efforts to collate and standardize trait data have also followed suit, including collaborations like the Open Traits Network, an open science community for gathering and standardizing trait datasets. While there are too many datasets to comprehensively describe here, we list some of the largest and most frequently used as an example of what is available (Table 1.1).

Table 1.1: Summary table of the attributes for major trait databases, informed by metadata collated by the Open Traits Network.

Trait Source	Taxa	Number of Species	Traits	Trait Resolution
Amphibio	Amphibians	6572	body mass, diet, active diel period	species
BIEN	Plants	464348	53 plant traits	individual
Coral Trait Database	Coral	1555	150 coral traits	individual
eFlower	Angiosperms	792	Sex, Ovary position, Number of perianth parts, Fusion of perianth, Symmetry of perianth, Perianth phyllotaxy, Number of perianth whorls, Perianth merism, Perianth differentiation, Number of fertile stamens, Filament, Anther orientation, Anther attachment, Anther dehiscence, Androecium structural phyllotaxy, Number of androecium structural whorls, Androecium structural merism, Gynoecium phyllotaxy, Number of structural carpels, Fusion of ovaries, Number of ovules per functional carpel	individual
Elton Traits	Mammals and Birds	15321	body mass, diet, nocturnality, forest foraging strata, habitat, active diel period, activity seasonality, body length, min maturation size, max maturation size, min offspring, size, max offspring size, reproductive output, breeding strategy	species
FishBase	Finfishes	>33,000	ecology, morphology, life history, habitat	species and individual
FishTraits	Freshwater Fish	809	trophic ecology, body size, reproductive ecology, life history, habitat preferences, salinity and temperature tolerances	species
PanTHERIA	Mammals	5416	size, diet, life history, environmental conditions, ecology	species
TRY	Vascular Plants, Mosses, Lichens	>69000	2091 plant traits	species and individual

Phylogenetic Diversity

Phylogenetic diversity captures the evolutionary lineage represented by each species in the community, thereby giving an indication of the future evolutionary potential of a community (Véron et al. 2019). Phylogenetic diversity also captures at least some aspects of a community's genetic scope, though likely not the significant intraspecific losses occurring across the globe (Miraldo et al. 2016, Theodoridis et al. 2020). Further exploration of patterns of genetic diversity will undoubtedly be critical for understanding biodiversity change, but are outside the scope of this review. Assessments of phylogenetic diversity have been greatly facilitated by the availability of phylogenetic trees that can be paired with existing species data. Patterns of phylogenetic diversity across scales illustrate alongside functional diversity the ways community structure can change independent of changes in species richness.

At the global scale, phylogenetic diversity patterns are broadly similar to species diversity. Speciation does not outpace losses of PD due to extinctions despite high rates for some taxa (Scholl and Wiens 2016). While the loss of any species results in at least a minor reduction in phylogenetic diversity, simulations of random species loss indicate that the majority of phylogenetic diversity can be maintained even after catastrophic species loss (Nee and May 1997). Still, estimates for mammals indicate that it would take millions of years to recover the PD already lost due to extinction, and that recent losses have resulted in reductions in PD far higher than expected by chance for random species extinctions (Davis et al. 2018). Generally the relationship between species and phylogenetic loss is heavily dependent both on the order in which species go extinct and the underlying phylogenetic structure (Erwin 2008, Maliet et al. 2018).

Work on regional and local phylogenetic diversity patterns reflect the complex relationship between species richness and underlying phylogenetic structure. Locally, phylogenetic diversity losses in response to land use change or environmental stress are common as phylogenetically distinct species are lost and replaced by less distinct species, if replaced at all (Winter et al. 2009, Li et al. 2019, Li et al. 2020). Significant phylogenetic losses can occur alongside species gains, leading to hidden phylogenetic impoverishment (Knapp et al. 2008). Phylogenetic diversity may be maintained regionally if species losses are only local (Li et al. 2019), however Winter et al. (2009) found that for European plants, phylogenetic diversity was lost at local, regional, and continental scales despite gains in species richness. Generally, phylogenetic diversity is lost when species go extinct or are extirpated even when net species richness at that scale remains the same, as replacement species do not make up for phylogenetic losses.

Data

With the advent of modern genomics, phylogenetic data is available for a wide variety of taxa. Databases such as TreeBASE (Piel et al. 2009) and the Open Tree of Life (McTavish et al. 2015) store phylogenetic trees and their underlying data. Tools such as Phylomatic make access to phylogenetic treeds even simpler, by requiring only lists of species names to construct a phylogenetic tree for the community based on existing phylogenetic estimates. While existing tree-based tools already represent a huge step forward in making phylogenetic data more accessible and usable, genomics data present another significant pool of phylogeny-relevant data. Genomics data from sources like GenBank are doubling every 18 months (Farley et al. 2018), providing an opportunity to improve phylogenetic trees with inclusion of more genes and more taxa. And though mapping of genomic data to phylogenetic trees is non-trivial, more comprehensive phylogenies taking advantage of this data are increasingly available (Kapli et al. 2020).

Species Interactions

Despite being one of the key mechanisms in ecological communities, species interactions are not often considered alongside other facets of biodiversity in conservation considerations. Work on interactions is severely data-limited, especially relative to the number of interactions a single species or individual may take part in, spanning for example competitive, predatory, and mutualistic relationships. The majority of ecological network studies treat species interactions as static in both time and space, dependent only on co-occurrence (Poisot et al. 2015), adding to difficulty in incorporating network concepts into our understanding of biodiversity change. As such, our inventory of species interactions and how they are changing is sparse.

There is a rich history of site and system focused work describing interactions and their response to perturbations, however geographic and taxonomic coverage is not comprehensive enough to establish general rules for network structure at any scale. Initial evidence suggests that some network characteristics such as connectance and nestedness are largely maintained through time (Trøjelsgaard and Olesen 2016). Network patterns seem inconsistent across latitude and dependent both on network type and habitat. Data limitations and ambiguous expectations of common macroecological rules for networks are both barriers for better understanding of the biogeography of networks (Baiser et al. 2019).

Predictions for consequences of human impact indicate that directly measuring changes in species interactions is critical for understanding biodiversity change. There is strong evidence that networks can rewire even when species composition remains largely the same, both in response to disturbance and as part of natural community fluctuation (CaraDonna et al. 2017, Tylianakis and Morris 2017, Bullock et al. 2018). Rare species and their interactions are often the first to be lost from communities and subsequently go extinct (Tylianakis and Morris 2017). Extinctions and extirpations may also have cascading effects on other interactions in the network, leading to further network deterioration.

Data

Species interaction data is available through a few key databases. GLOBI (Poelen et al. 2014), which stores interaction pairs between species, and Mangal (Poisot et al. 2016), which collects complete interaction networks with their metadata. Biases in network data reflect many of the issues also found in other ecological data including significant geographic and taxonomic biases. Poisot et al. (2021) took a comprehensive look at the Mangal database and found multiple other sampling limitations, including under sampling of some of the most common biomes, sampling of certain network types in only a subset of possible biomes, and a general tendency towards small networks.

Incorporating ecological context into synthesis work and interpretation

Debate about the role and efficacy of synthesis methods in biodiversity research has been highlighted in multiple recent exchanges in the literature. The first, described in detail in the species diversity section above, relates to our understanding of how biodiversity is changing at a local scale. Multiple studies found that for different taxa and community types the net change in diversity across communities is zero (Vellend et al. 2013, Dornelas et al. 2014, Supp and Ernest 2014). These findings were criticized in multiple responses based on a number of methodological grounds relating to the underlying data synthesis (Cardinale 2014, Gonzalez et al. 2016, Cardinale et al. 2018, Primack et al. 2018). A similar story played out in recent work around the nature of invertebrate population declines, where van Klink et al. (2020) found increases in freshwater invertebrate abundance across studies, a result that was also contested (Klink et al. 2020, Desquilbet et al. 2020). In both cases criticisms and defenses of the studies had some common themes surrounding the nature of biodiversity synthesis. We will discuss those themes and what they mean for the future of synthesis work.

Criticisms of synthesis approaches center around data limitations and how they are treated in analysis and interpretation. As outlined in the biodiversity knowledge section, available biodiversity data is profoundly geographically and taxonomically biased, with data missing more often for areas and taxa of highest vulnerability (Hughes et al. 2021). Studies that claim to make universal statements about global trends are therefore necessarily making inferences potentially far outside the scope of underlying data. Included data are also inherently missing some potentially important dimensions of ecological context, including level and type of anthropogenic impact, protection status, and site specific land use history (Cardinale et al. 2018). Large-scale analyses may also suffer from other widely acknowledged issues with processing of disparate data sources, including taxonomic inconsistencies, difficulty in accounting for fundamental sampling differences, reconciling data sources at different scales, and underlying coding errors (Specht et al. 2015). Skeptics of large-scale syntheses also raise concerns that they are unable to incorporate mechanisms that are known to be critical from system-specific studies. For example, the freshwater invertebrate analysis did not include potential upstream impacts despite the fact they are widely accepted as a key mechanism determining freshwater biodiversity (Desquilbet et al. 2020).

Proponents of synthesis argue that it is taking a first look at previously inaccessible questions using best available tools and data. Establishing broad-scale patterns of biodiversity change is critical for directing future scientific and conservation action, but often must make due with incomplete data (Chaplin-Kramer et al. 2021). Far from being the final word on the patterns in question, they serve as initial starting points upon which to build. Synthesis advocates argue that many of the criticisms have unrealistic expectations of available data, or fundamentally misunderstand synthesis as a scaling up of finer scale understanding, rather than an abstraction to assess general patterns (Vellend et al. 2017, Klink et al. 2020). Part of synthesis is exploring which dimensions of context are important and which are not.

We acknowledge the potential power of synthesis methods for identifying the broad-scale patterns critical for conservation alongside meaningful criticisms of their execution. We advocate for a few steps by the community to bridge the two perspectives and move synthesis work forward. First, synthesis work would greatly benefit from expansion and inclusion of more complete metadata from original data sources. Expectations for biodiversity patterns are strongly related to site characteristics, but there is often little to no metadata included in data aggregations about land use and disturbance histories or biodiversity change drivers. Expansion of metadata will be most meaningful after some consensus on which variables are most important and how they should be measured. For example, recent efforts to develop a standardized framework for classifying and measuring disturbance provide a strong starting point to identify key disturbance variables (Buma 2021). For many existing datasets metadata may need to be recovered from primary sources or measured *post hoc* from additional data sources such as remote sensing layers or datasets of human impact (Wildlife Conservation Society-WCS and Center For International Earth Science Information Network-CIESIN-Columbia University 2005).

Second, synthesis analysis should follow best practices in data management and coding. Code underpins almost all modern ecological work to some degree, but for synthesis work in particular the code is the scientific process. Data cleaning, merging, and analysis represent scientific decisions that must be documented, reproducible, and transparent. Code sharing and review is not only critical for ensuring efficacy of code products, but also speeds the scientific process by making code for common, shared tasks accessible for later researchers. Recognition of code as a fundamental part of a manuscript is increasing, however very few journals require code and data with submissions (but see American Naturalist, Methods in Ecology and Evolution, and ESA Journals) (Mislan et al. 2016). And while explicit and enforced standards are critical for achieving code archiving goals (Sholler et al. 2019, Tedersoo et al. 2021), not even they are sufficient to guarantee basic standards of reproducibility (Culina et al. 2020). Synthesis work should hold itself to a higher standard of code availability, reflecting the fundamental role of code in the scientific process.

Finally, we need greater clarity as a community on how to talk about broad-scale syntheses that are nevertheless missing key data and regions. While they represent a significant step forward and may be the most comprehensive looks at many biodiversity patterns so far, they cannot be global using currently available data. Results should be framed from the outset in terms of the biases of underlying data and what they may mean for measured phenomena. While this is by no means a novel call (Cardinale 2014), we feel it is worth explicit statement as it runs counter to publishing incentives, which push for broadest inference statements possible. Data limitations of conclusions should, to the best of our ability, be propagated through to subsequent references of the findings. Without both of these pieces we risk losing the thread of what we do and do not know about broad biodiversity patterns.

Improved synthesis for addressing biodiversity change questions

Survey of the four main biodiversity dimensions above illustrate multiple significant gaps in our understanding of broad-scale biodiversity and how it is changing. A few key questions emerge as being both common across the biodiversity facets and some of the most pressing for understanding anthropogenic impact on biodiversity. We discuss in further detail here two of those questions and how they could be better addressed by our proposed steps for synthesis improvement.

What are background rates of turnover and change in community structure?

One of the emerging questions of biodiversity change is what the typical background rate of change is for communities. All communities experience some level of background species and interaction turnover due to stochasticity and in response to normal environmental fluctuation. Typical rates will likely be heavily impacted by anthropogenic influence (Rapacciuolo et al. 2019). Indeed, initial assessments of turnover rates indicate that turnover is increasing over time in many communities, is generally lower in long-lived taxa, and that there is generally high variance in turnover rates (Dornelas et al. 2014, Blowes et al. 2019, Rishworth et al. 2020). Distinguishing elevated rates from base rates will be key for identifying communities undergoing rapid shifts, both due to elevated stress from external perturbation and as they adapt to novel environmental conditions due to climate change.

Quality study-level metadata is critical for assessing background rates of turnover, as rates are a function of multiple community characteristics including taxa, realm, organism life span, and climate (Blowes et al. 2019) and are likely perturbed by a number of drivers. A key challenge of determining base turnover rates is that all ecological communities on earth are experiencing at least some level of perturbation, making it difficult to empirically estimate the true background rate especially from synthesized data. Recent attempts to separate expected turnover from elevated turnover often turn to null model approaches using either mechanistic predictions of null turnover or community randomization models (Socolar et al. 2016, Magurran et al. 2019). Using datasets with detailed data on different change drivers would allow us to instead take an empirical approach, assessing how turnover rates may change as a function of specific drivers.

How does biodiversity change differ between systems experiencing different kinds of disturbance?

Identifying differences in general biodiversity trends under different kinds of disturbance is a long-time outstanding question of conservation and fundamentally requires explicit consideration of site-level characteristics (Newman 2019). Large-scale syntheses of biodiversity trends are frustrated by systems with multiple co-occurring disturbances. Further, differences in timing of disturbances mean that communities may be simultaneously recovering from one event while experiencing another, resulting in complex expectations for biodiversity trajectories (Graham et al. 2021). While we are prone to making sweeping statements about the impacts of anthropogenic and environmental change on ecosystems, in reality expectations for impact are highly heterogeneous across different ecological and disturbance contexts.

Metadata on study-level disturbance types and timing would shed significant light on the role different kinds of disturbance plays across systems. Metadata collection would build on extensive existing work for classifying disturbances and their interactions (Peters et al. 2011, Borics et al. 2013, Hobday et al. 2016, Jentsch and White 2019, Buma 2021, Graham et al. 2021), defining disturbance type, duration, and intensity. Categories for example may distinguish between relatively natural communities that experience little human intervention but are subject to climate change shifts from systems experiencing significant acute natural or human caused disturbance. Categories will likely be limited initially by the kinds of study metadata available, but could also critically inform the kinds of additional study-level data needed in future collection efforts.

Conclusion

Synthesis approaches are critical for most effectively leveraging biodiversity data to address the ongoing biodiversity crisis. Broad-scale patterns of biodiversity change in particular are both essential for conservation decision making and only accessible through synthesis approaches. We describe a few simple but powerful steps for reconciling synthesis limitations and strengths by having higher methodological standards and better incorporating ecological context in analysis and interpretation of results. Adoption of these suggestions by the community should provide a strong starting point from which to continue further biodiversity synthesis work.

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Transition between Chapter 1 and 2

In Chapter 1, I outlined the tension over synthesis approaches for addressing broad-scale patterns of biodiversity change. Synthesis methods offer a potential opportunity to leverage existing biodiversity data to assess aspects of biodiversity critical for conservation efforts. Synthesis also suffers from multiple limitations related to data biases and scope of inference. I laid out a few simple but powerful steps for reconciling synthesis need and limitations, including improving metadata for better incorporation of ecological context in synthesis, adoption of best practices in coding reproducibility, and explicit inclusion of inference limitations with results.

As discussed in Chapter 1, developing tools for biodiversity synthesis following best coding and open software practices is essential for improving efficacy of synthesis pipelines. By automating common tasks, scientists spend less time on data processing and reduce potential for human error. Chapter 2 outlines a project motivated by those goals and designed to address taxonomic inconsistencies in biodiversity synthesis. I outline the structure and use of `taxadb`, an R package that accesses providers of taxonomic data to translate scientific and common names to taxonomic ID's.

Chapter 2

taxadb: A High-Performance Local Taxonomic Database Interface

Kari E. A. Norman   Scott Chamberlain   Carl Boettiger

Abstract

1) A familiar and growing challenge in ecological and evolutionary research is that of establishing consistent taxonomy when combining data from separate sources. While this problem is already well understood and numerous naming authorities have been created to address the issue, most researchers lack a fast, consistent, and intuitive way to retrieve taxonomic names.
2) We present `taxadb` R package which creates a local database, managed automatically from within R, to provide fast operations on millions of taxonomic names.
3) `taxadb` provides access to established naming authorities to resolve synonyms, taxonomic identifiers, and hierarchical classification in a consistent and intuitive data format.
4) `taxadb` makes operation on millions of taxonomic names fast and manageable.

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Introduction

As ecologists and evolutionary biologists synthesize datasets across larger and larger assemblies of species, we face a continual challenge of maintaining consistent taxonomy. How many species are in the combined data? Do the studies use the same names for the same species, or do they use different synonyms for the same species? Failing to correct for such differences can lead to significant inflation of species counts and miss-aligned datasets. These challenges have become particularly acute as it becomes increasingly common for researchers to work across a larger number and diversity of species in any given analysis, which may preclude the resources or substantive taxonomic expertise for all clades needed to resolve scientific names (Patterson et al. 2010).

While these issues have long been recognized in the literature (Dayrat 2005, Bortolus 2008, Boyle et al. 2013, Maldonado et al. 2015, Remsen 2016), and a growing number of databases and tools have emerged over the past few decades (e.g. Gries et al. 2014, Rees 2014, Wagner 2016, Roskov Y. 2018, Alvarez and Luebert 2018, Foster et al. 2018, Biotechnology Information 2019, ITIS 2019), it remains difficult to resolve taxonomic names to a common authority in a transparent, efficient, and automatable manner. Here, we present an R package, `taxadb`, which seeks to address this gap.

Databases of taxonomic names such as the Integrated Taxonomic Information System (ITIS, ITIS 2019), the National Center for Biological Information's (NCBI) Taxonomy database (Biotechnology Information 2019), the Catalogue of Life (COL, Roskov Y. 2018), and over one hundred other providers have sought to address these problems by providing expert-curated lists of accepted taxonomic names, synonyms, associated taxonomic rank, hierarchical classifications, and scientific authority (e.g. author and date) establishing a scientific name. The R language (R Core Team 2019) is widely used in ecology and evolution (Lai et al. 2019) and the `taxize` package (Chamberlain and Szöcs 2013) has become a popular way for R users to interact with naming providers and name resolution services. `taxize` implements bindings to the web APIs (Application Programming Interface) hosted by many popular taxonomic name providers. Nevertheless, this means that functions in the `taxize` are impacted by several major drawbacks that are inherent in the implementation of these central API servers, such as:

- Queries require internet access at all times.
- Queries are slow and inefficient to implement and perform; frequently requiring separate API calls for each taxonomic name.
- The type of query is highly limited by the API design. For instance, it is usually impossible to make queries across the entire corpus of names, such as "which accepted name has the most known synonyms?"
- Both query formats and responses differ substantially across different naming providers, making it difficult to apply a script designed for one provider to different provider.
- Most queries are not reproducible, as the results depend on the state of the central server (and potentially the quality of the internet connection)(Rees and Cranston 2017b). Many names providers update the server data either continuously or at regular intervals, including both revising existing names (for spelling or changes in accepted name designation) and adding new names.

Instead of binding existing web APIs, `taxadb` is built around a set of compressed text files which are automatically downloaded, imported, and stored on a local database by `taxadb`. The largest of the taxonomic naming providers today contain under 6 million name records with uncompressed file sizes over a GB, which can be compressed to around 50 MB and downloaded in under a minute on a 1 MB/s connection. By using a local database as the backend, `taxadb` allows R users to interact with large data files without large memory (RAM) requirements. A query for a single name over the web API requires a remote server to respond, execute the query, and serialize the response, which can take several seconds. Thus it does not take many taxa before transferring the entire data set to query locally is more efficient. Moreover, this local copy can be cached on the user's machine, requiring only the one-time setup, and enabling offline use and reproducible queries. Rather than returning data in whatever format is given by the provider, `taxadb` provides a data structure following a consistent, standardized layout or schema following Darwin Core, which provides standard terms for biodiversity data (Wieczorek et al. 2012). Table 2.1 summarizes the list of all naming providers currently accessed by `taxadb`. More details are provided in the Data Sources Vignette, `https://docs.ropensci.org/taxadb/articles/data-sources.html`.

Table 2.1: Descriptions of the providers supported by taxadb with their reference abbreviation and the total number of identifiers contained by each provider.

Provider	Abbreviation	Number of Identifiers	Description
Integrated Taxonomic Information System (ITIS 2019)	itis	597120	originally formed to standardize taxonomic name usage across many agencies in the United States federal government
National Center for Biological Information's Taxonomy database (Biotechnology Information 2019)	ncbi	2175855	nomenclature for sequences in the International Nucleotide Sequence Database Collaboration database
Catalogue of Life (Roskov Y. 2018)	col	1998435	comprehensive taxonomic effort, includes some other providers (e.g. itis)
Global Biodiversity Information Facility Taxonomic Backbone (GBIF 2019)	gbif	3546672	taxonomic backbone of the GBIF database, assembled from other sources including COL
Open Tree Taxonomy (J. A. Rees and Cranston 2017)	ott	4455820	comprehensive tree of life based on phylogenetic trees and taxonomic data
International Union for Conservation of Nature and Natural Resources (IUCN 2019)	iucn	131927	taxonomy for classification of species status

Package Overview

```
library(tidyverse)
library(taxadb)
```

After loading our package and the tidyverse package for ease in manipulating function output, we look up the taxonomic identifier for Atlantic Cod, *Gadus morhua*, and the compliment:

```
get_ids("Gadus morhua")
get_names("ITIS:164712")
```

```
[1] "ITIS:164712"
```

```
[1] "Gadus morhua"
```

Our first call to any `taxadb` functions will automatically set up a local, persistent database if one has not yet been created. This one-time setup will download, extract, and import the compressed data into persistent database storage (using the appropriate location specified by the operating system (see Ratnakumar et al. 2016), or configured using the environmental variable `TAXADB_HOME`). The example above searches for names in ITIS, the default provider, which can be configured using the `provider` argument. Any future function calls to this function or any other function using data from the same provider will be able to access this data rapidly without the need for processing or an internet connection.

Users can also explicitly trigger this one-time setup using `td_create()` and specifying the provider abbreviation (see Table 2.1), or simply using `all` to install all available providers:

```
td_create("all")
```

`taxadb` functions like `get_ids()` and `td_create()` take an optional argument, `db`, to an external database connection. `taxadb` will work with most DBI-compliant databases such as MySQL or Postgres, but will be much faster when using a column-oriented database engine such as `duckdb` or `MonetDBLite`. These latter options are also much easier for most users, since each can be installed directly as an R package. `taxadb` will default to the fastest available option. `taxadb` can also run without a database backend by setting `db=NULL`, though some functions will require a lot (2-20 GB) of free RAM for this to work with many of the larger providers.

`taxadb` uses the widely known SQLite database by default, but users are encouraged to install the optional, suggested database backends by passing the option `dependencies =`

`TRUE` to the install command. This installs a MonetDBLite database instance (Raasveldt and Mühleisen 2018), a columnar-oriented relational database requiring no additional installation while also providing persistent disk-based storage. This also installs `duckdb`, another local columnar database which is rapidly emerging as an alternative to MonetDB and SQLite. `taxadb` will automatically detect and use these database engines if available, and automatically handles opening, caching, and closing the database connection. For large queries, MonetDBLite or `duckdb` deliver impressive improvements. Our benchmark on resolving the 750 species names in the Breeding Bird Survey against over 3 million names known in the 2019 Catalogue of Life takes 8 minutes in SQLite but less than a second in MonetDBLite.

Functions in `taxadb` are organized into several families:

- queries that return vectors: `get_ids()` and it's complement, `get_names()`,
- queries that filter the underlying taxonomic data frames: `filter_name()`, `filter_rank()`, `filter_id()`, and `filter_common()`,
- database functions `td_create()`, `td_connect()` and `taxa_tbl()`,
- and helper utilities, such as `clean_names()`.

Taxonomic Identifiers

Taxonomic identifiers provide a fundamental abstraction which lies at the heart of managing taxonomic names. For instance, by resolving scientific names to identifiers, we can identify which names are synonyms – different scientific names used to describe the same species – and which names are not recognized. Each naming authority provides its own identifiers for the names it recognizes. For example, the name Homo sapiens has the identifier 9606 in NCBI and 180092 in ITIS. To avoid possible confusion, `taxadb` always prefixes the naming provider, e.g. NCBI:9606. Some taxonomic naming providers include separate identifiers for synonyms, see Box 1. Unmatched names may indicate an error in data entry or otherwise warrant further investigation. Taxon identifiers are also easily resolved to the original authority (scientific publication) establishing the name. The common practice of appending an author and year to a scientific name, e.g. *Poa annua annua* (Smith 1912), serves a valuable role in disambiguating different uses of the same name but can be notoriously harder to resolve to the appropriate reference, while variation in this convention creates many distinct versions of the same name (Patterson et al. 2010).

These issues are best illustrated using a minimal example. We'll consider the task of combining data on bird extinction risk as assessed by the IUCN (International Union for Conservation of Nature and Natural Resources 2019) with data on average adult biomass, as estimated in the Elton Traits v1.0 database (Wilman et al. 2016). To keep the example concise enough for for visual presentation we will focus on a subset involving just 10 species (Table 2.2, 2.3).

```
trait_data <- read_tsv(
  system.file("extdata", "trait_data.tsv", package="taxadb"))
status_data <- read_tsv(
  system.file("extdata", "status_data.tsv", package="taxadb"))
```

Table 2.2: The subset of the IUCN status data used for subsequent taxonomic identifier examples.

iucn_name	category
Pipile pipile	CR
Pipile cumanensis	LC
Pipile cujubi	LC
Pipile jacutinga	EN
Megapodius decollatus	LC
Scleroptila gutturalis	LC
Margaroperdix madagarensis	LC
Falcipennis falcipennis	NT

Table 2.3: The subset of the Elton trait data used for subsequent taxonomic identifier examples.

elton_name	mass
Aburria pipile	1816.59
Aburria cumanensis	1239.22
Aburria cujubi	1195.82
Aburria jacutinga	1240.96
Megapodius reinwardt	666.34
Francolinus levalliantoides	376.69
Margaroperdix madagascariensis	245.00
Catreus wallichii	1436.88
Falcipennis falcipennis	685.61
Falcipennis canadensis	473.65

If we attempted to join these data directly on the species names provided by each table, we would find very little overlap, with only one species name having both a body mass and an IUCN threat status resolved (Table 2.4).

```
joined <- full_join(trait_data, status_data, by = c("elton_name" = "iucn_name"))
```

If we first resolve names used in each data set into shared identifiers, (for instance, using the Catalogue of Life), we discover that there is far more overlap in the species coverage

Table 2.4: Example IUCN and trait data joined directly on scientific name showing only one match. While common, joining on scientific name does not account for nomenclatural and taxonomic inconsistencies between databases and therefore results in seemingly very little overlap in species representation between the two.

elton_name	mass	category
Aburria pipile	1816.59	-
Aburria cumanensis	1239.22	-
Aburria cujubi	1195.82	-
Aburria jacutinga	1240.96	-
Megapodius reinwardt	666.34	-
Francolinus levalliantoides	376.69	-
Margaroperdix madagascariensis	245.00	-
Catreus wallichii	1436.88	-
Falcipennis falcipennis	685.61	NT
Falcipennis canadensis	473.65	-
Pipile pipile	-	CR
Pipile cumanensis	-	LC
Pipile cujubi	-	LC
Pipile jacutinga	-	EN
Megapodius decollatus	-	LC
Scleroptila gutturalis	-	LC
Margaroperdix madagarensis	-	LC

than we might have initially realized. First, we just add an ID column to each table by looking up the Catalog of Life identifier for the name provided:

```
traits <- trait_data %>% mutate(id = get_ids(elton_name, "col"))
status <- status_data %>% mutate(id = get_ids(iucn_name, "col"))
```

We can now join on the `id` column instead of names directly:

```
joined <- full_join(traits, status, by = "id")
```

This results in many more matches (Table 2.5), as different scientific names are recognized by the naming provider (Catalog of Life 2018 in this case), as *synonyms* for the same species, and thus resolve to the same taxonomic identifier. While we have focused on a small example for visual clarity here, the `get_ids()` function in `taxadb` can quickly resolve hundreds of thousands of species names to unique identifiers, thanks to the performance of fast joins in a local MonetDBLite database.

Table 2.5: Example IUCN and trait data joined on taxonomic ID. Multiple species have a different scientific name in the Elton and IUCN Redlist databases but can be match based on their COL taxonomic ID.

elton_name	iucn_name	mass	category	id
Aburria pipile	*Pipile pipile*	1816.59	CR	COL:35517887
Aburria cumanensis	*Pipile cumanensis*	1239.22	LC	COL:35537158
Aburria cujubi	*Pipile cujubi*	1195.82	LC	COL:35537159
Aburria jacutinga	*Pipile jacutinga*	1240.96	EN	COL:35517886
Megapodius reinwardt	-	666.34	-	COL:35521309
Francolinus levalliantoides	-	376.69	-	COL:35518087
Margaroperdix madagascariensis	*Margaroperdix madagarensis*	245.00	LC	COL:35521355
Catreus wallichii	-	1436.88	-	COL:35518185
Falcipennis falcipennis	*Falcipennis falcipennis*	685.61	NT	COL:35521380
Falcipennis canadensis	-	473.65	-	COL:35521381
-	*Megapodius decollatus*	-	LC	COL:35537166
-	*Scleroptila gutturalis*	-	LC	-

Box 1: Taxonomic Identifiers and Synonyms

`get_ids()` returns the `acceptedNameUsageID`, the identifier associated with the *accepted* name. Some naming providers, such as ITIS and NCBI, provide taxonomic identifiers to both synonyms and accepted names. Other providers, such as COL and GBIF, only provide identifiers for accepted names. Common practice in Darwin Core archives is to provide an `acceptedNameUsageID` only for names which are synonyms, and otherwise to provide a `taxonID`. For accepted names, the `acceptedNameUsageID` is then given as missing (`NA`), while for synonyms, the `taxonID` may be missing (`NA`). In contrast, `taxadb` lists the `acceptedNameUsageID` for accepted names (where it matches the `taxonID`), as well as known synonyms. This is semantically identical, but also more convenient for database interfaces, since it allows a name to mapped to its accepted identifier (or an identifier to map to it's accepted name usage) without the additional logic. For consistency, we will use the term "identifier" to mean the `acceptedNameUsageID` rather than the more ambiguous `taxonID` (which is undefined for synonyms listed by many providers), unless explicitly stated otherwise.

Unresolved names

`get_ids` offers a first pass at matching scientific names to id, but names may remain unresolved for a number of reasons. First, a name may match to multiple accepted names, as in the case of a species that has been split. By design, these cases are left to be resolved by the researcher using the `filter_` functions to filter underlying taxonomic tables for additional information. A name may also be unresolved due to typos or improper formatting. `clean_names` addresses common formatting issues such as the inclusion of missing species epithets (e.g. `Accipiter sp.`) that prevent matches to the Genus, or intraspecific epithets such as `Colaptes auratus cafer` that prevent matches to the binomial name. These modifications are not appropriate in all settings and should be used with care. Spell check of input names is outside the scope of `taxadb`, however existing tools such as those developed by the Global Names Architecture (`http://globalnames.org/apps/`) could be incorporated into a `taxadb` workflow.

Names may also have an ambiguous resolution wherein a name may be resolved by a different provider than the one specified, either as an accepted name or a synonym. Mapping between providers represent a meaningful scientific statement requiring an understanding of the underlying taxonomic concepts of each provider (Franz and Peet 2009, Lepage et al. 2014, Franz and Sterner 2018). The spirit of `taxadb` is not to automate steps that require expert knowledge, but provide access to multiple potential “taxonomic theories.”

`filter_` functions for access to underlying tables

Underlying data tables can be accessed through the family of `filter_` functions, which filter by certain attributes such as scientific name, id, common name, and rank. These functions allow us to ask general questions such as, how many bird species are there?

```
filter_rank("Aves", rank="class", provider = "col") %>%
  filter(taxonomicStatus == "accepted", taxonRank == "species") %>%
  pull(taxonID) %>%
  n_distinct()
```

```
[1] 10354
```

We can also use this to gain a detailed look at specific species or ids. For example, we can explore why `get_ids` fails to resolve a seemingly common species:

```
multi_match <- filter_name("Abies menziesii", provider = "col")
```

We see that *Abies menziesii* is a synonym for three accepted names which the user will have to choose between (Table 2.6). This is an example of how `taxadb` seeks to provide users with information from existing authorities and names providers, rather than make a potentially arbitrary decision. Because they return `data.frames`, `filter_` functions provide both potential matches. Note that the simpler `get_` functions (`get_ids()`) consider multiple name matches as `NA` for the `id`, making them suitable for automated pipelines where manual resolution of duplicates is not an option.

Table 2.6: Some names may not resolve to an identifier using get_ids() because they match to more than one accepted ID. In such cases filter_ functions give further detail, as in the example of *Abies menziesii* below which has three accepted ID matches.

sort	taxonID	scientificName	acceptedNameUsageID	taxonomicStatus	acceptedScientificName
1	COL:18159104	*Abies menziesii*	COL:18157974	synonym	Pseudotsuga menziesii
1	COL:18160542	*Abies menziesii*	COL:18158639	synonym	Picea pungens
1	COL:18161226	*Abies menziesii*	COL:18158652	synonym	Picea sitchensis

Direct database access

The full taxonomic record in the database can also be directly accessed by `taxa_tbl()`, allowing for whole-database queries that are not possible through the API or web interface of many providers. For example, we can easily check the coverage of accepted species names in each of the classes of vertebrates within the Catalogue of Life (Table 2.7):

```
verts <- taxa_tbl("col") %>%
  filter(taxonomicStatus == "accepted",
         phylum == "Chordata", taxonRank == "species") %>%
  count(class)
```

Table 2.7: taxadb also provides direct access to the database, allowing dplyr or SQL queries which can compute across the entire dataset, such as counting accepted species in all vertebrate classes shown here. This kind of query is effectively impossible in most REST API-based interfaces.

class	n
Actinopterygii	32474
Aves	10354
Reptilia	10233
Amphibia	6439
Mammalia	5852
Ascidiacea	2925
Elasmobranchii	1223
Myxini	81
Thaliacea	78
Appendicularia	68
Holocephali	56
Cephalaspidomorphi	45
Leptocardii	30
Sarcopterygii	8

Box 2: Common Names

`taxadb` can also resolve common names to their identifier by mapping common name to the accepted scientific name. Common names have many of the same issues as scientific names but even more frequent (e.g. matching to more than one accepted name, non-standardized formatting). Common names are accessed via `filter_common` which takes a vector of common names. The user can then resolve discrepancies.

Discussion

Some taxonomic name providers (e.g. OTT, COL, NCBI) offer periodic releases of a static names list, while many other providers (e.g. ITIS, FB, IUCN) offer name data on a rolling basis (i.e. the data returned by a given download URL is updated continuously or at arbitrary intervals without any additional indication if and how that data has changed.) `taxadb`'s `td_create()` function downloads and stores cached snapshots from each provider, which follow an annual release model to support reproducible analyses. All `taxadb` functions that download or access data include an optional argument `version` to indicate which version of the provider data should be used. By default, `taxadb` will determine the latest version available (at the time of writing this is version `2019`). Appropriate metadata is stored with each snapshot, including scripts used to access and reformat the data files, as described in the "Data Sources" vignette, `https://docs.ropensci.org/taxadb/articles/data-sources.html`.

Taxonomic identifiers are an essential first step for maintaining taxonomic consistency, a key task for a wide variety of applications. Despite multiple taxonomic standardization efforts, resolving names to taxonomic identifiers is often not a standard step in the research work flow due to difficulty in accessing providers and the time consuming API queries necessary for resolving even moderately sized data sets. `taxadb` fills an important gap between existing tools and typical research patterns by providing a fast, reproducible approach for matching names to taxonomic identifiers. It could also be used to verify that conclusions were robust to the choice of naming provider. `taxadb` is not intended as an improvement or replacement for any existing approaches to taxonomic name resolution. In particular, `taxadb` is not a replacement for the APIs or databases provided, but merely an interface to taxonomic naming information contained within that data.

Lastly, we note that local database design used in `taxadb` is not unique to taxonomic names. Despite the rapid expansion of REST API-based interfaces to ecological data (Boettiger et al. 2015), in our experience, much of the data relevant to ecologists and evolutionary biologists today would be also be amenable to the local database design. The local database approach is much easier for data providers (who can leverage static scientific database repositories instead of maintaining REST servers) and often much faster for data consumers.

Acknowledgments

We thank the many researchers who contributed to the data and infrastructure of the various taxonomic providers we access through our package. Support for the development of this package was provided by United States Department of Energy through the Computational Sciences Graduate Fellowship (DOE CSGF) under grant number DE-FG02-97ER25308 awarded to K.E.A.N..

Data Availability

Code for the R package can be found on GitHub at `https://github.com/ropensci/taxadb` and is archived on Zenodo at `DOI:10.5281/zenodo.3903858` (Boettiger et al. 2020). The taxonomic database is also stored on Github at `https://github.com/boettiger-lab/taxadb-cache`. The original taxonomic data are stored by the individual provider, see "Catalogue of Life," `http://www.catalogueoflife.org/` (Roskov Y. 2018), "ITIS," `https://www.itis.gov` (ITIS 2019), "NCBI," `https://www.ncbi.nlm.nih.gov/taxonomy` (Biotechnology Information 2019), "GBIF," `https://gbif.org` (GBIF 2019), "Fishbase," `https://fishbase.se` (Froese and Pauly 2019), "Open Tree Taxonomy," `https://tree.opentreeoflife.org` (Rees and Cranston 2017a), "IUCN," `https://www.iucnredlist.org/resources/tax-sources` (International Union for Conservation of Nature and Natural Resources 2019).

Authors' Contributions

K.E.A.N., S.C., and C.B. contributed to conceptual development of the package. K.E.A.N. and C.B. developed the package and contributed to the manuscript.

Transition between Chapter 2 and 3

Chapter 2 discusses the motivation behind and use of `taxadb`, an R package for dealing with taxonomic inconsistencies. Differences in taxonomic concepts between data providers presents a serious barrier to synthesizing multiple biodiversity datasets. Synthesis is further frustrated by existing tools that are not designed to deal with large volumes of data. `taxadb` moves beyond typical API approaches for accessing taxonomic data, using a local database approach for resolving scientific and common names to taxonomic ID's. This method can resolve millions of names to ID's in seconds.

In chapter 3, I use `taxadb` to pair time series of community data with databases of functional trait data to assess patterns of functional change through time. Multiple recent assessments of temporal biodiversity change have found that species-based diversity metrics are not fully able to capture the kinds of shifts happening in communities in recent decades. Functional diversity provides a potentially powerful alternative by describing differences in species traits rather than simply counting species and individuals. I calculate multiple metrics of functional diversity that describe complementary aspects of the trait space and assess prevailing trends across communities.

Chapter 3

Evaluating the evidence of widespread maintenance of functional composition in vertebrate communities

Kari E. A. Norman   Perry de Valpine   Carl Boettiger

Abstract

Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing species turnover but no overall trend in species diversity through time. Functional diversity provides a potentially powerful alternative approach for understanding this change in community composition by linking shifts in species identity to mechanisms of ecosystem processes. Here we present the first multi-taxa, multi-system analysis of functional change through time, pairing thousands of vertebrate assemblage time series from the BioTIME database with existing functional traits representitive of a species' functional role. We found no overall trend in any calculated functional diversity metric, despite similar species-based patterns of constant richness with increasing turnover. The lack of trend held even after correcting for changes in species richness and at the study-level, where only 3 of 54 studies experienced a significant trend in at least one functional diversity metric. Results give evidence that across a variety of taxa, climates, and biomes, these selected functional characteristics are maintained even in the face of significant environmental and community change. We also discuss the potential for underlying functional shifts to be obscured by current approaches and data and call for targeted data collection efforts to combat existing biases in monitoring and trait data.

Introduction

Ecological communities are experiencing unprecedented change as a result of anthropogenic pressures such as climate change, land use change, and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (Barnosky et al. 2011), and fundamental changes in some of the most well-studied systems (e.g. coral bleaching, Sully et al. 2019). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (Brown et al. 2001, Vellend et al. 2013, 2017, Dornelas et al. 2014) and evidence of significant shifts in community composition underlying consistent species richness (Brose and Hillebrand 2016, Gotelli et al. 2017, Li et al. 2020). While communities are clearly changing, our most common species-based approaches do not fully capture the nature of that change.

Functional diversity offers a potentially powerful alternative for detecting and describing community change by providing a mechanistic link between species' response to environmental change (response traits) and the processes they perform (effect traits) (Lavorel and Garnier 2002, Mcgill et al. 2006, Suding et al. 2008). By describing the functional trait space rather than species, functional diversity metrics capture the disproportionate impact of losses or gains of functionally unique species. Functional diversity metrics are therefore particularly well suited for assessing community shifts underlying even constant species richness trends.

Beyond simply characterizing changes in community structure, trends in functional composition also have important implications for ecosystem stability, function, and resilience. There is increasing evidence functional diversity is a better predictor of ecosystem function than species-based metrics (Cadotte et al. 2011, Gagic et al. 2015), and that different facets of functional diversity play essential roles in maintaining ecosystem stability (Morin et al. 2014, Craven et al. 2018). Indeed, almost all hypothesized mechanisms underpinning the relationship between species diversity and ecosystem function are trait-dependent (Hillebrand and Matthiessen 2009). Determining functional trends therefore gives a more complete picture of potential trends in critical ecosystem processes.

It is critical to establish whether or not functional loss is the general rule for communities. While functional loss is frequently cited as one of the most pressing concerns of the anthropocene (Cardinale et al. 2012, Dirzo et al. 2014, Young et al. 2016), it is not necessarily inevitable even in scenarios of species loss (Dıáz and Cabido 2001). Forecasts of functional loss range from negligible (Gallagher et al. 2013) to dire (Petchey and Gaston 2002, Pimiento et al. 2020b). And while some observed trends show significant functional loss (Flynn et al. 2009) others document no loss even in some of the most heavily impacted communities (Edwards et al. 2013, Matuoka et al. 2020). On paleoecological time scales functional composition shows mixed responses to environmental change and extinction events (Jackson and Blois 2015, Dornelas et al. 2018), with significant impacts of species extinctions on functional diversity in some taxa and not others (Pimiento et al. 2017). Some losses of functional diversity are indisputable on both paleocological and contemporary timescales such as continued trophic downgrading due to loss of large-bodied mammals, but implications of those losses for local diversity patterns are less clear (Estes et al. 2011, Smith et al. 2018) .

Assessments of broad-scale temporal change in functional diversity have previously been limited by a lack of functional trait data. The majority of work has therefore focused largely on system-specific studies with traits collected *in situ*. Ongoing efforts to assemble functional traits for a variety of taxa have made synthesis of existing community assemblage data and functional traits possible for the first time, providing initial insights into the ways functional diversity changes on a broad scale for specific taxa (e.g. fish, Trindade-Santos et al. 2020, birds, Jarzyna and Jetz 2016, Barnagaud et al. 2017). However, to date there has been no cross-taxa assessment of temporal functional change for a broad geographic and taxonomic extent.

Here we perform the first multi-taxa, multi-system assessment of functional diversity change through time. We focus on mammal, bird, and amphibian species as a significant subset of the world's biodiversity heavily impacted by anthropogenic change. While examining trends in plants, invertebrates, and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (FitzJohn et al. 2014), a lack of accepted species-level means, and differences in the types of traits collected. In order to ensure comparability across taxa in trait type and data quality we therefore focus on mammals, birds, and amphibians. Traits were intentionally selected to be representative of a species' Eltonian niche, thereby summarizing the functional role they play in the community (Wilman et al. 2014).

We assess thousands of mammal, bird, and amphibian functional diversity time series to determine whether or not there is a general trend of functional change, both in observed metrics and in metrics corrected for changes in species richness. We distinguish between three possible scenarios of functional change: 1) significant loss of functional diversity with accompanying shifts in other functional metrics, 2) no functional diversity loss, but significant shifts in other functional metrics, 3) maintenance of functional diversity and composition. Based on expectation due to human impacts, we expect to find a significant functional loss with further restructuring indicated by the additional metrics.

Material and Methods

Data

We obtained mammal, bird, and amphibian time series from the BioTIME database, a global repository of high quality assemblage time series. All studies included in the database follow consistent sampling protocols and represent full assemblages rather than populations of single species (Dornelas et al. 2018). Following best practices for the database (Blowes et al. 2019), studies with multiple sample locations were split into individual time series following a standardized spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see Dornelas et al. 2018 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. All samples from a study within a single cell were considered to be a single time series, and species abundances were combined for all samples. We gathered trait data from the Elton Trait Database (mammals and birds, Wilman et al. 2014) and Amphibio (amphibians, Oliveira et al. 2017). These databases include species-level means for traits that partially represent species' multifaceted function in the community including body size, diet, and behavioral characteristics. For the full list of traits included in the analysis for each taxon see Table 3.1.

Table 3.1: Summary of the data in the final trait database.

Taxa	Number of Time Series	Number of Species	Trait Source	Traits
Mammals	48	184	Elton Traits	body mass, diet, active diel period
Birds	2380	700	Elton Traits	body mass, diet, nocturnality, forest foraging strata, pelagic specialist
Amphibians	11	184	Amphibio	habitat, diet, active diel period, activity seasonality, body mass, body length, min maturation size, max maturation size, min offspring size, max offspring size, reproductive output, breeding strategy

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the on-line database, `https://doi.org/10.5066/F7KH0KBK`), obtained through the `taxadb` R package (Norman et al. 2020, R Core Team 2021). If more than one species in the assemblage data resolved to the same identifier, observations were considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies with at least 75% trait coverage were included and observations for species with no trait data were excluded. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded.

Many studies had a variable number of samples within years. To account for this inconsistency in sampling effort we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series.

Our final dataset included 2,443 time series from 53 studies in 21 countries and 15 biomes and 13 different traits (Fig 3.1). The earliest sample was in 1923 and the most recent was in 2016. Only four studies (consisting of 11 time series) came from Amphibian studies due to the limited availability of amphibian time series and low species richness values for

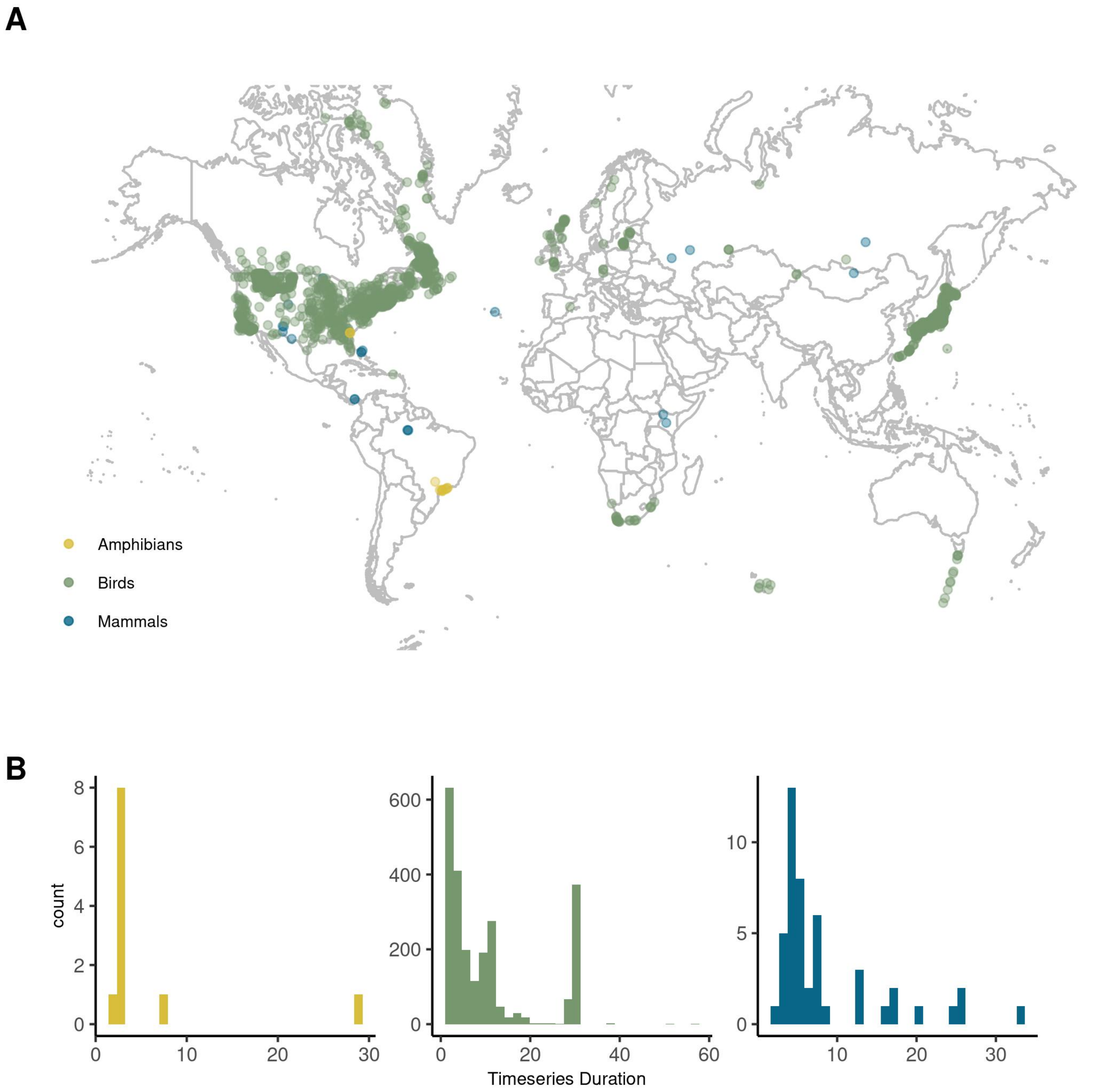

Figure 3.1: A) Map of time series locations with points colored by taxa, and B) histograms of time series duration broken down by taxa.

assemblages (Table 3.1). Amphibians are of particular concern due to impacts of habitat loss and pollution (Gibbons et al. 2000), so we include data while acknowledging that general inference for amphibians as a clade is not possible with the time series available. For a full breakdown of studies and their characteristics, see Supplement Table 3.5.

Diversity Metrics

We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate increasing turnover.

Functional diversity metrics were calculated using the *dbFD* function from the *FD* R package (Laliberté and Legendre 2010). Here we report functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) which together describe three complementary characteristics of the functional space (Mason et al. 2005, Hillebrand and Matthiessen 2009). FRic assesses the volume of the trait space occupied by species in the community, with higher values indicating communities with species of more extreme trait values. FEve describes how species are distributed across the trait space and how abundance is distributed across species. Higher values of FEve indicate more even spacing of species in the trait space and individuals across species. FDiv measures the degree to which species and their abundances maximize differences in the functional space. Higher values of FDiv therefore correspond to communities where many highly abundant species are on the edges of the trait space.

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. All continuous traits were z-score scaled to give each trait equal weight in the trait space (Leps et al. 2006, Schleuter et al. 2010). The number of trait axes was limited to the maximum number of traits that fulfills the criteria $s >= 2^t$, where s is the number of species and t is the number of traits. This restriction allows for a sufficient number of axes to capture the trait space while maintaining computational feasibility (Blonder 2018). Metrics incorporated weighting based on species abundance where available (three studies were presence only).

Null Models

To assess functional change independent of species richness we calculated the standardized effect size (SES) for each metric from null estimates (Swenson et al. 2012). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning observed abundances to species. Species pools included all species observed for a time series. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction for that time series. We used these values to calculate SES using the following formula: $SES = [F_{obs} - mean_{(F_{null})}]/SD_{(F_{null})}$. We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness.

Analysis

We estimated general trends for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each time series nested within the study. We obtained study-level estimates of temporal change from the Best Linear Unbiased Predictors (BLUPs) for each overall trend model. BLUP's provide an estimate for the conditional mean and variance of each level of a random effect from which we calculated 95% confidence intervals to determine significance of study-level slopes. To test for trends within and between different levels of taxa, biome, and realm we fit separate models with each of those covariates added as a predictor to the original model structure. We estimated within-level slopes and calculated between-level contrasts using the *emmeans* package (Lenth 2021). We assessed the impact of time series duration and start year on study-level trends using general linear models with duration and start year as predictors. All models were executed using the *lme4* package in R and p-values were calculated by Satterthwaite's degrees of freedom method using the *lmerTest* package with a significance level of $\alpha = 0.05$ (Bates et al. 2015, Kuznetsova et al. 2017, R Core Team 2021).

Results

We found no significant overall trend in species richness or functional diversity metrics (observed or standardized) (Fig 3.2). We did find a significant overall decrease in Jaccard similarity, indicating increasing turnover through time. Non-significant overall trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was plausibly 0 (Table 3.2). Trends for different taxa, biomes, or realms were also non-significant with the exception of a significantly increasing slope for functional evenness of global studies (characterized by having samples on multiple continents), and a significantly decreasing standardized functional richness slope for freshwater studies. However, with only two global studies and two freshwater studies these results are a characterization of the limited data rather than overall trends.

Table 3.2: Model estimates and statistics for general trend models for species richness (S) and standardized metrics. Additional model estimates can be found in the supplement.

metric	effect	group	term	estimate	std.error	p.value
Jaccard	fixed		Intercept	0.61	0.02	<0.001
Jaccard	fixed		Year	-0.05	0.01	<0.001

Jaccard	ran_pars	timeseries:study	Intercept sd	0.11		
Jaccard	ran_pars	timeseries:study	Intercept Year corr	0.02		
Jaccard	ran_pars	timeseries:study	Year sd	0.03		
Jaccard	ran_pars	study	Intercept sd	0.14		
Jaccard	ran_pars	study	Intercept Year corr	-0.48		
Jaccard	ran_pars	study	Year sd	0.03		
Jaccard	ran_pars	residual	Observation sd	0.10		
S	fixed		Intercept	2.49	0.09	<0.001
S	fixed		Year	-0.06	0.04	0.15
S	ran_pars	timeseries:study	Intercept sd	0.19		
S	ran_pars	timeseries:study	Intercept Year corr	0.36		
S	ran_pars	timeseries:study	Year sd	0.08		
S	ran_pars	study	Intercept sd	0.58		
S	ran_pars	study	Intercept Year corr	-0.71		
S	ran_pars	study	Year sd	0.24		
S	ran_pars	residual	Observation sd	0.17		
SES_FDiv	fixed		Intercept	-0.22	0.10	0.04
SES_FDiv	fixed		Year	0.01	0.04	0.88
SES_FDiv	ran_pars	timeseries:study	Intercept sd	0.60		
SES_FDiv	ran_pars	timeseries:study	Intercept Year corr	0.00		
SES_FDiv	ran_pars	timeseries:study	Year sd	0.23		
SES_FDiv	ran_pars	study	Intercept sd	0.56		
SES_FDiv	ran_pars	study	Intercept Year corr	-0.12		
SES_FDiv	ran_pars	study	Year sd	0.11		
SES_FDiv	ran_pars	residual	Observation sd	0.62		
SES_FEve	fixed		Intercept	0.09	0.16	0.58
SES_FEve	fixed		Year	-0.01	0.02	0.65
SES_FEve	ran_pars	timeseries:study	Intercept sd	0.40		
SES_FEve	ran_pars	timeseries:study	Intercept Year corr	-0.21		
SES_FEve	ran_pars	timeseries:study	Year sd	0.17		
SES_FEve	ran_pars	study	Intercept sd	1.05		
SES_FEve	ran_pars	study	Intercept Year corr	-0.62		
SES_FEve	ran_pars	study	Year sd	0.05		
SES_FEve	ran_pars	residual	Observation sd	0.90		
SES_FRic	fixed		Intercept	-0.25	0.07	<0.001
SES_FRic	fixed		Year	0.02	0.04	0.55
SES_FRic	ran_pars	timeseries:study	Intercept sd	0.54		
SES_FRic	ran_pars	timeseries:study	Intercept Year corr	0.06		
SES_FRic	ran_pars	timeseries:study	Year sd	0.18		
SES_FRic	ran_pars	study	Intercept sd	0.27		
SES_FRic	ran_pars	study	Intercept Year corr	-0.28		
SES_FRic	ran_pars	study	Year sd	0.11		
SES_FRic	ran_pars	residual	Observation sd	0.81		

At the study level, 4 studies experienced a significant trend in species richness and only 10 of 54 studies for observed metrics and 3 of 54 studies for standardized metrics expe-

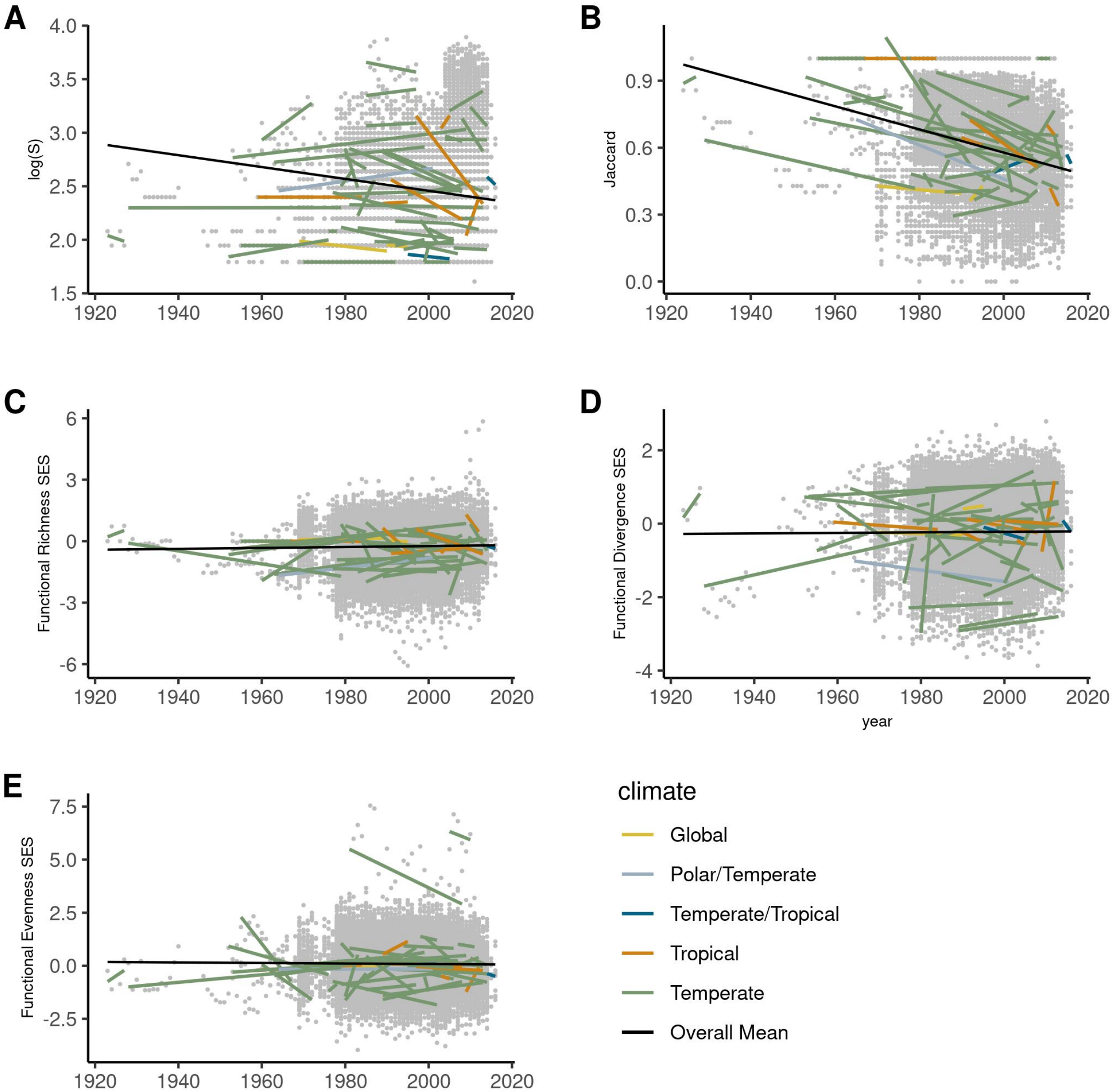

Figure 3.2: Plots of time series-level trends with line color corresponding to climatic region, with data points in grey and the overall metric mean in black for A) log species richness, B) Jaccard similarity, C) Functional Richness SES, D) Functional Divergence SES, and E) Functional Evenness SES

rienced a significant trend for a metric other than Jaccard similarity (Table 3.3). Most significant trends for observed functional metrics are in functional richness and disappeared after standardization, indicating that richness increases were likely due to changes in the number of species. Hypothesis testing for study-level trends is likely affected by multiple testing issues and some trends identified as significant are therefore potentially erroneous. Rather than interpreting changes in specific studies, we present these results as a general picture of the small number of studies experiencing a trend and highlight that even those studies are likely an overestimate of the number of significant trends. Study-level slopes for multiple metrics were significantly related to the duration and start year of studies. Slopes for species richness were significantly more negative with later start date and more positive shorter duration studies. Jaccard similarity and functional evenness both had significantly more negative slopes with more recent start year, whereas functional divergence was significantly more positive. Slopes for functional evenness were also significantly more positive for longer duration studies. Results were consistent between standardized and observed metrics with exception of functional evenness, which was negatively related to duration for observed data and positively related for standardized data. See Supplement Table 3.4 for estimates and p-values for all models.

Table 3.3: Model estimates and statistics for general trend models for species richness (S) and standardized metrics.

	S	Jaccard.Similarity	FRic	FEve	FDiv	SES.FRic	SES.FEve	SES.FDiv
+	1	0	2	1	0	0	0	0
-	3	37	6	0	1	1	2	1

Discussion

Our study represents the largest broad-scale multi-taxa assessment of functional change through time to date, giving a first look at aggregate and local trends in functional diversity in mammal, bird, and amphibian communities. Surprisingly, we did not detect an overall trend in any of the calculated functional diversity metrics. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by increasing turnover through time (Dornelas et al. 2018), indicating that non-significant trends in functional metrics may be consistent with similar well-documented species derived trends. We found no evidence of systemic functional richness loss or functional change. A lack of trend for almost all realms, biomes, and taxonomic groups gives further evidence that directional functional change is absent from all systems observed in our dataset.

This striking result could be a product of two possible processes, one ecological and one methodological. Null trends appear to give strong evidence of systemic maintenance of functional structure due to common ecological processes, however multiple limitations of current approaches in synthesis could potentially be obscuring a true underlying global trend. We discuss both options further here.

Evidence of Ecological Processes

Communities demonstrated almost universal maintenance of functional composition. While the majority of the studies (~70%) included in our data experienced significant species turnover, only three (for standardized metrics) experienced a significant shift in any functional dimension. This suggests certain characteristics of the functional space are maintained even in the face of significant change in species identity, specifically the size of the functional space occupied by the community (FRic) and the distribution of species and individuals within that space (FEve and FDiv). On average, species additions have similar functional characteristics as lost species and therefore maintain the structure of the functional space.

These results challenge assumptions that functional loss is the default state of all or even many communities. While we do not directly assess the disturbance histories of included communities, trends were consistent even for the longest running and most heavily impacted studies. The North American Breeding Survey for example is considered an authoritative dataset on the state of bird populations on the continent and underpins policy decisions about bird conservation (Sauer et al. 2017, Rosenberg et al. 2019, Pardieck et al. 2020). No more robust dataset exists to capture North American avian community change, yet we detected no general shifts in functional structure across the dataset. Further, none of the 5 included studies that experienced a manual manipulation (e.g. burning, grazing exclosure, etc) experienced any significant functional trends.

While we did not directly measure changes in rare species, our results also contradict likely scenarios of loss predicted due to rare species extinction. Rare species, defined by small populations and geographic restriction, are simultaneously more likely to be functionally distinct and at higher risk for extinction (Davies et al. 2004, Harnik et al. 2012, Loiseau et al. 2020). Locally, communities losing functionally rare species should exhibit strong functional shifts as lost species can eventually no longer be replaced by functionally similar species (Leitão et al. 2016). Observed patterns were instead consistent with species replacement by functionally redundant species from the species pool. Still, for many timeseries we likely did not have a large enough time window to capture community and species pool impoverishment due to extinction.

What does local maintenance of functional structure mean for ecosystem function? The vast majority of experimental and observational work links declines in function to declines in functional or species diversity (Duffy et al. 2007, Cadotte et al. 2011, Brose and Hillebrand 2016). By those criteria very few communities in our dataset are in a state of concern for loss of functionality. However, shifts in metrics are only relevant if the underlying traits are those most critical for ecosystem function. We were limited in this analysis to the traits available rather than those with strong empirical links to function. Similarly, the dimensions of functional space most important for ecosystem function are still a topic of ongoing debate, and at least some known aspects important for multifunctionality were not measured here (e.g. dispersion, rarity, abundance of dominant species, Bagousse-Pinguet et al. 2021). Still, the fact that we observed so many communities maintaining structure across the most commonly used metrics for linking biodiversity and function calls into question how previous work translates to natural communities. Metrics need to be both closely linked to changes in ecosystem function and also experiencing shifts in natural communities to be meaningful.

Potential Methodological Limitations

Here we approach the question of functional change using the best available data and biodiversity synthesis approaches. However, a number of gaps in best practices may be obscuring a true underlying trend. First, the BioTIME database, while the most comprehensive data source of time series available, is limited in temporal and geographic scope. Most time series span only a few years (Figure 3.1) and may not provide the statistical power necessary to detect trends. The database is also not a representative sample of the world's biodiversity or areas of greatest threat (Gonzalez et al. 2016, Vellend et al. 2017), and the subset of data in this study exhibits a strong Northern Hemisphere bias. We may simply not have data from those areas experiencing the greatest perturbation (Hughes et al. 2021), particularly scenarios of conversion to urban, human-dominated landscapes. While evidence from other work shows even disturbed communities can maintain functional structure (Edwards et al. 2013, Matuoka et al. 2020), these results should not be interpreted as evidence of low functional impact in areas of heavy human disturbance.

Second, despite using the most comprehensive trait databases for these taxa, we were still limited to species-level means of the traits deemed important by database creators. The importance of intraspecific variation is well documented (Violle et al. 2012, Des Roches et al. 2018), however individual-level traits are rarely collected alongside monitoring data, especially for the longest running efforts. Species-level traits may be obscuring more subtle shifts in the trait space happening within species. Likewise, available trait data may not capture the traits experiencing the greatest change.

Third, while we use here the most common metrics for describing functional diversity they do not measure some potentially important aspects of the functional space. Most notably, the metrics we calculated do not capture shifts in the location of the functional space. For example, two communities could have very similar metric values but no overlap in their trait spaces. This is especially relevant in the context of biodiversity change as a species loss could be replaced by a species with very different functional attributes, but the replacement would go undetected if the new species expanded the trait space by the same degree and had similar abundance. This scenario may be common in communities tracking changing environmental conditions. Approaches for assessing shifts and overlaps in functional space are still relatively new (Barros et al. 2016, Blonder 2018, Mammola 2019) but could shed critical insight into functional composition changes of this nature.

Policy Implications

Our results should not be interpreted as an indication that the ongoing biodiversity crisis is less severe than described, or that there is no concern for functional change as a result of anthropogenic impact. These findings do not negate a substantial body of work linking functional degradation to direct human intervention in the form of land use change and intensification or habitat fragmentation (Flynn et al. 2009, Tinoco et al. 2018, Magioli et al. 2021), but rather illustrate the prevailing functional state for communities experiencing background levels of environmental change. Rather than assuming functional structure will be maintained in areas of concern, our work indicates that when measurements of functional diversity show significant shifts, it should be considered outside the normal expectation and a potential indicator of a system in distress.

Future Work

Here we make a significant first step in establishing a general trend for functional diversity through time across a variety of taxa and systems. We present the conclusion best supported by available data and acknowledge that it is still too early to confidently distinguish between true ecological pattern and methodological limitations. The most pressing next step is for intentional and targeted data collection efforts. We join others in the call for increased monitoring in under sampled areas and continued efforts to centralize existing data sources (Gonzalez et al. 2016, Vellend et al. 2017, Hughes et al. 2021). Data that fill geographic, taxonomic and trait gaps should be prioritized over further collection of data that replicate existing biases. One relatively low-cost high-reward data investment is collation of additional species-level trait means. Intentional trait selection is critical for linking functional patterns to ecological processes (Zhu et al. 2017), however synthesis is constrained to the traits in a few taxa-specific databases. Trait collection should explicitly consider existing frameworks for linking traits to processes (e.g. the response and effect framework Lavorel and Garnier 2002) to facilitate clear ecological interpretation of potential functional changes.

Data Availability

Code for the analyses in this chapter is archived on Zenodo at `DOI:10.5281/zenodo.5514335` (Norman 2021). Data products are on Github at `https://github.com/karinorman/biodivTS_data`. Original data sources are open access and available at their respective providers.

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Conclusion

My dissertation focuses on the role of synthesis in understanding biodiversity change. Assessing general patterns of local-scale biodiversity change is critical for informing management and giving us a broad view of human impacts on ecological process. Synthesis methods are uniquely suited to examine biodiversity questions on a comprehensive scale. Here, I explored multiple facets of synthesis work, advancing both the tools for and application of synthesis for improved biodiversity understanding.

Synthesis will necessarily play a critical role in how we assess biodiversity in the years to come, giving us an approach to leverage increasingly large volumes of biodiversity data. Rather than replacing highly valuable place-based work, rooted in a deep understanding of a system's natural history, synthesis gives us tools to explore fundamentally different questions. Much like the give and take between theory and empirical work, synthesis should both inform and be informed by local-scale studies (Grainger et al. 2021). In chapter 1, I discussed ways in which synthesis can incorporate greater site-level fidelity by including important characteristics of constituent studies. Local-scale work further plays the critical role of exploring the mechanisms by which patterns from large-scale studies occur and identifying variables or processes that may have been overlooked.

Synthesis has traditionally focused on changes in species-level measures of biodiversity, reflecting both the kinds of data available and a deep history of species as the unit of ecological understanding. With improved computational tools and an expansion in available data, synthesis is now equipped to move beyond the limitations of a species lens. In chapter 2, I presented one such tool I developed to facilitate synthesis of different types of biodiversity data by resolving taxonomic inconsistencies between data sources. In chapter 3, I used that R package `taxadb` to bridge community assemblage time series and functional trait data, taking a first look at broad-scale patterns in functional change through time. Through a functional lens, I found that most communities exhibit maintenance of functional structure alongside maintenance of species diversity, regardless of taxa, climate, or realm.

In this dissertation I demonstrated some of the ways in which synthesis allow us to address previously inaccessible broad-scale trends, and the kinds of tools that would facilitate further synthesis. Future work should focus on developing tools for improved reproducibility and transparency of synthesis workflows, improving richness of study metadata, and creatively incorporating data sources beyond traditional biodiversity surveys. The next decades will see an explosion of automated biodiversity data from passive acoustic and camera trap monitoring, remote sensing, and Long Term Ecological Research networks (LTER's) (Farley et al. 2018). How we leverage this data alongside existing biodiversity data sources will determine how effectively we can respond to the coming years of the biodiversity crisis.

Supplement

Table 3.4: Complete table of all models run in Chapter 3.

metric	effect	group	term	estimate	std.error	statistic	df	p.value
Jaccard	fixed		Intercept	0.61	0.02	25.7422027	56.0351890	<0.001
Jaccard	fixed		Year	-0.05	0.01	-6.8309185	19.2530973	<0.001
Jaccard	ran_pars	timeseries:study	Intercept sd	0.11				
Jaccard	ran_pars	timeseries:study	Intercept Year corr	0.02				
Jaccard	ran_pars	timeseries:study	Year sd	0.03				
Jaccard	ran_pars	study	Intercept sd	0.14				
Jaccard	ran_pars	study	Intercept Year corr	-0.48				
Jaccard	ran_pars	study	Year sd	0.03				
Jaccard	ran_pars	residual	Observation sd	0.10				
Jaccard	fixed		Intercept	0.63	0.05	11.5582422	2.1925767	0.01
Jaccard	fixed		Year	-0.05	0.01	-6.4834470	8.6992765	<0.001
Jaccard	ran_pars	timeseries:study	Intercept sd	0.11				
Jaccard	ran_pars	timeseries:study	Intercept Year corr	0.02				
Jaccard	ran_pars	timeseries:study	Year sd	0.03				
Jaccard	ran_pars	study	Intercept sd	0.13				
Jaccard	ran_pars	study	Intercept Year corr	-0.50				
Jaccard	ran_pars	study	Year sd	0.03				
Jaccard	ran_pars	taxa	Intercept sd	0.08				
Jaccard	ran_pars	taxa	Intercept Year corr	1.00				
Jaccard	ran_pars	taxa	Year sd	0.00				
Jaccard	ran_pars	residual	Observation sd	0.10				
Jaccard	fixed		Intercept	0.59	0.07	8.7459136	1.6027167	0.02
Jaccard	fixed		Year	-0.05	0.02	-2.8837019	1.4558223	0.15
Jaccard	ran_pars	timeseries:study	Intercept sd	0.11				
Jaccard	ran_pars	timeseries:study	Intercept Year corr	0.02				
Jaccard	ran_pars	timeseries:study	Year sd	0.03				
Jaccard	ran_pars	study	Intercept sd	0.12				
Jaccard	ran_pars	study	Intercept Year corr	-0.27				
Jaccard	ran_pars	study	Year sd	0.02				
Jaccard	ran_pars	realm	Intercept sd	0.10				
Jaccard	ran_pars	realm	Intercept Year corr	-1.00				
Jaccard	ran_pars	realm	Year sd	0.02				
Jaccard	ran_pars	residual	Observation sd	0.10				
Jaccard	fixed		Intercept	0.58	0.05	11.9504215	1.8144360	0.01
Jaccard	fixed		Year	-0.05	0.01	-4.0741171	1.0825525	0.14
Jaccard	ran_pars	timeseries:study	Intercept sd	0.11				
Jaccard	ran_pars	timeseries:study	Intercept Year corr	0.02				
Jaccard	ran_pars	timeseries:study	Year sd	0.03				
Jaccard	ran_pars	study	Intercept sd	0.13				

Jaccard	ran_pars	study	Intercept Year corr	-0.40				
Jaccard	ran_pars	study	Year sd	0.02				
Jaccard	ran_pars	climate	Intercept sd	0.07				
Jaccard	ran_pars	climate	Intercept Year corr	-1.00				
Jaccard	ran_pars	climate	Year sd	0.01				
Jaccard	ran_pars	residual	Observation sd	0.10				
S	fixed		Intercept	2.49	0.09	28.8288070	53.5701148	<0.001
S	fixed		Year	-0.06	0.04	-1.4352855	52.5996525	0.16
S	ran_pars	timeseries:study	Intercept sd	0.19				
S	ran_pars	timeseries:study	Intercept Year corr	0.36				
S	ran_pars	timeseries:study	Year sd	0.08				
S	ran_pars	study	Intercept sd	0.58				
S	ran_pars	study	Intercept Year corr	-0.70				
S	ran_pars	study	Year sd	0.25				
S	ran_pars	climate	Intercept sd	0.00				
S	ran_pars	climate	Intercept Year corr	-1.00				
S	ran_pars	climate	Year sd	0.00				
S	ran_pars	residual	Observation sd	0.17				
S	fixed		Intercept	2.49	0.09	29.1417981	54.9920877	<0.001
S	fixed		Year	-0.06	0.04	-1.4535101	53.6850668	0.15
S	ran_pars	timeseries:study	Intercept sd	0.19				
S	ran_pars	timeseries:study	Intercept Year corr	0.36				
S	ran_pars	timeseries:study	Year sd	0.08				
S	ran_pars	study	Intercept sd	0.58				
S	ran_pars	study	Intercept Year corr	-0.71				
S	ran_pars	study	Year sd	0.24				
S	ran_pars	residual	Observation sd	0.17				
S	fixed		Intercept	2.33	0.18	13.2783848	2.7761230	<0.001
S	fixed		Year	-0.05	0.04	-1.2382369	17.4916017	0.23
S	ran_pars	timeseries:study	Intercept sd	0.19				
S	ran_pars	timeseries:study	Intercept Year corr	0.36				
S	ran_pars	timeseries:study	Year sd	0.08				
S	ran_pars	study	Intercept sd	0.54				
S	ran_pars	study	Intercept Year corr	-0.73				
S	ran_pars	study	Year sd	0.24				
S	ran_pars	realm	Intercept sd	0.24				
S	ran_pars	realm	Intercept Year corr	-1.00				
S	ran_pars	realm	Year sd	0.01				
S	ran_pars	residual	Observation sd	0.17				
S	fixed		Intercept	2.46	0.12	20.1627311	1.9033415	<0.001
S	fixed		Year	-0.06	0.04	-1.4250548	50.1995551	0.16
S	ran_pars	timeseries:study	Intercept sd	0.19				
S	ran_pars	timeseries:study	Intercept Year corr	0.36				
S	ran_pars	timeseries:study	Year sd	0.08				
S	ran_pars	study	Intercept sd	0.58				
S	ran_pars	study	Intercept Year corr	-0.71				
S	ran_pars	study	Year sd	0.25				
S	ran_pars	taxa	Intercept sd	0.13				
S	ran_pars	taxa	Intercept Year corr	-1.00				
S	ran_pars	taxa	Year sd	0.00				
S	ran_pars	residual	Observation sd	0.17				
SES_FDiv	fixed		Intercept	-0.29	0.26	-1.1140885	2.0524273	0.38
SES_FDiv	fixed		Year	0.04	0.06	0.7072293	1.4772563	0.57
SES_FDiv	ran_pars	timeseries:study	Intercept sd	0.60				
SES_FDiv	ran_pars	timeseries:study	Intercept Year corr	0.00				

SES_FDiv	ran_pars	timeseries:study	Year sd	0.23				
SES_FDiv	ran_pars	study	Intercept sd	0.45				
SES_FDiv	ran_pars	study	Intercept Year corr	0.06				
SES_FDiv	ran_pars	study	Year sd	0.11				
SES_FDiv	ran_pars	taxa	Intercept sd	0.39				
SES_FDiv	ran_pars	taxa	Intercept Year corr	-1.00				
SES_FDiv	ran_pars	taxa	Year sd	0.07				
SES_FDiv	ran_pars	residual	Observation sd	0.62				
SES_FDiv	fixed		Intercept	-0.23	0.11	-2.1347994	30.8012895	0.04
SES_FDiv	fixed		Year	0.01	0.04	0.1977322	16.9250898	0.85
SES_FDiv	ran_pars	timeseries:study	Intercept sd	0.60				
SES_FDiv	ran_pars	timeseries:study	Intercept Year corr	0.00				
SES_FDiv	ran_pars	timeseries:study	Year sd	0.23				
SES_FDiv	ran_pars	study	Intercept sd	0.57				
SES_FDiv	ran_pars	study	Intercept Year corr	-0.12				
SES_FDiv	ran_pars	study	Year sd	0.11				
SES_FDiv	ran_pars	realm	Intercept sd	0.00				
SES_FDiv	ran_pars	realm	Intercept Year corr					
SES_FDiv	ran_pars	realm	Year sd	0.00				
SES_FDiv	ran_pars	residual	Observation sd	0.62				
SES_FDiv	fixed		Intercept	-0.23	0.11	-2.1347978	30.8013822	0.04
SES_FDiv	fixed		Year	0.01	0.04	0.1977648	16.9157297	0.85
SES_FDiv	ran_pars	timeseries:study	Intercept sd	0.60				
SES_FDiv	ran_pars	timeseries:study	Intercept Year corr	0.00				
SES_FDiv	ran_pars	timeseries:study	Year sd	0.23				
SES_FDiv	ran_pars	study	Intercept sd	0.57				
SES_FDiv	ran_pars	study	Intercept Year corr	-0.12				
SES_FDiv	ran_pars	study	Year sd	0.11				
SES_FDiv	ran_pars	climate	Intercept sd	0.00				
SES_FDiv	ran_pars	climate	Intercept Year corr					
SES_FDiv	ran_pars	climate	Year sd	0.00				
SES_FDiv	ran_pars	residual	Observation sd	0.62				
SES_FDiv	fixed		Intercept	-0.22	0.10	-2.1239478	30.2380329	0.04
SES_FDiv	fixed		Year	0.01	0.04	0.1521845	16.1078718	0.88
SES_FDiv	ran_pars	timeseries:study	Intercept sd	0.60				
SES_FDiv	ran_pars	timeseries:study	Intercept Year corr	0.00				
SES_FDiv	ran_pars	timeseries:study	Year sd	0.23				
SES_FDiv	ran_pars	study	Intercept sd	0.56				
SES_FDiv	ran_pars	study	Intercept Year corr	-0.12				
SES_FDiv	ran_pars	study	Year sd	0.11				
SES_FDiv	ran_pars	residual	Observation sd	0.62				
SES_FEve	fixed		Intercept	0.09	0.16	0.5614426	40.7147487	0.58
SES_FEve	fixed		Year	-0.01	0.02	-0.5302651	1.9508512	0.65
SES_FEve	ran_pars	timeseries:study	Intercept sd	0.40				
SES_FEve	ran_pars	timeseries:study	Intercept Year corr	-0.21				
SES_FEve	ran_pars	timeseries:study	Year sd	0.17				
SES_FEve	ran_pars	study	Intercept sd	1.05				
SES_FEve	ran_pars	study	Intercept Year corr	-0.62				
SES_FEve	ran_pars	study	Year sd	0.05				
SES_FEve	ran_pars	residual	Observation sd	0.90				
SES_FEve	fixed		Intercept	0.08	0.17	0.4951251	3.1373722	0.65
SES_FEve	fixed		Year	-0.02	0.03	-0.6423262	0.2137335	0.8
SES_FEve	ran_pars	timeseries:study	Intercept sd	0.40				
SES_FEve	ran_pars	timeseries:study	Intercept Year corr	-0.21				
SES_FEve	ran_pars	timeseries:study	Year sd	0.17				

SES_FEve	ran_pars	study	Intercept sd	1.05				
SES_FEve	ran_pars	study	Intercept Year corr	-0.64				
SES_FEve	ran_pars	study	Year sd	0.05				
SES_FEve	ran_pars	taxa	Intercept sd	0.09				
SES_FEve	ran_pars	taxa	Intercept Year corr	1.00				
SES_FEve	ran_pars	taxa	Year sd	0.03				
SES_FEve	ran_pars	residual	Observation sd	0.90				
SES_FEve	fixed		Intercept	0.09	0.16	0.5613774	40.3844781	0.58
SES_FEve	fixed		Year	-0.01	0.02	-0.5305799	1.9528686	0.65
SES_FEve	ran_pars	timeseries:study	Intercept sd	0.40				
SES_FEve	ran_pars	timeseries:study	Intercept Year corr	-0.21				
SES_FEve	ran_pars	timeseries:study	Year sd	0.17				
SES_FEve	ran_pars	study	Intercept sd	1.05				
SES_FEve	ran_pars	study	Intercept Year corr	-0.62				
SES_FEve	ran_pars	study	Year sd	0.05				
SES_FEve	ran_pars	climate	Intercept sd	0.00				
SES_FEve	ran_pars	climate	Intercept Year corr	-1.00				
SES_FEve	ran_pars	climate	Year sd	0.00				
SES_FEve	ran_pars	residual	Observation sd	0.90				
SES_FEve	fixed		Intercept	0.08	0.15	0.5234394	43.9007306	0.6
SES_FEve	fixed		Year	0.01	0.01	0.4375161	27.2700294	0.67
SES_FEve	ran_pars	timeseries:study	Intercept sd	0.40				
SES_FEve	ran_pars	timeseries:study	Intercept Year corr	-0.21				
SES_FEve	ran_pars	timeseries:study	Year sd	0.17				
SES_FEve	ran_pars	study	Intercept sd	1.01				
SES_FEve	ran_pars	study	Intercept Year corr	1.00				
SES_FEve	ran_pars	study	Year sd	0.01				
SES_FEve	ran_pars	realm	Intercept sd	0.00				
SES_FEve	ran_pars	realm	Intercept Year corr					
SES_FEve	ran_pars	realm	Year sd	0.00				
SES_FEve	ran_pars	residual	Observation sd	0.90				
SES_FRic	fixed		Intercept	-0.23	0.09	-2.4264361	0.6001519	0.36
SES_FRic	fixed		Year	0.02	0.04	0.4567764	1.3686001	0.71
SES_FRic	ran_pars	timeseries:study	Intercept sd	0.54				
SES_FRic	ran_pars	timeseries:study	Intercept Year corr	0.06				
SES_FRic	ran_pars	timeseries:study	Year sd	0.18				
SES_FRic	ran_pars	study	Intercept sd	0.28				
SES_FRic	ran_pars	study	Intercept Year corr	-0.27				
SES_FRic	ran_pars	study	Year sd	0.12				
SES_FRic	ran_pars	climate	Intercept sd	0.09				
SES_FRic	ran_pars	climate	Intercept Year corr	-1.00				
SES_FRic	ran_pars	climate	Year sd	0.02				
SES_FRic	ran_pars	residual	Observation sd	0.81				
SES_FRic	fixed		Intercept	-0.25	0.07	-3.6991139	38.0641105	<0.001
SES_FRic	fixed		Year	0.02	0.04	0.6154086	10.9427859	0.55
SES_FRic	ran_pars	timeseries:study	Intercept sd	0.54				
SES_FRic	ran_pars	timeseries:study	Intercept Year corr	0.06				
SES_FRic	ran_pars	timeseries:study	Year sd	0.18				
SES_FRic	ran_pars	study	Intercept sd	0.27				
SES_FRic	ran_pars	study	Intercept Year corr	-0.28				
SES_FRic	ran_pars	study	Year sd	0.11				
SES_FRic	ran_pars	residual	Observation sd	0.81				
SES_FRic	fixed		Intercept	-0.25	0.07	-3.6989768	38.0642115	<0.001
SES_FRic	fixed		Year	0.02	0.04	0.6153911	10.9377906	0.55
SES_FRic	ran_pars	timeseries:study	Intercept sd	0.54				

SES_FRic	ran_pars	timeseries:study	Intercept Year corr	0.06				
SES_FRic	ran_pars	timeseries:study	Year sd	0.18				
SES_FRic	ran_pars	study	Intercept sd	0.27				
SES_FRic	ran_pars	study	Intercept Year corr	-0.28				
SES_FRic	ran_pars	study	Year sd	0.11				
SES_FRic	ran_pars	taxa	Intercept sd	0.00				
SES_FRic	ran_pars	taxa	Intercept Year corr	0.02				
SES_FRic	ran_pars	taxa	Year sd	0.00				
SES_FRic	ran_pars	residual	Observation sd	0.81				
SES_FRic	fixed		Intercept	-0.18	0.12	-1.5069779	2.2609264	0.26
SES_FRic	fixed		Year	0.00	0.05	0.0373018	1.6402024	0.97
SES_FRic	ran_pars	timeseries:study	Intercept sd	0.54				
SES_FRic	ran_pars	timeseries:study	Intercept Year corr	0.06				
SES_FRic	ran_pars	timeseries:study	Year sd	0.18				
SES_FRic	ran_pars	study	Intercept sd	0.22				
SES_FRic	ran_pars	study	Intercept Year corr	-0.14				
SES_FRic	ran_pars	study	Year sd	0.12				
SES_FRic	ran_pars	realm	Intercept sd	0.15				
SES_FRic	ran_pars	realm	Intercept Year corr	-1.00				
SES_FRic	ran_pars	realm	Year sd	0.05				
SES_FRic	ran_pars	residual	Observation sd	0.81				

Table 3.5: Details for all assemblage timeseries included in Chapter 3 analysis, adapted from the original BioTIME metadata.

study_id	realm	climate	taxa	title
39	Terrestrial	Temperate	Birds	Bird community dynamics in a temperate deciduous forest Long-term trends at Hubbard Brook
41	Terrestrial	Temperate	Birds	Time and space and the variation of species
46	Terrestrial	Temperate	Birds	Skokholm Bird Observatory
47	Terrestrial	Temperate	Birds	Detection of Density-Dependent Effects in Annual Duck Censuses
56	Terrestrial	Temperate	Mammals	Small Mammal Mark-Recapture Population Dynamics at Core Research Sites
58	Terrestrial	Tropical	Birds	Avian populations long-term monitoring dataset. San Juan. Puerto Rico Luquillo Long Term Ecological Research Site Database Grid points bird counts DBAS 23
59	Terrestrial	Temperate	Mammals	Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal. Arizona. USA
67	Terrestrial	Temperate	Birds	Animal Demography Unit - Coordinated Waterbird Counts (CWAC) (AfrOBIS)
69	Marine	Temperate	Birds	Seabird 2000 (EurOBIS)
77	Marine	Temperate	Birds	MEDITS Seabird surveys 1999 - 2000 - 2002
91	Marine	Temperate	Birds	Baltic seabirds transect surveys
108	Marine	Global	Birds	Seabirds of the Southern and South Indian Ocean (Australian Antarctic Data Centre)
166	Marine	Global	All	PIROP Northwest Atlantic 1965-1992 (SEAMAP)
169	Marine	Temperate	All	CalCOFI and NMFS Seabird and Marine Mammal Observation Data. 1987-2006 (SEAMAP)
171	Marine	Temperate/Tropical	Mammals	Bahamas Marine Mammal Research Organisation Opportunistic Sightings (SEAMAP)

172	Marine	Temperate	All	POPA cetacean. seabird. and sea turtle sightings in the Azores area 1998-2009 (OBIS SEAMAP)
195	Terrestrial	Temperate	Birds	Breeding birds survey North America
217	Terrestrial	Temperate	Birds	Landbird Monitoring Program (UMT-LBMP)
311	Terrestrial	Temperate	Mammals	Seasonal summary of numbers of small mammals on 14 LTER traplines in prairie habitats at Konza Prairie
312	Terrestrial	Tropical	Mammals	Stability in a Multi-Species Assemblage of Large Herbivores in East Africa
321	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study. Jornada LTER. SMES rodent trapping data
328	Freshwater	Temperate	Amphibians	The Rainbow Bay Long-term Study
333	Terrestrial	Temperate	Birds	Weekly record of bird species observed on Konza Prairie
337	Terrestrial	Temperate	Birds	Mountain Birdwatch
339	Terrestrial	Temperate	Birds	Species trends turnover and composition of a woodland bird community in southern Sweden during a period of 57 years.
341	Terrestrial	Temperate/Tropical	Amphibians	Brazil Dataset 1
357	Terrestrial	Temperate	Mammals	Small Mammal Trapping Webs on the Central Plains Experimental Range
362	Terrestrial	Tropical	Mammals	Plant and small-mammal responses to large-herbivore exclusion in an African savanna
363	Terrestrial	Temperate	Birds	The 37-year dynamics of a subalpine bird community with special emphasis on the influence of environmental temperature and Epirrita autumnata cycles.
366	Terrestrial	Temperate	Mammals	Small Mammal Exclosure Study (SMES)
372	Terrestrial	Temperate	Birds	Monitoring site 1000 Village survey - Bird survey data
373	Terrestrial	Temperate	Mammals	Village survey Medium and large mammal survey data
374	Marine	Temperate	Birds	Monitoring site 1000 Shorebird Survey
376	Terrestrial	Temperate	Birds	Monitoring site 1000 forest and grassland research - Bird survey data -1st phase
377	Terrestrial	Temperate	Birds	Monitoring site 1000 forest and grassland research - Bird survey data -2nd phase
382	Terrestrial	Temperate	Mammals	Small Mammals and Vegetation Changes After Fire in a Mixed Conifer-Hardwood Forest
403	Freshwater	Tropical	Amphibians	Community ecology of anura amphibia at Northwest region of Sao Paulo state
420	Terrestrial	Polar/Temperate	Birds	Species composition and population fluctuations of alpine bird communities during 38 years in the Scandinavian mountain range
439	Terrestrial	Temperate	Birds	Long-term dynamics of bird populations in pine forests of Ilmen Nature Reserve during the breeding period individuals / km2
440	Terrestrial	Temperate	Birds	Long-term dynamics of bird populations in pine-birch forests of Ilmen Nature Reserve during the breeding period individuals / km2
441	Terrestrial	Temperate	Birds	Long-term dynamics of bird populations in birch forests of Ilmen Nature Reserve during the breeding period individuals / km2
442	Terrestrial	Temperate	Birds	Composition and abundance of bird species in the village Matabay in June 1980-1985 (absolute indicators (area 025 km2))
443	Terrestrial	Temperate	Birds	Composition and abundance of bird species in the village Verhnjaja Elovka in June 1980-1985 (absolute indicators (area 025 km2))

444	Terrestrial	Temperate	Birds	The dynamics of species composition and abundance of migratory birds of prey in the Irkut River mouth (absolute figures)
445	Terrestrial	Temperate	Birds	A number of waterfowl after periods of breeding and molting in the lower reaches of Ob River (thous. individuals / 22 thous. km2)
446	Terrestrial	Temperate	Mammals	The density of population (ind/1000ha.) of hunting species of mammals in the Republic of Mordovia (Chamzinsky district)
447	Terrestrial	Temperate	Mammals	Long-term population dynamics of small mammals in the Natural Boundary Morozova Gora (individuals / 100 trap-nights)
448	Terrestrial	Temperate	Mammals	Number of small mammals in Verkhnyaya Angara basin (accounting period since 20.07 to 20.08 individuals /100 trap-nights
449	Terrestrial	Temperate	Mammals	Indicators of abundance (individuals / 100 trap-nights) of different species of small mammals in different years with using trap grooves and a coefficient characterizing the adverse conditions winter
459	Terrestrial	Temperate	Birds	Birds from the Bavarian Forest
475	Terrestrial	Temperate	Birds	Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest
515	Terrestrial	Tropical	Mammals	Assemblage-level responses of phyllostomid bats to tropical forest fragmentation
516	Terrestrial	Tropical	Mammals	A large-scale fragmentation experiment for Neotropical bats

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