



# Exploring the data demands and global opportunities for reconstructing morphological responses to climate change

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## Abstract

There is growing evidence that morphological change is a widespread response to the warming climate. The empirical basis for understanding this process has, to date, largely been correlative analyses of morphological time series. However, it is not clear what constitutes sufficient temporal sampling for assessing long-term morphological change. We analyzed two long-term high-quality morphological datasets, one including 33 species of birds collected over 37 years and one including 11 species of mammals collected over 40 years. We find that the number of years of data needed to accurately characterize trends in functional traits varies by trait and taxonomic group. For birds, accurately estimating the trend of morphological changes 95% of the time requires data from a minimum of 14 years for bill length, 19 years for tarsus length, and 20 years for wing length. For mammals, 31 years of hind-foot length data and 36 years of weight data are needed to achieve the same level of accuracy in trend estimates. Using these minimum sampling thresholds, we identify where in the world there are sufficient museum holdings to reconstruct long-term trends in morphology. Museum specimens have a critical benefit that is not available from other long-term data sources: collected, vouchered, specimens can be analyzed in new and standardized ways designed to understand morphological responses to climate change. We find that there are many opportunities to reconstruct morphological change in birds and, to a smaller degree, in mammals using museum specimens though sufficient sampling is not available for the vast majority of the globe. Most of the sites at which there is sufficient sampling are in the Northern Hemisphere and are concentrated in the United States and Europe. Expanding long-term animal capture efforts will be critical to enabling a more holistic understanding of biotic responses to global change in the future.

**Keywords** Morphology · Climate change · Sampling · Functional traits · Museum specimens · Birds · Mammals

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## Introduction

Understanding biotic responses to rapid large-scale environmental change is a critical conservation challenge that affords opportunities to advance our understanding of the environmental determinants of the phenotype. As global temperatures have increased, hypothesized general biotic responses to climate change have emerged. These include consistent shifts in phenology (Cohen et al. 2018), distributional ranges (Parmesan and Yohe 2003; Lenoir et al. 2020), and morphology (Gardner et al. 2011; Ryding et al. 2021). However, the magnitude of the spatiotemporal scale of these processes poses a challenge. Generating datasets that have the spatial, taxonomic, and temporal breadth necessary to characterize these types of large-scale changes, as well as the diversity of data types necessary to speak to potential interactions between shifts in phenology, range, and morphology, exceeds the scope of what is possible for single individuals, research labs, and even most institutions.

To date, the morphological data used to estimate long-term change have come from a variety of sources, including banding efforts (Yom-Tov et al. 2006; Van Buskirk et al. 2010; Jirinec et al. 2021; McQueen et al. 2022, 2024; Youngflesh et al. 2022; Neate-Clegg et al. 2024), live trapping initiatives (Ozgul et al. 2010; Hoy et al. 2018; Archer et al. 2025), and natural history museum specimens (Weeks et al. 2020; Hantak et al. 2021; Dubiner and Meiri 2022; Theriot et al. 2023; Ryding et al. 2024; Dias et al. 2025). All of these methods, which enable measuring individuals (as opposed to occurrence records, for example), have been critical sources of data and all have distinct advantages and disadvantages (e.g., standardized spatiotemporal sampling in many banding efforts as opposed to museum specimens, which tend to have been collected irregularly across space and time). However, of these, museum specimens are uniquely well-suited to contribute to a more holistic understanding of morphological responses to global change at the scale and density necessary to understand this global phenomenon. Specimens, along with their metadata, have the potential to provide multi-dimensional data that can be used to link axes of adaptation. For example, by comparing trends in specimen morphology with the timing of their collection during migration, Zimova et al. (2021) were able to test whether observed shifts in the flight apparatus could be explained by selection for advancing migratory phenology. These same specimens could be analyzed using isotopic approaches (Hobson et al. 2004) or genomic approaches (Ruegg et al. 2014) to integrate range shift dynamics, providing a richer assessment of the inter-relationships among changes in phenology, morphology, and range.

While museum specimens have the potential to be powerful sources of data on biotic responses to global change, they are likely to be limited by a history of uneven collection efforts across space and time. For much of their history, most natural history museums have aimed to discover, describe, and understand the relationships and origins of the world's biodiversity (National Academies of Sciences Engineering and Medicine 2021). While monitoring biotic responses to global change has not tended to be a primary focus of past collecting efforts, the sheer magnitude of these collections, which include hundreds of millions of specimens collected over centuries, gives them the potential to be potent sources of long-term datasets for a range of topics for which they were not intended to be used (e.g., environmental pollution; DuBay et al. 2025). Recent changes in how specimens are collected have implications for understanding long-term changes, and shifts in the sources of specimens have the potential to introduce biases into datasets derived from specimens collected over long time periods. For example, birds are increasingly collected in

urban areas, largely due to increased efforts to monitor and prepare specimens from repeated window collisions – which may not be representative samples of the broader population—and wildlife rehabilitation centers, while mammals continue to be collected in more rural and presumably less disturbed habitats (Shultz et al. 2021). To understand the potential that museum holdings have to quantify contemporary shifts in morphology, it is critical to understand the sampling effort required and identify regions across the globe where these sampling requirements are met.

Understanding the sampling requirements for quantifying morphological responses to climate change is challenging. For example, over the past four decades, birds in the mid-western United States have become smaller in a number of morphological traits, but these shifts have been non-linear due to temporal variation in temperature (Weeks et al. 2020). Additionally, the rates of change across these species and traits have been variable in their consistency, strength, uniformity, and linearity (Weeks et al. 2020). Such complexities, which are likely common in nature, influence sampling requirements and make it difficult to simply use power tests to determine the necessary sampling to reconstruct changes in morphology through time. One way to address this challenge is to subsample existing datasets to understand the impacts of variation in data availability on estimates of morphological trends.

Once the sampling requirements are known, we can identify regions worldwide where existing resources enable opportunities to quantify morphological change. Furthermore, identifying these regions will allow us to better understand the spatial biases that exist in available specimen-based datasets. Analogous biases in other data sources likely impact—and constrain—our ability to understand other biotic responses to climate change (e.g., range shifts; Parker et al. 2024). Understanding the biases in global specimen time series that are long enough to reconstruct morphological responses to climate change can both provide context for interpreting the growing number of specimen-based studies on morphological responses to climate change and can inform prioritization of future collection of long-term specimen time series.

Here, we first take advantage of two long-term morphological datasets in birds (Weeks et al. 2020) and mammals (Ernest et al. 2020) to characterize how many years of sampling are necessary to recover the same trends in morphology that occur across the full datasets. We do this for five traits: wing length, tarsus length, and bill length for birds, and mass and hind-foot length for mammals. We then use the minimum sampling thresholds we discover to identify locations across the world with sufficient sampling of specimens through time in museum collections to reconstruct long-term morphological change.

## Methods

### Estimating minimum sampling requirements for long-term trend recovery

Using two long-term datasets of bird and mammal morphology, we estimated: 1) how many years of data are necessary to consistently recover the long-term trend in morphology that occurred across the full dataset, and 2) how the error in long-term trend estimates declines with additional years of data. For birds, we used a dataset derived from specimens salvaged from window collisions in Chicago, IL, USA. This dataset spans nearly four decades, start-

ing in the late 1970s, and consists of 70,716 specimens from 52 species of North American migratory birds that were collected after migrating birds collided with buildings during their spring and fall migrations (Weeks et al. 2020). For these birds, prior to preparation as museum specimens, tarsus length, bill length, and the length of the relaxed wing chord (the distance from the carpal joint to the tip of the longest unflattened primary feather) were measured, and sex and age (hatch year, HY, or after hatch year, AHY) were recorded (Weeks et al. 2020). We only considered species within this dataset with a mean of at least 10 individuals per year across the duration of the dataset.

For mammals, we retrieved data from a long-term experimental study of rodents, plants, and ants in the Chihuahuan desert near Portal, AZ, USA (Ernest et al. 2020). We used the data on all rodents that were live-trapped within the approximately 20-ha study area, with age, sex, weight, and hind-foot length measured on > 70,000 individuals representing more than 40 species of mammals from 1977 to 2024 (version 5.108.0 of the dataset; <https://doi.org/10.5281/zenodo.13988418>). All animals were given an individual ID and we removed recaptures by only using the first observation of any individual animal. As with the bird dataset, we only considered species with a mean of at least 10 individuals per year across the duration of the dataset.

To understand the effect of time series duration on our ability to accurately characterize long-term morphological trends, we randomly selected  $n$  consecutive years of data and considered values of  $n$  spanning from 2 to the full length of the dataset. For each duration  $n$ , we repeated this random sampling process 500 times, then estimated the rate of morphological change in the logarithm of each trait ( $X$ ) for each species ( $i$ ) using a linear model with year, age, and sex as predictors:

$$\log(X_i) \sim \text{year} + \text{age} + \text{sex} \quad (1)$$

We considered each species separately to avoid complications that would arise in trying to generalize species-level results derived from a hierarchical model, in which the estimated dynamics of individual species are influenced by other species in the model. This would make it difficult to understand how the results might relate to non-hierarchical modelling approaches in other studies or hierarchical models with different species sets. We only retained random subsets that included both age and sex classes. In cases where the random subset only contained individuals of one age class or sex, we resampled the dataset until we reached 500 successful random subsets or 100 failures; if there were 100 failures for a species at that time series length ( $n$ ) we would not include data for that species at that time series length.

To assess whether the morphological trend through time was accurately recovered in each random subset, we compared the year effect to the year effect in an analogous model (Eq. 1), fit with the full-length dataset for the species. We then calculated two metrics: 1) we classified a subset time trend as “correct” if it had the same sign as the trend in the species’ full-length dataset, and 2) for each subset of years ( $n$ ), we calculated the root mean square error (RMSE) of the subset slope estimates (i.e., the parameter for year in Eq. 1) compared to the trend in the species’ full-length dataset as follows:

$$RMSE = \frac{\sum_{s=1}^{500} (\text{subset}_s - \text{full})^2}{500} \quad (2)$$

where  $\text{subset}_s$  is the parameter for  $\text{year}$  from Eq. 1 for each of the 500 random subsets ( $s$ ) of each length ( $n$ ), and  $\text{full}$  is the year parameter estimate derived from the complete time series.

To estimate the minimum sampling threshold for accurately recovering the direction of morphological change for each trait, we first calculated the species-specific percentage of the 500 subsets for each duration  $n$  that recovered the correct trend. We then summarized the minimum sampling threshold ( $n$ ) across bird and mammal species separately by taking the median percentage of correct estimates among species at each value of  $n$  for each trait. Finally, we calculated the minimum number of years needed to achieve a median percentage of correct estimates of morphological change in each trait that exceeded 95% among all bird or mammal species. To understand the effect of additional years of sampling on the RMSE of the trend estimates, for each species, we calculated the proportional difference in species-specific median RMSE of the 500 subsets for each duration  $n$  compared to  $n-1$ . We then identified the convergence “threshold”, defined as the length of the subset at which point the inclusion of an additional year of sampling led to a less than 10% reduction in the median RMSE. Finally, we calculated the median threshold across all species separately for birds and mammals (separately).

## Opportunities to reconstruct morphological change through time across the globe

We used the minimum sampling thresholds for each trait to identify locations around the world with sufficient temporal sampling to reconstruct long-term morphological change. We did this by downloading all records for Aves and Mammalia from the Global Biodiversity Information Facility (GBIF), for which the basis of record is “Preserved specimen” (GBIF.org 2024, 2025). To ensure that all records can be traced to a specific specimen, we then filtered the data to only retain rows with a catalog number, institution code, and species key, and that included latitude and longitude values that were numeric. To remove potential duplicate records, we only retained one record for each combination of catalog number and institution code and discarded records for which we found duplicated combinations of catalog number and institution codes outside the same 1-degree of latitude and longitude. We then removed specimen records from within 2 km of institutional locations (e.g., zoos), those georeferenced to country capitals, and those with low-precision or highly uncertain geographic coordinates using the CoordinateCleaner package (Zizka et al. 2019) in R (R Core Team 2024). This filtering process limited the dataset to records that can be linked to museum specimens and removed the most common issues in coding specimen localities. To identify geographic locations with sufficient sampling, we built an R pipeline (R Core Team 2024) to assign and assess species occurrences across a global grid using the h3 hexagonal geospatial indexing system (Uber Technologies 2018). Our pipeline includes a series of new functions (available in the supplemental R code) and efficiently processes millions of GBIF records using numerous R packages, including data.table (Barrett et al. 2024), h3 (Kueth 2022; Cooley and Shao 2024), h3jsr (O’Brien 2023), sf (Pebesma 2018; Pebesma and Bivand 2023), pbmcapply (Kuang et al. 2022), ggplot2 (Wickham 2016), rnaturalearth (Massicotte and South 2023), CoordinateCleaner (Zizka et al. 2019), and dplyr (Wickham et al. 2023). In sum, we assign each GBIF ‘speciesKey’ occurrence (as of March 2025) to one of 5,882 grid cells defined at h3 resolution level “2”, corresponding to grid cells with an edge length of approximately 180 km. The speciesKey is a unique GBIF identifier that

links any taxon to its corresponding species-level entry in the GBIF Backbone Taxonomy. For each grid cell, we count the number of bird and mammal species with at least one set of consecutive years in which the species was sampled at that location that is as long, or longer, than the minimum sampling threshold for each trait.

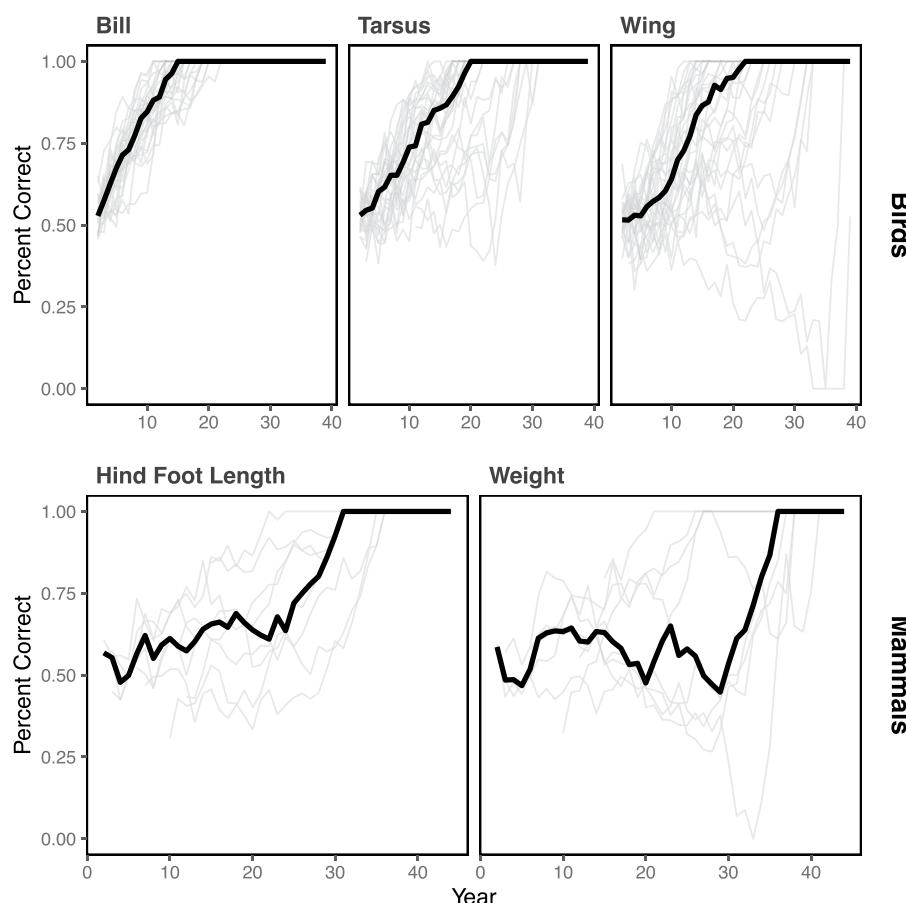
## Results

### Minimum sampling thresholds

Using the Weeks et al. (2020) dataset, we analyzed 33 species of birds that were sampled for a mean of 36.9 years (ranging from 34 to 38 years). Each species included, on average, 1,797.8 individuals measured per species over the duration of the sampling (ranging from 364 to 9,269 individuals), with a mean of 47.5 individuals per species per year (Table S1). Using the Ernest et al. (2020) dataset, we analyzed morphological traits of 11 species of mammals that were sampled at the same location for a mean of 40.45 years (ranging from 25 to 43 years). Each species included, on average, 2,224 individuals (ranging from 549 to 7,373 individuals), with a mean of 57 individuals per species per year (Table S2).

The minimum sampling threshold for accurately estimating the correct direction of the trend varied across traits and taxa (Fig. 1). In birds, the number of years that it took to recover the correct trend in 95% of the 500 random subsets within species ranged from 9 to 20 years for bill length (median=14 years), 13 to 31 years for tarsus length (median=19 years), and 10 to 38 years for wing length (median=20 years). For mammals, the number of years required to recover the correct trend in 95% of the 500 random subsets within species ranged from 21 to 38 years (median=36 years) for mass and from 22 to 36 years (median=31 years) for hind-foot length. Estimated morphological trends using the full dataset varied by species and trait (mean slopes: tarsus length= $-0.006$  [min= $-0.0018$ , max= $0.0015$ ]; wing length= $0.0003$  [min= $-0.0002$ , max= $0.0008$ ]; bill length= $-0.0033$  [min= $-0.0052$ , max= $-0.0006$ ]; hind-foot length= $-0.0007$  [min= $-0.0012$ , max= $0.0002$ ]; weight= $0.0025$  [min= $-0.0018$ , max= $0.0047$ ]). Similarly, the relative signal to noise in our estimates also varied among species and traits (mean  $R^2$ : tarsus length= $0.125$  [min= $0.035$ , max= $0.243$ ], wing length= $0.410$  [min= $0.010$ , max= $0.602$ ], bill length= $0.309$  [min= $0.093$ , max= $0.522$ ], hind-foot length= $0.025$  [min= $0.006$ , max= $0.064$ ], weight= $0.039$  [min= $0.003$ , max= $0.087$ ]). Trends through time for each species, as well as estimated slopes and  $R^2$  values for each species-trait combination, can be found in the Supporting Information.

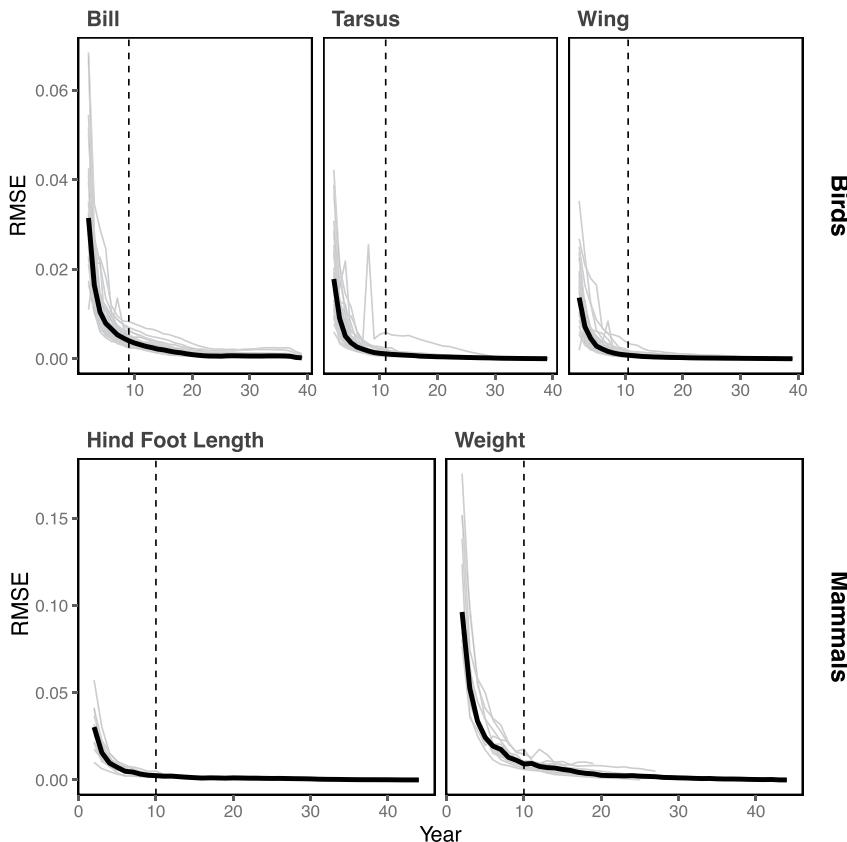
The thresholds beyond which additional years of sampling led to <10% reduction in RMSE were relatively consistent across traits and taxa (Fig. 2). In birds, the number of years of sampling it took to reach the point at which the median RMSE stopped declining appreciably with additional years of data ranged from 4–14 years for bill length (median=9 years), 3–13 for tarsus length (median=11 years), and 5–16 years for wing length (median=10.5 years). For mammals, the number of years beyond which RMSE stopped declining appreciably with additional data ranged from 7–15 years for weight (median=10) and 6–13 years for hind-foot length (median=10).



**Fig. 1** The relationship between sampling effort and trend accuracy. In birds, there is variation in the number of years of consecutive sampling needed to recover the correct long-term morphological trend 95% of the time ( $n_T$ ) for bill ( $n_T=14$ ), tarsus ( $n_T=19$ ) and wing length ( $n_T=20$ ). In mammals, fewer years are needed to accurately recover the trend for hind-foot length ( $n_T=31$ ) than for weight ( $n_T=36$ ). The minimum sampling thresholds for mammals tend to be longer than for birds. In all plots, grey lines are the median numbers of 500 random subsets that yielded the correct trend at each duration  $n$  (in consecutive years) for each species, and the black lines are the medians of those species-specific medians

### Spatial distribution of potential sampling sites

To identify opportunities to assess long-term trends in morphological change using museum specimens, we focus on the minimum data thresholds for confidently recovering the direction of the trend, as these are longer and thus provide a more conservative assessment of potential. In birds, we find globally distributed opportunities to confidently assess long-term trends in bill, tarsus, and wing lengths, though the bulk of this opportunity is within North America and Europe. Sampling is available for a large number of bird species, with over 100 species having sufficient sampling to reconstruct bill length trends in some places (Fig. 3). Opportunities to assess morphological trends across a high diversity of species are concentrated in the Southwestern United States, but there are also opportunities for high-



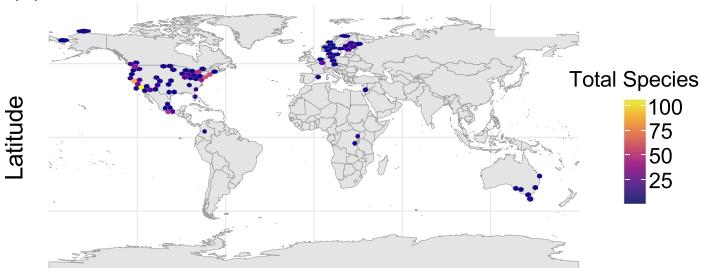
**Fig. 2** The relationship between root mean square error (RMSE) of slope estimates and sampling length. For each species (grey lines), we calculated the median RMSE for the slope estimates of the 500 random subsets of each sampling length ( $n$ ) and the median among all species (black line). We identified the convergence “threshold” as the length of the subset at which point the inclusion of an additional year of sampling led to a less than 10% reduction in the median RMSE. Dashed line represents the trait-specific, among-species median convergence threshold

diversity sampling in the Midwestern and Eastern United States, Europe, and eastern and Southeastern Australia (Fig. 3). Additionally, there are some opportunities to reconstruct long-term trends in bird morphology in the tropics, with sufficient sampling for some cells in tropical South America (0–1 cells across traits) and Central Africa (1–2 cells across traits; Fig. 3). In cells with adequate sampling, there tends to be data for multiple species, with a mean of 9.6 species with adequate sampling for bill length, 9.4 species for tarsus length, and 9.8 species for wing length.

Mammals are comparatively poorly represented in museum collection time series; we find sites that have sufficient sampling to confidently recover long-term trends in mammal mass and hind-foot length on three continents. As with birds, the locations with sampling that exceeds the minimal sampling thresholds are concentrated in North America and Europe, with sites with the highest diversity of species concentrated in the Southwestern

### Grid Cells with Total Species Counts

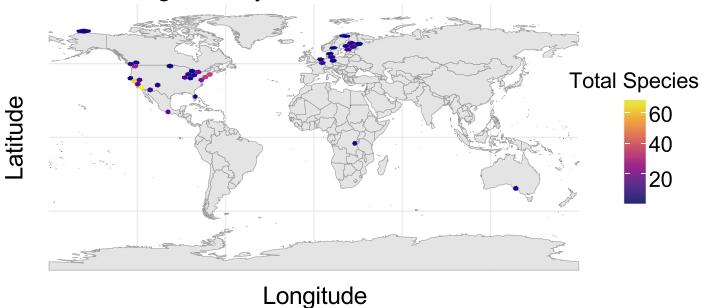
(a) Streak length  $\geq 14$  years



(b) Streak length  $\geq 19$  years

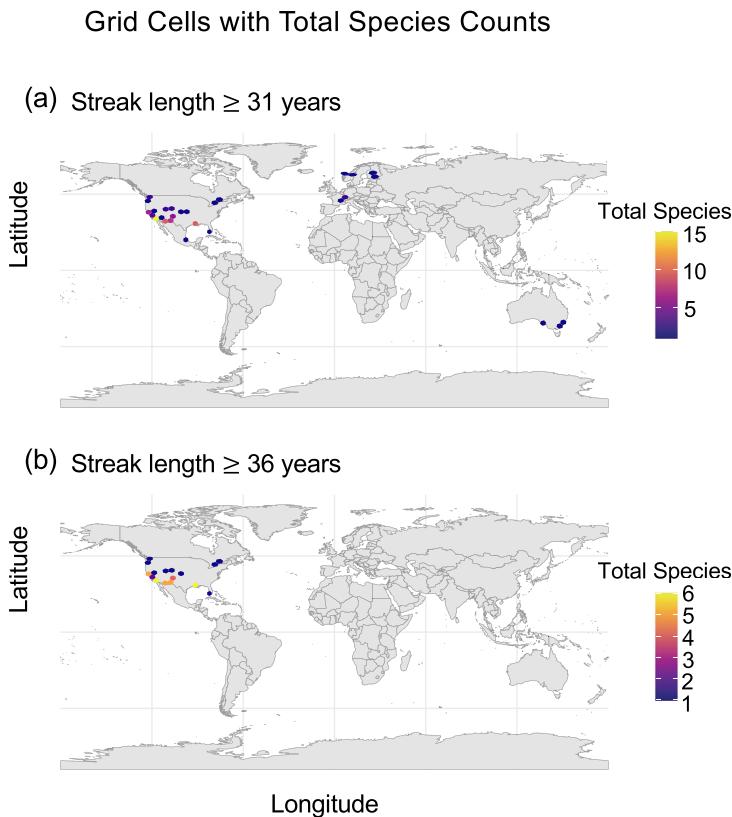


(c) Streak length  $\geq 20$  years



**Fig. 3** Locations where time series of bird specimens exceed the estimated minimum sampling threshold. Birds are comparatively well represented in museum holdings, and there are widespread opportunities to reconstruct long-term changes in bill length (a), tarsus length (b), and wing length (c), though most opportunities are in the Northern Hemisphere, with a bias toward North America and Europe, though there are some limited opportunities in the tropics

United States and Northern Europe. In the Southern Hemisphere, the only locations with specimen series exceeding the minimal sampling thresholds are located on the southeastern and southern coast of Australia (0–3 cells across traits; Fig. 4). On average, these sites contain 2.7 species with adequate sampling for mass and 2.8 species with adequate sampling for hind-foot length.



**Fig. 4** Locations where time series of mammalian specimens exceed the estimated minimum sampling threshold. For both mass (a) and hind-foot length (b), opportunities to reconstruct long-term morphological change are concentrated in the Northern Hemisphere, in particular North America and Europe

## Discussion

### Sampling demands for reconstructing morphological change

Morphological change associated with warming temperatures is emerging as a general response to climate change (Daufresne et al. 2009; Gardner et al. 2011; Caruso et al. 2014; Ryding et al. 2021). While much can be learned about the link between temperature and morphology experimentally (Weeks et al. 2022) and by applying principles from ecophysiology (Nord et al. 2024), analyses of long-term datasets have emerged as a significant basis for understanding long-term morphological responses to environmental change. Correlational studies have been conducted across a wide range of taxa, traits, and temporal breadths (Table 1). We find that taxon identity and the trait being studied can impact the temporal sampling needed to accurately characterize long-term changes in morphology in birds and mammals.

In the bird data we analyzed, fewer years of data are needed to characterize long-term trends in bill length (14 years) than tarsus length (19 years) or wing length (20 years; Fig. 1).

**Table 1** Past efforts to reconstruct morphological change using field- and specimen-based datasets

	Data type	Over/Under minimum sampling threshold	Trait measured	Mean number of years	Number of studies
<i>Mammals</i>					
	Field Data	Under	Body Mass	17	7
	Field Data	Over	Body Mass	42	1
	Specimen Data	Under	Body Mass	–	0
	Specimen Data	Over	Body Mass	78	5
	Field Data	Under	Foot Length	3	1
	Field Data	Over	Foot Length	57	3
	Specimen Data	Under	Foot Length	–	0
	Specimen Data	Over	Foot Length	89	3
<i>Birds</i>					
	Field Data	Under	Tarsus Length	7	1
	Field Data	Over	Tarsus Length	33	3
	Specimen Data	Under	Tarsus Length	–	0
	Specimen Data	Over	Tarsus Length	86	6
	Field Data	Under	Wing Length	9	3
	Field Data	Over	Wing Length	37	17
	Specimen Data	Under	Wing Length	–	0
	Specimen Data	Over	Wing Length	91	12
	Field Data	Under	Bill Length	13	1
	Field Data	Over	Bill Length	36	4
	Specimen Data	Under	Bill Length	–	0
	Specimen Data	Over	Bill Length	91	6

We reviewed 71 assessments of long-term trait change from the literature (see Supporting Information and Table S3 for more detail) and classified the dataset as over or under the minimum sampling threshold we identify for that trait

This may be because bill length has changed significantly faster than tarsus and wing lengths in this dataset and more consistently among species than wing length (Zimova et al. 2023). Although tarsus and bill lengths have changed with a similar consistency among species, it is possible that the longer time series necessary for tarsus length could be influenced both by the strength of the trends and the presence of highly correlated non-linear fluctuations in tarsus length (Weeks et al. 2020). In estimating range shifts related to climate change, similar among-species correlations in population size fluctuations obscure long-term population-level spatial shifts through time (McCain et al. 2016).

In mammals, while there is slight variation in the temporal sampling necessary to confidently recover trends (31 years for hind-foot length and 36 years for mass), the difference between these minimum sampling thresholds is much less pronounced than in birds (Fig. 1). Interestingly, analyses of morphological shifts in mammals require longer time series than those of birds. While this could be due to differences in the strength or consistency of morphological change in mammals and birds, it could also be the result of increased noise in measuring traits like hind-foot length on live animals and the potential for body mass to vary in relation to reproductive status and due to short-term variation in the environment (Wirminghaus and Perrin 1993; Zuercher et al. 1999). Further, we expect that inter-individual heterogeneity is likely an important factor in how detectable a long-term trend is; it is possible that greater within-population variation in mammal traits leads to longer minimum temporal sampling periods.

There is some potential for these sources of variation in sampling thresholds to have biased our understanding of morphological responses to climate change. Traits that are changing faster may appear to be changing more consistently across species than traits that are changing more slowly simply because more data are needed to accurately characterize the trajectories of change for slower changing traits. Similarly, traits that are changing in complex ways through time (e.g., responding to short-term cyclical fluctuations in temperature; Weeks et al. 2020) may similarly appear to be changing less consistently across taxa simply because of the increased data requirements to accurately characterize those trends.

While it is possible that these different thresholds have impacted our understanding of trait change, based on a sample of studies that have characterized long-term trends in morphology across birds and mammals, it seems like this is unlikely to be a widespread problem. Across traits and for both birds and mammals, long-term studies of morphological change have by and large exceeded the minimum sampling thresholds (Table 1). With the exception of field data-based assessments of mammal body mass, most studies of mammal hind-foot length and bird tarsus, wing, and bill lengths have used sufficiently long datasets to reliably capture long-term trends. In particular, the specimen-based analyses of morphological change that we found were uniformly long enough to exceed the minimum sampling thresholds we identified.

In contrast to the variation seen among traits and taxa in the number of years of sampling necessary to recover the correct sign of the trend, there is comparatively little variation in the sampling duration at which RMSE stabilizes. Across all traits and both taxa, the threshold we identify lies between 9 and 11 years. This may reflect relatively small slope estimates in the trends, resulting in sign changes even with small differences in slope estimates. In thinking about global opportunities to reconstruct morphological change, we focus on the thresholds for accurately characterizing the long-term trends rather than RMSE stabilization, as this results in the most conservative characterization of potential opportunities.

## Global opportunities to reconstruct morphological change using museum specimens

When we apply the minimum sampling thresholds to identify opportunities to reconstruct morphological change through time across the globe, we find that the potential to use specimens is extensive but biased and that there are large gaps in coverage (Fig. 3, Fig. 4). Most opportunities to accurately characterize morphological trends using museum specimens exist in the United States and Europe. It is also important to note that, although a location may have enough specimens to analyze morphological change through time, these specimens may not necessarily be housed at that location, or even in a single collection, potentially complicating efforts to access the relevant specimens. Given that there are major gaps in spatial coverage, data limitations are likely to be a significant constraint in understanding global phenomena like climate change. These spatially biased limitations support recent calls for increasing biodiversity monitoring to enable a more just future (Chapman et al. 2024) and highlight the importance and value of arduous and resource-intensive efforts being undertaken by museums to georeference older specimens. However, it is also worth noting that because our analyses were restricted to specimen metadata made available through GBIF, some apparent gaps may be due to under-representation of specimen holdings that have not yet been digitized (Ball et al. 2025), or the result of countries or institutions that do not participate in GBIF.

Additionally, there are likely biases that are less apparent from our global scale map. For example, in herbarium specimens, there is a strong bias toward collecting near features like roads that facilitate collecting activities (Daru et al. 2018). Whether or not these biases are likely to impact efforts to understand long-term trends in animal morphology is complex. For example, in mammals, urbanization is associated with intra-specific variation in size (Hantak et al. 2021), while for birds, the impacts of urbanization are more nuanced (Zhao et al. 2021). If biases in collecting influence the size of specimens relative to the rest of the population, it is unclear whether this bias would impact efforts to understand long-term trends in morphology as long as the biases remain consistent through time. Among species, smaller species are changing faster through time (Zimova et al. 2023), and this size effect appears to be independent of generation length effects. Thus, it is possible that within species there may be a similar pattern, and if collections are biased toward larger or smaller populations, they may result in biased species-level estimates of rates of change. Absent a better understanding of the mechanisms driving the trends we observe, it is not currently possible to determine the extent to which this may impact assessments of morphological change.

In addition to providing opportunities for reconstructing patterns of morphological change, long-term specimen time series can enable more mechanistic assessments of change than are typically possible with non-specimen-based datasets. For example, a key question about long-term morphological change is how plasticity and selection contribute to observed changes. These questions can certainly be addressed with non-specimen-based data, but doing so typically requires extraordinary datasets (e.g., long-term pedigree data on populations over many decades (Teplitsky et al. 2008) or combinations of experimental interventions and recapturing of individuals (Shipley et al. 2022)), which can limit the taxa that can be studied. Huge advances in using historical DNA have made, and will continue to make, specimens powerful sources of data for genomic analyses (Raxworthy and Smith 2021). Because of this, specimen-based DNA from long-term collection efforts can be used to search for genomic signatures of selection that may explain morphological responses to environmental change (Adams et al. 2025). Coupling these genomic analyses with phenological (Zimova et al. 2021) and isotopic data (Hobson et al. 2004) may advance a more mechanistic and predictive understanding of the drivers of morphological change.

There are several limitations to our study that are worth considering. To estimate the minimum sampling thresholds, we based our findings on two single-location studies, each including multiple bird and mammal species. However, the extent to which these thresholds vary from system to system is unknown. Further, our mammal data come from a long-term experimental study, in which a variety of plot-level treatments occurred. The most relevant of these treatments occurred during certain years in which experimental gates excluded large species; however, these species remained present in the larger sampled area, and if they were not present in any plot, data would simply not have been used that year for that species. We also assume that the linear trend in the longest time series is the "correct" trend, and we base our analyses on simple linear models of individual species; the use of hierarchical models may influence sampling thresholds, but the impacts of different analytical approaches are likely to depend on the details of the approaches. Next, there are important caveats to note regarding the global specimen database we used to map the availability of specimen time series. First, individual specimens can be prepared as multiple preparation types (e.g., stuffed skin and tissue samples), and in some cases, different preparation types

may have been assigned distinct collection codes, potentially inflating the number of individuals thought to have been collected at a location. Second, our reliance on the speciesKey identifier assumes a consistent, species-centered taxonomy where each taxon at or below species rank maps reliably to a single species in the GBIF Backbone Taxonomy. Undoubtedly, there are taxonomic mismatches within the database, and these may have reduced the individual counts at a location. In addition to those limitations, our analyses were restricted to specimen metadata made available through GBIF, which may have resulted in a significant under-representation of specimen holdings in biased ways as digitization of collections is certainly incomplete and there may be spatial biases in where collections have been digitized (Ball et al. 2025). Finally, not all preparation types include information on all traits (e.g., a skeletal preparation of a bird cannot be used to measure the length of the relaxed wing chord); the extent to which this is an issue will be dependent on the trait and taxon of interest.

## Conclusions

Confidently reconstructing long-term trends in morphological traits of birds and mammals is critical to understanding the drivers of biotic responses to climate change. We find that, in general, multiple decades of morphological data are needed to confidently assess these trends. Importantly, there is significant variation in the sampling demands depending on the taxon and trait being examined, and these differences may have impacted our understanding of species responses to global change and limit our ability to generate ecological forecasts across locations and ecological contexts. Finally, specimen time series of sufficient length to confidently reconstruct long-term morphological change exist for many species around the globe. Although these series are fairly sparse and are unevenly distributed geographically, they represent promising opportunities for developing a more holistic understanding of species' responses to global change.

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## Declarations

**Competing interests** The authors declare no competing interests.

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