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RESEARCH PAPER

How has bird biodiversity changed over time? A review across spatio-temporal scales

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Abstract

Empirical quantification of biodiversity changes remains a challenge even in well surveyed groups such as birds. This may be because the change depends on spatio-temporal scales, specifically on spatial grain (i.e. average unit of area of the sampling or the analysis), geographic extent (i.e. size of the area of interest), temporal grain (i.e. average unit of duration of the sampling or the analysis), and temporal extent (i.e. length of the time series). Further, different metrics of biodiversity may exhibit different trends. Here we review the literature assessing the temporal trends of avian biodiversity from ca. 1900 AD to present, focusing on studies summarising trends across many locations within a larger region (i.e. spatially replicated). From each study we extracted direction of average trend (increase, decrease, stable), spatial and temporal grains and extents at which the trends have been assessed, metrics of biodiversity, and location. We then discuss the trends as a function of the spatio-temporal grains and extents they are defined at. We found 59 trends of 12 metrics, where each trend is an average of trends from multiple sites (spatial replicates). There was a tendency of biodiversity metrics to increase at local and regional spatial scales, and to decrease globally. We thus confirmed that biodiversity dynamics can have opposite trends at different spatial scales. Concerning temporal grain, it was poorly documented across the studies, with inconsistent and/or confusing definitions. We suggest a common framework to better understand the link between temporal scales and biodiversity dynamics. We have also identified underrepresented regions (those outside North America and Europe), periods (those before the 70′s), and biodiversity metrics that need further attention. We highlight the importance of considering both spatial and temporal scaling jointly in any assessment of biodiversity change, and provide guidelines for specifying spatio-temporal features (i.e. grain, lag and extent) effectively both in birds, and in other taxa.

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Introduction

We have reasons to suspect that the global alteration of biodiversity due to anthropogenic pressures is unprecedented (Barnosky et al., 2011), and political goals have been declared in order to mitigate it (Convention on Biological Diversity, 2021). However, a data-driven basis for these policies remains a challenge, mainly due to severe gaps and biases in empirical biodiversity data (Meyer et al., 2015). To complicate matters further, current scientific literature has shown that temporal trends of local biodiversity can be different from and sometimes even opposite to trends at larger spatial scales (e.g. Cardinale et al., 2018; Finderup Nielsen et al., 2019; Keil et al., 2011, 2018; Vellend et al., 2013). Thus, we should expect local and regional changes of biodiversity to be more complex than the simple global decrease in species number (Chase et al., 2019). In addition, biodiversity can be measured by many metrics, and these can differ in their temporal trends (McGill et al., 2015): for instance, while there may be small average net change in local species richness, ecosystems can still undergo significant changes in species composition (Blowes et al., 2019; Dornelas et al., 2014; Vaidyanathan, 2021).

The scale at which biodiversity is assessed is critical (Levin, 1992). Since Arrhenius (1921) and Preston (1960), who formulated the species-area and species-time relationships, we know that spatial and temporal scaling of biodiversity affect macroecological patterns. While the *static* spatial scaling of biodiversity has been of great interest (e.g. Rahbek, 2005; Storch et al., 2007), it is still unclear how spatial and temporal scales affect the perceived dynamics of biodiversity. In other words: how the observed temporal biodiversity trends differ when we zoom out from local communities to regions, countries, or continents? In fact, the magnitude of ecological processes such as colonization, extinction, persistence, dispersal or extirpation is scale dependant, leading to different possible relationships between scale and biodiversity change (Chase et al., 2019; Jarzyna et al., 2015; Jarzyna & Jetz, 2017; Keil et al., 2018). This can be illustrated on an example of scale-dependant extinction: if a rare species goes extinct, it reduces diversity of the whole region, but not diversity in an average local spot, and thus the region has a higher extinction rate than a local spot (Keil et al., 2018). Inversely, if a widespread species contracts its distribution, it reduces diversity in many localities, but not diversity of the region, and a local spot has higher extinction rates than the whole region (Keil et al., 2018).

Importantly, scale has several facets, specifically grain, extent and lag (Dungan et al., 2002). Here, we use the term *spatial grain* to refer to the average area of multiple sites (or regions) at which biodiversity is assessed in the field or at which an analysis is made (Fig. 1(B), (A), respectively). One should not confuse spatial grain with the *spatial extent* of a study, i.e. the total area over which samples or analyses are conducted (Fig. 1(A), (B)). The same terminology can be applied to the temporal features: *temporal grain* is the average duration of an event during which biodiversity is measured, i.e. the duration of a one-time sampling session or the duration for which a metric is computed (Fig. 1(D), (C), respectively), while *temporal extent* of a study refers to the duration of the study period (Adler & Lauenroth, 2003; Fig. 1(C), (D)). Another aspect of scale is temporal or spatial *lag*, which refers to the average spatial or temporal distance between sampling sites or events respectively. The term average is important here: we only get to grain by averaging area across multiple sites, or averaging durations across multiple events. This means that grain can be defined even when area of sites or duration of events varies, and lag can be defined even when distance varies. In contrast to spatial scaling, temporal scaling has been much less studied, although it is expected to affect observed biodiversity trends, similarly as spatial scaling (Foote, 1994).

Definition of biodiversity is officially given by the Convention of Biological Diversity: "*"Biological diversity" means the variability among living organisms from all sources [. . .]; this includes diversity within species, between species and of ecosystems.*" A significant number of metrics follow this definition, all focusing on a specific aspect of biodiversity. Measures of static biodiversity metrics are commonly used such as local species richness (α diversity), regional richness (γ diversity, Whittaker, 1960), by indices that consider relative abundances (e.g. Shannon, 1948; Simpson, 1949), or by Hill numbers (Hill, 1973). Change of species composition in space and time can be expressed as $\beta = \frac{\gamma}{\alpha}$ (hereafter beta-diversity, Whittaker, 1972), or by pairwise dissimilarity among locations or time periods (Koleff et al., 2003). In addition, functional and phylogenetic diversity can provide supplementary information on the community structure and its dynamic (e.g. McGill et al., 2006; Mouquet et al., 2012; Webb et al., 2002). Even though abundance does not represent diversity *per se*, population abundance metrics have seen an increase in usage (Fraixedas et al., 2020). However, they often focus on either restricted communities (e.g. farmland/woodland bird indicators, Gregory et al., 2007; Gregory & van Strien, 2010) or on addressing particular problems (e.g. community temperature index that tracks community shifts caused by climate change, Bowler & Böhning-Gaese, 2017; Devictor et al., 2008).

While spatio-temporal scaling of static biodiversity metrics is well-known (i.e. species-area, species-time, and species-time-area relationships, Adler et al., 2005), scaling of their temporal trends is not. Here, to address this issue, we review the literature assessing the temporal trends of biodiversity, with focus on the variety of species-based biodiversity metrics (McGill et al., 2015) that they use, and spatial and temporal scales at which trends have been assessed. We focus our review on diversity metrics (i.e. incidence-based metrics such as species richness, or diversity metrics considering relative abundances such as evenness, Shannon's or Simpson's indices) as they aim at assessing biodiversity of entire metacommunities. Also, we caution that metrics of absolute population abundance (including those aggregated

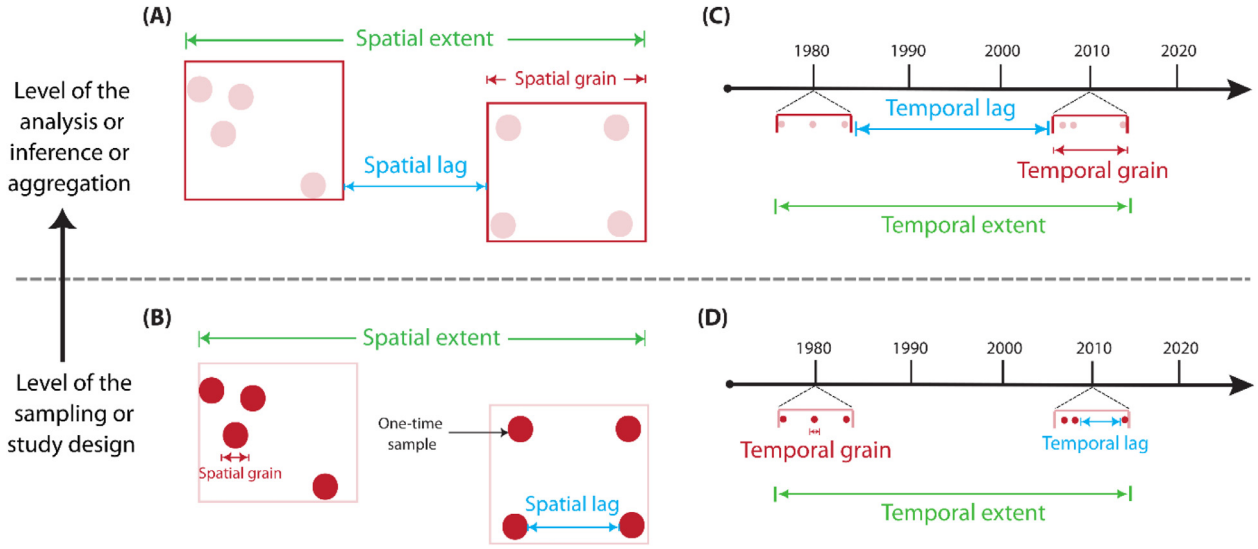

Fig. 1. Illustration of spatial (A, B) and temporal (C, D) features used in this review. Spatial and temporal grain, extent, and lags are defined as averages over multiple areas or distances. For instance, temporal distance between samples can vary (D), but there is only one lag, i.e. the average temporal distance between sample. Grain, extent, and lag also differ according to whether one refers to an analysis conducted (A, C) or to the study design (B, D).

over multiple species, e.g. as in Gregory et al., 2005) represent other phenomena than biodiversity, and that the sign of their change can be opposite to diversity. We show (1) that the most common trend across all metrics within the studied regions is an increase at local and regional scales. These local diversity increases are contrasting with global decreases. (2) Studies lack consensus about specification of spatial and temporal grains, where particularly the temporal scale of the dynamics is seldom considered, leading to confused conclusions about temporal trends. Moreover, we show that (3) studies lack spatial replication that would make reported trends robust and general and that (4) the studies assessing biodiversity trends with spatial replicates are mainly from North America and Europe, leading to spatially biased interpretation of biodiversity trends.

We focus our review on birds, as they represent the most surveyed taxa. Thanks to the many ornithological monitoring initiatives and surveys, we have a large number of high-quality time series on bird populations (e.g. Bejček & Šťastný, Karel, 2016; Jiguet et al., 2012; Kamp et al., 2021; Sauer et al., 2013, and many more). This is because birds are easy to observe and identify, and thus many volunteers are motivated to conduct standardised sampling or to participate in citizen-science projects (e.g. eBird, Sullivan et al., 2009; iNaturalist, https://www.inaturalist.org/). Also, birds are important for ecosystem functioning (e.g. seed dispersal) and sensitive to ecosystem perturbations, making them of interest when studying community dynamics in a context of increasing anthropogenic impact and climate change (Fricke et al., 2022). Finally, they represent a large spectrum of functional traits (e.g. diets, morphology, ecology), habitats, and responses to perturbations, and are thus suitable for tests of macroecological theories.

Materials and methods

We focused on articles that assess temporal trends of the most common metrics of biodiversity, and that are also explicit about spatial and temporal scales that they use. We considered the following categories of biodiversity metrics: *species richness (sR), functional richness (fR), evenness (Eve), functional evenness (fEve), diversity (Div), functional diversity (fDiv), temporal beta-diversity (tBetaDiv), spatial beta-diversity (sBetaDiv), functional spatial beta-diversity (fsBetaDiv), gamma-diversity* (*GammaDiv*, as used in, Monnet et al., 2014), *functional gamma-diversity (fGammaDiv)* and *phylogenetic diversity (pDiv)*. Some of these categories contain several indices. For instance, *diversity (Div)* designates either the Shannon or Simpson index here (see Table 1 for the metrics and their definitions). In the reviewed articles, both spatial and temporal *beta-diversity* are measured either as similarity (e.g. Jaccard index) or dissimilarity indices (e.g. Bray-Curtis index). Here, we consider *beta-diversity* as dissimilarity indices.

We followed selection steps in order to process the references. First, we only considered articles for which there were **spatial replicates**, i.e. where the trend of the metric was *assessed at several locations at a given spatial grain* (except for the global scale). For instance, Barnagaud et al. (2017) uses 807 routes, which are spatial replicates, and the overall trend is assessed by averaging across these replicates. Also, Keller et al. (2020) use 2972 grid cells as spatial replicates and the overall trend is the most common trend across all the cells. By assessing trends over spatial replicates, the trend reported at one spatial grain is more general and statistically reliable. Second, we omitted studies which were assessing the temporal trend after a perturbation (e.g.

Table 1. Definition of the metrics used in this review.

Metric name	Definition
Species richness (sR)	Number of species.
Functional richness (fR)	Number of morphological, physiological, and/or ecological traits spread across species.
Evenness (Eve)	Similarity of the relative abundances between species. The closer are abundances of species to each other, the higher the evenness. Examples are Pielou's (Pielou, 1966) or Simpson's (Simpson, 1949) evenness indices.
Functional evenness (fEve)	Evenness applied to functional richness.
Diversity (Div)	Diversity metrics which combine both richness and evenness. Examples are the Simpson's (Simpson, 1949) and Shannon's (Shannon, 1948) indices.
Functional diversity (fDiv)	Diversity metrics which combine functional richness and functional evenness.
Phylogenetic diversity (pDiv)	Diversity of evolutionary lineages, often measured as the sum of branch lengths of a phylogenetic tree. Example is Faith's phylogenetic diversity (Faith, 2006).
Temporal beta-diversity (tBetaDiv)	A measure of dissimilarity of species composition between two time periods at a single location. Example is the temporal Bray-Curtis distance (Bray & Curtis, 1957).
Spatial beta-diversity (sBetaDiv)	A measure of dissimilarity of species composition between two locations in space at a single temporal snapshot. Example is the spatial Bray-Curtis distance (Bray & Curtis, 1957).
Functional spatial beta-diversity (fsBetaDiv)	Spatial beta-diversity applied to composition of functional traits in communities.
Gamma diversity (GammaDiv)	Total diversity of all communities in a larger region.
Functional gamma diversity (fGammaDiv)	Total functional diversity of a larger region.

impact of logging in Hill & Hamer, 2004; tree planting in Roels et al., 2019; shrub encroachment in Sirami & Monadjem, 2012; urbanisation in Xu et al., 2018. . .). Also we omitted studies which were assessing temporal trends for a single type of ecosystem (e.g. Latta et al., 2011; Scarton, 2017).

We used the quantitative "advanced search" tool of the ISI Web of Science Core collection database with these following queries:

1 ALL = (birds AND species richness AND temporal trend) which resulted in 88 references.
2 ALL = (birds AND diversity AND temporal trend) which resulted in 156 references.

The search was run on August 11th, 2021. For each query, the title and abstract of the articles were reviewed. In addition, we used our knowledge about scientific literature on the topic for finding further studies. Additionally, for each article, we scanned its References section for other potentially relevant literature.

When the average temporal trend over spatial replicates was explicitly reported (either in a graph or text), we extracted the type of metric (Table 1), the spatial grain of the analysis (i.e. the area at which the metric trend was assessed in km^2; Fig 1(A)), its temporal grain (i.e. in decimal hours; Fig. 1(C)), spatial extent of the study (i.e. the entire area on which the study applies), temporal extent of the study, temporal lag of the study (i.e. the distance in time between two measures of the metric) and the beginning and ending years of the study (i.e. temporal coverage) as well as the trend of the metric (i.e. either increase, stable or decrease, see Appendix A: Table 1). We discretized spatial grains into four levels: local $\leq 50 \times 50$ km, regional $\geq 50 \times 50$ km, *national* when entire countries are considered, and *global* at the worldwide scale (in this latter case grain = extent). As definitions of temporal grain in the articles vary, we consider the temporal grain of the smallest unit of area at which the analysis is conducted (in decimal hours, Fig. 1. C)). For instance, articles using the North American Breeding Birds Survey summarise the data at the grain of the routes. Each route is divided into 50 census points surveyed for 3 min each, thus the temporal grain is: $(3 \times 50)/\ 60\ = 2.5$ h. Other example: in Monnet et al. (2014), the temporal grain is 5 min., thus $5/60\ = 0.08$ h.

We ended up with 59 trends of 12 metrics from 24 studies in total (see Appendix A: Table 1). Studies with spatial replicates were sometimes using the same datasets (e.g. Barnagaud et al., 2017; Blowes et al., 2019; Chase et al., 2019; Jarzyna & Jetz, 2017, 2018; La Sorte, 2006; La Sorte & Boecklen, 2005; McGill et al., 2015; Schipper et al., 2016). In order to avoid pseudoreplication, we discarded trends assessed at the same spatial grain with the same dataset and reporting the same direction of the trend; for instance, La Sorte (2006) and La Sorte et al. (2009) reported an increase of species richness at local scales using the North American Breeding Bird Survey (BBS) and thus we decided to keep only the latter. Both discussion about the trends and Fig. 3 account for pseudo-replication and are based on 46 trends of 12 metrics from 22 references.

Concerning the trend assessment, different papers contain the *p*-value, confidence interval or directly specify the significance of a trend of a metric. We used these to classify trends into 3 categories: *Increase* (significantly higher than 0), *Stable* (not significantly different from 0), or *Decrease* (significantly lower than 0). However, some papers give only graphical representations of the trend. In this case, the confidence interval was used when given (i.e. ending point

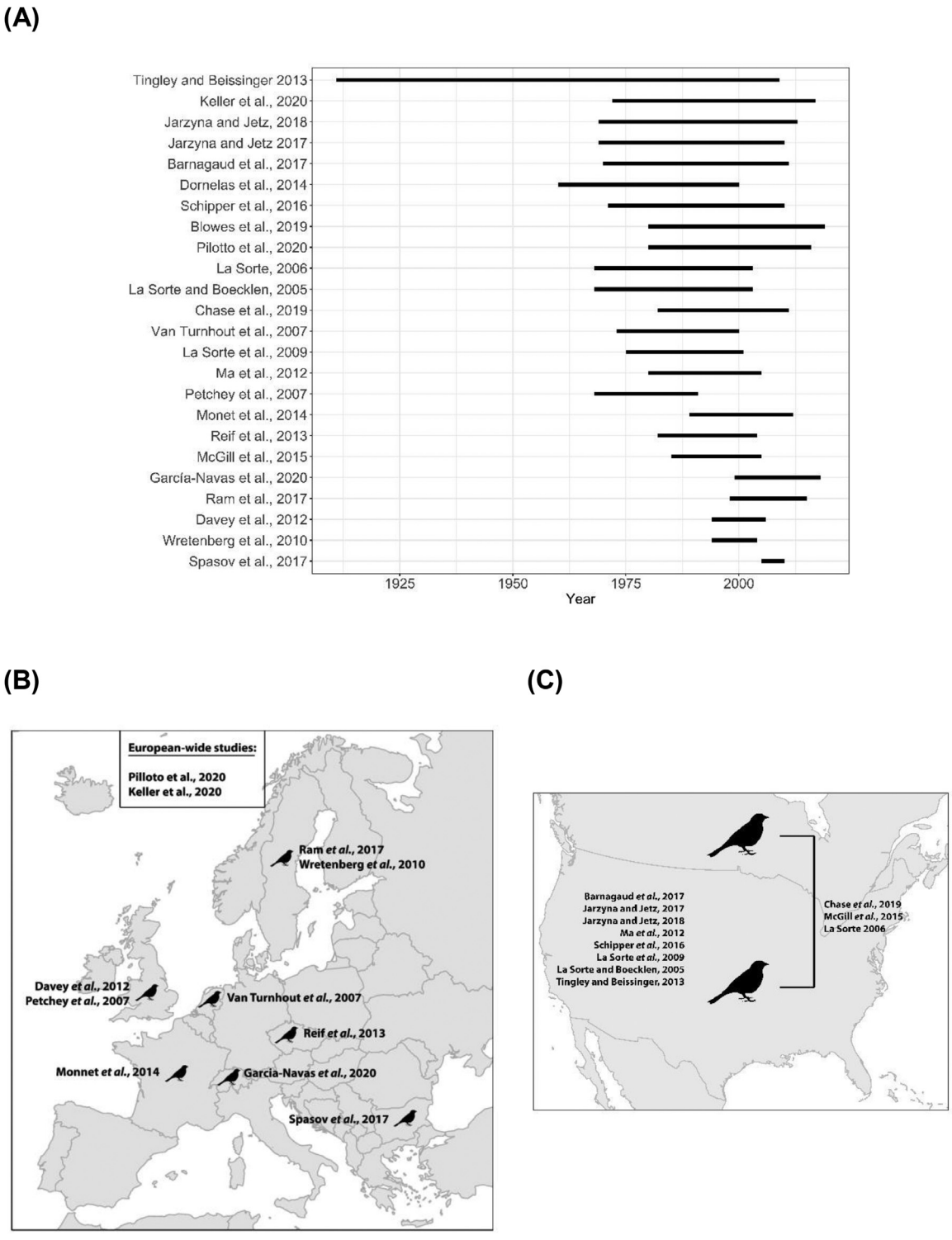

Fig. 2. Maximum temporal extent ranked by duration (A), and geographic extent (B, C) of 24 studies that we reviewed. In (A), as each reference assesses temporal trends with spatial replicates, some trends can be shorter than the maximum displayed. In (B) and (C), birds indicate countries where the studies were conducted. Worldwide studies (i.e. Dornelas et al., 2014; Blowes et al., 2019; Jarzyna & Jetz, 2018) are not represented.

of the trend outside of the confidence interval of the starting point). We note that we reported the overall trend of each study, i.e. with a temporal lag equal to the temporal extent (Fig. 1(C)), even though an overall trend is composed of increases and decreases throughout the temporal extent. We then summarised the trends by counting the increases, stable trends, and decreases within categories of spatial and temporal grains, and metric type.

Results

The oldest and longest study (Tingley & Beissinger, 2013) started in 1911, but most of the studies used datasets starting in the 1970s–1980s and ending in the 2000s–2010s (Fig. 2(A)). The median temporal extent among the 59 assessed trends is 28 years, with a minimum temporal extent of 6 years and a maximum of 99 years (Fig. 2(A)). among all the studies, only three different temporal grains of the analysis (Fig. 1(D)) were clearly specified (2.5, 3.4, 0.08 decimal hours). The median spatial extent of the 24 articles is ca. 300,000 km^2, with the smallest area of 267 km^2 and the greatest representing the global land surface (Fig. 2(B), (C)). Altogether, the 59 trends consist of 18 combinations of spatial grains and metrics. Studies reporting trends with spatial replicates were almost only found for Europe and North America. Only Blowes et al. (2019), Dornelas et al. (2014), Jarzyna and Jetz (2018) conducted worldwide analysis.

Overall trends

Overall, we found 36 *Increases,* 13 *Stable* and 10 *Decreases* trends (each trend is based on spatially replicated data) across the literature (see Appendix A: Fig. 2A). After accounting for pseudo-replicates, there were 26 *Increases*, 10 *Stable* and 10 *Decreases* (Fig. 3(A)). Remarkably, studies with spatial replicates at *National* grain (i.e. averaging trends across several countries) were absent. In our case, local grains were more represented than the others, and the number of articles decreases with the increasing spatial

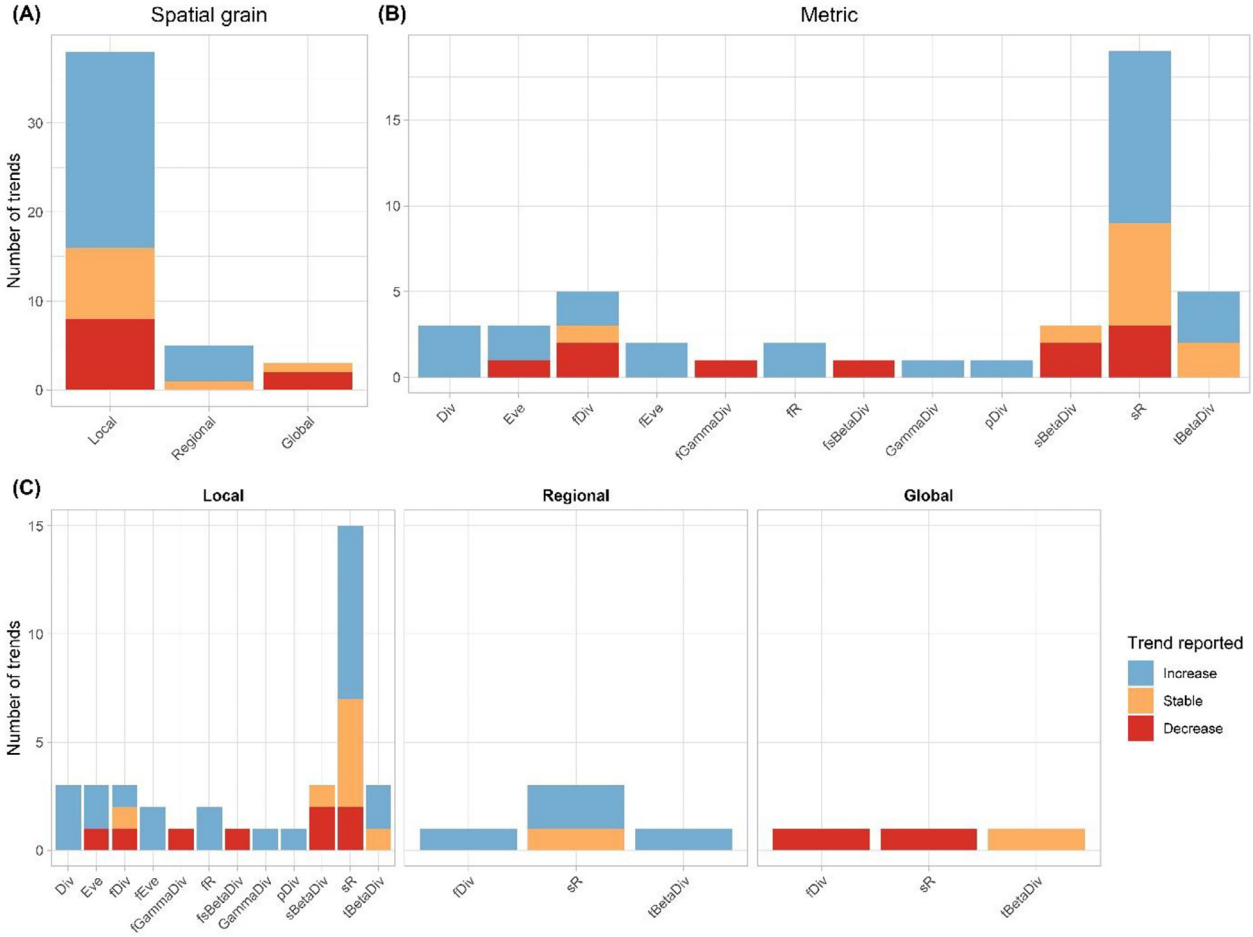

Fig. 3. Numbers of trends in each category (increase, stable, decrease) (A) for each spatial grain, (B) for each of the 12 metrics and (C) for each metric in each spatial grain. We accounted for pseudoreplication by removing the trends using the same datasets at the same spatial grain. Here, 46 trends from 21 articles are reported (out of 59 and 24, respectively). Note that each trend is an average trend from a given study, scale, and for a given metric, calculated over multiple sites (i.e. spatial replicates). Abbreviations: species richness (sR), functional richness (fR), evenness (Eve), functional evenness (fEve), taxonomic diversity (Div), functional diversity (fDiv), temporal beta-diversity (tBetaDiv), spatial beta-diversity (sBetaDiv), functional spatial beta-diversity (fsBetaDiv), gamma-diversity (GammaDiv), functional gamma-diversity (fGammaDiv), phylogenetic diversity (pDiv).

grain. From the selected articles, local spatial grains exhibited the highest variation in the trend sign. Surprisingly, trends at regional grains were mainly increasing and no decreases were found. At the *Global* scale, as expected, we found no *Increase*. Also, we did not find any relationship between the starting year and the sign of the temporal trend (Appendix A: Fig. 1). We caution that the direction of a trend has different meaning according to the metric considered (e.g. an increase of species richness does not bear the same meaning than an increase of spatial beta-diversity).

Trends by metric

Among the different metrics, most of the examined studies deal with temporal trends of species richness (Fig. 3(B), sR = 41%; Appendix A: Fig. 2B, sR = 54%). We seldom found trends of the other metrics with spatial replicates. Even when accounting for pseudo-replicates, the most common trend of richness (both taxonomic and functional) is *Increase*, whilst *Decrease* is the less common. Evenness indices (both taxonomic and functional) are also found mainly increasing. Interestingly, local taxonomic diversity is only increasing whilst functional diversity is reported increasing, decreasing and stable. Spatial β-diversity indices (both taxonomic and functional) mainly decrease whilst temporal β-diversity mainly increases.

Trends by spatial grain

Trends of only three metrics are comparable through spatial scales (Fig. 3(C)): species richness, functional diversity and temporal β-diversity. In the studies that we reviewed, at local and regional grains, species richness mostly increases while it decreases at global scale. At local grain, functional diversity shows as many decreases as increases, whilst it is increasing at regional grain and decreasing at global scale. Temporal β-diversity is mainly increasing at local and regional grains and is stable at global scale.

Discussion

Dynamics of avian biodiversity

While global species richness is undoubtedly decreasing (e.g. Barnosky et al., 2011; Diamond, 1989; Smith et al., 1993), there is still no evidence of such a negative trend at local and regional scales (Blowes et al., 2019; Cardinale et al., 2018; Dornelas et al., 2014; Finderup Nielsen et al., 2019; Vellend et al., 2013). Using literature on bird biodiversity trends, here we show that: **1)** the direction of local diversity trends varies considerably, **2)** intermediate (i.e. regional) spatial grains exhibit positive trends and **3)** this is in contrast with global diversity (i.e. species richness and functional diversity) which is declining. We further show that **4)** at local grains, taxonomic diversity metrics (i.e. species richness, diversity, evenness) are mainly increasing. This is also the case of functional richness and phylogenetic diversity, which we found to be reported only increasing at local scales. We note that the global decrease of species richness, mainly due to anthropogenic disturbances (e.g. Wilting et al., 2017), is inevitable as it can increase only through speciation, which is too slow to influence recent trends. Also, we warn that the sign of the *preferred trend* of a metric (i.e. indicating restoration/stability of biodiversity) can be different according to the metric considered.

Given the prevailing notion of the current biodiversity crisis (Barnosky et al., 2011; Ceballos et al., 2020; Cowie et al., 2022), the predominating increases of species richness and other diversity indices at local grains are surprising. The mismatch between global vs. local trends of diversity was hypothesised for the first time by Sax and Gaines (2003) and empirically demonstrated afterwards (Chase et al., 2019; Dornelas et al., 2014; Vellend et al., 2013). However, our review is the first to confirm this hypothesis based on published results, putting together studies assessing bird biodiversity trends using spatial replications along with their spatio-temporal features, study designs, and modeling methods.

We have several reasons to think that these local increases are human-induced (Pereira et al., 2012). For instance, local and regional increase of temporal β-diversity has been attributed to change in land use, overexploitation, introduction of invasive species or climate change (Pereira et al., 2012; Vaidyanathan, 2021). While we expected an increase of temporal β-diversity at global grain due to anthropogenic disturbances (McGill et al., 2015), we found it to be stable. Besides, in the reviewed literature, we observed a decrease of local spatial β-diversity which indicates homogenisation of bird communities (Rigal et al., 2021), likely due to replacement of endemic specialists by generalists after ecosystem perturbations, habitat fragmentation, and/or land-use homogenization (Davey et al., 2012; Devictor et al., 2008; McGill et al., 2015; McKinney & Lockwood, 1999). This local homogenization can be seen as a threat for ecosystems, as the new species do not necessarily provide the same ecosystem functions as the replaced ones (e.g. Clavel et al., 2011). Indeed, in Fig. 3(C), we found that local functional diversity was reported increasing, stable or decreasing, while diversity and species richness were mainly increasing. Thus, new species are introduced, but they do not necessarily add new functions, and can even reduce functional diversity. The lack of decrease of species richness at regional scale can be explained by the decrease of extinction rate with increasing spatial scale (Jarzyna et al., 2015; Jarzyna & Jetz, 2018; Keil et al., 2018). This can happen when species contract their distributions, but do not disappear completely, which affects local communities but not regional species pools (Keil et al., 2018).

We suspect that the local increases of diversity metrics (i.e. species richness, diversity, evenness and their functional

equivalents) could be temporary. Increase of those metrics has been partly attributed to generalist species colonisation in a context of climate change (Davey et al., 2012), and colonisation by generalists of disturbed landscapes is usually faster than specialists' extinction due to several mechanisms including extinction debt of specialists (Semper-Pascual et al., 2018; Warkentin & Reed, 1999). Thus, the observed diversity increase could be attributed to the variable speed of gains vs. losses. Another possibility is that communities are recovering from a massive decline driven by strong pressures on ecosystems during the mid-twentieth century (Gonzalez et al., 2016), which is the beginning of most of the analyses that we reviewed (Fig. 2(A)). Also, changes in environmental conditions induced by climate change lead to species range shifts that colonise new areas, leading to a (presumably temporary) increase of biodiversity (Walther et al., 2002). Besides, we reported species-based, not population-based metrics (e.g. multi-species indicators such as farmland/woodland/urban birds indicator, the Living Planet Index. . .), and potentially other metrics (e.g. trait-based indicators). We stress that those population abundance metrics show clear decline (Barnagaud et al., 2017; Burns et al., 2021; La Sorte & Boecklen, 2005; Rosenberg et al., 2019), confirming that increases of diversity metrics can be observed together with decreases of abundances. Also, we see an opportunity for future comparisons of trends of both diversity and population abundance metrics in order to better understand how they influence each other's.

Issues of temporal grain

The importance of temporal scaling of biodiversity is known since Grinnell (1922), who used California birds to demonstrate the species-time relationship (i.e. relationship between temporal grain and species richness), which has later been proven to be common (White, 2004). However, we found that the description of the temporal grain in the studies was not straightforward (see Appendix A: Table 1 & 2). Sometimes, the temporal grain of the sampling was specified precisely (e.g. time of each census point, as in Schipper et al., 2016), and sometimes with inaccuracies (e.g. *"During the survey, each observer records birds along two 1-km transect routes through each 1-km square."*, Davey et al., 2012).

Even if precisely specified, the temporal grain of the sampling does not always represent the temporal grain of the analysis conducted (see the difference between Fig. 1(C) and (D)). Some samples are combined over a certain area (e.g. combining the species richness in an atlas square, such as in Van Turnhout et al., 2007) and sometimes over both an area and a period of time (Chase et al., 2019). Analogically, the temporal grain of the analysis should be the result of the same combination of the temporal extent of the samples (e.g. Fig. 1(C), the analysis is made at the temporal grain of the red boxes which is different from the temporal grain of the samples in Fig. 1(D)). However, the process of how the temporal grain of the analysis is obtained from the temporal grain of the sampling was seldom specified in the papers that we reviewed. Usually, only the lag at the analysis level is reported (Fig. 1(C)). It is also important to consider the temporal lag of the sampling as well as how those samples are clumped in time (Fig. 1(D), the samples can be spread homogeneously or clumped in the red box). That is, the temporal lag between samples, and aggregation of the samples, can vary and we can expect different temporal distance decay of similarity for a given temporal grain of the analysis (i.e. temporal autocorrelation; Nekola & White, 1999).

If one wants to study the temporal scaling of biodiversity trends (Thompson et al., 2002), a clear definition and description of all the temporal features (i.e. grain, lag and extent) of both the study design **and** the analysis needs to be considered (Fig. 1(C), (D)). Thus, future studies should provide the following features: 1) the temporal grain of the sampling (i.e. red dots in Fig. 1(D)), 2) the temporal grain of the analysis (red boxes in Fig. 1(C)), 3) the number of samples used to form the temporal grain of the analysis (i.e. the number of red dots in a red box in Fig. 1(D)), 4) how these samples have been processed to obtain the temporal grain of the analysis (summed/averaged/modeled), 5) the temporal lag of the analysis (Fig. 1(C)), and 6) the temporal lag of the sampling (Fig. 1(D)). We argue that these guidelines allow for a complete representation of temporal structure, as they differentiate the temporal features of the sampling from those of the analysis (i.e. difference between Fig. 1(C) and (D)). This would allow a better assessment of the influence of the temporal features on biodiversity and its trends in the future. These recommendations also apply to spatial features, which are more often considered and simpler to display with maps.

Lack of spatial replication

In order to better understand the link between spatial scales and biodiversity trends, we focused on articles reporting and summarising trends from more than a single location, since a trend from a single locality gives little information on the patterns and can be driven by the site's specific features. However, these spatially replicated studies are uncommon (we found 24 studies out of 244 resulting from the queries made in Web of Science). This is partly due to a lack of data, especially outside of North America and Europe, but also to the way the data are processed. For instance, the North American BBS (Sauer et al., 2013) follows a standardised sampling plan with spatial replications (i.e. multiple census plots representing roads). However, authors can decide to aggregate and summarise the trends at the scale of a state or of the entire US, resulting in no spatial replication (e.g. Rosenberg et al., 2017). Additionally, a common method encountered is to learn a predictive model from the data, predict the target feature (e.g. species richness, spatial β-diversity) and then compute the trend from

the output of the model at the national spatial extent (this is very common for population abundance metrics, e.g. Doxa et al., 2010; Eglington & Pearce-Higgins, 2012; Jiguet et al., 2012; Sauer et al., 2017). These analyses are useful for conservation practice, and are common (Fraixedas et al., 2020). However, by reducing the number of trends computed, they also reduce the information on biodiversity dynamics at local grains. Only a few authors analysed the trends of metrics with spatial replicates across more than one spatial grain. This is the case of Chase et al. (2019), Jarzyna and Jetz (2018), McGill et al. (2015) and Van Turnhout et al. (2007), who show mismatching trends through spatial grains. For that reason and in order to have a general overview of the current biodiversity crisis magnitude, this cross-scale approach deserves more attention.

We found no studies using spatial replicates at the national spatial grain, i.e. using countries as observational units and summarising the trends across them. This is expected for two reasons. First, as the spatial replications get more demanding in organisation and resources with increasing grain size, the number of datasets available is reduced. Second, biodiversity datasets are usually standardised at the scale of the country, but the standardisation criteria of the spatio-temporal features are often specific to each country, making international merging of datasets and comparisons difficult. Fortunately, initiatives like the European Breeding Bird Atlas (Hagemeyer & Blair, 1997; Keller et al., 2020) or other citizen science projects (e.g. GBIF, https://www.gbif.org) are now making this possible by providing data at large spatial extent, and we hope to see trends with spatial replicates at regional or national grains soon.

Lack of spatio-temporal coverage

A striking but expected result (see Meyer et al., 2015), was the lack of studies with spatial replicates from outside of the high-income global North. Out of 24 papers, 11 assess trends in North America, 11 in Europe and 3 of them consider the globe, leading to biased spatial representativeness of biodiversity trends (Gonzalez et al., 2016). This gap was also reported in the literature review by Fraixedas et al. (2020). Even the "worldwide" studies often consider considerably more data from Europe and North America (Blowes et al., 2019; Dornelas et al., 2014). Yet, local biodiversity dynamics in Europe and North America may not be representative of local dynamics on other continents as most of the pressure on biodiveristy are currently happening in the global south (Marques et al., 2019). We have reason to think that the dominant increase of diversity (e.g. species richness, Shannon index…) reported in the reviewed studies only applies to the north hemisphere, especially due to temperature increase that impact positively species richness through species' range shifts (Walther et al., 2002) and because most of the extinctions in Europe and North America might have happened before data collection. Thus, studies of biodiversity trends at several spatio-temporal scales are needed in other parts of the world, at local grains as well as at the spatial grain of regions, nations and continents (e.g. see Alroy, 2015 for amphibians and reptiles). Finally, most of the studies covered only the last ca. 50 years, while only the longest study (i.e. 99 years) shows a clear decline of species richness at local grains (Tingley & Beissinger, 2013). These short temporal scope can bias assessment of temporal trends (Gonzalez et al., 2016) and the lack of data before the industrial era prevents us from comparing the trends reported here with historical changes of biodiversity.

Conclusion

As observers, we only directly experience biodiversity at local scale, but focusing only on local trends can be misleading. Indeed, the reviewed literature indicates that avian diversity has different trends, i.e. mainly local increases vs. global decreases. Besides, increases of species richness at local and regional scales should not be interpreted as ecosystem well-being without considering the trend of other metrics (e.g. spatial and temporal beta-diversity) and all spatial scales. We have reason to think that anthropogenic disturbances drive the local trends of biodiversity that is whether recovering from previous disturbances or is impacted by current ones. Temporal grain of the analysis has either been confused with the temporal grain of the sampling plan, or not properly considered at all. This can be addressed by following our guidelines for specifying the full temporal features of a study. Finally, the gaps in spatio-temporal coverage need to be filled with more data or interpolated over by cross-scale models (e.g. Keil & Chase, 2019). We hope that this review improves the current knowledge on spatio-temporal scaling of biodiversity trends and illustrates that the current biodiversity change needs to be considered across both spatial and temporal grains.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2023.03.004.

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