Basic and Applied Ecology

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

Manuscript Number:	BAAE-D-22-00038
Article Type:	VSI:Scales and Heterogeneity
Keywords:	macroecology; cross scale; taxonomic diversity; functional diversity; richness; turnover; resolution; extinction; biodiversity crisis; breeding bird survey
Corresponding Author:	François LEROY Czech University of Life Sciences Prague Prague, CZECH REPUBLIC
First Author:	François LEROY
Order of Authors:	François LEROY
	Jiři Reif
	David Storch
	Petr Keil
Manuscript Region of Origin:	Europe
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.
Suggested Reviewers:	

Cover Letter

Czech university of Life Sciences
Faculty of Environmental Sciences
Kamýcká 1176
165 00, Prague
✆ +420737480623
✉ leroy@fzp.czu.cz

Dr. Holger Kreft, Dr. Catrin Westphal, Dr. Kerstin Wiegand
Editors
Basic and Applied Ecology
Special issue: *Scales and heterogeneity*

February 14, 2022

Dear editors,

Hereby, we submit a literature review entitled *"How has bird biodiversity changed over time? A review across spatio-temporal scales"* for consideration for the special issue *Scales and heterogeneity* of *Basic and Applied Ecology.*

There are numerous analyses that assess biodiversity trends of birds, they come from different countries, and most of them use a single spatial scale (*e.g.* only local). They have never been put together, and never compared while also considering their spatial and temporal features (*i.e.* grain, extent, lag, …). Here, we review these studies, and we show that for birds, biodiversity can have opposing trends depending on the scale at which these trends are assessed. Given the current debate about biodiversity loss, we believe that demonstrating the influence of spatial scales on biodiversity change will motivate researchers to measure biodiversity trends across scales.

Moreover, we highlight a lack of consensus about temporal scale (*i.e.* confusion between temporal grain of the sampling effort and of the metric), and we give guidelines for authors to better consider it. Finally, we show an insufficient spatio-temporal coverage of bird biodiversity datasets, which can lead to biased assessment of temporal biodiversity trends.

By considering spatio-temporal scales and heterogeneity of macroecological metrics, we believe that this literature review is relevant for the special issue "*Scales and heterogeneity*".

We have no conflict of interest to disclose. We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

Thank you for the consideration of our manuscript.

Sincerely,

François Leroy
PhD candidate
On behalf of the co-authors.

1 **How has bird biodiversity changed over time? A review across**

2 **spatio-temporal scales**

3 *François Leroy[1,*], Jiři Reif[2,3], David Storch[4,5], Petr Keil[1]*

4 [1] Department of Spatial Sciences, Faculty of Environmental Sciences, Czech University of Life

5 Sciences Prague, Kamýcká 129, 16500 Praha-Suchdol, Czech Republic

6 [2] Faculty of Science, Institute for Environmental Studies, Charles University, Prague, Czechia

7 [3] Department of Zoology, Faculty of Science, Palacky University, Olomouc, Czechia

8 [4] Center for Theoretical Study, Charles University, Jilská 1, 110 00-CZ Praha 1, Czech

9 Republic

10 [5] Department of ecology, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2,

11 Czech Republic

12 * Correspondence :

13 Email: leroy@fzp.czu.cz

14 Mail: Czech University of Life Sciences Prague

15 Faculty of Environmental Sciences

16 Kamycka 129

17 165 00 Prague - Suchdol

18

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

20

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; Finderup 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

69   of the measured biodiversity, while *temporal extent* refers to the duration of the study period

70   (Adler & Lauenroth, 2003, Fig. 1b). In contrast to spatial scaling, temporal scaling has been

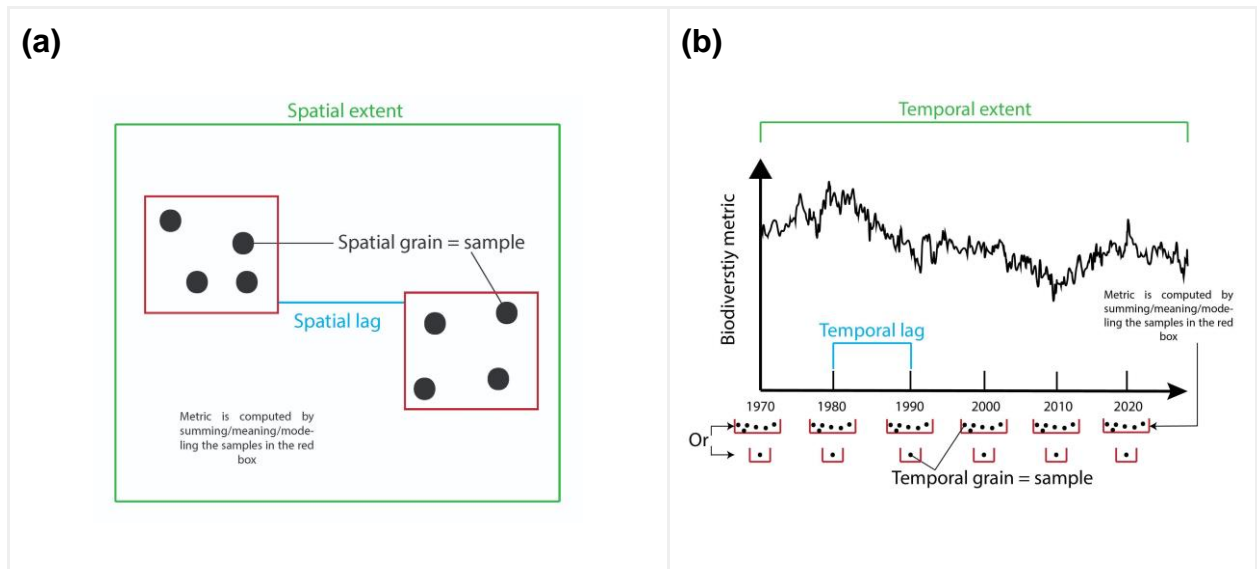71   much less studied, although it should also strongly affect observed biodiversity trends (Foote,

72   1994).

73   **Figure 1 (in colours)**: *Illustration of the concepts of spatial (a) and temporal (b) scales used*

74   *in this review.*

75   Definition of biodiversity is officially given by the Convention of Biological Diversity:

76   ""*Biological diversity" means the variability among living organisms from all sources [...];*

77   *this includes diversity within species, between species and of ecosystems.*" A significant

78   amount of metrics follow this definition, all focusing on a specific aspect of biodiversity.

79   Measures of static biodiversity are commonly used such as local species richness (α diversity),

80   regional richness (ɣ diversity, Whittaker, 1960), by indices that consider relative abundances

81   (*e.g.* Shannon, 1948; Simpson, 1949), or by Hill numbers (Hill, 1973). Change of species

82   composition in space and time can be expressed as $\beta = \frac{\gamma}{\alpha}$ (hereafter beta-diversity, Whittaker,

83   1972), or by pairwise dissimilarity among locations or time periods (Koleff *et al.*, 2003). In

84   addition, functional and phylogenetic diversity can provide supplementary information on the

85   community structure and its dynamic (*e.g.* McGill *et al.*, 2006; Mouquet *et al.*, 2012; Webb *et*

4

86 *al.*, 2002). Finally, abundance-based or population-based metrics have seen an increase in

87 usage (Fraixedas *et al.*, 2020), although most of these metrics are focused on specific

88 communities (*e.g.* farmland/woodland bird indicators, Gregory *et al.*, 2007; Gregory & Strien,

89 2010) or on addressing particular problems (*e.g.* community temperature index that tracks

90 community shifts caused by climate change, Bowler & Böhning-Gaese, 2017; Devictor *et al.*,

91 2008).

92 While spatio-temporal scaling of static biodiversity metrics is well-known (*e.g.* species-area,

93 species-time, and species-time-area relationships, Adler *et al.*, 2005), scaling of their temporal

94 trends is not. Here, to address this issue, we review articles assessing the temporal trends of

95 biodiversity, with focus on the variety of species-based biodiversity metrics (McGill *et al.*,

96 2015) that they use, and spatial and temporal scales at which trends have been assessed. We

97 show 1) that the most common trend across all metrics within the studied regions is an increase

98 for local and regional scales. These local increases are contrasting with global trends. 2) We

99 emphasise a lack of consensus about specifications and definitions of spatial and temporal

100 grains (respectively), where particularly the temporal scale of the dynamics is seldom

101 considered, leading to confused conclusions about temporal trends. Moreover, we show that 3)

102 studies lack spatial replication that would make reported trends robust and general and that 4)

103 the studies assessing biodiversity trends with spatial replicates are mainly from North America

104 and Europe, leading to spatially biased interpretation of biodiversity trends.

105 We focus our review on birds, as they represent one of the most surveyed taxa. Thanks to the

106 many ornithological monitoring initiatives and surveys, we have a large number of high-quality

107 time series on bird populations (*e.g.* Bejček & Stastný, 2016; Jiguet *et al.*, 2012; Kamp *et al.*,

108 2021; Sauer *et al.*, 2013, and many more). This is because birds are easy to observe and identify,

109 and thus many volunteers are motivated to participate on citizen-science projects (*e.g.* eBird,

110 Sullivan *et al.*, 2009; iNaturalist, https://www.inaturalist.org/) or to conduct standardised

111 sampling. Moreover, birds are key for ecosystem functioning (*e.g.* seed dispersal) and sensitive

112 to ecosystem perturbations, making them of interest when studying community dynamic in a

113 context of increasing anthropogenic impacts and climate change (Fricke *et al.*, 2022).

Material and Methods

115 We focused on articles that assess temporal trends of the most common metrics of biodiversity,

116 and that are also explicit about spatial and temporal scales that they use. We considered the

117 following categories of biodiversity metrics: *species richness (sR), functional richness (fR),*

118 *evenness (Eve), functional evenness (fEve), diversity (Div), functional diversity (fDiv),*

119 *temporal beta-diversity (tBetaDiv), spatial beta-diversity (sBetaDiv), functional spatial beta-*

120 *diversity (fsBetaDiv), gamma-diversity (gammaDiv,* as used in Monnet *et al.*, 2014*), functional*

121 *gamma-diversity (fgammaDiv)* and *phylogenetic diversity (pDiv)*. Some of these categories

122 contain several indices. For instance, *diversity (Div)* designates either the Shannon or Simpson

123 index here (see Appendices Table 1 for the notes). In the reviewed articles, both spatial and

124 temporal □-diversity are measured either by similarity or dissimilarity indices (*e.g.* Jaccard

125 similarity index, turnover). Here, we consider *beta-diversity* as dissimilarity indices.

126 We only considered articles for which there were **spatial replicates**, *i.e.* where the trend of the

127 metric was *assessed at several locations at a given spatial grain* (except for the global scale).

128 For instance, Barnagaud *et al.* (2017) uses 807 routes, which are spatial replicates, and the

129 overall trend is assessed by averaging across these replicates. In contrast, Keller *et al.* (2020)

130 uses 2,972 grid cells as spatial replicates and the overall trend is the most common trend across

131 all the cells. With these replications, the trend reported at one spatial grain is more general and

132 reliable.

133 We used the quantitative "advanced search" tool of the ISI Web of Science Core collection

134 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 ≤ 50×50 km², regional > 50×50 km², 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.*

159   (2009) reported an increase of species richness at local scales using the North American

160   Breeding Bird Survey (BBS) and thus we decided to keep only the latter. Both discussion about

161   the trends and Fig. 3 account for pseudo-replication and are based on 46 trends of 12 metrics

162   from 22 references.

163   Concerning the trend assessment, different papers contain the *p-value*, confidence interval or

164   directly specify the significance of a trend of a metric. We used these to classify trends into 3

165   categories: *Increase* (significantly higher than 0), *Stable* (not significantly different from 0), or

166   *Decrease* (significantly lower than 0). However, some papers give only graphical

167   representations of the trend. In this case, the confidence interval was used when given (*i.e.*

168   ending point of the trend outside of the confidence interval of the starting point means an

169   increase or a decrease). We note that these trends do not reflect all the fluctuations of the metric

170   through time but rather the difference between the starting and ending points. Thus, they can

171   be seen at the *overall trends* across the temporal extent of the studies. We then summarised the

172   trends by counting the increases, stable trends, and decreases within categories of spatial and

173   temporal grains, and metric type.

Results

175   The oldest and longest study (Tingley & Beissinger, 2013) started in 1911, but most of the

176   studies considered datasets starting in the 1970s-1980s and ending in the 2000s-2010s (Fig.

177   2a). The median temporal extent among the 59 assessed trends is 28 years, with a minimum

178   temporal extent of 6 years and a maximum of 99 years (Fig. 2a). Among all the studies, only

179   three different temporal grains were clearly specified (2.5, 3.4, 0.09 hours). The median spatial

180   extent of the 20 articles is *ca.* 300,000 *km²*, with the smallest area of 267 *km²* and the greatest

181   representing the global land surface (Fig. 2b,c). Altogether, the 59 trends consist of 18

182   combinations of spatial grains and metrics. Studies reporting trends with spatial replicates were

183 almost only found for Europe and North America. Only Jarzyna and Jetz (2018), Dornelas *et*

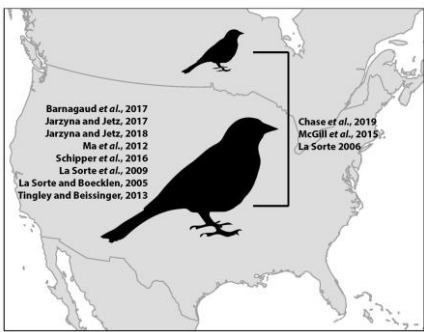184 *al.* (2014) and Blowes *et al.* (2019) conducted worldwide analysis.
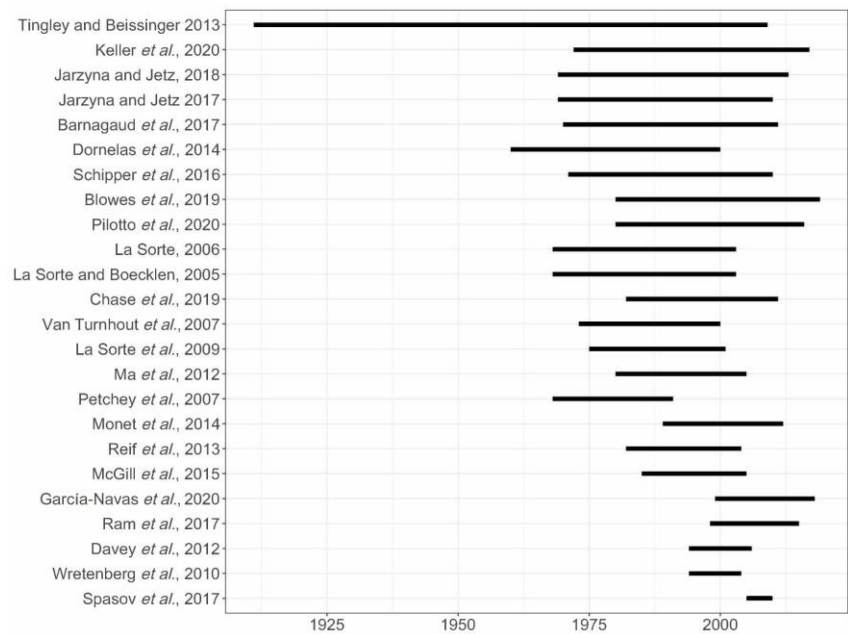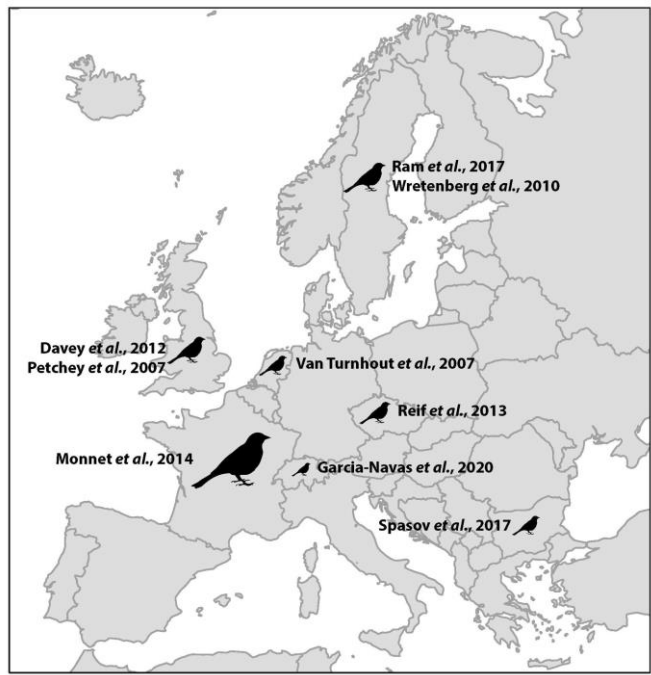
185　*Figure 2 Temporal extents ranked by duration (a), and geographic extents (b, c) of 24 studies*

186　*that we reviewed. Worldwide (i.e. Dornelas et al., 2014; Blowes et al., 2019; Jarzyna and Jetz*

187　*2018) and European-wide (i.e. Pilotto et al., 2020; Keller et al., 2020) studies are not*

188　*represented. The size of the bird varies for aesthetic reasons, and bears no meaning.*

Overall trends

190　Overall, we found 36 *Increases,* 14 *Stable* and 9 *Decreases* trends (each trend is based on

191　spatially replicated data) across the literature (supplementary Fig. 1a). After accounting for

192　pseudo-replicates, there were 26 *Increases*, 11 *Stable* and 9 *Decreases* (Fig. 3a). Remarkably,

193　studies with spatial replicates at *National* grain (*i.e.* averaging trends across several countries)

194　were absent. In our case, local grains were more represented than the others, and the number

195　of articles decreases with the increasing spatial grain. From the selected articles, local spatial

196　grains exhibited the highest variation in the trend sign. Surprisingly, trends at regional grains

197　were mainly increasing and no decreases were found. At the *Global* scale, as expected, we

198　found no *Increase*.

Trends by metric

200　Among the different metrics, most of the examined studies deal with temporal trends of species

201　richness (Fig. 3b, *sR = 41%;* Supplementary Fig. 1b, *sR = 54%*). We seldom found trends of

202　the other metrics with spatial replicates. Even when accounting for pseudo-replicates, the most

203　common trend of richness (both taxonomic and functional) is *Increase*, whilst *Decrease* is the

204　less common. Evenness indices (both taxonomic and functional) are also found mainly

205　increasing. Interestingly, taxonomic diversity is only increasing whilst functional diversity is

206　reported increasing, decreasing and stable. Spatial □-diversity indices (both taxonomic and

207　functional) mainly decrease whilst temporal □-diversity mainly increases.

208 Trends by spatial grain

209 Trends of only three metrics are comparable through spatial scales (Fig. 3c): species richness,

210 functional diversity and temporal □-diversity. In the studies that we reviewed, at local and

211 regional grains, species richness mostly increases while it decreases at global scale. At local

212 grain, functional diversity shows as many decreases as increases, whilst it is increasing at

213 regional grain and decreasing at global scale. Temporal □-diversity is mainly increasing at

214 local and regional grains and is stable at global scale.

215
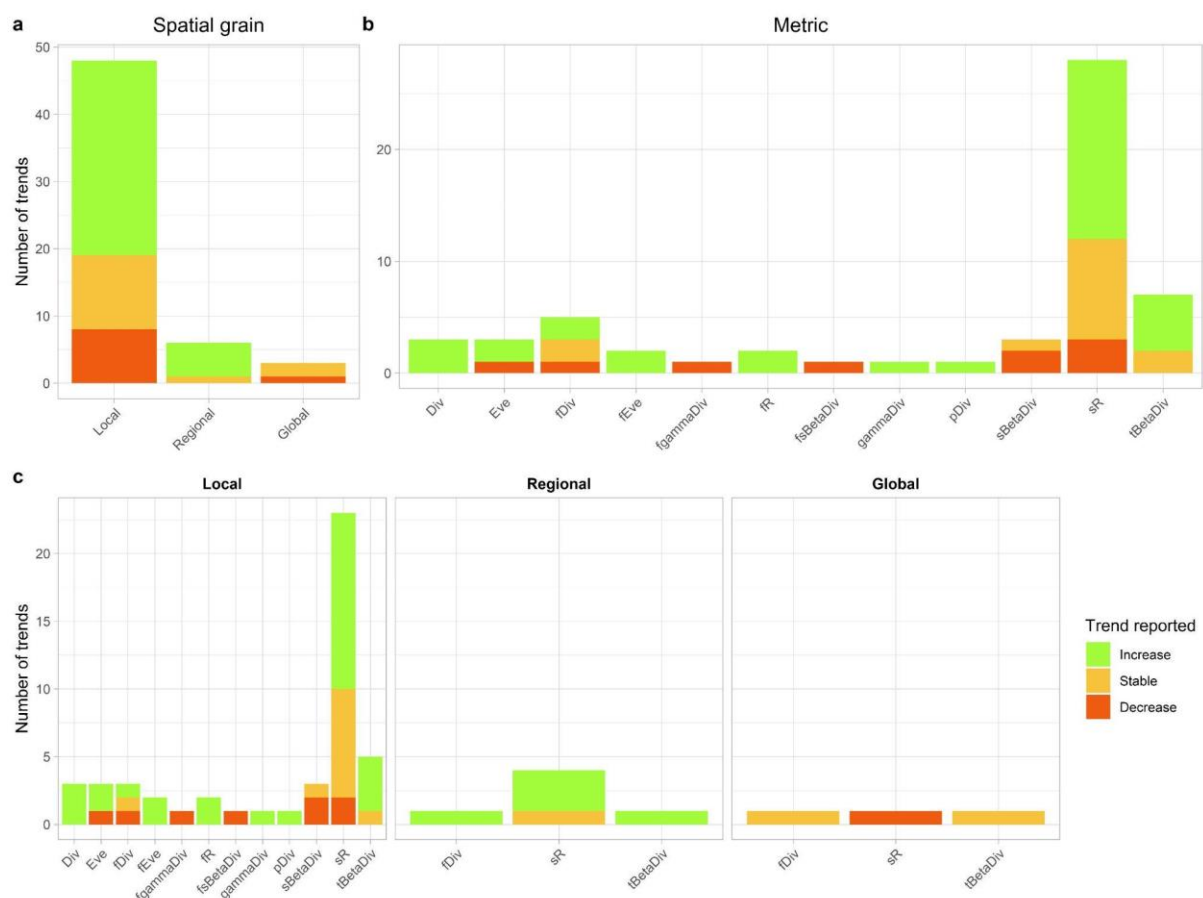
216 ***Figure 3 (in colours): Numbers of trends in each category (increase, stable, decrease) (a) for***

217 *each spatial grain, (b) for each of the 12 metrics and (c) for each metric in each spatial grain.*

218 *We accounted for pseudoreplication by removing the trends using the same datasets at the*

219 *same spatial grain. Here, 46 trends from 21 articles are reported (out of 59 and 24,*

220 *respectively). Note that each trend is an average trend from a given study, scale, and for a*

221 *given metric, calculated over multiple sites (i.e. spatial replicates). Abbreviations: species*

222 *richness (sR), functional richness (fR), evenness (Eve), functional evenness (fEve), taxonomic*

223 *diversity (Div), functional diversity (fDiv), temporal beta-diversity (tBetaDiv), spatial beta-*

224 *diversity (sBetaDiv), functional spatial beta-diversity (fsBetaDiv), gamma-diversity*

225 *(gammaDiv), functional Gamma-diversity (fgammaDiv), phylogenetic diversity (pDiv).*

Discussion

226

Dynamics of avian biodiversity

227

228 While global biodiversity is undoubtedly decreasing, there is still no evidence of this negative

229 trend at local and regional scales (Blowes *et al.*, 2019; Cardinale *et al.*, 2018; Dornelas *et al.*,

230 2014; Finderup Nielsen *et al.*, 2019; Vellend *et al.*, 2013). Using literature on bird biodiversity

231 trends, here we show that: **1)** the direction of local diversity dynamics varies considerably, **2)**

232 intermediate (*i.e.* regional) spatial grains exhibit positive trends and **3)** this is in contrast with

233 global richness which is declining. We further show that **4)** at local grains, taxonomic diversity

234 metrics (*i.e.* species richness, diversity, evenness) are mainly increasing. This is also the case

235 of functional richness and phylogenetic diversity, which we found to be only reported

236 increasing at local scales. We note that the global decrease is inevitable as it can only increase

237 through speciation, which is too slow to influence recent trends.

238 Given the prevailing notion of the current biodiversity crisis (Barnosky *et al.*, 2011; Ceballos

239 *et al.*, 2020; Cowie *et al.*, 2022), the predominating increases of species richness and other

240 biodiversity indices at local grains are surprising. However, we have reasons to think that these

241 local increases are human-induced (Pereira *et al.*, 2012). Local and regional increase of

242 temporal □-diversity has been attributed to change in land use, overexploitation, introduction

243 of invasive species or climate change (Pereira *et al.*, 2012; Vaidyanathan, 2021). While we

244 expected to find an increase of temporal β-diversity due to anthropogenic disturbances (McGill

245 et al., 2015), we found it to be stable. Besides, in the reviewed literature, we observed a

246 decrease of local spatial □-diversity which indicates homogenisation of bird communities

247 (Rigal *et al.*, 2021), likely due to replacement of endemic specialists by generalists after

248 ecosystem perturbations, habitat fragmentation, and/or land-use homogenization (Davey *et al.*,

249 2012; Devictor *et al.*, 2008; McGill *et al.*, 2015; McKinney & Lockwood, 1999). This local

250 homogenization can be seen as a decrease of *'quality'* of biodiversity, as the replacing species

251 do not necessarily provide the same ecosystem services as the replaced ones (*e.g.* Clavel *et al.*,

252 2011). For instance, in Fig 3c, we found that local functional diversity was reported increasing,

253 stable or decreasing, while diversity and species richness are mainly increasing. Thus, new

254 species are introduced, but they do not necessarily add new functions, and can even reduce

255 functional diversity. Finally, the lack of decrease of species richness at regional scale can be

256 explained by the decrease of extinction rate with increasing spatial scale. This can happen when

257 species contract their distributions, but do not disappear completely, which affects local

258 communities but not regional species pools (Keil *et al.*, 2018).

259 We suspect that the local increases of biodiversity could be temporary. Increase of diversity

260 has been partly attributed to generalist species colonisation in a context of climate change

261 (Davey *et al.*, 2012) and generalists' colonisation of disturbed landscapes is usually faster than

262 specialists' extinction due to several mechanisms including extinction debt of specialists

263 (Semper-Pascual *et al.*, 2018; Warkentin & Reed, 1999). Thus, the observed biodiversity

264 increase could be attributed to the variable speed of gains *vs.* losses. Another possibility is that

265 communities are recovering from a massive decline driven by strong pressures on ecosystems

266 during the mid-twentieth century (Gonzalez et al., 2016), which is the beginning of most of the

267 analyses that we reviewed (Fig. 2a). Besides, we reported species-based, not population-based

268 metrics (*e.g.* multi-species indicators), and potentially other metrics (*e.g.* trait-based

269 indicators). We thus see an opportunity for future comparisons of trends of both species-based

13

270 and non species-based metrics. For example, it is possible to have, on average, species richness

271 increase together with abundance decline (Barnagaud *et al.*, 2017; La Sorte & Boecklen, 2005)

272 or abundance stability (Pilotto *et al.*, 2020).

Issues of temporal grain

274 The importance of temporal scaling of biodiversity is known since Grinnell (1922), who used

275 California birds to demonstrate the species-time relationship, which has since been proven to

276 be common with other communities (White, 2004). However, we found that description of the

277 temporal grain in the studies was not straightforward (Table 1). Sometimes, the temporal grain

278 of the sampling was specified precisely (*e.g.* time of each census point, as in Schipper *et al.*,

279 2016), and sometimes with inaccuracies (*e.g. "All sites were visited six times [...] during early*

280 *morning (mainly from sunrise to 10 am)...)",* Wretenberg *et al.*, 2010).

281 Even if precisely specified, the temporal grain of the sampling does not always represent the

282 temporal grain of the computed metric. Some metrics are combined over a certain area (*e.g.*

283 combining the species richness in an atlas square, such as in Van Turnhout *et al.*, 2007) and

284 sometimes over both an area and a period of time (*e.g.* Chase *et al.*, 2019). Analogically, the

285 temporal grain is summed over all the sampling censuses embedded in this area/time span (*e.g.*

286 Fig. 1, the metric is computed by using all the samples in the red boxes). For instance, let's

287 assume that a location is sampled twice a year during five minutes, and the species richness per

288 year is computed by combining those two samples. In this specific case the temporal grain of

289 the metric is ten minutes (*i.e.* the sum of the two census periods). However, this final temporal

290 grain was seldom specified in the papers that we reviewed. Usually, only the lag was reported

291 (*i.e.* the time between two computations of the metric, Fig. 1a).

292 If one wants to study the temporal scaling of biodiversity trends, a clear assessment of the

293 temporal grain needs to be done systematically. That is: if a biodiversity metric is computed

294   by combining samples together, the temporal grain (*i.e.* time span) of samples is summed, and

295   this sum should be considered as the final temporal grain of the metric (*i.e.* Fig. 1, sum of the

296   temporal grains of the black dots in the red boxes). Likewise, if the metric is averaged over

297   several samples, the mean temporal grain of the samples should be specified (*i.e.* Fig. 1, mean

298   of the temporal grains of the black dots in the red boxes). Finally, if the metric is predicted by

299   a statistical model, the temporal grain of the model should be specified. These

300   recommendations also apply to spatial grain.

Lack of spatial replication

302   In order to better understand the link between spatial scales and biodiversity trends, we focused

303   on articles reporting and summarising trends from more than a single location, as a trend from

304   a single locality is hard to generalize and can be driven by the site's specific features. However,

305   these spatially replicated studies are uncommon (we found 24 of them). This is partly due to a

306   lack of data, especially outside of North America and Europe, but also to the way the data are

307   processed. For instance, the North American BBS (Sauer *et al.*, 2013) follows a standardised

308   sampling plan with spatial replications (*i.e.* multiple census plots representing roads).

309   However, not all the trends reported for the North American BBS are summarised at the

310   specific spatial grain of the road, and are sometimes aggregated over the US, thus with no

311   spatial replication. Additionally, a common method encountered is to learn a predictive model

312   from the data, predict the target feature (*e.g.* species richness, spatial □-diversity) and then

313   compute the trend from the output of the model at the national spatial extent (this is very

314   common for abundance-based metrics, *e.g.* Doxa *et al.*, 2010; Eglington & Pearce-Higgins,

315   2012; Jiguet *et al.*, 2012; Sauer *et al.*, 2017). These analyses are useful for conservation

316   practice, and are common (Fraixedas *et al.*, 2020). However, by reducing the number of trends

317   computed, they also reduce the generality of the trend at the given scale. Finally, only a few

318   authors computed the trends of metrics with spatial replicates across more than one spatial

15

319 grain. This was the case for Chase *et al.* (2019), Jarzyna and Jetz (2018), Van Turnhout *et al.*

320 (2007) and McGill *et al.* (2015). Yet, as we show here, biodiversity trends can be different

321 according to the spatio-temporal grains they are assessed at. For that reason and in order to

322 have a general overview of the current biodiversity crisis magnitude, this cross-scale approach

323 deserves more attention.

324

325 We found no studies using spatial replicates at the national spatial grain, *i.e.* using countries as

326 observational units and summarising the trends across them. This is expected for two reasons.

327 First, as the spatial replications get more demanding in organisation and resources with

328 increasing grain size, the number of datasets available is reduced. Second, biodiversity datasets

329 are usually standardised at the scale of the country, which makes international merging of

330 datasets and comparisons more demanding in terms of homogenization. Fortunately, initiatives

331 like the European Breeding Bird Atlas (Hagemeyer & Blair, 1997; Keller *et al.*, 2020) or other

332 citizen science projects (*e.g.* GBIF, https://www.gbif.org) are now making this possible, and

333 we hope to see trends with spatial replicates at the national grain soon.

334 Lack of spatio-temporal coverage.

335 A striking but expected result (see Meyer *et al.*, 2015), was the lack of studies with spatial

336 replicates from outside of the high-income global North. Out of 24 papers, 11 assess trends in

337 North America, 12 in Europe and 3 of them consider the globe, leading to biased spatial

338 representativeness of biodiversity trends (Gonzalez *et al.*, 2016). This gap was also reported by

339 Fraixedas *et al.* (2020). Even the "worldwide" studies often consider relatively more data from

340 Europe and North America (Blowes *et al.*, 2019; Dornelas *et al.*, 2014). Yet, local biodiversity

341 dynamics in Europe and North America is not representative of local dynamics on other

342 continents. We have reasons to think that the dominant increase of biodiversity reported in the

343 reviewed studies applies only on north hemisphere, especially due to temperature increase that

16

344 impact positively species richness through species-energy relationship (Currie, 1991; Storch &

345 Gaston, 2004; Whittaker *et al.*, 2001). Thus, studies of biodiversity trends at several spatio-

346 temporal scales are needed in other parts of the world. These studies are needed at local grains,

347 as well as at the spatial grain of regions, nations and continents (*e.g.* see Alroy, 2015 for

348 amphibians and reptiles). Finally, most of the studies covered only *ca.* the last 50 years. This

349 lack of data before the industrial era prevents us from comparing the trends reported here with

350 *baseline* biodiversity trends. These short time series can lead to biased assessment of temporal

351 trends (Gonzalez *et al.*, 2016). Indeed, here, the only significantly long study (*i.e.* 99 years)

352 shows a clear decline of species richness at local grains (Tingley & Beissinger, 2013).

353 Conclusion

354 As observers, we only directly experience biodiversity at local scale but focusing only on local

355 trends can be misleading. Indeed, the reviewed literature indicates that avian biodiversity has

356 different trends between local (*i.e.* mainly increases) and global (*i.e.* no increase) spatial scales.

357 Besides, increases of species richness at local and regional scales should not be interpreted as

358 ecosystems well-being without considering the trend of other metrics (*e.g.* spatial and temporal

359 beta-diversity) at all spatial scales. We have reasons to think that anthropogenic disturbances

360 drive local biodiversity trends which are either recovering from previous disturbances or being

361 impacted by current ones. Unfortunately, little is known about the resilience of bird

362 biodiversity. Temporal grain of the metrics has either been confused with the temporal grain

363 of the sampling plan, or not properly considered at all, and this needs to be addressed. Finally,

364 the gaps in spatio-temporal coverage need to be filled with more data or interpolated over by

365 models. We hope that this review improves the current knowledge on spatio-temporal scaling

366 of biodiversity trends and illustrates that the current biodiversity change needs to be considered

367 across both spatial and temporal grains.

372 ***Table 1:*** Trends of different metrics of biodiversity at various spatial and temporal scales.

373 Abbreviations: *species richness (sR), functional richness (fR), evenness (Eve), functional*

374 *evenness (fEve), diversity (Div), functional diversity (fDiv), temporal beta-diversity (tBetaDiv),*

375 *spatial beta-diversity (sBetaDiv), functional spatial beta-diversity (fsBetaDiv), gamma-*

376 *diversity (gammaDiv), functional Gamma-diversity (fgammaDiv), phylogenetic diversity*

377 *(pDiv).*

Reference	Metric	Spatial grain (Km²)	Spatial extent (Km²)	Temporal lag (year)	Temporal grain (hour)	Temporal extent (year)	Temporal coverage	Location	Trend
Barnagaud *et al.* (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 *et al.* (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 *et al.* (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 *et al.* (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 *et al.* (2017)	sR	Local	350,000	1		18	1998-2015	Sweden	Increase
Reif *et al.* (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 *et al.* (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

Study	Metric	Scale	Area			N	Period	Country	Trend
	sR	Local	9,834,000	1	2.50	36	1968-2003	USA	Increase
Van Turnhout *et al.* (2007)	sR	Regional	41,543	4		28	1973-2000	Netherlands	Increase
	sR	Local	41,543	4		28	1973-2000	Netherlands	Increase
Wretenberg *et al.* (2010)	sR	Local	1,800	1		11	1994-2004	Sweden	Decrease
Keller *et al.* (2020)	sR	Local	11,075,000	30		46	1972-2017	Europe	Increase
Monnet *et al.* (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 *et al.* (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 *et al.* (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 *et al.* (2012)	sR	Local	125,384	20		26	1980-2005	USA	Increase
Dornelas *et al.* (2014)	sR	Local	148,940,000			41	1960-2000	World	Stable

|									
	tBetaDiv	Local	148,940,000			41	1960-2000	World	Increase
García-Navas *et al.* (2020)	sBetaDiv	Local	267	1	1.00	20	1999-2018	Switzerland	Decrease
Blowes *et al.* (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 *et al.* (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 *et al.* (2007)	sR	Local	229,800	20		24	1968-1991	UK	Stable
	fDiv	Local	229,800	20		24	1968-1991	UK	Stable

378

379

380

381

382

383

384

385

386

387

Appendices
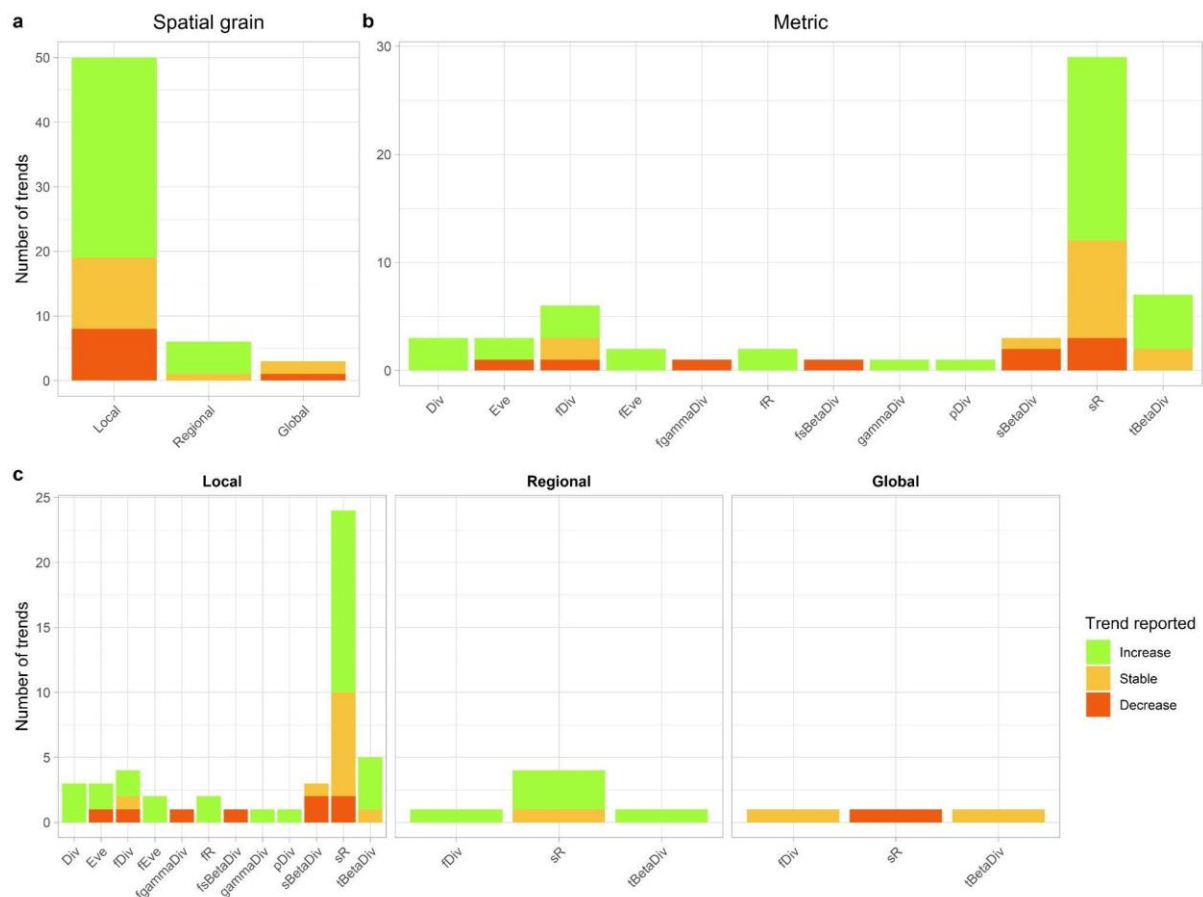
389

***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).*

400

401 **_Supplementary Table 1:_** _table containing the notes about the trends and articles used in this_

402 _literature review. Abbreviations: BBS = Breeding Bird Survey, species richness (sR),_

403 _functional richness (fR), evenness (Eve), functional evenness (fEve), diversity (Div), functional_

404 _diversity (fDiv), temporal beta-diversity (tBetaDiv), spatial beta-diversity (sBetaDiv),_

405 _functional spatial beta-diversity (fsBetaDiv), gamma-diversity (gammaDiv), functional_

406 _Gamma-diversity (fgammaDiv), phylogenetic diversity (pDiv)._

Reference	Metric	Spatial grain (Km²)	Note
Barnagaud *et al.* (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 *et al.* (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 *et al.* (2012)	Div	Local	British BBS. Metric = Simpson. They predict the metric using a GAM with spatial resolution of 1 Km². 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 *et al.* 2012
	fDiv	Local	

	fDiv	Regional	
	fDiv	Global	Data from Szabo *et al.* 2012
	tBetaDiv	Local	
	tBetaDiv	Regional	
	tBetaDiv	Global	Data from Szabo *et al.* 2012
Pilotto *et al.* (2020)	Div	Local	Metric = Simpson
	sR	Local	
	tBetaDiv	Local	
Ram *et al.* (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 *et al.* (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 *et al.* (2016)	Div	Local	North American BBS. Metric = Shannon. The metric is meaned over each road. Area of the road = 50*(pi*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*(pi*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*(pi*400\^2) with 50 census point per road and a census radius of 400m.
Van Turnhout *et al.* (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 *et al.* (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 *et al.* (2020)	sR	Local	Change in number of species between EBBA1 (1972-1995) and EBBA2 (2013-2017), grid cell = 50*50 Km
Monnet *et al.* (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*0.2^2) and Gamma-diversity at the site scale
	sBetaDiv	Local	
	fsBetaDiv	Local	
	gammaDiv	Local	
	fgammaDiv	Local	
Spasov *et al.* (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"
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 = 10x(pi x 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%; χ2 test, P = 0.007)."
La Sorte *et al.* (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 *et al.* (2012)	sR	Local	New York State Breeding Bird Atlas
Dornelas *et al.* (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 *et al.* (2020)	sBetaDiv	Local	Sørensen score

Blowes *et al.* (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 *et al.* (2015)	sR	Regional	North American BBS, spatial grain of 5x5°
	sR	Local	
Petchey *et al.* (2007)	sR	Local	Summer (breeding) distribution of the British avifauna, 2298 grid cells of 10*10 Km. "Species richness [...] from [...] (mean ± 1 SD = 80·6 ± 13·1) in Atlas 1 and from [...] (80·0 ± 15·2) in Atlas 2. "
	fDiv	Local	"FD ranged from [...](mean ± 1 SD = 0·58 ± 0·08) in Atlas 1 and from [...] (mean ± 1 SD = 0·59 ± 0·09) in Atlas 2"

407

References

Adler, P. B., & Lauenroth, W. K. (2003). The power of time: Spatiotemporal scaling of species diversity. *Ecology Letters*, *6*(8), 749–756. https://doi.org/10.1046/j.1461-0248.2003.00497.x

Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman, D. M., Rassweiler, A., & Rusak, J. A. (2005). Evidence for a General Species–Time–Area Relationship. *Ecology*, *86*(8), 2032–2039. https://doi.org/10.1890/05-0067

Alroy, J. (2015). Current extinction rates of reptiles and amphibians. *Proceedings of the National Academy of Sciences*, *112*(42), 13003–13008. https://doi.org/10.1073/pnas.1508681112

Arrhenius, O. (1921). Species and Area. *Journal of Ecology*, *9*(1), 95–99. https://doi.org/10.2307/2255763

420 Barnagaud, J.-Y., Gaüzère, P., Zuckerberg, B., Princé, K., & Svenning, J.-C. (2017). Temporal

421 changes in bird functional diversity across the United States. *Oecologia*, *185*(4), 737–

422 748. https://doi.org/10.1007/s00442-017-3967-4

423 Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B.,

424 Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E.

425 A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336),

426 51–57. https://doi.org/10.1038/nature09678

427 Bejček, V. & Stastný. (2016). Velké ptačí mapování. *Vesmír*. https://vesmir.cz/cz/on-line-

428 clanky/2016/04/velke-ptaci-mapovani.html

429 Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F.,

430 Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler,

431 D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L. M.,

432 … Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial

433 assemblages. *Science*, *366*(6463), 339–345. https://doi.org/10.1126/science.aaw1620

434 Bowler, D., & Böhning-Gaese, K. (2017). Improving the community-temperature index as a

435 climate change indicator. *PLOS ONE*, *12*(9), e0184275.

436 https://doi.org/10.1371/journal.pone.0184275

437 Cardinale, B. J., Gonzalez, A., Allington, G. R. H., & Loreau, M. (2018). Is local biodiversity

438 declining or not? A summary of the debate over analysis of species richness time trends.

439 *Biological Conservation*, *219*, 175–183. https://doi.org/10.1016/j.biocon.2017.12.021

440 Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of

441 biological annihilation and the sixth mass extinction. *Proceedings of the National*

442 *Academy of Sciences*, *117*(24), 13596–13602.

443 https://doi.org/10.1073/pnas.1922686117

444   Chase, J. M., McGill, B. J., Thompson, P. L., Antão, L. H., Bates, A. E., Blowes, S. A.,

445   Dornelas, M., Gonzalez, A., Magurran, A. E., Supp, S. R., Winter, M., Bjorkman, A.

446   D., Bruelheide, H., Byrnes, J. E. K., Cabral, J. S., Elahi, R., Gomez, C., Guzman, H.

447   M., Isbell, F., … O'Connor, M. (2019). Species richness change across spatial scales.

448   *Oikos*, *128*(8), 1079–1091. https://doi.org/10.1111/oik.05968

449   Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward

450   a global functional homogenization? *Frontiers in Ecology and the Environment*, *9*(4),

451   222–228. https://doi.org/10.1890/080216

452   Cowie, R. H., Bouchet, P., & Fontaine, B. (2022). The Sixth Mass Extinction: Fact, fiction or

453   speculation? *Biological Reviews*, *n/a*(n/a). https://doi.org/10.1111/brv.12816

454   Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. (2012). Rise

455   of the generalists: Evidence for climate driven homogenization in avian communities.

456   *Global Ecology and Biogeography*, *21*(5), 568–578. https://doi.org/10.1111/j.1466-

457   8238.2011.00693.x

458   Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic

459   homogenization of bird communities in disturbed landscapes. *Global Ecology and*

460   *Biogeography*, *17*(2), 252–261. https://doi.org/10.1111/j.1466-8238.2007.00364.x

461   Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A.

462   E. (2014). Assemblage Time Series Reveal Biodiversity Change but Not Systematic

463   Loss. *Science*, *344*(6181), 296–299. https://doi.org/10.1126/science.1248484

464   Doxa, A., Bas, Y., Paracchini, M. L., Pointereau, P., Terres, J.-M., & Jiguet, F. (2010). Low-

465   intensity agriculture increases farmland bird abundances in France. *Journal of Applied*

466   *Ecology*, *47*(6), 1348–1356. https://doi.org/10.1111/j.1365-2664.2010.01869.x

467   Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S., Fortin, M.-J.,

468   Jakomulska, A., Miriti, M., & Rosenberg, M. S. (2002). A balanced view of scale in

469   spatial statistical analysis. *Ecography*, *25*(5), 626–640. https://doi.org/10.1034/j.1600-

470   0587.2002.250510.x

471 Eglington, S. M., & Pearce-Higgins, J. W. (2012). Disentangling the Relative Importance of

472   Changes in Climate and Land-Use Intensity in Driving Recent Bird Population Trends.

473   *PLoS ONE*, *7*(3), e30407. https://doi.org/10.1371/journal.pone.0030407

474 Finderup Nielsen, T., Sand- Jensen, K., Dornelas, M., & Bruun, H. H. (2019). More is less:

475   Net gain in species richness, but biotic homogenization over 140 years. *Ecology Letters*,

476   *22*(10), 1650–1657. https://doi.org/10.1111/ele.13361

477 Foote, M. (1994). Temporal variation in extinction risk and temporal scaling of extinction

478   metrics. *Paleobiology*, *20*(4), 424–444. https://doi.org/10.1017/S0094837300012914

479 Fraixedas, S., Lindén, A., Piha, M., Cabeza, M., Gregory, R., & Lehikoinen, A. (2020). A state

480   of the art review on birds as indicators of biodiversity: Advances, challenges, and future

481   directions.   *Ecological   Indicators*,   *118*,   106728.

482   https://doi.org/10.1016/j.ecolind.2020.106728

483 Fricke, E. C., Ordonez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation

484   on   plants'   capacity   to   track   climate   change.   *Science*.

485   https://doi.org/10.1126/science.abk3510

486 García-Navas, V., Sattler, T., Schmid, H., & Ozgul, A. (2020). Temporal homogenization of

487   functional and beta diversity in bird communities of the Swiss Alps. *Diversity and*

488   *Distributions*, *26*(8), 900–911. https://doi.org/10.1111/ddi.13076

489 Gonzalez, A., Cardinale, B. J., Allington, G. R. H., Byrnes, J., Arthur Endsley, K., Brown, D.

490   G., Hooper, D. U., Isbell, F., O'Connor, M. I., & Loreau, M. (2016). Estimating local

491   biodiversity change: A critique of papers claiming no net loss of local diversity.

492   *Ecology*, *97*(8), 1949–1960. https://doi.org/10.1890/15-1759.1

493   Gregory, R. D., & Strien, A. van. (2010). Wild bird indicators: Using composite population

494   trends of birds as measures of environmental health. *Ornithological Science*, *9*(1), 3–

495   22. https://doi.org/10.2326/osj.9.3

496   Gregory, R. D., Vorisek, P., Strien, A. V., Meyling, A. W. G., Jiguet, F., Fornasari, L., Reif, J.,

497   Chylarecki, P., & Burfield, I. J. (2007). Population trends of widespread woodland birds

498   in Europe. *Ibis*, *149*(s2), 78–97. https://doi.org/10.1111/j.1474-919X.2007.00698.x

499   Grinnell, J. (1922). The Role of the "Accidental." *The Auk*, *39*(3), 373–380.

500   https://doi.org/10.2307/4073434

501   Hagemeyer, W., & Blair, M. (1997). *EBCC Atlas of European Breeding Birds*.

502   https://doi.org/10.15468/adtfvf

503   Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences.

504   *Ecology*, *54*(2), 427–432. https://doi.org/10.2307/1934352

505   Jarzyna, M. A., & Jetz, W. (2017). A near half-century of temporal change in different facets

506   of avian diversity. *Global Change Biology*, *23*(8), 2999–3011.

507   https://doi.org/10.1111/gcb.13571

508   Jarzyna, M. A., & Jetz, W. (2018). Taxonomic and functional diversity change is scale

509   dependent. *Nature Communications*, *9*(1), 2565. https://doi.org/10.1038/s41467-018-

510   04889-z

511   Jiguet, F., Devictor, V., Julliard, R., & Couvet, D. (2012). French citizens monitoring ordinary

512   birds provide tools for conservation and ecological sciences. *Acta Oecologica*, *44*, 58–

513   66. https://doi.org/10.1016/j.actao.2011.05.003

514   Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B.,

515   Karthäuser, J., Kunz, F., Mitschke, A., Schwarz, J., & Sudfeldt, C. (2021). Population

516   trends of common breeding birds in Germany 1990–2018. *Journal of Ornithology*,

517   *162*(1), 1–15. https://doi.org/10.1007/s10336-020-01830-4

Keil, P., Biesmeijer, J. C., Barendregt, A., Reemer, M., & Kunin, W. E. (2011). Biodiversity change is scale-dependent: An example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography*, *34*(3), 392–401. https://doi.org/10.1111/j.1600-0587.2010.06554.x

Keil, P., Pereira, H. M., Cabral, J. S., Chase, J. M., May, F., Martins, I. S., & Winter, M. (2018). Spatial scaling of extinction rates: Theory and data reveal nonlinearity and a major upscaling and downscaling challenge. *Global Ecology and Biogeography*, *27*(1), 2–13. https://doi.org/10.1111/geb.12669

Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M. V., Bauer, H.-G., & Foppen, R. P. B. (2020). *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Lynx Edicions. https://www.ebba2.info/results/

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, *72*(3), 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

La Sorte, F. A. (2006). Geographical expansion and increased prevalence of common species in avian assemblages: Implications for large-scale patterns of species richness. *Journal of Biogeography*, *33*(7), 1183–1191. https://doi.org/10.1111/j.1365-2699.2006.01480.x

La Sorte, F. A., & Boecklen, W. J. (2005). Changes in the diversity structure of avian assemblages in North America. *Global Ecology and Biogeography*, *14*(4), 367–378. https://doi.org/10.1111/j.1466-822X.2005.00160.x

La Sorte, F. A., Lee, T. M., Wilman, H., & Jetz, W. (2009). Disparities between observed and predicted impacts of climate change on winter bird assemblages. *Proceedings of the*

Royal Society B: Biological Sciences, *276*(1670), 3167–3174. https://doi.org/10.1098/rspb.2009.0162

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*, *73*(6), 1943–1967. https://doi.org/10.2307/1941447

Ma, Z., Zuckerberg, B., Porter, W. F., & Zhang, L. (2012). Use of localized descriptive statistics for exploring the spatial pattern changes of bird species richness at multiple scales. *Applied Geography*, *32*(2), 185–194. https://doi.org/10.1016/j.apgeog.2011.05.005

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, *30*(2), 104–113. https://doi.org/10.1016/j.tree.2014.11.006

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Meyer, C., Kreft, H., Guralnick, R., & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nature Communications*, *6*(1), 8221. https://doi.org/10.1038/ncomms9221

Monnet, A.-C., Jiguet, F., Meynard, C. N., Mouillot, D., Mouquet, N., Thuiller, W., & Devictor, V. (2014). Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Global Ecology and Biogeography*, *23*(7), 780–788. https://doi.org/10.1111/geb.12179

566 Mouquet, N., Devictor, V., Meynard, C. N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P.,

567   Dalecky, A., Fontaine, C., Gravel, D., Hardy, O. J., Jabot, F., Lavergne, S., Leibold,

568   M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A. S. L., …

569   Thuiller, W. (2012). Ecophylogenetics: Advances and perspectives. *Biological*

570   *Reviews*, *87*(4), 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

571 Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global Biodiversity Change: The Bad,

572   the Good, and the Unknown. *Annual Review of Environment and Resources*, *37*(1), 25–

573   50. https://doi.org/10.1146/annurev-environ-042911-093511

574 Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity

575   and no redundancy in British avian assemblages. *Journal of Animal Ecology*, *76*(5),

576   977–985. https://doi.org/10.1111/j.1365-2656.2007.01271.x

577 Pilotto, F., Kühn, I., Adrian, R., Alber, R., Alignier, A., Andrews, C., Bäck, J., Barbaro, L.,

578   Beaumont, D., Beenaerts, N., Benham, S., Boukal, D. S., Bretagnolle, V., Camatti, E.,

579   Canullo, R., Cardoso, P. G., Ens, B. J., Everaert, G., Evtimova, V., … Haase, P. (2020).

580   Meta-analysis of multidecadal biodiversity trends in Europe. *Nature Communications*,

581   *11*(1), 3486. https://doi.org/10.1038/s41467-020-17171-y

582 Preston, F. W. (1960). Time and Space and the Variation of Species. *Ecology*, *41*(4), 611–627.

583   https://doi.org/10.2307/1931793

584 Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness

585   patterns.   *Ecology   Letters*,   *8*(2),   224–239.   https://doi.org/10.1111/j.1461-

586   0248.2004.00701.x

587 Ram, D., Axelsson, A.-L., Green, M., Smith, H. G., & Lindström, Å. (2017). What drives

588   current population trends in forest birds – forest quantity, quality or climate? A large-

589   scale analysis from northern Europe. *Forest Ecology and Management*, *385*, 177–188.

590   https://doi.org/10.1016/j.foreco.2016.11.013

591   Reif, J., Prylová, K., Šizling, A. L., Vermouzek, Z., Šťastný, K., & Bejček, V. (2013). Changes

592   in bird community composition in the Czech Republic from 1982 to 2004: Increasing

593   biotic homogenization, impacts of warming climate, but no trend in species richness.

594   *Journal of Ornithology*, *154*(2), 359–370. https://doi.org/10.1007/s10336-012-0900-9

595   Rigal, S., Devictor, V., Gaüzère, P., Kéfi, S., Forsman, J. T., Kajanus, M. H., Mönkkönen, M.,

596   & Dakos, V. (2021). Biotic homogenisation in bird communities leads to large-scale

597   changes in species associations. *Oikos*, *n/a*(n/a). https://doi.org/10.1111/oik.08756

598   Sauer, J. R., Link, W. A., Fallon, J. E., Pardieck, K. L., & Ziolkowski, D. J., Jr. (2013). The

599   North American Breeding Bird Survey 1966–2011: Summary Analysis and Species

600   Accounts. *North American Fauna*, *79 (79)*, 1–32. https://doi.org/10.3996/nafa.79.0001

601   Sauer, J. R., Pardieck, K. L., Ziolkowski, D. J., Jr., Smith, A. C., Hudson, M.-A. R., Rodriguez,

602   V., Berlanga, H., Niven, D. K., & Link, W. A. (2017). The first 50 years of the North

603   American   Breeding   Bird   Survey.   *The   Condor*,   *119*(3),   576–593.

604   https://doi.org/10.1650/CONDOR-17-83.1

605   Schipper, A. M., Belmaker, J., Miranda, M. D. de, Navarro, L. M., Böhning-Gaese, K.,

606   Costello, M. J., Dornelas, M., Foppen, R., Hortal, J., Huijbregts, M. A. J., Martín-

607   López, B., Pettorelli, N., Queiroz, C., Rossberg, A. G., Santini, L., Schiffers, K.,

608   Steinmann, Z. J. N., Visconti, P., Rondinini, C., & Pereira, H. M. (2016). Contrasting

609   changes in the abundance and diversity of North American bird assemblages from 1971

610   to   2010.   *Global   Change   Biology*,   *22*(12),   3948–3959.

611   https://doi.org/10.1111/gcb.13292

612   CBD, 2006. Global Biodiversity Outlook 2 Secretariat of the Convention on Biological

613   Diversity, Montreal, 81 + vii pages

614   Semper-Pascual, A., Macchi, L., Sabatini, F. M., Decarre, J., Baumann, M., Blendinger, P. G.,

615   Gómez-Valencia, B., Mastrangelo, M. E., & Kuemmerle, T. (2018). Mapping

extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. *Journal of Applied Ecology*, *55*(3), 1218–1229. https://doi.org/10.1111/1365-2664.13074

Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Simpson, E. H. (1949). Measurement of Diversity. *Nature*, *163*(4148), 688–688. https://doi.org/10.1038/163688a0

Spasov, S., Hristov, I., Eaton, M., & Nikolov, S. C. (2017). Population Trends of Common Birds in Bulgaria: Is Their Status Improving after the EU Accession? *Acta Zoologica Bulgarica*, *69*(1), 10.

Storch, D., Marquet, P., & Brown, J. (Eds.). (2007). *Scaling Biodiversity*. Cambridge University Press. https://doi.org/10.1017/CBO9780511814938

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, *142*(10), 2282–2292. https://doi.org/10.1016/j.biocon.2009.05.006

Tingley, M. W., & Beissinger, S. R. (2013). Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology*, *94*(3), 598–609. https://doi.org/10.1890/12-0928.1

Vaidyanathan, G. (2021). The world's species are playing musical chairs: How will it end? *Nature*, *596*(7870), 22–25. https://doi.org/10.1038/d41586-021-02088-3

Van Turnhout, C. A. M., Foppen, R. P. B., Leuven, R. S. E. W., Siepel, H., & Esselink, H. (2007). Scale-dependent homogenization: Changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation*, *134*(4), 505–516. https://doi.org/10.1016/j.biocon.2006.09.011

640 Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beausejour, R., Brown, C. D.,

641   De Frenne, P., Verheyen, K., & Wipf, S. (2013). Global meta-analysis reveals no net

642   change in local-scale plant biodiversity over time. *Proceedings of the National*

643   *Academy*   *of*   *Sciences*,   *110*(48),   19456–19459.

644   https://doi.org/10.1073/pnas.1312779110

645 Warkentin, I. G., & Reed, J. M. (1999). Effects of habitat type and degradation on avian species

646   richness in great basin riparian habitats. *The Great Basin Naturalist*, *59*(3), 205–212.

647   https://www.jstor.org/stable/41713111

648 Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and

649   Community Ecology. *Annual Review of Ecology and Systematics*, *33*(1), 475–505.

650   https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

651 White, E. P. (2004). Two-phase species–time relationships in North American land birds.

652   *Ecology Letters*, *7*(4), 329–336. https://doi.org/10.1111/j.1461-0248.2004.00581.x

653 Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California.

654   *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

655 Whittaker, R. H. (1972). Evolution and Measurement of Species Diversity. *TAXON*, *21*(2–3),

656   213–251. https://doi.org/10.2307/1218190

657 Wretenberg, J., Pärt, T., & Berg, Å. (2010). Changes in local species richness of farmland birds

658   in relation to land-use changes and landscape structure. *Biological Conservation*,

659   *143*(2), 375–381. https://doi.org/10.1016/j.biocon.2009.11.001

660

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: