

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

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Data, code and figures are available here: https://github.com/FrsLry/BAAE_SI_litrev

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.* area of a sampling unit), geographic extent (*i.e.* size of the area of interest), temporal grain (*i.e.* duration of a sampling event), and temporal extent (*i.e.* length of the time series). Further, different metrics of biodiversity may exhibit different trends. Here we review global 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 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 not increase 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 definitions, and 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 how to do this effectively both in birds, and in other taxa.

Keywords: macroecology, cross scale, taxonomic diversity, functional diversity, richness, turnover, resolution, extinction, biodiversity crisis, breeding bird survey

Introduction

We have reasons to suspect that the global alteration of biodiversity due to anthropogenic pressures is unprecedented, and political goals have been declared in order to mitigate it (CBD, 2006). 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; Funderup Nielsen *et al.*, 2019; Keil *et al.*, 2011, 2018; Vellend *et al.*, 2013). Thus, we should expect changes in biodiversity to be more complex than a simple global decrease (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).

Particularly the scale is critical (Levin, 1992). Since Arrhenius (1921) and Preston (1960), we know that spatial and temporal scaling of biodiversity affects macroecological patterns. While the *static* spatial scaling of biodiversity has been of great interest (Rahbek, 2005; Storch *et al.*, 2007), it is still unclear how spatial and temporal scales affect the *dynamic* of biodiversity. In other words: how the observed temporal biodiversity trends differ when we zoom out from local communities to regions, countries, or continents? Here, the term *spatial grain* is also used to refer to the spatial scale of biodiversity, *i.e.* the area at which the biodiversity is assessed on the field. One should be careful to not confuse spatial grain with the *spatial extent* of a study, *i.e.* the total area which is observed or analysed (Dungan *et al.*, 2002, Fig. 1a). The same terminology can be applied for the temporal scale: *temporal grain* refers to the temporal unit of the measured biodiversity, while *temporal extent* refers to the duration of the study period (Adler & Lauenroth, 2003, Fig. 1b). In contrast to spatial scaling, temporal scaling has been much less studied, although it should also strongly affect observed biodiversity trends (Foote, 1994).

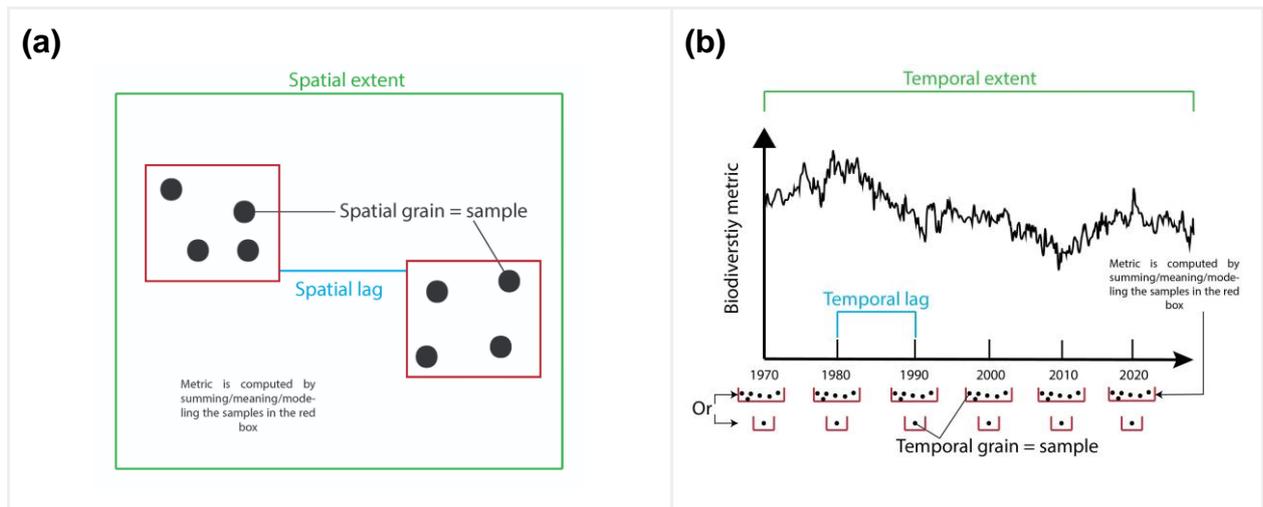


Figure 1 (in colours): Illustration of the concepts of spatial (a) and temporal (b) scales used in this review.

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 amount of metrics follow this definition, all focusing on a specific aspect of biodiversity. Measures of static biodiversity 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). Finally, abundance-based or population-based metrics have seen an increase in usage (Fraixedas *et al.*, 2020), although most of these metrics are focused on specific communities (e.g. farmland/woodland bird indicators, Gregory *et al.*, 2007; Gregory & 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 (e.g. 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 articles 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 show 1) that the most common trend across all metrics within the studied regions is an increase for local and regional scales. These local increases are contrasting with global trends. 2) We emphasise a lack of consensus about specifications and definitions of spatial and temporal grains (respectively), 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 one of 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 & Stastný, 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 participate on citizen-science projects (*e.g.* eBird, Sullivan *et al.*, 2009; iNaturalist, <https://www.inaturalist.org/>) or to conduct standardised sampling. Moreover, birds are key for ecosystem functioning (*e.g.* seed dispersal) and sensitive to ecosystem perturbations, making them of interest when studying community dynamic in a context of increasing anthropogenic impacts and climate change (Fricke *et al.*, 2022).

Material 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 Appendices Table 1 for the notes). In the reviewed articles, both spatial and temporal β -diversity are measured either by similarity or dissimilarity indices (*e.g.* Jaccard similarity index, turnover). Here, we consider *beta-diversity* as dissimilarity indices.

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. In contrast, Keller *et al.* (2020) uses 2,972 grid cells as spatial replicates and the overall trend is the most common trend across all the cells. With these replications, the trend reported at one spatial grain is more general and reliable.

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 11th August 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, the spatial grain of the trend (*i.e.* the area at which the metric trend is assessed), its temporal grain (*i.e.* the temporal unit of the sampling plan), spatial extent (*i.e.* the entire area on which the study applies), temporal extent, temporal lag (*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 (Table 1). We discretized spatial grains into four levels: *local* $\leq 50 \times 50$ km, *regional* $> 50 \times 50$ km, *national* when entire countries are considered, and *global* at the worldwide scale (for the latter, grain = extent).

After discarding all studies which reported trends for only a single spatial location, we ended up with 59 trends of 12 metrics from 24 studies in total (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 *et al.*, 2009; 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 of the trend outside of the confidence interval of the starting point means an increase or a decrease). We note that these trends do not reflect all the fluctuations of the metric through time but rather the difference between the starting and ending points. Thus, they can be seen at the *overall trends* across the temporal extent of the studies. 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 considered datasets starting in the 1970s-1980s and ending in the 2000s-2010s (Fig. 2a). 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. 2a). Among all the studies, only three different temporal grains were clearly specified (2.5, 3.4, 0.09 hours). The median spatial extent of the 20 articles is *ca.* 300,000 km², with the smallest area of 267 km² and the greatest representing the global land surface (Fig. 2b,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 Jarzyna and Jetz (2018), Dornelas *et al.* (2014) and Blowes *et al.* (2019) conducted worldwide analysis.

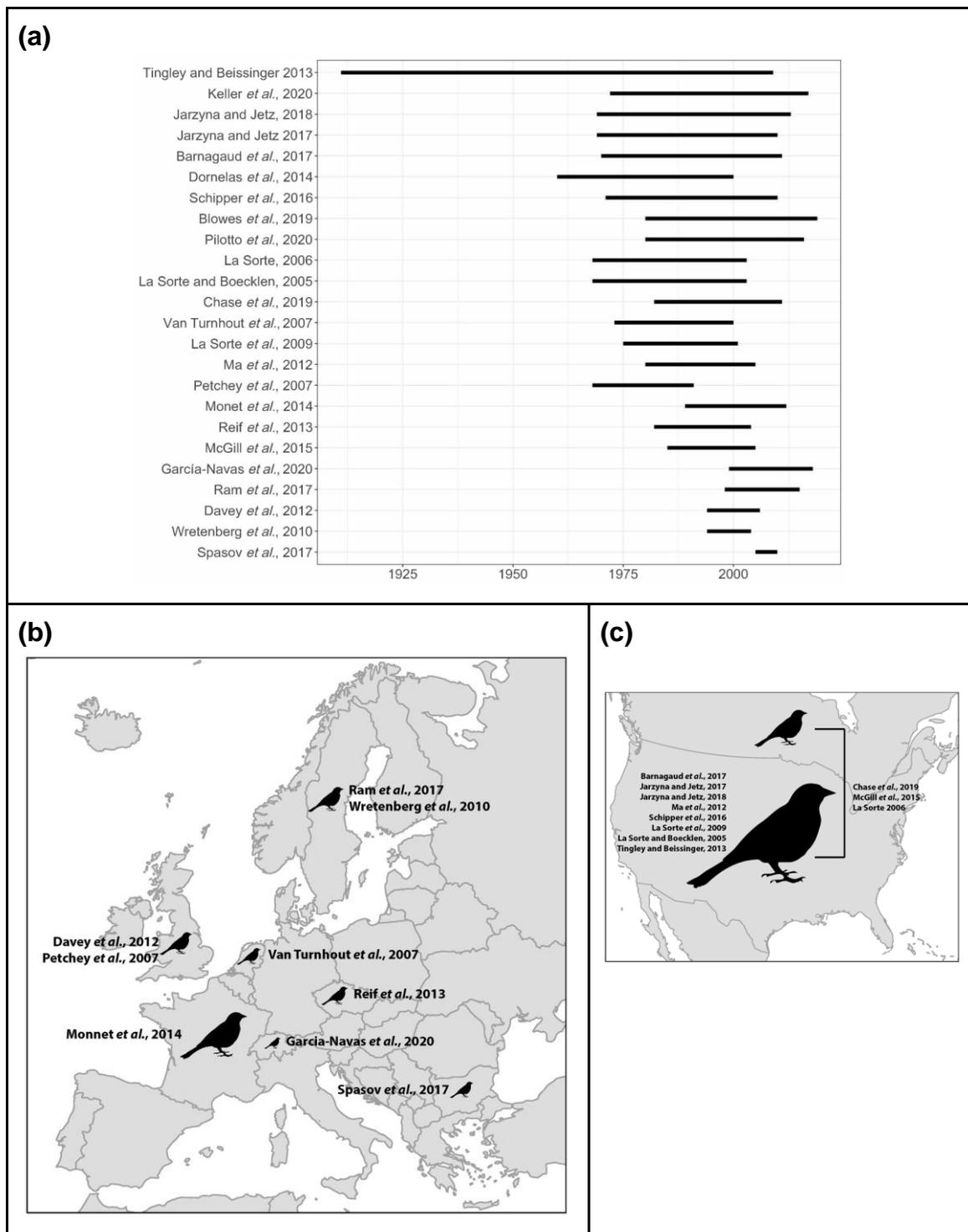


Figure 2 Temporal extents ranked by duration (a), and geographic extents (b, c) of 24 studies that we reviewed. Worldwide (i.e. Dornelas *et al.*, 2014; Blowes *et al.*, 2019; Jarzyna and Jetz 2018) and European-wide (i.e. Pilotto *et al.*, 2020; Keller *et al.*, 2020) studies are not represented. The size of the bird varies for aesthetic reasons, and bears no meaning.

Overall trends

Overall, we found 36 *Increases*, 14 *Stable* and 9 *Decreases* trends (each trend is based on spatially replicated data) across the literature (supplementary Fig. 1a). After accounting for pseudo-replicates, there were 26 *Increases*, 11 *Stable* and 9 *Decreases* (Fig. 3a). 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 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*.

Trends by metric

Among the different metrics, most of the examined studies deal with temporal trends of species richness (Fig. 3b, $sR = 41\%$; Supplementary Fig. 1b, $sR = 54\%$). 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, 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. 3c): 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.

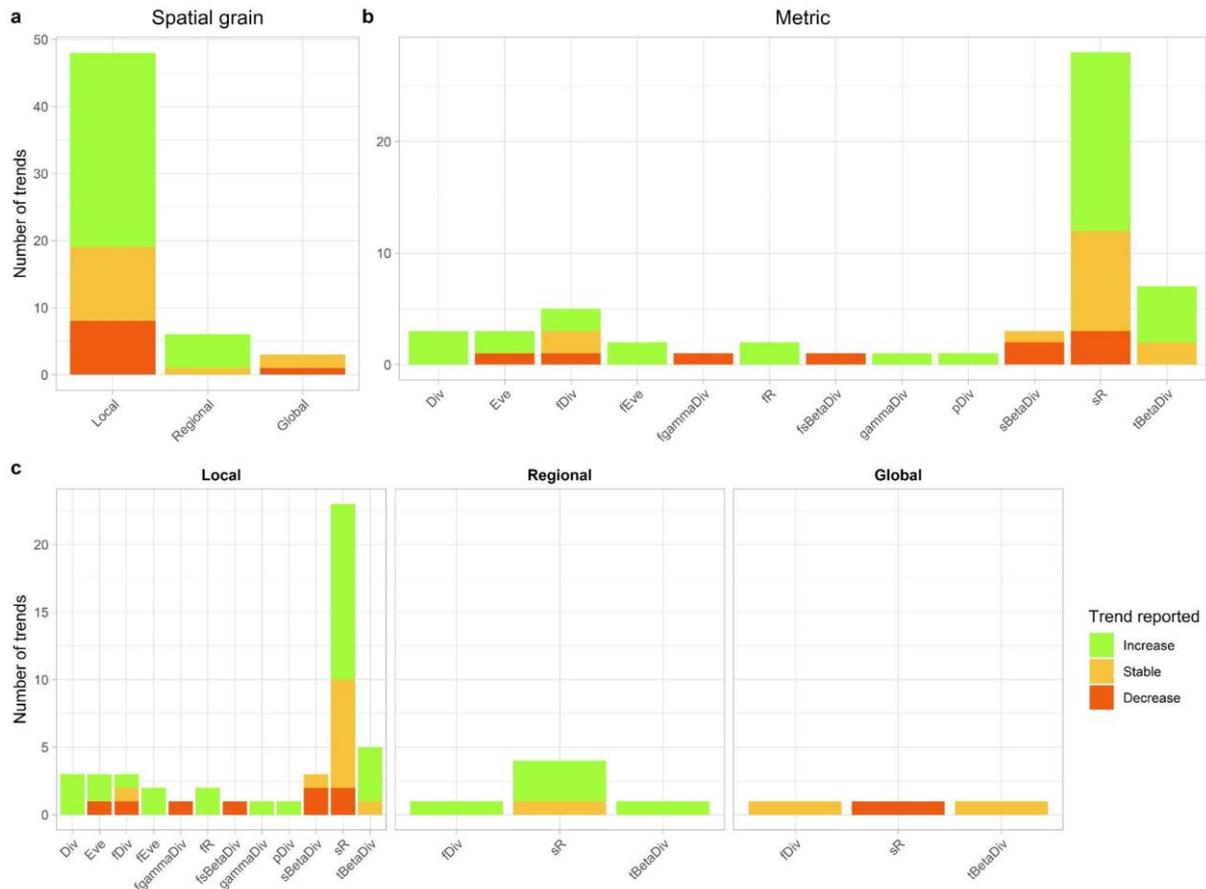


Figure 3 (in colours): Numbers of trends in each category (increase, stable, decrease) (a) for each spatial grain, (b) for each of the 12 metrics and (c) for each metric in each spatial grain. We accounted for pseudoreplication by removing the trends using the same datasets at the same spatial grain. 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*).

Discussion

Dynamics of avian biodiversity

While global biodiversity is undoubtedly decreasing, there is still no evidence of this 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 dynamics varies considerably, **2)** intermediate (*i.e.* regional) spatial grains exhibit positive trends and **3)** this is in contrast with global richness 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 only reported increasing at local scales. We note that the global decrease is inevitable as it can only increase through speciation, which is too slow to influence recent trends.

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 biodiversity indices at local grains are surprising. However, we have reasons to think that these local increases are human-induced (Pereira *et al.*, 2012). 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 to find an increase of temporal β -diversity 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 decrease of 'quality' of biodiversity, as the replacing species do not necessarily provide the same ecosystem services as the replaced ones (*e.g.* Clavel *et al.*, 2011). For instance, in Fig 3c, we found that local functional diversity was reported increasing, stable or decreasing, while diversity and species richness are mainly increasing. Thus, new species are introduced, but they do not necessarily add new functions, and can even reduce functional diversity. Finally, the lack of decrease of species richness at regional scale can be explained by the decrease of extinction rate with increasing spatial scale. 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 biodiversity could be temporary. Increase of diversity has been partly attributed to generalist species colonisation in a context of climate change (Davey *et al.*, 2012) and generalists' colonisation 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 biodiversity 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. 2a). Besides, we reported species-based, not population-based metrics (*e.g.* multi-species indicators), and potentially other metrics (*e.g.* trait-based indicators). We thus see an opportunity for future comparisons of trends of both species-based and non species-based metrics. For example, it is possible to have, on average, species richness increase together with abundance decline (Barnagaud *et al.*, 2017; La Sorte & Boecklen, 2005) or abundance stability (Pilotto *et al.*, 2020).

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, which has since been proven to

be common with other communities (White, 2004). However, we found that description of the temporal grain in the studies was not straightforward (Table 1). 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.* “All sites were visited six times [...] during early morning (mainly from sunrise to 10 am)...”), Wretenberg *et al.*, 2010).

Even if precisely specified, the temporal grain of the sampling does not always represent the temporal grain of the computed metric. Some metrics 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 (*e.g.* Chase *et al.*, 2019). Analogically, the temporal grain is summed over all the sampling censuses embedded in this area/time span (*e.g.* Fig. 1, the metric is computed by using all the samples in the red boxes). For instance, let's assume that a location is sampled twice a year during five minutes, and the species richness per year is computed by combining those two samples. In this specific case the temporal grain of the metric is ten minutes (*i.e.* the sum of the two census periods). However, this final temporal grain was seldom specified in the papers that we reviewed. Usually, only the lag was reported (*i.e.* the time between two computations of the metric, Fig. 1a).

If one wants to study the temporal scaling of biodiversity trends, a clear assessment of the temporal grain needs to be done systematically. That is: if a biodiversity metric is computed by combining samples together, the temporal grain (*i.e.* time span) of samples is summed, and this sum should be considered as the final temporal grain of the metric (*i.e.* Fig. 1, sum of the temporal grains of the black dots in the red boxes). Likewise, if the metric is averaged over several samples, the mean temporal grain of the samples should be specified (*i.e.* Fig. 1, mean of the temporal grains of the black dots in the red boxes). Finally, if the metric is predicted by a statistical model, the temporal grain of the model should be specified. These recommendations also apply to spatial grain.

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, as a trend from a single locality is hard to generalize and can be driven by the site's specific features. However, these spatially replicated studies are uncommon (we found 24 of them). 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, not all the trends reported for the North American BBS are summarised at the specific spatial grain of the road, and are sometimes aggregated over the US, thus with no spatial replication. 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 abundance-based 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 generality of the trend at the given scale. Finally, only a few authors computed the trends of metrics with spatial replicates across more than one spatial grain. This was the case for Chase *et al.* (2019), Jarzyna and Jetz (2018), Van Turnhout *et al.* (2007) and McGill *et al.* (2015). Yet, as we show here, biodiversity trends can be different according to the spatio-temporal grains they are assessed at. 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, which makes international merging of datasets and comparisons more demanding in terms of homogenization. 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, and we hope to see trends with spatial replicates at the national grain 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, 12 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 by Fraixedas *et al.* (2020). Even the “worldwide” studies often consider relatively more data from Europe and North America (Blowes *et al.*, 2019; Dornelas *et al.*, 2014). Yet, local biodiversity dynamics in Europe and North America is not representative of local dynamics on other continents. We have reasons to think that the dominant increase of biodiversity reported in the reviewed studies applies only on north hemisphere, especially due to temperature increase that impact positively species richness through species-energy relationship (Currie, 1991; Storch & Gaston, 2004; Whittaker *et al.*, 2001). Thus, studies of biodiversity trends at several spatio-temporal scales are needed in other parts of the world. These studies are needed 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 *ca.* the last 50 years. This lack of data before the industrial era prevents us from comparing the trends reported here with *baseline* biodiversity trends. These short time series can lead to biased assessment of temporal trends (Gonzalez *et al.*, 2016). Indeed, here, the only significantly long study (*i.e.* 99 years) shows a clear decline of species richness at local grains (Tingley & Beissinger, 2013).

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 biodiversity has different trends between local (*i.e.* mainly increases) and global (*i.e.* no increase) spatial scales. Besides, increases of species richness at local and regional scales should not be interpreted as

ecosystems well-being without considering the trend of other metrics (*e.g.* spatial and temporal beta-diversity) at all spatial scales. We have reasons to think that anthropogenic disturbances drive local biodiversity trends which are either recovering from previous disturbances or being impacted by current ones. Unfortunately, little is known about the resilience of bird biodiversity. Temporal grain of the metrics has either been confused with the temporal grain of the sampling plan, or not properly considered at all, and this needs to be addressed. Finally, the gaps in spatio-temporal coverage need to be filled with more data or interpolated over by models. 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.

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Table 1: Trends of different metrics of biodiversity at various spatial and temporal scales. Abbreviations: *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)*, *functional Gamma-diversity (fgammaDiv)*, *phylogenetic diversity (pDiv)*.

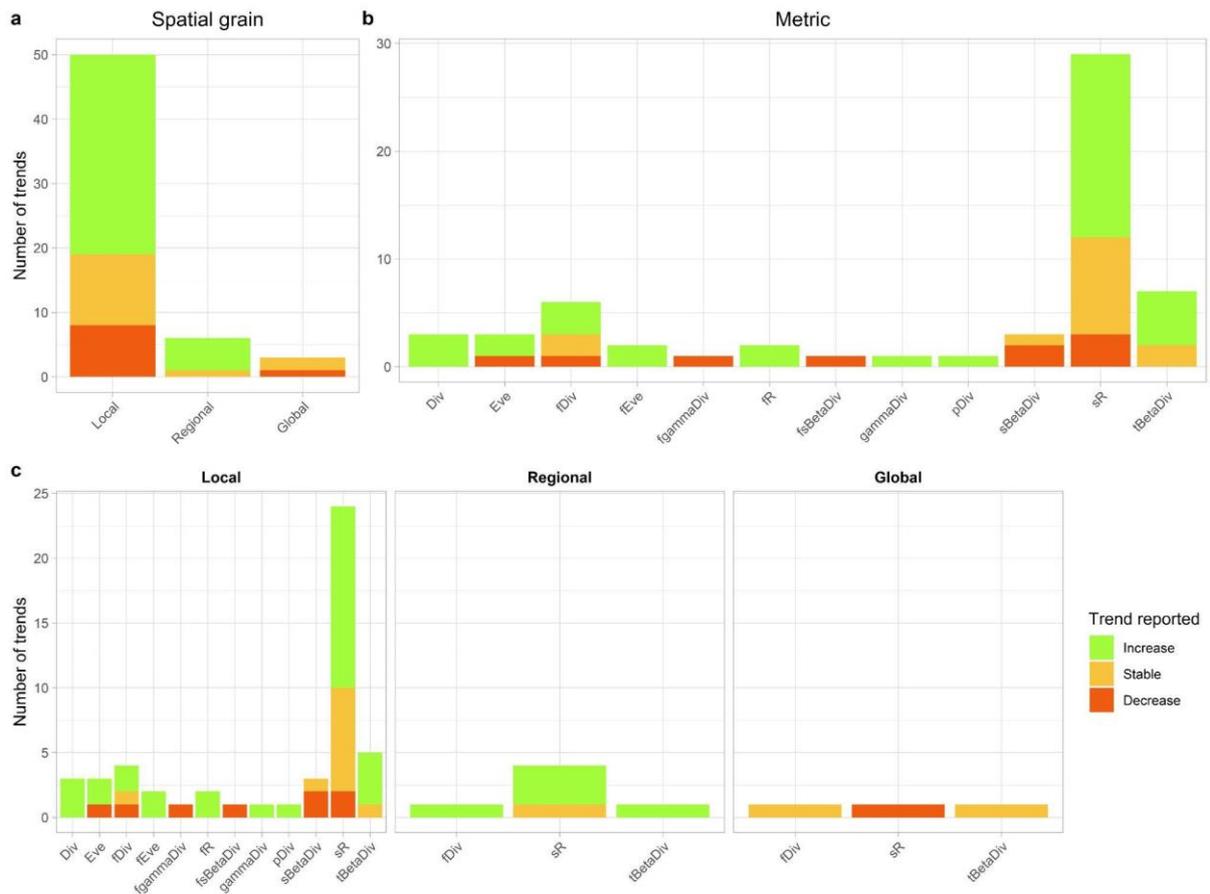
Reference	Metric	Spatial grain (Km ²)	Spatial extent (Km ²)	Temporal lag (year)	Temporal grain (hour)	Temporal extent (year)	Temporal coverage	Location	Trend
Barnagaud <i>et al.</i> (2017)	fR	Local	9,834,000	1	2.50	42	1970-2011	USA	Increase
	fEve	Local	9,834,000	1	2.50	42	1970-2011	USA	Increase
	Eve	Local	9,834,000	1	2.50	42	1970-2011	USA	Increase
	sR	Local	9,834,000	1	2.50	42	1970-2011	USA	Increase
Chase <i>et al.</i> (2019)	sR	Local	2,800,000	5	2.50	30	1982-2011	USA, Canada	Stable
	sR	Regional	2,800,000	5	2.50	30	1982-2011	USA, Canada	Increase
Davey <i>et al.</i> (2012)	Div	Local	242,495	1		13	1994-2006	UK	Increase
	Eve	Local	242,495	1		13	1994-2006	UK	Increase

	sR	Local	242,495	1		13	1994-2006	UK	Increase
Jarzyna & Jetz (2018)	sR	Local	9,834,000		2.50	45	1969-2013	USA	Increase
	sR	Regional	9,834,000		2.50	45	1969-2013	USA	Increase
	sR	Global	148,940,000			45	1969-2013	World	Decrease
	fDiv	Local	9,834,000		2.50	45	1969-2013	USA	Increase
	fDiv	Regional	9,834,000		2.50	45	1969-2013	USA	Increase
	fDiv	Global	148,940,000			45	1969-2013	World	Decrease
	tBetaDiv	Local	9,834,000		2.50	45	1969-2013	USA	Increase
	tBetaDiv	Regional	9,834,000		2.50	45	1969-2013	USA	Increase
	tBetaDiv	Global	148,940,000			45	1969-2013	World	Stable
Pilotto <i>et al.</i> (2020)	Div	Local	10,180,000			37	1980-2016	Europe	Increase
	sR	Local	10,180,000			37	1980-2016	Europe	Increase
	tBetaDiv	Local	10,180,000			37	1980-2016	Europe	Stable
Ram <i>et al.</i> (2017)	sR	Local	350,000	1		18	1998-2015	Sweden	Increase
Reif <i>et al.</i> (2013)	sBetaDiv	Local	79,000	1	3.40	23	1982-2004	Czech Rep.	Stable
	sR	Local	79,000	1	3.40	23	1982-2004	Czech Rep.	Stable
Schipper <i>et al.</i> (2016)	Div	Local	24,710,000	5	2.50	40	1971-2010	USA	Increase
	fDiv	Local	24,710,000	5	2.50	40	1971-2010	USA	Decrease
	fEve	Local	24,710,000	5	2.50	40	1971-2010	USA	Increase
	fR	Local	24,710,000	5	2.50	40	1971-2010	USA	Increase

	sR	Local	24,710,000	5	2.50	40	1971-2010	USA	Increase
La Sorte & Boecklen (2005)	Eve	Local	9,834,000	1	2.50	36	1968-2003	USA	Decrease
	sR	Local	9,834,000	1	2.50	36	1968-2003	USA	Increase
Van Turnhout <i>et al.</i> (2007)	sR	Regional	41,543	4		28	1973-2000	Netherlands	Increase
	sR	Local	41,543	4		28	1973-2000	Netherlands	Increase
Wretenberg <i>et al.</i> (2010)	sR	Local	1,800	1		11	1994-2004	Sweden	Decrease
Keller <i>et al.</i> (2020)	sR	Local	11,075,000	30		46	1972-2017	Europe	Increase
Monnet <i>et al.</i> (2014)	sR	Local	551,695	1	0.09	24	1989-2012	France	Increase
	sBetaDiv	Local	551,695	1	0.09	24	1989-2012	France	Decrease
	fsBetaDiv	Local	551,695	1	0.09	24	1989-2012	France	Decrease
	gammaDiv	Local	551,695	1	0.09	24	1989-2012	France	Increase
	fgammaDiv	Local	551,695	1	0.09	24	1989-2012	France	Decrease
Spasov <i>et al.</i> (2017)	sR	Local	110,994	1		6	2005-2010	Bulgaria	Stable
Jarzyna & Jetz, (2017)	sR	Local	9,834,000	1	2.50	42	1969-2010	USA	Increase
	fDiv	Local	9,834,000	1	2.50	42	1969-2010	USA	Increase
Tingley & Beissinger (2013)	sR	Local				99	1911-2009	USA	Decrease
La Sorte <i>et al.</i> (2009)	sR	Local	9,834,000	1	2.50	27	1975-2001	USA	Increase
La Sorte (2006)	sR	Local	9,834,000	1	2.50	36	1968-2003	USA, Canada	Increase

Ma <i>et al.</i> (2012)	sR	Local	125,384	20		26	1980-2005	USA	Increase
Dornelas <i>et al.</i> (2014)	sR	Local	148,940,000			41	1960-2000	World	Stable
	tBetaDiv	Local	148,940,000			41	1960-2000	World	Increase
García-Navas <i>et al.</i> (2020)	sBetaDiv	Local	267	1	1.00	20	1999-2018	Switzerland	Decrease
Blowes <i>et al.</i> (2019)	sR	Local		1		6	1980-2019	Polar realm	Stable
	sR	Local		1		6	1980-2019	Temperate realm	Stable
	tBetaDiv	Local		1		6	1980-2019	Polar realm	Increase
	tBetaDiv	Local		1		6	1980-2019	Temperate realm	Increase
McGill <i>et al.</i> (2015)	sR	Regional	9,834,000	5	2.5	20	1985-2020	USA	Stable
	sR	Local	9,834,000	5	2.5	20	1985-2020	USA	Stable
Petchey <i>et al.</i> (2007)	sR	Local	229,800	20		24	1968-1991	UK	Stable
	fDiv	Local	229,800	20		24	1968-1991	UK	Stable

Appendices



Supplementary Figure 1 (in colours): Numbers of trends in each category (increase, stable, decrease) for the 59 trends across 24 articles. 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). We also note that some trends reported here are based on the same dataset, but come from different studies; this is a potential source of pseudoreplication. For summary of trends that accounts for this pseudoreplication see Fig. 3. 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).

Supplementary Table 1: table containing the notes about the trends and articles used in this literature review. Abbreviations: *BBS* = *Breeding Bird Survey*, *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*), *functional Gamma-diversity* (*fgammaDiv*), *phylogenetic diversity* (*pDiv*).

Reference	Metric	Spatial grain (Km ²)	Note
Barnagaud <i>et al.</i> (2017)	fR	Local	North American BBS, there are 50 census points sampled for 3 minutes, Mean change of SR at the road scales. Area of the road = $(40/0.8) * (\pi * 0.4^2)$ with a road of 40 Km with point counts spaced by 0.8 Km and a census radius of 400m
	fEve	Local	
	Eve	Local	
	sR	Local	
Chase <i>et al.</i> (2019)	sR	Local	North American BBS restricted to a rectangle between 95°W to 70°W and 30°N to 50°N. They binned by 5 years and by quadrats, so the temporal grain of the metric should be different than from the sampling plan
	sR	Regional	
Davey <i>et al.</i> (2012)	Div	Local	British BBS. Metric = Simpson. They predict the metric using a GAM with spatial resolution of 1 Km ² . Then they show the trend for the mean value of the metric per year
	Eve	Local	
	sR	Local	
Jarzyna & Jetz (2018)	sR	Local	North American BBS
	sR	Regional	
	sR	Global	Data from Szabo <i>et al.</i> 2012
	fDiv	Local	
	fDiv	Regional	
	fDiv	Global	Data from Szabo <i>et al.</i> 2012

	tBetaDiv	Local	
	tBetaDiv	Regional	
	tBetaDiv	Global	Data from Szabo <i>et al.</i> 2012
Pilotto <i>et al.</i> (2020)	Div	Local	Metric = Simpson
	sR	Local	
	tBetaDiv	Local	
Ram <i>et al.</i> (2017)	sR	Local	Swedish BBS, "The number of observations for each sampling route is the sum of observed pair equivalents of birds at the counting points (5 min counting period at each point) and while moving between counting points". SR for forest species meaned over roads, spatial grain = 8* .4 with road of 8 Km and census radius "no limitations" so assumed 200m.
Reif <i>et al.</i> (2013)	sBetaDiv	Local	Breeding Bird Monitoring Programme. Jaccard similarity index (pairwise comparisons between transects), first increase then decrease. "A census transect consists of 20 points, which are visited twice per breeding season to sample early and late breeders. Observers register all birds seen or heard for 5 min at each census point"
	sR	Local	"species richness on both the local and national scales did not show any clear temporal trend"
Schipper <i>et al.</i> (2016)	Div	Local	North American BBS. Metric = Shannon. The metric is meaned over each road. Area of the road = $50 \cdot (\pi \cdot 400^2)$ with 50 census points per road and a census radius of 400m
	fDiv	Local	
	fEve	Local	
	fR	Local	
	sR	Local	
La Sorte & Boecklen (2005)	Eve	Local	North American BBS. The metric is meaned over each road. Area of the road = $50 \cdot (\pi \cdot 400^2)$ with 50 census point per road and a census radius of 400m.
	sR	Local	North American BBS. The metric is meaned over each road. Area of the road = $50 \cdot (\pi \cdot 400^2)$ with 50 census point per road and a census radius of 400m.
Van Turnhout <i>et al.</i> (2007)	sR	Regional	Dutch BBS, " two census periods". For each region, the trend is computed using the mean number of species per atlas square
	sR	Local	Mainly increase of SR but the proportion of negative trend were higher than for the regional scale

Wretenberg <i>et al.</i> (2010)	sR	Local	"All sites were visited six times in 1994 and five times in 2004 during early morning". Looking at the trend through different environmental policies, " local species richness (i.e. at the scale of sites = 3 hectares) decreased significantly probably as a result of an overall reduced abundance of several species. "
Keller <i>et al.</i> (2020)	sR	Local	Change in number of species between EBBA1 (1972-1995) and EBBA2 (2013-2017), grid cell = 50*50 Km
Monnet <i>et al.</i> (2014)	sR	Local	French BBS, Metrics are modelled at the point and site scales with GAMMs, Beta-diversity at the point scale (no indications of the spatial scale so assuming a 200m radius so spatial scale = $\pi \cdot 0.2^2$) and Gamma-diversity at the site scale
	sBetaDiv	Local	
	fsBetaDiv	Local	
	gammaDiv	Local	
Spasov <i>et al.</i> (2017)	sR	Local	Trend of the mean species richness per study plot, "The mean abundance of birds per sample declined over the years (Table 2, Fig. 3) but there was no significant trend in species richness (Table 2)." Unclear temporal grain: "All birds seen or heard while walking along the two line transects were counted"
	fDiv	Local	Functional diversity resulting from summing the length of the branches of a pruned clustering tree
Jarzyna & Jetz (2017)	sR	Local	American BBS, trend at the road scale. For taxonomic diversity trend: "35 years of significant increase and 7 years of significant decrease"
	fDiv	Local	Functional diversity resulting from summing the length of the branches of a pruned clustering tree
Tingley & Beissinger (2013)	sR	Local	Spatial grain: 10 counting points per site, with radius of observation assumed to 200m = $10 \times (\pi \times 0.2^2)$. "Modern species richness was significantly less than historical richness (i.e., 95% credible intervals of richness differences nonoverlapping with 0) at 21 sites (27%), while only seven sites (9%) gained a significant number of species. More generally, using mean posterior estimates of richness change, significantly more sites lost species than gained species (57% vs. 43%; χ^2 test, $P = 0.007$)."
La Sorte <i>et al.</i> (2009)	sR	Local	North American BBS, "our findings indicate a general trend of increasing species richness"
La Sorte (2006)	sR	Local	North American BBS, "In general, the results indicate that, during the time of the survey, more species expanded their geographical ranges within the study area"
Ma <i>et al.</i> (2012)	sR	Local	New York State Breeding Bird Atlas
Dornelas <i>et al.</i> (2014)	sR	Local	For species richness, Fig. S5 shows the slope for birds. For the temporal beta-diversity, trends only for birds is not given so we took the global trend.
	tBetaDiv	Local	Index used Jaccard similarity index. In this review, temporal beta-diversity is assessed as dissimilarity.
García-Navas <i>et al.</i> (2020)	sBetaDiv	Local	Sørensen score
Blowes <i>et al.</i> (2019)	sR	Local	Temporal extent is the median time serie. Tropical realm is represented only by 5 trends, so we decided to not take it into account.

	sR	Local	
	tBetaDiv	Local	
	tBetaDiv	Local	
McGill <i>et al.</i> (2015)	sR	Regional	North American BBS, spatial grain of 5x5°
	sR	Local	
Petchey <i>et al.</i> (2007)	sR	Local	Summer (breeding) distribution of the British avifauna, 2298 grid cells of 10*10 Km. "Species richness [...] from [...] (mean \pm 1 SD = 80.6 \pm 13.1) in Atlas 1 and from [...] (80.0 \pm 15.2) in Atlas 2. "
	fDiv	Local	"FD ranged from [...] (mean \pm 1 SD = 0.58 \pm 0.08) in Atlas 1 and from [...] (mean \pm 1 SD = 0.59 \pm 0.09) in Atlas 2"

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