Scaling Biodiversity Trends

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# 1 Introduction

Our life quality is intrinsically linked to the state of ecosystems that we live in. Ecosystem services to humans ([Díaz et al. 2018](#ref-diaz_assessing_2018)), as well as their inner functioning, involve a spectrum of mechanisms including nutrient cycles or ecosystem stability ([Pereira, Navarro, and Martins 2012](#ref-pereira_global_2012)). Some of these functions, such as seed dispersal, control of pests, scavenging, or pollination, depend on birds and their diversity. Birds also have a significant esthetical value, with most countries having numerous iconic/charismatic species of conservation interest (<https://www.iucnredlist.org/>). Moreover, given their ability to quickly move between locations, their presence is also a good indicator for ecosystem health. Unfortunately, anthropogenic stressors like habitat loss, over-exploitation, pollution, or introduction of invasive species are a threat to birds and their biodiversity ([Donald, Green, and Heath 2001](#ref-donald_agricultural_2001); [Frédéric Jiguet et al. 2010](#ref-jiguet_population_2010)), with concerns that they could face a sixth mass extinction ([Barnosky et al. 2011](#ref-barnosky_has_2011)).

We have reasons to suspect that the global alteration of biodiversity due to anthropogenic stressors is unprecedented, and political goals have been declared in order to limit it (*e.g.* [Convention on Biological Diversity and Centre 2006](#X9d9998b2a18109011522d670b75978c5cd32ed0)). However, data-driven basis for these policies remains a challenge, mainly due to severe gaps and biases in empirical biodiversity data ([Meyer et al. 2015](#ref-meyer_global_2015)). To complicate matters further, current scientific literature has shown that temporal trends of local biodiversity can be opposite to trends at larger spatial scales (*e.g.* [Chase et al. 2019](#ref-chase_species_2019); [Keil et al. 2011](#ref-keil_biodiversity_2011), [2018](#ref-keil_spatial_2018)). Thus, we should expect changes in biodiversity to be far more complex than a simple global decrease. Finally, biodiversity can be measured by many metrics, and these can differ in their temporal trends ([McGill et al. 2015](#ref-mcgill_fifteen_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](#ref-blowes_geography_2019); [Dornelas et al. 2013](#ref-dornelas_quantifying_2013); [Vaidyanathan 2021](#ref-vaidyanathan_worlds_2021)).

Particularly the issue of scale is critical ([Levin 1992](#ref-levin_problem_1992)). Since [Arrhenius](#ref-arrhenius_species_1921) ([1921](#ref-arrhenius_species_1921)) and [Grinnell](#ref-grinnell_role_1922) ([1922](#ref-grinnell_role_1922)), we know that spatial and temporal scaling of biodiversity affects macroecological patterns. Even though particularly the static spatial scaling of biodiversity has been of great interest (*e.g.* [Storch, Marquet, and Brown 2007](#ref-storch_scaling_2007)), wonders persist about how temporal trends of biodiversity are linked to the spatial and temporal scales. In other words: does the observed biodiversity trends differ if 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 metric of biodiversity is assessed. One should be careful to not confuse spatial grain with the spatial extent of a study, *i.e.* the total area of the ecosystem which is observed or analyzed ([Dungan et al. 2002](#ref-dungan_balanced_2002)). The same terminology is applied for the temporal scale: temporal grain refers to the temporal unit of the measured biodiversity ([Adler and Lauenroth 2003](#ref-adler_power_2003)). Compared to spatial scaling, the temporal scaling is much less studied, which is mostly due to the lack of temporally replicated data. This review will, in part, show how the definition of temporal grain has still no consensus in the scientific literature.

To investigate the link between spatio-temporal grains and trends of biodiversity, birds are a relevant taxon. Thanks to the many ornithological monitoring initiatives and surveys, we have a large number of high-quality time series on bird populations ([Bejček and Stastný 2016](#ref-bejcek_velke_2016); [Kamp et al. 2021](#ref-kamp_population_2021); [Sauer et al. 2013](#ref-sauer_north_2013)…). This is because birds are easy to observe, easy to identify and thus many volunteers are motivated to participate on citizen-science projects ([Sullivan et al. 2009](#ref-sullivan_ebird_2009), <https://www.inaturalist.org/>) or to conduct standardized sampling (*e.g.* most of the breeding bird surveys are conducted by volunteers).

Given birds importance to assess ecosystem health, several standardized metrics have been created to assess their populations. [Fraixedas et al.](#ref-fraixedas_state_2020) ([2020](#ref-fraixedas_state_2020)) reviewed this wide spectrum of bird biodiversity indicators, without considerations to their link with spatial and temporal grains. Here, we review articles assessing the temporal trends of avian biodiversity, with species focus on the variety of metrics that they use, and spatial and temporal scales at which temporal trends have been assessed. We consider the most common macroecological indicators used to assess biodiversity at the community level and higher, such as diversity indexes (*e.g.* species richness, functional diversity…) or population indexes ([McGill et al. 2015](#ref-mcgill_fifteen_2015)). We highlight a lack of consensus about specifications and definitions of both spatial and temporal grains (respectively) of trends, we demonstrate that the scaling of trends is seldom considered, leading to confused messages about overall trends. Moreover, we show that studies lack spatial replication that would make reported trends robust and general. We believe that this review will improve the current knowledge on spatio-temporal scaling of trends biodiversity, and thus be useful for the ornithological field community and the conservation decision making.

# 2 Metrics and indicators

Studying biodiversity can be confusing as it exists many ways to measure it. The different metrics and indicators have diverse features, and one should consider which one is the most suited to its study. First, the type of biodiversity studied must be chosen (*e.g.* taxonomic, functional, phylogenetic diversity). Only then, one must choose the metric(s).

**Classical metrics.** Measures of static biodiversity are commonly used such as local species richness ( diversity), regional richness ( diversity, [Whittaker 1960](#ref-whittaker_vegetation_1960)), by indices that consider abundances (*e.g.* [Shannon 1948](#ref-shannon_mathematical_1948); [Simpson 1949](#ref-simpson_measurement_1949)), or by Hill numbers ([M. O. Hill 1973](#ref-hill_diversity_1973)). On the other hand, change of species composition in space and time can be expressed as ([Whittaker 1972](#ref-whittaker_evolution_1972)), or by pairwise dissimilarity among locations or time periods ([Koleff, Gaston, and Lennon 2003](#ref-koleff_measuring_2003)). All these metrics assess species-based metrics, *i.e.* they use the species as a unit. However, it has also been shown that functional and phylogenetic diversity can provide supplementary information on the community structure and its dynamic (*e.g.* [McGill et al. 2006](#ref-mcgill_rebuilding_2006); [Mouquet et al. 2012](#ref-mouquet_ecophylogenetics_2012); [Webb et al. 2002](#ref-webb_phylogenies_2002)).

**Composite and multi-species indicators.** The composite indicators are made to summarize several ecosystem information into one informative index. The most known ones are the Red List Index ([Stuart H. M. Butchart et al. 2007](#ref-butchart_improvements_2007); [Stuart H. M. Butchart et al. 2004](#ref-butchart_measuring_2004); [S. h. m. Butchart et al. 2005](#ref-butchart_using_2005)), the Living Planet Index ([Loh et al. 2005](#ref-loh_living_2005)) or the Biodiversity Change Index ([Normander et al. 2012](#ref-normander_indicator_2012)). In these composite indicators, metrics of great interest are the abundance-based or population-based metrics. As individuals react to stress or disturbances, the population trends reflect ecosystems health. The population decline that a species undergoes before going locally extinct is not captured by species-based metrics. Thus, population trends are usually efficient at assessing finer biodiversity declines. Although overall abundance is often hard to assess, the abundance of few indicator species can reflect processes in an entire ecosystem ([Richard D. Gregory et al. 2005](#ref-gregory_developing_2005)). This has led to a proposition of a family of metrics called the multi-species indicators (MSI, [Landres, Verner, and Thomas 1988](#ref-landres_ecological_1988)). Examples are the farmland bird indicator, woodland bird indicator or Wildland Bird Indicator which summarizes the latter two ([Richard D. Gregory et al. 1999](#ref-gregory_generation_1999); [Richard D. Gregory and Strien 2010](#ref-gregory_wild_2010)). These metrics compute the geometric mean of abundance of few key species over time.

# 3 Quantitative literature review

For this review, we focused on articles assessing temporal trends of the most common metrics of avian biodiversity and specifying spatial and temporal scales, which are at the same time consistent with broader macroecological scaling and theory ([Storch, Marquet, and Brown 2007](#ref-storch_scaling_2007); [Storch and Gaston 2004](#ref-storch_untangling_2004)), and thus can be compared across studies and scales. Namely, these were: *Species richness, Functional richness, Abundance, Evenness, SR, Diversity, Temporal beta-diversity, Spatial beta-diversity, Functional diversity, Functional beta-diversity, Gamma-diversity, Functional Gamma-diversity*. Some of these classes contain several different indexes. For instance, the class *Diversity*, which contains either the Shannon or Simpson index, or the class *Abundance*, which contains various multi-species indicators (see Table 9.1 for the notes).

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. With these replications, the trend reported at one spatial grain is more reliable and general. However, at larger spatial grains (*i.e.* national, continental or global scales), spatial replicates are rare. Thus, we considered these trends from a single location only when based on a large set of observations from smaller spatial scales.

We used the “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.

For each query, the title and abstract of these articles were reviewed. In addition, we scanned the references of these articles for other potentially relevant literature. When the temporal trend was explicitly reported (either in a graph or text), we extracted from the material and methods 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), the spatial extent (*i.e.* the entire area on which the study applies), the temporal extent and the beginning and ending years of the study as well as the general trend of the metric (Table 3.1). The temporal lag of the trend, *i.e.* the time-span between two time steps, was also reported ([Dungan et al. 2002](#ref-dungan_balanced_2002)). We discretized spatial grain sizes discretized into four levels: local , regional , national when an entire country was considered, and global at the worldwide scale (grain = extent = the entire Earth’s mainland).

Concerning the trend assessment, different papers contain the or directly specify the significance of a trend of a metric. However, some papers give only graphical representations of the trend. Moreover, the final trend retained (*i.e.* either *Increase*, *Stable* or *Decrease*) doesn’t reflect all the fluctuations of the metric through time but rather the difference between the starting and ending points.

We found 31 references in which authors were both determining the temporal trend of a metric and explicitly defining the spatial grain size. However, only 19 of them used spatial replicates and were thus relevant for this study (Table 3.1).

Table 3.1: Trends of different metrics of biodiversity at various spatial and temporal scales

| Reference | Metric | Spatial grain (Km²) | Spatial extent (Km²) | Temporal lag (year) | Temporal grain (hour) | Temporal extent (year) | Years | Country | Trend |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Barnagaud et al. (2017) | Functional richness | Local | 9,834,000 | 1.0 | 2.50 | 41 | 1970-2011 | USA | Increase |
|  | Functional evenness | Local | 9,834,000 | 1.0 | 2.50 | 41 | 1970-2011 | USA | Increase |
|  | Abundance | Local | 9,834,000 | 1.0 | 2.50 | 41 | 1970-2011 | USA | Decrease |
|  | Evenness | Local | 9,834,000 | 1.0 | 2.50 | 41 | 1970-2011 | USA | Increase |
|  | SR | Local | 9,834,000 | 1.0 | 2.50 | 41 | 1970-2011 | USA | Increase |
| Bowler et al. (2021) | Abundance | National | 520,475 |  |  | 27 | 1990-2016 | Czech Rep., Switzerland, Denmark, Germany | Stable |
| Chase et al. (2019) | SR | Local | 2,800,000 | 5.0 | 2.50 | 30 | 1982–2011 | USA, Canada | Stable |
|  | SR | Regional | 2,800,000 | 5.0 | 2.50 | 30 | 1982–2011 | USA, Canada | Stable |
|  | SR | Regional | 2,800,000 | 5.0 | 2.50 | 30 | 1982–2011 | USA, Canada | Stable |
|  | SR | Local | 2,800,000 | 5.0 | 2.50 | 30 | 1982–2011 | USA, Canada | Increase |
|  | SR | Local | 2,800,000 | 5.0 | 2.50 | 30 | 1982–2011 | USA, Canada | Increase |
| Chiron et al. (2013) | Abundance | Regional | 643,801 | 1.0 | 1.70 | 14 | 2007-2020 | France | Decrease |
|  | Abundance | Regional | 643,801 | 1.0 | 1.70 | 14 | 2007-2020 | France | Decrease |
|  | Abundance | Regional | 643,801 | 1.0 | 1.70 | 14 | 2007-2020 | France | Decrease |
|  | Abundance | Regional | 643,801 | 1.0 | 1.70 | 14 | 2007-2020 | France | Decrease |
| Davey et al. (2012) | Diversity | Local | 242,495 | 1.0 |  | 13 | 1994-2006 | UK | Increase |
|  | Evenness | Local | 242,495 | 1.0 |  | 13 | 1994-2006 | UK | Increase |
|  | SR | Local | 242,495 | 1.0 |  | 13 | 1994-2006 | UK | Increase |
| Harrison et al. (2014) | Abundance | Local | 200,000 | 1.0 |  | 18 | 1994-2011 | Great Britain, UK | Increase |
|  | Abundance | Local | 200,000 | 1.0 |  | 18 | 1994-2011 | Great Britain, UK | Stable |
|  | Abundance | Local | 200,000 | 1.0 |  | 18 | 1994-2011 | Great Britain, UK | Stable |
| Harrison et al. (2016) | Abundance | Local | 242,495 | 0.5 |  | 20 | 1994-2013 | UK | Increase |
|  | Abundance | Local | 242,495 | 0.5 |  | 20 | 1994-2013 | UK | Stable |
|  | Abundance | Local | 242,495 | 0.5 |  | 20 | 1994-2013 | UK | Stable |
| Jarzyna and Jetz (2018) | SR | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | SR | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | SR | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | SR | National | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | SR | Global | 148,940,000 |  |  | 45 | 1969-2013 | World | Decrease |
|  | Temporal beta-diversity | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | Temporal beta-diversity | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | Temporal beta-diversity | Regional | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | Temporal beta-diversity | National | 9,834,000 |  | 2.50 | 45 | 1969-2013 | USA | Increase |
|  | Temporal beta-diversity | Global | 148,940,000 |  |  | 45 | 1969-2013 | World | Stable |
| Pilotto et al. (2020) | Abundance | Local | 10,180,000 |  |  |  | NA | Europe | Stable |
|  | Diversity | Local | 10,180,000 |  |  |  | NA | Europe | Increase |
|  | SR | Local | 10,180,000 |  |  |  | NA | Europe | Increase |
|  | Temporal beta-diversity | Local | 10,180,000 |  |  |  | NA | Europe | Stable |
| Ram et al. (2017) | Abundance | Local | 350,000 | 1.0 |  | 18 | 1998-2015 | Sweden | Increase |
|  | SR | Regional | 350,000 | 1.0 |  | 18 | 1998-2015 | Sweden | Increase |
| Reif et al. (2013) | Spatial beta-diversity | Local | 79,000 | 1.0 | 3.40 | 23 | 1982-2004 | Czech Rep. | Stable |
|  | SR | Local | 79,000 | 1.0 | 3.40 | 23 | 1982-2004 | Czech Rep. | Stable |
|  | SR | National | 79,000 | 1.0 | 3.40 | 23 | 1982-2004 | Czech Rep. | Stable |
| Schipper et al. (2016) | Abundance | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
|  | Diversity | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
|  | Diversity | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
|  | Functional diversity | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Decrease |
|  | Functional evenness | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
|  | Functional richness | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
|  | SR | Local | 24,710,000 | 5.0 | 2.50 | 40 | 1971-2010 | Canada, USA, Mexico | Increase |
| Sorte and Boecklen (2005) | Abundance | Local | 9,834,000 | 1.0 | 2.50 | 36 | 1968-2003 | USA | Decrease |
|  | Evenness | Local | 9,834,000 | 1.0 | 2.50 | 36 | 1968-2003 | USA | Decrease |
|  | SR | Local | 9,834,000 | 1.0 | 2.50 | 36 | 1968-2003 | USA | Increase |
| Van Turnhout et al. (2007) | SR | Regional | 41,543 | 4.0 |  | 28 | 1973-2000 | Netherlands | Increase |
|  | SR | Local | 41,543 | 4.0 |  | 28 | 1973-2000 | Netherlands | Increase |
|  | SR | National | 41,543 | 4.0 |  | 28 | 1973-2000 | Netherlands | Increase |
| Wretenberg, Pärt, and Berg (2010) | SR | Local | 1,800 | 1.0 |  | 11 | 1994-2004 | Sweden | Decrease |
| Inger et al. (2015) | Abundance | National | 10,180,000 | 1.0 |  | 22 | 1980-2001 | Europe | Decrease |
| Donald, Green, and Heath (2001) | Abundance | National | 10,180,000 |  |  | 21 | 1970-1990 | Europe | Decrease |
| Keller et al. (2020) | SR | Regional | 11,075,000 | 30.0 |  | 45 | 1972-2017 | Europe | Increase |
| Monnet et al. (2014) | SR | Local | 551,695 | 1.0 | 0.09 | 22 | 1989-2012 | France | Increase |
|  | Spatial beta-diversity | Local | 551,695 | 1.0 | 0.09 | 22 | 1989-2012 | France | Decrease |
|  | Functional beta-diversity | Local | 551,695 | 1.0 | 0.09 | 22 | 1989-2012 | France | Decrease |
|  | Gamma-diversity | Regional | 551,695 | 1.0 | 0.09 | 22 | 1989-2012 | France | Increase |
|  | Functional Gamma-diversity | Regional | 551,695 | 1.0 | 0.09 | 22 | 1989-2012 | France | Decrease |

# 4 Spatial scale and temporal trends

**Overall trends.** The median spatial extent of the 19 articles is 5.51695^{5} , with the smallest area of 1800 and the greatest representing the global emerged surface (*i.e.* 1.4894^{8} ). These articles reported 20 combinations of scales and metrics. Overall, there were 15 *Decrease*, 36 *Increase* and 14 *Stable* reliable trends (*i.e.* spatially replicated) across the literature. In our case, local scales are more represented than the others and the number of articles decreases with the increasing spatial scale (Figure 4.1). This is expected, as the spatial replications get more demanding in organization and resources as the grain size enlarges. The *Increase* of the metrics seems to be dominating at smaller scales. On the other hand, the proportion of *Decrease* is larger at regional scales than at local scales. At the global scale, no *Increase* was found.

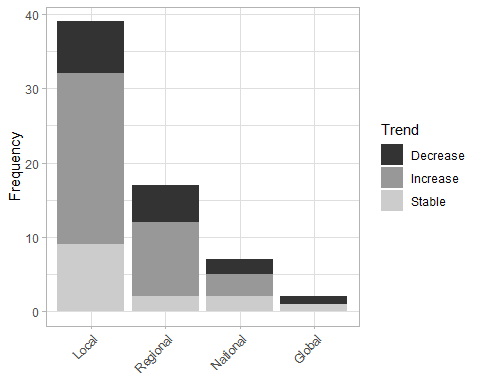


Figure 4.1: Proportion of Increase, Decrease or Stable trends for each spatial scale

**Trends by metric.** Among the different metrics, most of the examined studies deal with temporal trends of species richness and abundance (Figure 4.2). The use of the other metrics was rare. The less common trend of abundance is *Increase*, whilst *Decrease* and *Stability* are almost as common. In general, all the diversity indexes (*i.e.* taxonomic and functional richness, evenness and diversity) are mostly found increasing.

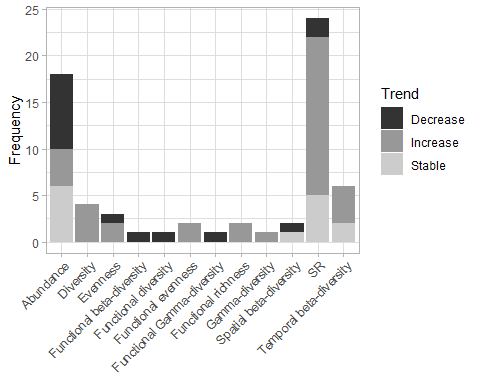


Figure 4.2: Proportion of Increase, Decrease or Stable trends for each of the metric

**Trends by spatial grain.** In the studies that we reviewed, at *local grains*, taxonomic and functional richness mostly increased (Figure 4.3). Evenness indices, *i.e.* taxonomic and functional evenness, were also mostly increasing. Concerning the abundance indices, we found mostly no trend, or increases. At *regional grains*, abundance metrics always decreased, temporal -diversity always increased, and species richness mostly increased. At *national and global grains*, studies analyzing multiple locations are rare, and most trends reported here for these two spatial scales are not replicated. Exceptions are [Bowler et al.](#ref-bowler_geographic_2021) ([2021](#ref-bowler_geographic_2021)) and [Donald, Green, and Heath](#ref-donald_agricultural_2001) ([2001](#ref-donald_agricultural_2001)). The former showed negative trends in abundance indices for Denmark and Germany, and positive trends for Switzerland and Czech Republic, *i.e.* no clear direction of the trend (here referred as *Stable*). However, for [Donald, Green, and Heath](#ref-donald_agricultural_2001) ([2001](#ref-donald_agricultural_2001)), trends of mean population size were computed for 30 European countries and the majority was negative. Global trends only come from [Jarzyna and Jetz](#ref-jarzyna_taxonomic_2018) ([2018](#ref-jarzyna_taxonomic_2018)), who report a global decrease of species richness and a stable temporal -diversity.

Concerning species richness, we can see that the decrease is global, but that this decrease is rare at finer spatial scales. In fact, we observe more often increases, confirming the high perturbations that biodiversity is undergoing ([Dornelas et al. 2014](#ref-dornelas_assemblage_2014); [Vaidyanathan 2021](#ref-vaidyanathan_worlds_2021)). This analysis goes along with the temporal -diversity which is always observed either stable or increasing. Indeed, increasing turnover through time is a sign of an increasing perturbation of the ecosystems.

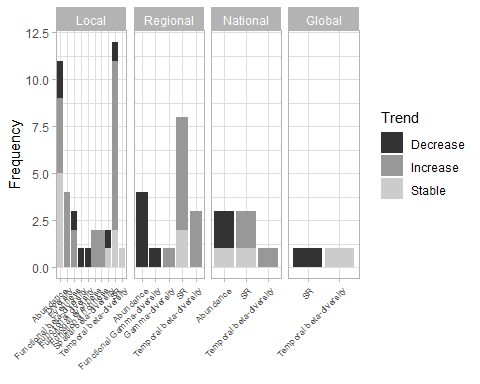


Figure 4.3: Proportion of Increase, Decrease or Stable trends for each metric. Each panel represent one spatial scale

# 5 Temporal scale and temporal trends

The oldest study started in 1968 and the median duration is 23 years, with a minimum time-span of 11 years and a maximum of 45. As the studies use mainly the same datasets (generally from Breeding Bird Surveys), only three different temporal grains were found (2.5, 1.7, 3.4, 0.09 hours).

We found longest temporal lags in studies with large spatial extent (Figure 5.1). This is because data used in the selected article are mainly structured data, *i.e.* data following a well established sampling plan. This type of survey is sparse since it needs resources and organization. Increasing the spatial extent thus increases both the temporal extent and the time to sample all the sampling units. This explains this positive correlation between spatial extent and temporal lag. This limitation can be overcome thanks to citizen science data, which have increasingly been used (*e.g.* [Bowler et al. 2021](#ref-bowler_geographic_2021); [Isaac et al. 2020](#ref-isaac_data_2020), [2014](#ref-isaac_statistics_2014)). The opportunistic nature of these data allows for short census times, even over a large area. These data, with high temporal grain resolution for large spatial scales, could in future be used to explore in more details the temporal scaling of biodiversity trends, especially for low temporal lags.

Determination of the temporal grain in the studies in Table 1 was complicated. Usually, the temporal grain of the sampling was specified, but sometimes with inaccuracies (*e.g.* *“The sites are visited twice a year (April to early May and late May to June), during which volunteers walk two parallel 1-km-long transect lines”*, [Harrison et al. 2014](#ref-harrison_assessing_2014)). Moreover, the temporal grain of the sampling doesn’t represent the temporal grain of the metric. For instance, some metrics are summed over a certain area (*e.g.* summing the species richness over an atlas square, such as in [Van Turnhout et al. 2007](#ref-van_turnhout_scale-dependent_2007)) and sometimes over both an area and a period of time (*e.g.* [Chase et al. 2019](#ref-chase_species_2019)). Analogically, the temporal grain should have also been summed over all the sampling censuses englobed in this area/time span, but this was never specified. Moreover, when the trend is computed, usually the lag (*i.e.* the time between two computation of the metric, [Dungan et al. 2002](#ref-dungan_balanced_2002)) is clearly specified, but the temporal grain is not. For the cases where the metric of biodiversity is determined out of model (*e.g.* [Harrison et al. 2014](#ref-harrison_assessing_2014)), it is easier to assess the temporal grain, since predictions are based on the sampling temporal grain. Thus, for these cases, the final temporal grain was most of the time explicitly given.

In short, temporal grain of the sampling plan is sometimes specified. However, when the metric and its trend are computed, temporal grains are occasionally merged. In this case, the value wasn’t specified.

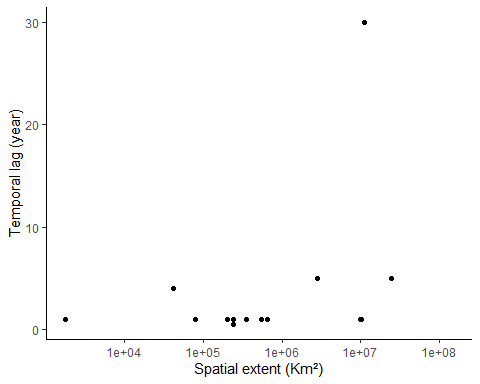


Figure 5.1: Relationship between temporal lag and spatial extent

# 6 Lack of spatial replication

Articles reporting trends from more than a single location are uncommon (we only found 19 of them), either due to a lack of data, or because the trend was assessed for the spatial extent of the data. For instance, the US Breeding Bird Survey (*e.g.* [Kamp et al. 2021](#ref-kamp_population_2021); [Sauer et al. 2013](#ref-sauer_north_2013)) follows a standardized sampling plan with spatial replications (*i.e.* multiple census plots). However, not all the trends reported for the BBS are summarized at their specific grain, and were sometimes aggregated over their respective national scales, reducing spatial replication. For instance, the common method encountered to assess population abundance trends (*i.e.* abundance indexes) is to learn a predictive model from the data, predict the target feature (*i.e.* abundance) and then compute the metric and its trend from the output of the model at the national spatial extent (*e.g.* [Doxa et al. 2010](#ref-doxa_low-intensity_2010); [Eglington and Pearce-Higgins 2012](#ref-eglington_disentangling_2012); [Frédéric Jiguet et al. 2012](#ref-jiguet_french_2012); [Frederic Jiguet et al. 2005](#ref-jiguet_modeling_2005); [Sauer et al. 2017](#ref-sauer_first_2017)). These analyses are practically useful for conservation, and are common ([Fraixedas et al. 2020](#ref-fraixedas_state_2020)): they give inform about ecosystem health at national extent, and are thus useful for decision-makers.

Another common type of study uses the *space-for-time substitution* ([Walker et al. 2010](#ref-walker_use_2010)) to assess the trend of a metric (one of the best example is [J. K. Hill and Hamer 2004](#ref-hill_determining_2004)). This method consists in considering sampling in different places as representing a temporal trend. One could think that using theses studies could increase significantly the spatial replicates. However, the space-for-time substitution is mainly used to assess the impact of a processes (*e.g.* before/after logging, before/after urbanization etc) meaning that the trend computed is highly biased, which we try to avoid for our topic.

Even fewer articles computed the trends of metrics with spatial replicates across more than one spatial grain. So far this was the case for only [Chase et al.](#ref-chase_species_2019) ([2019](#ref-chase_species_2019)) and [Jarzyna and Jetz](#ref-jarzyna_taxonomic_2018) ([2018](#ref-jarzyna_taxonomic_2018)). Importantly, [Jarzyna et al.](#ref-jarzyna_spatial_2015) ([2015](#ref-jarzyna_spatial_2015)) did spatial replicates of temporal change community metrics (*i.e.* temporal dissimilarity, temporal turnover, extinction and colonization) at several spatial scales. However, the temporal trend of these metrics weren’t considered and are therefore not reported in Table 3.1.

# 7 Metric heterogeneity

In contrast to macroecology, applied ecology has offered multiparametric indices that aim to reflect multiple components of an ecosystem, the so-called *composite indicators*. For birds, these indices have been widely used (see review by [Fraixedas et al. 2020](#ref-fraixedas_state_2020)) and have proven to be effective for conservation policies. Some of these metrics either reduce (*e.g.* MSI which use a limited number of species) or increase (*e.g.* the Biodiversity change index which takes into account habitat features) the complexity of the metric. In order to study the link between biodiversity trends and spatio-temporal grains, we need to use the common macroecology metrics, such as species richness, diversity or abundance indices.

# 8 Future directions

A striking but expected result (see [Meyer et al. 2015](#ref-meyer_global_2015)), was the lack of studies form outside of the high-income global North. Out of 17 papers, 5 were located in North America and 12 in Europe. This is gap was also reported by [Fraixedas et al.](#ref-fraixedas_state_2020) ([2020](#ref-fraixedas_state_2020)). Yet, biodiversity dynamic in Europe may not be representative of global dynamic, and studies of biodiversity trends at several spatio-temporal scales are needed outside of Europe. These studies are needed on local grains, as well as at the spatial grain of continents (*e.g.* see [Alroy 2015](#ref-alroy_current_2015) for amphibians and reptiles).

The spatial grain of biodiversity trends is critical, yet this has not always been specified in the articles. One should consider the way a metric was computed, *e.g.* if it was summed, modeled, averaged over the sampling units. According to the method, the spatial grain can vary from the sampling unit to the sampling extent. Given the importance of spatial scaling of biodiversity patterns ([Storch and Gaston 2004](#ref-storch_untangling_2004)), one has to expect that it will be also important for its dynamic (*e.g.* [Chase et al. 2019](#ref-chase_species_2019)). We thus argue that authors should pay extra attention to specifying the spatial grain for every metric of biodiversity trends.

The importance of temporal scaling of biodiversity is known since [Grinnell](#ref-grinnell_role_1922) ([1922](#ref-grinnell_role_1922)), who used California birds to demonstrate the species-time relationship, which has since been proven to be common with other bird populations ([White 2004](#ref-white_two-phase_2004)). Thus, as spatial grain, temporal grain is known to be important to explicit. However, there is no consensus on the definition of temporal grain and is thus specified in various ways: sometimes very precised (*e.g.* time of each census point, as in [Schipper et al. 2016](#ref-schipper_contrasting_2016)) and sometimes without explicit information (*e.g.* [Wretenberg, Pärt, and Berg 2010](#ref-wretenberg_changes_2010): *“All sites were visited six times in 1994 and five times in 2004 during early morning”*). As for the spatial grain, the temporal grain can vary according to the way the metric is assessed (*e.g.* if the data is aggregated over an area and/or a period of time). However, when temporal trend of a metric is assessed, the temporal lag of the trend is often only specified (*i.e.* time-span between and ). In other words, when computing a trend, one usually uses a single point either every day, every month or every year. However, this temporal lag doesn’t represent the temporal grain that interests us. If one wants to study the temporal scaling of biodiversity trends, a clear assessment of the temporal grain needs to be done systematically.

# 9 Conclusion

Reviewing the scientific literature on avian biodiversity trends give us a glimpse of what needs to be done to better understand the scaling of biodiversity dynamic. The first challenge is to find a common definition of spatial and temporal grain when computing the trend. We showed that these definitions vary according to the way the metric is computed. Whilst spatial grain of a trend is intuitively important for biodiversity, temporal grain is less often considered, especially when the temporal trend is computed. Finally, as birds are one of the most data-rich taxa of vertebrates, the challenges highlighted here will be even more severe for other groups.

# Supplementary materials

Table 9.1: Supplementary informations about each article

| Reference | Spatial grain (Km²) | Temporal grain (hour) | Trend | Note |
| --- | --- | --- | --- | --- |
| Barnagaud et al. (2017) | Local | 2.5 | Increase | 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\*400\^2) with a road of 40 Km with point counts spaced by 0.8 Km and a census radius of 400m |
|  | Local | 2.5 | Increase |  |
|  | Local | 2.5 | Decrease |  |
|  | Local | 2.5 | Increase |  |
|  | Local | 2.5 | Increase |  |
| Bowler et al. (2021) | National | NA | Stable | Metric = MSI, as many and as intense increase (i.e. Czech Rep. and Switzerland) than decrease (i.e. Germany and Denmarl) |
| Chase et al. (2019) | Local | 2.5 | Stable | American BBS, but they binned by 5 years and by quadrats, so the temporal grain of the metric should be different than from the sampling plan |
|  | Regional | 2.5 | Stable |  |
|  | Regional | 2.5 | Stable |  |
|  | Local | 2.5 | Increase |  |
|  | Local | 2.5 | Increase |  |
| Chiron et al. (2013) | Regional | 1.7 | Decrease | Concerning the spatial scale, predictions are made using the spatial unit of 4 Km² and the FBI is computed for each region of France, then meanned. French BBS, twice 10 point counts of 5 minutes. Prediction with baseline scenario |
|  | Regional | 1.7 | Decrease | FBI prediction with CAP greening cenario |
|  | Regional | 1.7 | Decrease | FBI prediction with No Pillar I scenario |
|  | Regional | 1.7 | Decrease | FBI prediction with biofuel scenario |
| Davey et al. (2012) | Local | NA | Increase | Britain 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 |
|  | Local | NA | Increase |  |
|  | Local | NA | Increase |  |
| Harrison et al. (2014) | Local | NA | Increase | Britain BBS, "The sites are visited twice a year (April to early May and late May to June), during which volunteers walk two parallel 1-km-long transect lines". To assess the metric, they use a GAM to predict the abundance over the entire area of interest (spatial resolution = 1 Km²) and then compute the geometric mean of species abundance = Multi Species Index from the prediction. Data used to learn the GAM are sampled from plots of 1 Km². Farmland communities. |
|  | Local | NA | Stable | Farmland communities, GoF ($\lambda$ = −1) = weighted towards the rare species |
|  | Local | NA | Stable | Farmland communities, GoF ( $\lambda$ = −2) weighted towards the common species |
| Harrison et al. (2016) | Local | NA | Increase | Britain BBS, "In each year, the sites are visited twice (once in April to early May and once in late May to June), during which volunteers walk two parallel 1-km transect lines". Geomteric mean of species abundance, they predict the abundance with resolution of 1 Km² and then computed the metric for each 10000 Km² cell across Great Britain. |
|  | Local | NA | Stable | GoF ( $\lambda$ = −1) = toward rare species" The goodness-of-fit-based measure of biodiversity suggests that both rare and common species made gains through much of Britain in the first half of the time period, and losses in the second half.", Visited twice a year / Increase first half and second second halfGoF ( $\lambda$ = −1) |
|  | Local | NA | Stable | GoF ( $\lambda$ = −2) = toward common species " The goodness-of-fit-based measure of biodiversity suggests that both rare and common species made gains through much of Britain in the first half of the time period, and losses in the second half.", Visited twice a year / Increase first half and second second half |
| Jarzyna and Jetz (2018) | Regional | 2.5 | Increase | American BBS |
|  | Regional | 2.5 | Increase |  |
|  | Regional | 2.5 | Increase |  |
|  | National | 2.5 | Increase |  |
|  | Global | NA | Decrease |  |
|  | Regional | 2.5 | Increase |  |
|  | Regional | 2.5 | Increase |  |
|  | Regional | 2.5 | Increase |  |
|  | National | 2.5 | Increase |  |
|  | Global | NA | Stable |  |
| Pilotto et al. (2020) | Local | NA | Stable | "Analyses of the trends in local biodiversity over large spatial scales" |
|  | Local | NA | Increase | Metric = Simpson |
|  | Local | NA | Increase |  |
|  | Local | NA | Stable |  |
| Ram et al. (2017) | Local | NA | Increase | 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". MSI for forest species, road of 8 Km with no limitations so assumed 200m |
|  | Regional | NA | Increase | 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) | Local | 3.4 | Stable | Jaccard index (pairwise comparisions between transects), first increase then decrease. BBMP = JPSP, "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" |
|  | Local | 3.4 | Stable | JPSP data, transect scale, "species richness on both the local and national scales did not show any clear temporal trend" |
|  | National | 3.4 | Stable | JPSP data, national scale, "species richness on both the local and national scales did not show any clear temporal trend" |
| Schipper et al. (2016) | Local | 2.5 | Increase | American BBS. The metric (i.e. geometric mean) 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 |
|  | Local | 2.5 | Increase | Metric = Shannon |
|  | Local | 2.5 | Increase | Metric = Simpson |
|  | Local | 2.5 | Decrease |  |
|  | Local | 2.5 | Increase |  |
|  | Local | 2.5 | Increase |  |
|  | Local | 2.5 | Increase |  |
| Sorte and Boecklen (2005) | Local | 2.5 | Decrease | American BBS |
|  | Local | 2.5 | Decrease | Metric = evenness |
|  | Local | 2.5 | Increase | 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) | Regional | NA | Increase | Dutch BBS, " two census periods". For each region, the trend is computed using the mean number of species per atlas square |
|  | Local | NA | Increase | Mainly increase of SR but the proportion of negative trend were higher than for the regional scale |
|  | National | NA | Increase | National scale |
| Wretenberg, Pärt, and Berg (2010) | Local | NA | Decrease | "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. " |
| Inger et al. (2015) | National | NA | Decrease |  |
| Donald, Green, and Heath (2001) | National | NA | Decrease | The metric is referred as "Mean population" and the trend is estimated for each european country |
| Keller et al. (2020) | Regional | NA | Increase | Change in number of species between EBBA1 (1972-1995) and EBBA2 (2013-2017) |
| Monnet et al. (2014) | Local | 0.09 | Increase | 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 |
|  | Local | 0.09 | Decrease | 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 |
|  | Local | 0.09 | Decrease |  |
|  | Regional | 0.09 | Increase |  |
|  | Regional | 0.09 | Decrease |  |

# References

Adler, Peter B., and William K. Lauenroth. 2003. “The Power of Time: Spatiotemporal Scaling of Species Diversity.” *Ecology Letters* 6 (8): 749–56. https://doi.org/<https://doi.org/10.1046/j.1461-0248.2003.00497.x>.

Alroy, John. 2015. “Current Extinction Rates of Reptiles and Amphibians.” *Proceedings of the National Academy of Sciences* 112 (42): 13003–8. <https://doi.org/10.1073/pnas.1508681112>.

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

Barnagaud, Jean-Yves, Pierre Gaüzère, Benjamin Zuckerberg, Karine Princé, and Jens-Christian Svenning. 2017. “Temporal Changes in Bird Functional Diversity Across the United States.” *Oecologia* 185 (4): 737–48. <https://doi.org/10.1007/s00442-017-3967-4>.

Barnosky, Anthony D., Nicholas Matzke, Susumu Tomiya, Guinevere O. U. Wogan, Brian Swartz, Tiago B. Quental, Charles Marshall, et al. 2011. “Has the Earth’s Sixth Mass Extinction Already Arrived?” *Nature* 471 (7336): 51–57. <https://doi.org/10.1038/nature09678>.

Bejček, Vladimír, and Stastný. 2016. “Velké Ptačí Mapování.” *Vesmír*. <https://vesmir.cz/cz/on-line-clanky/2016/04/velke-ptaci-mapovani.html>.

Blowes, Shane A., Sarah R. Supp, Laura H. Antão, Amanda Bates, Helge Bruelheide, Jonathan M. Chase, Faye Moyes, et al. 2019. “The Geography of Biodiversity Change in Marine and Terrestrial Assemblages.” *Science* 366 (6463): 339–45. <https://doi.org/10.1126/science.aaw1620>.

Bowler, Diana, Raja Lorena Richter, Daniel Eskildsen, Johannes Kamp, Charlotte M. Moshøj, Jiří Reif, Nicolas Strebel, Sven Trautmann, and Petr Voříšek. 2021. “Geographic Variation in the Population Trends of Common Breeding Birds Across Central Europe.” *Basic and Applied Ecology* 56 (November): 72–84. <https://doi.org/10.1016/j.baae.2021.07.004>.

Butchart, S.h.m, A.j Stattersfield, J Baillie, L.a Bennun, S.n Stuart, H.r Akçakaya, C Hilton-Taylor, and G.m Mace. 2005. “Using Red List Indices to Measure Progress Towards the 2010 Target and Beyond.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 360 (1454): 255–68. <https://doi.org/10.1098/rstb.2004.1583>.

Butchart, Stuart H. M., H. Resit Akçakaya, Janice Chanson, Jonathan E. M. Baillie, Ben Collen, Suhel Quader, Will R. Turner, Rajan Amin, Simon N. Stuart, and Craig Hilton-Taylor. 2007. “Improvements to the Red List Index.” *PLOS ONE* 2 (1): e140. <https://doi.org/10.1371/journal.pone.0000140>.

Butchart, Stuart H. M, Alison J Stattersfield, Leon A Bennun, Sue M Shutes, H. Resit Akçakaya, Jonathan E. M Baillie, Simon N Stuart, Craig Hilton-Taylor, and Georgina M Mace. 2004. “Measuring Global Trends in the Status of Biodiversity: Red List Indices for Birds.” Edited by Walt V. Reid. *PLoS Biology* 2 (12): e383. <https://doi.org/10.1371/journal.pbio.0020383>.

Chase, Jonathan M., Brian J. McGill, Patrick L. Thompson, Laura H. Antão, Amanda E. Bates, Shane A. Blowes, Maria Dornelas, et al. 2019. “Species Richness Change Across Spatial Scales.” *Oikos* 128 (8): 1079–91. <https://doi.org/10.1111/oik.05968>.

Chiron, François, Karine Princé, Maria Luisa Paracchini, Claudia Bulgheroni, and Frédéric Jiguet. 2013. “Forecasting the Potential Impacts of CAP-Associated Land Use Changes on Farmland Birds at the National Level.” *Agriculture, Ecosystems & Environment* 176 (August): 17–23. <https://doi.org/10.1016/j.agee.2013.05.018>.

Convention on Biological Diversity, Secretariat of the, and UNEP World Conservation Monitoring Centre, eds. 2006. *Global Biodiversity Outlook 2*. Montreal: Secretariat of the Convention on Biological Diversity.

Davey, Catherine M., Dan E. Chamberlain, Stuart E. Newson, David G. Noble, and Alison Johnston. 2012. “Rise of the Generalists: Evidence for Climate Driven Homogenization in Avian Communities.” *Global Ecology and Biogeography* 21 (5): 568–78. <https://doi.org/10.1111/j.1466-8238.2011.00693.x>.

Díaz, Sandra, Unai Pascual, Marie Stenseke, Berta Martín-López, Robert T. Watson, Zsolt Molnár, Rosemary Hill, et al. 2018. “Assessing Nature’s Contributions to People.” *Science* 359 (6373): 270–72. <https://doi.org/10.1126/science.aap8826>.

Donald, P. F., R. E. Green, and M. F. Heath. 2001. “Agricultural Intensification and the Collapse of Europe’s Farmland Bird Populations.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268 (1462): 25–29. <https://doi.org/10.1098/rspb.2000.1325>.

Dornelas, Maria, Nicholas J. Gotelli, Brian McGill, Hideyasu Shimadzu, Faye Moyes, Caya Sievers, and Anne E. Magurran. 2014. “Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss.” *Science* 344 (6181): 296–99. <https://doi.org/10.1126/science.1248484>.

Dornelas, Maria, Anne E. Magurran, Stephen T. Buckland, Anne Chao, Robin L. Chazdon, Robert K. Colwell, Tom Curtis, et al. 2013. “Quantifying Temporal Change in Biodiversity: Challenges and Opportunities.” *Proceedings of the Royal Society B: Biological Sciences* 280 (1750): 20121931. <https://doi.org/10.1098/rspb.2012.1931>.

Doxa, Aggeliki, Yves Bas, Maria Luisa Paracchini, Philippe Pointereau, Jean-Michel Terres, and Frédéric Jiguet. 2010. “Low-Intensity Agriculture Increases Farmland Bird Abundances in France.” *Journal of Applied Ecology* 47 (6): 1348–56. <https://doi.org/10.1111/j.1365-2664.2010.01869.x>.

Dungan, J. L., J. N. Perry, M. R. T. Dale, P. Legendre, S. Citron-Pousty, M.-J. Fortin, A. Jakomulska, M. Miriti, and M. S. Rosenberg. 2002. “A Balanced View of Scale in Spatial Statistical Analysis.” *Ecography* 25 (5): 626–40. <https://doi.org/10.1034/j.1600-0587.2002.250510.x>.

Eglington, Sarah M., and James W. Pearce-Higgins. 2012. “Disentangling the Relative Importance of Changes in Climate and Land-Use Intensity in Driving Recent Bird Population Trends.” Edited by Raphaël Arlettaz. *PLoS ONE* 7 (3): e30407. <https://doi.org/10.1371/journal.pone.0030407>.

Fraixedas, Sara, Andreas Lindén, Markus Piha, Mar Cabeza, Richard Gregory, and Aleksi Lehikoinen. 2020. “A State of the Art Review on Birds as Indicators of Biodiversity: Advances, Challenges, and Future Directions.” *Ecological Indicators* 118 (November): 106728. <https://doi.org/10.1016/j.ecolind.2020.106728>.

Gregory, Richard D., and Arco van Strien. 2010. “Wild Bird Indicators: Using Composite Population Trends of Birds as Measures of Environmental Health.” *Ornithological Science* 9 (1): 3–22. <https://doi.org/10.2326/osj.9.3>.

Gregory, Richard D, David W Gibbons, Andrew Impey, and John H Marchant. 1999. “Generation of the Headline Indicator of Wild Bird Populations,” 48.

Gregory, Richard D, Arco van Strien, Petr Vorisek, Adriaan W Gmelig Meyling, David G Noble, Ruud P. B Foppen, and David W Gibbons. 2005. “Developing Indicators for European Birds.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 360 (1454): 269–88. <https://doi.org/10.1098/rstb.2004.1602>.

Grinnell, Joseph. 1922. “The Role of the ‘Accidental’.” *The Auk* 39 (3): 373–80. <https://doi.org/10.2307/4073434>.

Harrison, Philip J., Stephen T. Buckland, Yuan Yuan, David A. Elston, Mark J. Brewer, Alison Johnston, and James W. Pearce-Higgins. 2014. “Assessing Trends in Biodiversity over Space and Time Using the Example of British Breeding Birds.” *Journal of Applied Ecology* 51 (6): 1650–60. <https://doi.org/10.1111/1365-2664.12316>.

Harrison, Philip J., Yuan Yuan, Stephen T. Buckland, Cornelia S. Oedekoven, David A. Elston, Mark J. Brewer, Alison Johnston, and James W. Pearce-Higgins. 2016. “Quantifying Turnover in Biodiversity of British Breeding Birds.” *Journal of Applied Ecology* 53 (2): 469–78. <https://doi.org/10.1111/1365-2664.12539>.

Hill, Jane K., and Keith C. Hamer. 2004. “Determining Impacts of Habitat Modification on Diversity of Tropical Forest Fauna: The Importance of Spatial Scale.” *Journal of Applied Ecology* 41 (4): 744–54. <https://doi.org/10.1111/j.0021-8901.2004.00926.x>.

Hill, M. O. 1973. “Diversity and Evenness: A Unifying Notation and Its Consequences.” *Ecology* 54 (2): 427–32. <https://doi.org/10.2307/1934352>.

Inger, Richard, Richard Gregory, James P. Duffy, Iain Stott, Petr Voříšek, and Kevin J. Gaston. 2015. “Common European Birds Are Declining Rapidly While Less Abundant Species’ Numbers Are Rising.” *Ecology Letters* 18 (1): 28–36. <https://doi.org/10.1111/ele.12387>.

Isaac, Nick J. B., Marta A. Jarzyna, Petr Keil, Lea I. Dambly, Philipp H. Boersch-Supan, Ella Browning, Stephen N. Freeman, et al. 2020. “Data Integration for Large-Scale Models of Species Distributions.” *Trends in Ecology & Evolution* 35 (1): 56–67. <https://doi.org/10.1016/j.tree.2019.08.006>.

Isaac, Nick J. B., Arco J. van Strien, Tom A. August, Marnix P. de Zeeuw, and David B. Roy. 2014. “Statistics for Citizen Science: Extracting Signals of Change from Noisy Ecological Data.” *Methods in Ecology and Evolution* 5 (10): 1052–60. <https://doi.org/10.1111/2041-210X.12254>.

Jarzyna, Marta A., and Walter Jetz. 2018. “Taxonomic and Functional Diversity Change Is Scale Dependent.” *Nature Communications* 9 (1): 2565. <https://doi.org/10.1038/s41467-018-04889-z>.

Jarzyna, Marta A., Benjamin Zuckerberg, William F. Porter, Andrew O. Finley, and Brian A. Maurer. 2015. “Spatial Scaling of Temporal Changes in Avian Communities: Scale Dependence of Community Turnover.” *Global Ecology and Biogeography* 24 (11): 1236–48. <https://doi.org/10.1111/geb.12361>.

Jiguet, Frederic, Romain Julliard, Denis Couvet, and Aurelie Petiau. 2005. “Modeling Spatial Trends in Estimated Species Richness Using Breeding Bird Survey Data: A Valuable Tool in Biodiversity Assessment.” *Biodiversity and Conservation* 14 (13): 3305–24. <https://doi.org/10.1007/s10531-004-0448-y>.

Jiguet, Frédéric, Vincent Devictor, Romain Julliard, and Denis Couvet. 2012. “French Citizens Monitoring Ordinary Birds Provide Tools for Conservation and Ecological Sciences.” *Acta Oecologica*, Sino-French Cooperation on Biodiversity and Natural Resource Management, 44 (October): 58–66. <https://doi.org/10.1016/j.actao.2011.05.003>.

Jiguet, Frédéric, Richard D. Gregory, Vincent Devictor, Rhys E. Green, Petr Voříšek, Arco Van Strien, and Denis Couvet. 2010. “Population Trends of European Common Birds Are Predicted by Characteristics of Their Climatic Niche.” *Global Change Biology* 16 (2): 497–505. <https://doi.org/10.1111/j.1365-2486.2009.01963.x>.

Kamp, Johannes, Claudia Frank, Sven Trautmann, Malte Busch, Rainer Dröschmeister, Martin Flade, Bettina Gerlach, et al. 2021. “Population Trends of Common Breeding Birds in Germany 1990–2018.” *Journal of Ornithology* 162 (1): 1–15. <https://doi.org/10.1007/s10336-020-01830-4>.

Keil, Petr, Jacobus C. Biesmeijer, Aat Barendregt, Menno Reemer, and William E. Kunin. 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, Petr, Henrique M. Pereira, Juliano S. Cabral, Jonathan M. Chase, Felix May, Inês S. Martins, and Marten Winter. 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., S. Herrando, P. Voříšek, M. Franch, M. Kipson, P. Milanesi, D. Martí, et al. 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Lynx Edicions. <https://www.ebba2.info/results/>.

Koleff, Patricia, Kevin J. Gaston, and Jack J. Lennon. 2003. “Measuring Beta Diversity for Presence–Absence Data.” *Journal of Animal Ecology* 72 (3): 367–82. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>.

Landres, Peter B., Jared Verner, and Jack Ward Thomas. 1988. “Ecological Uses of Vertebrate Indicator Species: A Critique.” *Conservation Biology* 2 (4): 316–28. <https://doi.org/10.1111/j.1523-1739.1988.tb00195.x>.

Levin, Simon A. 1992. “The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture.” *Ecology* 73 (6): 1943–67. https://doi.org/<https://doi.org/10.2307/1941447>.

Loh, Jonathan, Rhys E Green, Taylor Ricketts, John Lamoreux, Martin Jenkins, Valerie Kapos, and Jorgen Randers. 2005. “The Living Planet Index: Using Species Population Time Series to Track Trends in Biodiversity.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 360 (1454): 289–95. <https://doi.org/10.1098/rstb.2004.1584>.

McGill, Brian J., Maria Dornelas, Nicholas J. Gotelli, and Anne E. Magurran. 2015. “Fifteen Forms of Biodiversity Trend in the Anthropocene.” *Trends in Ecology & Evolution* 30 (2): 104–13. <https://doi.org/10.1016/j.tree.2014.11.006>.

McGill, Brian J., Brian J. Enquist, Evan Weiher, and Mark Westoby. 2006. “Rebuilding Community Ecology from Functional Traits.” *Trends in Ecology & Evolution* 21 (4): 178–85. <https://doi.org/10.1016/j.tree.2006.02.002>.

Meyer, Carsten, Holger Kreft, Robert Guralnick, and Walter Jetz. 2015. “Global Priorities for an Effective Information Basis of Biodiversity Distributions.” *Nature Communications* 6 (1): 8221. <https://doi.org/10.1038/ncomms9221>.

Monnet, Anne-Christine, Frédéric Jiguet, Christine N. Meynard, David Mouillot, Nicolas Mouquet, Wilfried Thuiller, and Vincent Devictor. 2014. “Asynchrony of Taxonomic, Functional and Phylogenetic Diversity in Birds.” *Global Ecology and Biogeography* 23 (7): 780–88. <https://doi.org/10.1111/geb.12179>.

Mouquet, Nicolas, Vincent Devictor, Christine N. Meynard, Francois Munoz, Louis-Félix Bersier, Jérôme Chave, Pierre Couteron, et al. 2012. “Ecophylogenetics: Advances and Perspectives.” *Biological Reviews* 87 (4): 769–85. <https://doi.org/10.1111/j.1469-185X.2012.00224.x>.

Normander, Bo, Gregor Levin, Ari-Pekka Auvinen, Harald Bratli, Odd Stabbetorp, Marcus Hedblom, Anders Glimskär, and Gudmundur A. Gudmundsson. 2012. “Indicator Framework for Measuring Quantity and Quality of Biodiversity—Exemplified in the Nordic Countries.” *Ecological Indicators* 13 (1): 104–16. <https://doi.org/10.1016/j.ecolind.2011.05.017>.

Pereira, Henrique Miguel, Laetitia Marie Navarro, and Inês Santos Martins. 2012. “Global Biodiversity Change: The Bad, the Good, and the Unknown.” *Annual Review of Environment and Resources* 37 (1): 25–50. <https://doi.org/10.1146/annurev-environ-042911-093511>.

Pilotto, Francesca, Ingolf Kühn, Rita Adrian, Renate Alber, Audrey Alignier, Christopher Andrews, Jaana Bäck, et al. 2020. “Meta-Analysis of Multidecadal Biodiversity Trends in Europe.” *Nature Communications* 11 (1): 3486. <https://doi.org/10.1038/s41467-020-17171-y>.

Ram, Dafne, Anna-Lena Axelsson, Martin Green, Henrik G. Smith, and Åke Lindström. 2017. “What Drives Current Population Trends in Forest Birds – Forest Quantity, Quality or Climate? A Large-Scale Analysis from Northern Europe.” *Forest Ecology and Management* 385 (February): 177–88. <https://doi.org/10.1016/j.foreco.2016.11.013>.

Reif, Jiří, Kristýna Prylová, Arnošt L. Šizling, Zdeněk Vermouzek, Karel Šťastný, and Vladimír Bejček. 2013. “Changes in Bird Community Composition in the Czech Republic from 1982 to 2004: Increasing Biotic Homogenization, Impacts of Warming Climate, but No Trend in Species Richness.” *Journal of Ornithology* 154 (2): 359–70. <https://doi.org/10.1007/s10336-012-0900-9>.

Sauer, John R., William A. Link, Jane E. Fallon, Keith L. Pardieck, and David J. Ziolkowski Jr. 2013. “The North American Breeding Bird Survey 1966–2011: Summary Analysis and Species Accounts.” *North American Fauna*, no. 79 (79) (August): 1–32. <https://doi.org/10.3996/nafa.79.0001>.

Sauer, John R., Keith L. Pardieck, David J. Ziolkowski Jr., Adam C. Smith, Marie-Anne R. Hudson, Vicente Rodriguez, Humberto Berlanga, Daniel K. Niven, and William A. Link. 2017. “The First 50 Years of the North American Breeding Bird Survey.” *The Condor* 119 (3): 576–93. <https://doi.org/10.1650/CONDOR-17-83.1>.

Schipper, Aafke M., Jonathan Belmaker, Murilo Dantas de Miranda, Laetitia M. Navarro, Katrin Böhning-Gaese, Mark J. Costello, Maria Dornelas, et al. 2016. “Contrasting Changes in the Abundance and Diversity of North American Bird Assemblages from 1971 to 2010.” *Global Change Biology* 22 (12): 3948–59. <https://doi.org/10.1111/gcb.13292>.

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): 688–88. <https://doi.org/10.1038/163688a0>.

Sorte, Frank A. La, and William J. Boecklen. 2005. “Changes in the Diversity Structure of Avian Assemblages in North America.” *Global Ecology and Biogeography* 14 (4): 367–78. <https://doi.org/10.1111/j.1466-822X.2005.00160.x>.

Storch, David, and Kevin J. Gaston. 2004. “Untangling Ecological Complexity on Different Scales of Space and Time.” *Basic and Applied Ecology* 5 (5): 389–400. <https://doi.org/10.1016/j.baae.2004.08.001>.

Storch, David, Pablo Marquet, and James Brown, eds. 2007. *Scaling Biodiversity*. Ecological Reviews. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511814938>.

Sullivan, Brian L., Christopher L. Wood, Marshall J. Iliff, Rick E. Bonney, Daniel Fink, and Steve Kelling. 2009. “eBird: A Citizen-Based Bird Observation Network in the Biological Sciences.” *Biological Conservation* 142 (10): 2282–92. <https://doi.org/10.1016/j.biocon.2009.05.006>.

Vaidyanathan, Gayathri. 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, Chris A. M., Ruud P. B. Foppen, Rob S. E. W. Leuven, Henk Siepel, and Hans Esselink. 2007. “Scale-Dependent Homogenization: Changes in Breeding Bird Diversity in the Netherlands over a 25-Year Period.” *Biological Conservation* 134 (4): 505–16. <https://doi.org/10.1016/j.biocon.2006.09.011>.

Walker, Lawrence R., David A. Wardle, Richard D. Bardgett, and Bruce D. Clarkson. 2010. “The Use of Chronosequences in Studies of Ecological Succession and Soil Development.” *Journal of Ecology* 98 (4): 725–36. <https://doi.org/10.1111/j.1365-2745.2010.01664.x>.

Webb, Campbell O., David D. Ackerly, Mark A. McPeek, and Michael J. Donoghue. 2002. “Phylogenies and Community Ecology.” *Annual Review of Ecology and Systematics* 33 (1): 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>.

White, Ethan P. 2004. “Two-Phase Species–Time Relationships in North American Land Birds.” *Ecology Letters* 7 (4): 329–36. https://doi.org/<https://doi.org/10.1111/j.1461-0248.2004.00581.x>.

Whittaker, R. H. 1960. “Vegetation of the Siskiyou Mountains, Oregon and California.” *Ecological Monographs* 30 (3): 279–338. <https://doi.org/10.2307/1943563>.

———. 1972. “Evolution and Measurement of Species Diversity.” *TAXON* 21 (2-3): 213–51. <https://doi.org/10.2307/1218190>.

Wretenberg, Johan, Tomas Pärt, and Åke Berg. 2010. “Changes in Local Species Richness of Farmland Birds in Relation to Land-Use Changes and Landscape Structure.” *Biological Conservation* 143 (2): 375–81. <https://doi.org/10.1016/j.biocon.2009.11.001>.