

Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010

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Abstract

Although it is generally recognized that global biodiversity is declining, few studies have examined long-term changes in multiple biodiversity dimensions simultaneously. In this study, we quantified and compared temporal changes in the abundance, taxonomic diversity, functional diversity, and phylogenetic diversity of bird assemblages, using roadside monitoring data of the North American Breeding Bird Survey from 1971 to 2010. We calculated 12 abundance and diversity metrics based on 5-year average abundances of 519 species for each of 768 monitoring routes. We did this for all bird species together as well as for four subgroups based on breeding habitat affinity (grassland, woodland, wetland, and shrubland breeders). The majority of the biodiversity metrics increased or remained constant over the study period, whereas the overall abundance of birds showed a pronounced decrease, primarily driven by declines of the most abundant species. These results highlight how stable or even increasing metrics of taxonomic, functional, or phylogenetic diversity may occur in parallel with substantial losses of individuals. We further found that patterns of change differed among the species subgroups, with both abundance and diversity increasing for woodland birds and decreasing for grassland breeders. The contrasting changes between abundance and diversity and among the breeding habitat groups underscore the relevance of a multifaceted approach to measuring biodiversity change. Our findings further stress the importance of monitoring the overall abundance of individuals in addition to metrics of taxonomic, functional, or phylogenetic diversity, thus confirming the importance of population abundance as an essential biodiversity variable.

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Introduction

It is generally acknowledged that global biodiversity is currently declining at an unusually high rate (Barnosky *et al.*, 2011; Pereira *et al.*, 2012; Tittensor *et al.*, 2014). This decline includes local extirpations as well as complete extinctions of species and is so substantial that it has been referred to as 'defaunation' (Dirzo *et al.*, 2014; McCauley *et al.*, 2015; Newbold *et al.*, 2015). National and international agreements to counteract this decline, like the Convention on Biological Diversity (CBD), call for biodiversity changes to be accurately quantified (Walpole *et al.*, 2009; Dornelas *et al.*, 2013). So far, biodiversity has typically been quantified based on taxonomic composition, using the number of species and their relative abundances to derive metrics like species richness or Shannon's diversity index. However, as it is increasingly recognized that taxonomic diversity represents only one of the multiple dimensions of biodiversity, aspects of functional and phylogenetic diversity are increasingly included in biodiversity research and assessments (Purvis & Hector, 2000; Devictor *et al.*, 2010; Wahl *et al.*, 2011; Purschke *et al.*, 2013; Calba *et al.*, 2014; Monnet *et al.*, 2014). Functional diversity represents the distribution of the functional traits of the organisms present in an assemblage (Villéger *et al.*, 2008). Functional traits are the morphological, physiological, or phenological characteristics of an organism that strongly influence its performance (McGill *et al.*, 2006; Luck *et al.*, 2012). Hence, metrics of functional diversity are considered relevant particularly in the context of ecosystem functioning (Diaz & Cabido, 2001; Cardinale *et al.*, 2012). Phylogenetic diversity represents the degree of evolutionary divergence of the organisms within an assemblage (Faith, 1992). Metrics of phylogenetic diversity have been used as proxies for functional diversity as well as measures of conservation interest on their own, representing the evolutionary heritage and potential of species' assemblages (Diaz *et al.*, 2013; Winter *et al.*, 2013; Mace *et al.*, 2014).

Although no single metric can be expected to adequately describe the multidimensionality of biodiversity, at least some redundancy among the large variety of metrics is likely, either for formal mathematical reasons or because different metrics may respond similarly to environmental change. Hence, there is a clear need to identify a nonredundant yet representative set of metrics to adequately capture biodiversity change (Buckland *et al.*, 2005; Lyashevskaya & Farnsworth, 2012;

Pereira *et al.*, 2013; Stevens & Tello, 2014). Yet, comparative assessments of temporal trends in multiple biodiversity metrics have hardly been made (Magurran *et al.*, 2010; Monnet *et al.*, 2014). The few studies conducted so far are inconclusive, as they show that temporal changes may or may not be congruent among taxonomic, functional, and phylogenetic diversity (Petchey *et al.*, 2007; Winter *et al.*, 2009; Villéger *et al.*, 2010; Monnet *et al.*, 2014). Moreover, these studies all focused on metrics reflecting species composition and ignored the overall abundance of individuals, which influences the organisms' contribution to ecosystem functioning (McIntyre *et al.*, 2007; Dirzo *et al.*, 2014; Inger *et al.*, 2015). Hence, there is a clear need for comparative studies of temporal changes in both the diversity of species assemblages and the overall abundance of individuals.

In this study, we used large-scale and long-term bird monitoring data in, to our knowledge, the largest comparative assessment to date of temporal changes in abundance, taxonomic diversity, functional diversity, and phylogenetic diversity. Birds provide an excellent case to investigate biodiversity changes: They have been documented and studied more intensively than most other taxa, resulting in a relatively large availability of monitoring data as well as information on functional traits and phylogeny (Gregory *et al.*, 2005; Petchey *et al.*, 2007; Gregory & Van Strien, 2010; Szabo *et al.*, 2012; Illan *et al.*, 2014; Monnet *et al.*, 2014; Inger *et al.*, 2015). We used a large-scale dataset encompassing 40 years of monitoring from the North American Breeding Bird Survey (BBS). Our specific aims were twofold: 1) to quantify and compare the changes in multiple metrics of abundance and diversity, and 2) to identify a nonredundant set of key metrics most representative of the changes. Thus, the results of our study enhance our understanding of how different biodiversity metrics may replicate or complement each other in their ability to reflect biodiversity change, which in turn helps to select an optimum set of metrics to adopt for monitoring (Lyashevskaya & Farnsworth, 2012; Van Strien *et al.*, 2012).

Material and methods

Bird monitoring data

The North American Breeding Bird Survey (BBS) is a cooperative effort of the United States Geological Survey,

the Canadian Wildlife Service, and, since 2008, the Mexican National Commission for the Knowledge and Use of Biodiversity, with the aim to monitor the status and trends of North American bird populations (Sauer *et al.*, 2013). Initiated in 1966, the BBS monitoring program has been collecting yearly population counts from an increasing number of roadside routes. Each roadside route has a length of 24.5 miles (approximately 40 km), along which fifty regularly spaced sites are monitored each year in June. At each site, the observer records all birds heard or seen within a 400 m radius and within 3 min (Sauer *et al.*, 1997; Rittenhouse *et al.*, 2012). For this study, we used monitoring data from the conterminous United States from 1971 through 2010, thus excluding the early years of the survey, when relatively few routes were visited (Illan *et al.*, 2014). The BBS data comprise raw counts, which are a function of both population size and detection probability, the latter being dependent on characteristics of routes, observers, and meteorological conditions (Phillips *et al.*, 2010; Rittenhouse *et al.*, 2010, 2012). To obtain a spatially consistent dataset covering the entire study period, we selected routes with at least one observation in each 5-year interval. Then, we reduced sampling variation in abundance induced by observed and weather effects by calculating 5-year average abundances per species per route (Illan *et al.*, 2014). This resulted in a dataset of 768 routes each with eight 5-year average abundances of in total 519 species. A list of species is provided in the Supporting Information (Table S1).

Biodiversity metrics

We calculated 12 biodiversity metrics for each monitoring route and for each of the eight time periods. The set of metrics was selected to represent abundance, taxonomic diversity, functional diversity, and phylogenetic diversity (Table 1). Because temporal trends may differ between or be driven by particular species groups, we calculated the metrics not only for all bird species together, but also for four subgroups based on breeding habitat preferences (Table S1): grassland (27 species), woodland (129 species), wetland (83 species), and shrubland (81 species). Breeding habitat preferences were derived from the Patuxent Bird Identification Infocenter (Gough *et al.*, 1998). This database also distinguishes species using urban breeding habitats; however, there were too few urban breeders in our dataset to perform meaningful metric calculations. Urban breeders ($n = 13$) were therefore not included in the separate breeding habitat group analyses, but they were included in the overall assessment. To assess the sensitivity of our findings to occasional observations of rare or vagrant species, we performed the metric calculations and subsequent analyses also based on only those 439 species that were observed consistently throughout all eight 5-year intervals.

Abundance. To quantify abundance, we used the total abundance and the geometric mean abundance. We calculated total abundance by simply summing the abundances of all species

Table 1 Overview of the biodiversity metrics calculated in this study

Biodiversity metric		Description *
Total abundance	TA	$\sum_{i=1}^{i=n} a_i$
Geometric mean abundance	GMA	$\left(\prod_{i=1}^{i=n} \ln(a_i + c) \right)^{1/n}$
Species richness	SR	Total number of species present
Shannon index	Shan	$\exp\left(-\sum_{i=1}^{i=SR} p_i \cdot \log p_i\right)$
Simpson index	Simp	$\frac{1}{\sum_{i=1}^{i=n} p_i^2}$
Functional richness	FRic	The convex hull volume of the individual species in multidimensional trait space (Villéger <i>et al.</i> , 2008).
Functional evenness	FEve	The regularity with which species abundances are distributed along the minimum spanning tree which links all the species in the multidimensional functional space (Villéger <i>et al.</i> , 2008).
Functional divergence	FDiv	Species deviance from the mean distance to the center of gravity within multidimensional trait space, weighted by relative abundance (Villéger <i>et al.</i> , 2008).
Functional dispersion	FDis	The weighted mean distance in multidimensional trait space of individual species to the centroid of all species. Weights are species' relative abundances (Laliberté & Legendre, 2010).
Proportion of carnivores	PC	The abundance of carnivorous species (i.e., species with a diet consisting of at least 60% meat, fish, and/or carrion) relative to the total abundance of all species (%).
Community-weighted mean body mass	CWMm	The mean body mass of species weighted by the species' abundances.
Phylogenetic diversity	PD	The total length of the phylogenetic branches connecting all species of a given assemblage (Faith, 1992).

* a_i is the abundance of species i ; p_i is the proportional abundance of species i ; n is the total number of species in the dataset; c is a constant.

at each route, thus obtaining a measure representing the total number of individuals. Because changes in abundance have been shown to differ among common and less common bird

species (Inger *et al.*, 2015), we calculated the total abundance not only based on all bird species together, but also for common and less common species separately. To that end, we assigned each species to an abundance quartile based on its overall abundance (i.e., the total abundance over all routes and the entire study period), with the least abundant species occupying quartile one (q1) and the most abundant occupying quartile four (q4) (Inger *et al.*, 2015). Because the geometric mean abundance is a multiplicative rather than an additive measure, it reflects relative rather than absolute abundances. As such, it is a composite measure of abundance and evenness: It declines not only if all species decline proportionally (i.e., lower total abundance, same evenness), but also if the abundance distribution becomes less even for a given number of individuals (Buckland *et al.*, 2005, 2011). We calculated the geometric mean abundance based on all species within the entire set or particular habitat subgroup; that is, a species absent from a particular route in a particular time period was counted as zero. Because a geometric mean cannot be calculated if there are zeros in the data, we applied an $X + 1$ transformation prior to the calculation (Jongman *et al.*, 1995). As the geometric mean may change with the constant chosen for the transformation (Buckland *et al.*, 2011), we evaluated the effect of alternative transformations of $X + 0.1$, $X + 0.01$, and $X + 0.001$ on our results.

Taxonomic diversity. As metrics of taxonomic diversity, we calculated species richness, Shannon diversity index, and Simpson diversity index, using the 'vegan' package in R, version 2.2-1 (Oksanen *et al.*, 2015). We took the exponential of Shannon index and the inverse of Simpson index to make them comparable to species richness (Jost, 2006).

Functional diversity. We followed the framework of Villéger *et al.* (2008) to obtain a set of complementary and orthogonal metrics of functional diversity (FD): functional richness, functional divergence, and functional evenness. These metrics account for the total volume of functional trait space occupied by the species present in the community, the abundance distribution of the species in functional trait space, and the regularity of this abundance distribution, respectively (Table 1). We further included functional dispersion to represent the dispersion of the species in the trait space (Laliberté & Legendre, 2010). We calculated the FD metrics based on functional traits related to feeding behavior and resource use as reported in the ELTONTRAITS 1.0 database, which contains trait values for all 9993 extant bird species (Wilman *et al.*, 2014). Traits used in the FD calculations were diet composition (percentage; seven categories), foraging height prevalence (percentage; seven layers), foraging activity period (nocturnal or diurnal), and body mass (g) (Table S1). This combination of traits reflects foraging behavior and quantity of resources consumed (Petchey *et al.*, 2007; Calba *et al.*, 2014), which in turn influence both the species' responses to environmental change and their effects on ecosystem functioning (Vetter *et al.*, 2011; Luck *et al.*, 2012). For traits expressed as proportions or prevalence, each category was included as a separate variable in the FD calculations and weighted according to the total number of categories per

trait (for example, a weight of 1/7 was assigned to each of the seven diet categories). We calculated the FD measures based on a Gower dissimilarity matrix using the package 'FD' in R, version 1.0-12 (Laliberté *et al.*, 2015). In addition to the four composite functional diversity metrics listed above, we calculated the proportion of carnivores and the community-weighted mean body mass. The proportion of carnivores was calculated as the proportion of individuals with a diet consisting of at least 60% meat, fish, and/or carrion, following the data and classification of the ELTONTRAITS database.

Phylogenetic diversity. We calculated phylogenetic diversity as the total length of the phylogenetic branches connecting all species of a given assemblage (Faith, 1992). The larger the total branch length of a given assemblage, the more evolutionarily divergent the species (Cadotte *et al.*, 2009). We sampled 10 trees from the full posterior distribution of phylogenetic trees from Jetz *et al.* (2012). Per assemblage, we then calculated phylogenetic diversity as the total branch length averaged over the 10 trees. We used no more than 10 trees because the computation time strongly increased with the number of trees. To assess the extent to which phylogenetic diversity depended on the number of phylogenetic trees, we took a random sample of 30 assemblages for which we calculated phylogenetic diversity based on a number of trees ranging from 1 to 10. Compared to differences in phylogenetic diversity among the assemblages, fluctuations in phylogenetic diversity related to the number of trees were negligible (Fig. S1). Moreover, fluctuations levelled off at about seven trees, indicating that 10 trees were enough to obtain a representative estimate of phylogenetic diversity.

Biodiversity changes

We quantified the temporal changes in the biodiversity metrics in two ways. First, we calculated the overall temporal change for each metric per route, that is the change from the first to the last 5-year interval, as

$$ES_{M,x} = \frac{M_{x,t=8} - M_{x,t=1}}{0.5 \cdot (M_{x,t=1} + M_{x,t=8})} \quad (1)$$

where $ES_{M,x}$ represents the effect size for biodiversity metric M at route x , and $M_{x,t=1}$ and $M_{x,t=8}$ are the values calculated for biodiversity metric M at route x for the intervals 1971–1975 and 2006–2010, respectively. This effect size measure yields a symmetrical index of decrease or increase between -2 and 2 (Böhning-Gaese & Bauer, 1996; Van Turnhout *et al.*, 2007). Second, we estimated the temporal trends in the metrics across all routes throughout the eight 5-year intervals. To that end, we first calculated mean metric values over all routes for each 5-year interval (Table S2). To facilitate comparison among the metrics, we then standardized the metric values over time (zero mean and unit variance). Because we were interested in the overall direction and strength of the trends, we fitted ordinary least squares (OLS) regression models to the standardized metric values. Note that this approach results in slopes and intercepts identical to those resulting from an approach where OLS models are first fitted for each route and slopes

and intercepts are then averaged over the routes. For comparison, we also fitted generalized least squares (GLS) models with temporally autocorrelated error structure (AR1), to account for possible nonindependence of observations closer in time. GLS models tend to have slopes similar to those of OLS regression models, yet GLS models have more conservative *P*-values because the temporal autocorrelation is accounted for (Dornelas *et al.*, 2013).

Key metrics

To quantify the redundancy and complementarity among the changes in the various metrics, we applied a combination of principal component analysis (PCA), variable reduction, and cluster analysis. We did this based on the overall changes of the metrics across the routes (i.e., the effect sizes, Eqn 1). First, we determined the dimensionality of the biodiversity changes with PCA, based on Spearman rank correlations among the effect sizes (Lyashevskaya & Farnsworth, 2012; Stevens & Tello, 2014). To determine the number of nontrivial or significant principal components, we randomly permuted the effect sizes per metric, conducted a PCA, retained the eigenvalues, and repeated this procedure 1000 times to create distributions of eigenvalues for each principal component that would be expected by chance. If the eigenvalue of a principal component based on the original dataset was larger than the 95th percentile of the eigenvalues based on the randomized data, then we considered that particular principal component significant (Peres-Neto *et al.*, 2005). Next, we clustered the metrics based on the similarity of their loadings on the significant components using a hierarchical clustering algorithm (Ward's method) based on Euclidean distance and we identified a number of clusters equal to the number of significant components. Finally, we identified which of the metrics were most representative of the changes. A common approach to identify the most representative variables in a set is to select those variables that have high loadings on the first (few) principal components. However, by considering one principal component at a time, this approach may lead to a suboptimal or larger subset of the original variables than is strictly necessary (Cadima & Jolliffe, 2001). To avoid this, we used the 'improve' algorithm (with criterion 'Rm') from the 'subselect' package (version 0.12-5), which is specifically designed to identify which variables are most representative of the total variation in a dataset (Cadima & Jolliffe, 2001). As a benchmark for the number of key metrics to retain, we used the number of significant components. All statistical analyses were performed in R, version 3.0.3 (R Core Team, 2014).

Results

Biodiversity changes

The biodiversity changes showed considerable spatial variation, as exemplified by the effect sizes ranging from -2 to 2 (i.e., the minimum and maximum values possible) for several of the metrics (Figs 1 and 2). However, when averaged over all routes, and when

considering all species together, we found the majority of the metrics to increase over the study period (Fig. 3, Table S2–S4). Pronounced increases were observed in particular for the proportion of carnivores (which, on average, more than doubled from 1.3% in 1971–1975 to 2.8% in 2006–2010), the functional richness (which increased by nearly 60% over the study period), the community-weighted mean body mass (which increased from 100 to 150 g), and the total abundance of birds in quartile 3 (from 28 to 36 individuals). In contrast, distinct decreases were observed for the total abundance of all birds (from 901 individuals in 1971–1975 to 804 individuals in 2006–2010) as well as the abundance of the most common species (from 868 to 762 individuals). Highly similar results were obtained when excluding species that were not consistently observed throughout all 5-year intervals (Figs 1 and 3, Table S2–S4). Yet, changes were clearly different between the breeding habitat groups (Figs 2 and 3). Grassland birds showed, on average, decreases in various metrics, including the total abundance, geometric mean abundance, species richness, and phylogenetic diversity, whereas these metrics increased for woodland birds. Wetland birds tended to decrease in abundance, although not as sharply as the grassland birds. Yet, this group showed increases in various measures of both taxonomic and functional diversity, including Shannon index, Simpson index, functional richness, functional evenness, functional divergence, proportion of carnivores, and community-weighted mean body mass. For shrubland birds, the most pronounced change was a clear decrease in the community-weighted mean body mass.

Key metrics

The PCA yielded three significant principal components for all species together and for three of the four breeding habitat groups. For the shrubland breeders, four principal components were retained (Table S5). The cumulative proportion of variance explained by the nontrivial components was between 59% and 63%, with the first component explaining between 30% (shrubland breeders) and 37% (woodland breeders) of the total variance (Table S5). Clusters of metrics slightly differed among the species groups and with the data transformation applied to calculate the geometric mean abundance (Figs 4 and 5, Fig. S2). Yet, particular metrics were in all cases closely associated with each other, such as the total abundance and the abundance of the most common species, or the Shannon index and the Simpson index. Metrics depending on the number of species or traits without any abundance weighting (species richness, phylogenetic diversity, and functional

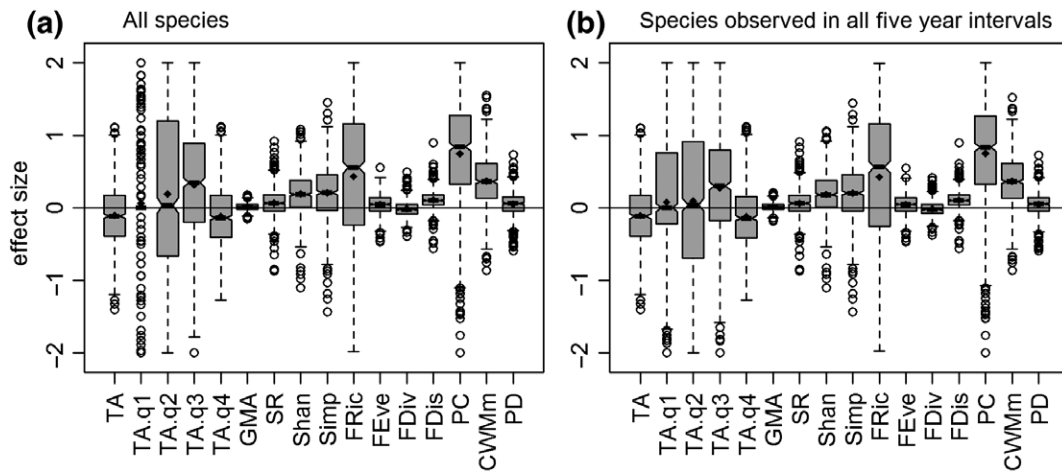


Fig. 1 Changes in biodiversity metrics from 1971–1975 to 2006–2010, showing increases in diversity and a decrease in overall abundance. Black diamonds represent the mean; boxplots show the median and its 95% confidence interval (thick black line and notch), the interquartile distance (boxes), 1.5 times the interquartile distance from the 25th or 75th percentile (whiskers) and the outliers (open dots). Full names of the metrics are provided in Table 1.

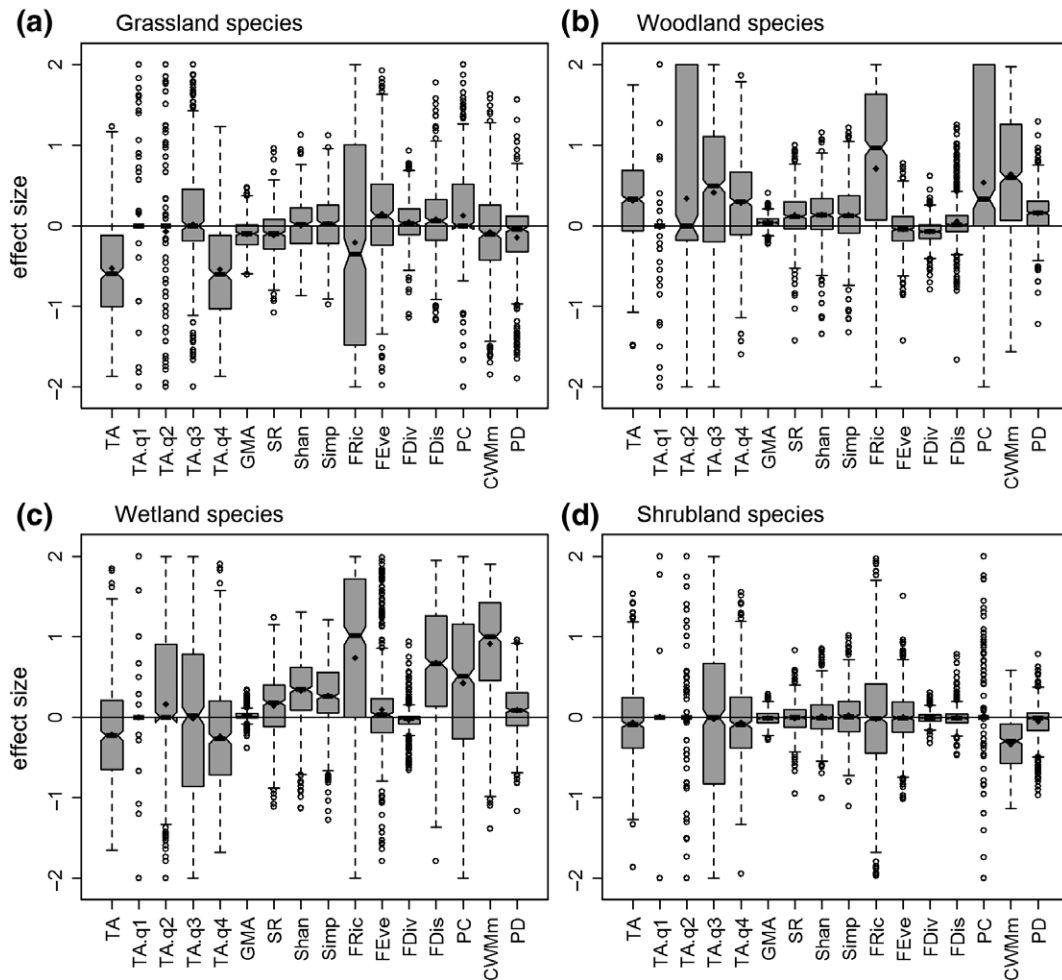


Fig. 2 Changes in biodiversity metrics differ among the four breeding habitat groups. Black diamonds represent the mean; boxplots show the median and its 95% confidence interval (thick black line and notch), the interquartile distance (boxes), 1.5 times the interquartile distance from the 25th or 75th percentile (whiskers) and the outliers (open dots). Full names of the metrics are provided in Table 1.

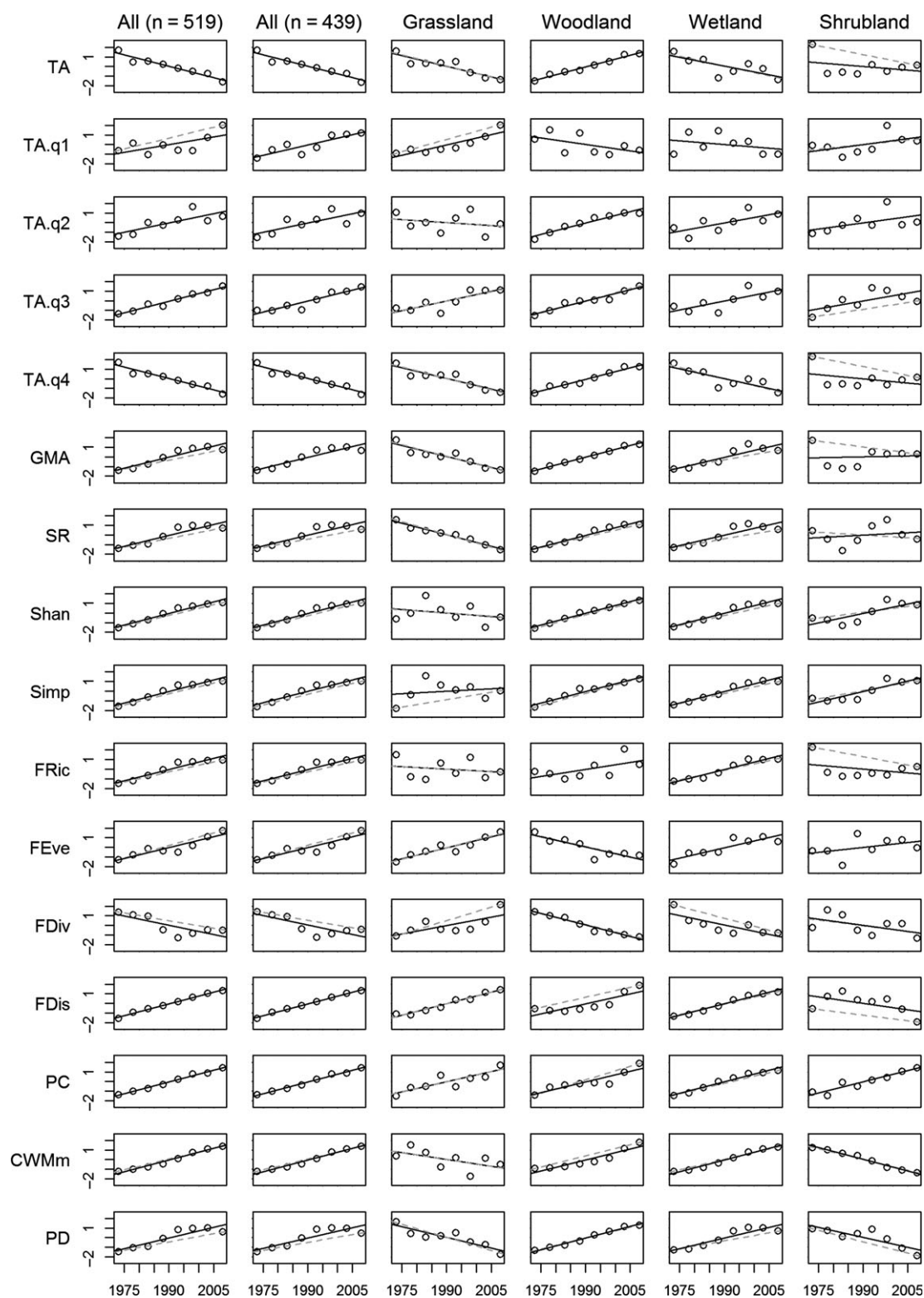


Fig. 3 Trends in North American bird assemblages based on metrics of abundance, taxonomic diversity, functional diversity, and phylogenetic diversity, for all species together as well as for specific breeding habitat groups. Metric values were calculated as mean values over the 768 monitoring routes and then standardized (zero mean and unit variance) over time, to facilitate comparison. Solid and dashed lines represent OLS and GLS regression lines, respectively. If no dashed line is visible, the two lines overlap. Full names of the metrics are provided in Table 1.

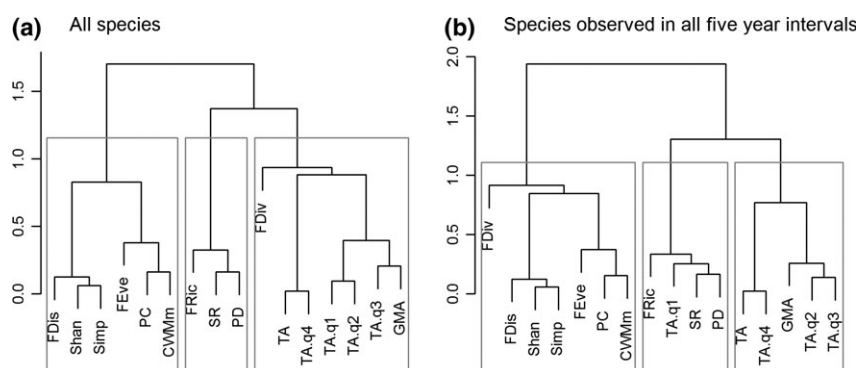


Fig. 4 Three clusters of biodiversity metrics based on the overall changes observed across the monitoring routes. The number of clusters corresponds with the number of significant components as identified by PCA. Full names of the metrics are provided in Table 1.

richness) were always in the same cluster. In many cases, the richness metrics were also in the same group as the abundance of the less common species, reflecting that changes in the abundance of those species in particular coincided with changes in species composition. Finally, irrespective of the species group, the nonredundant set of metrics most representative of the overall changes included a metric of overall abundance (mostly total abundance), a richness metric (species richness, phylogenetic diversity, or functional richness), and a metric relying on both richness and evenness (Shannon index) (Table 2). These results did not change with the data transformation applied to calculate the geometric mean abundance.

Discussion

Biodiversity trends

Based on long-term roadside monitoring data of the North American BBS, we found contrasting trends between the overall abundance of birds and the diversity of assemblages. Among the most pronounced trends was a distinct decrease in overall bird abundance, mainly driven by declines of the most abundant species. This finding is in line with the results of a recent study in Europe (Inger *et al.*, 2015), indicating that declines of common bird species constitute a widespread phenomenon. In our dataset, we observed strong declines mainly for common grassland breeders, like eastern meadowlark (*Sturnella magna*), as well as highly abundant generalists, including the common grackle (*Quiscalus quiscula*), common nighthawk (*Chordeiles minor*), chimney swift (*Chaetura pelagica*), and house sparrow (*Passer domesticus*) (Table S1). Declines of generalists as well as farmland birds have been reported before, in both North America and Europe (Donald *et al.*, 2001; De Laet & Summers-Smith, 2007; Reif, 2013). Agricultural intensification has been identi-

fied as a main driver, for example through increased drainage of grasslands, increased livestock densities, and increased use of pesticides, which reduce food availability for aerial insectivores in particular (Donald *et al.*, 2001; Newton, 2004; Reif, 2013, North American Bird Conservation Initiative U.S. Committee, 2014). Trends may have been amplified by farmland abandonment in less productive or remote areas, which occurred across much of eastern North America (Flinn & Vellend, 2005). Forest regrowth in these abandoned farmlands may, in turn, explain why the overall abundance of woodland birds has increased, in contrast to the other habitat groups (Figs 2 and 3).

In contrast to the decline in overall abundance, we found various metrics to remain stable or increase over the study period (Fig. 1–3). Because species richness, phylogenetic diversity, and functional richness are derived from species composition without any abundance weighting, the overall increases in these metrics indicate that the assemblages have been subject to colonization by new bird species with new combinations of traits or distinct phylogenies (Mouillot *et al.*, 2013). Underlying factors may include changes in habitat characteristics, shifts in species ranges, for example due to climate change, species recovery due to targeted conservation actions (e.g., forest restoration within the Conservation Reserve Program), or changes in observer skills (Böhning-Gaese & Bauer, 1996; Buckland *et al.*, 2005; Van Turnhout *et al.*, 2007; Rittenhouse *et al.*, 2012; Reif, 2013; Inger *et al.*, 2015). We cannot rule out the possibility that the proficiency of the observers has changed over the years. Yet, the BBS monitoring protocol is highly standardized, and given the large spatial and temporal scale of our analysis, we see no particular reasons for a directional observer bias.

All metrics other than overall abundance, species richness, functional richness, and phylogenetic diversity account for the proportional abundance of species or traits; hence, changes in these metrics may reflect species'

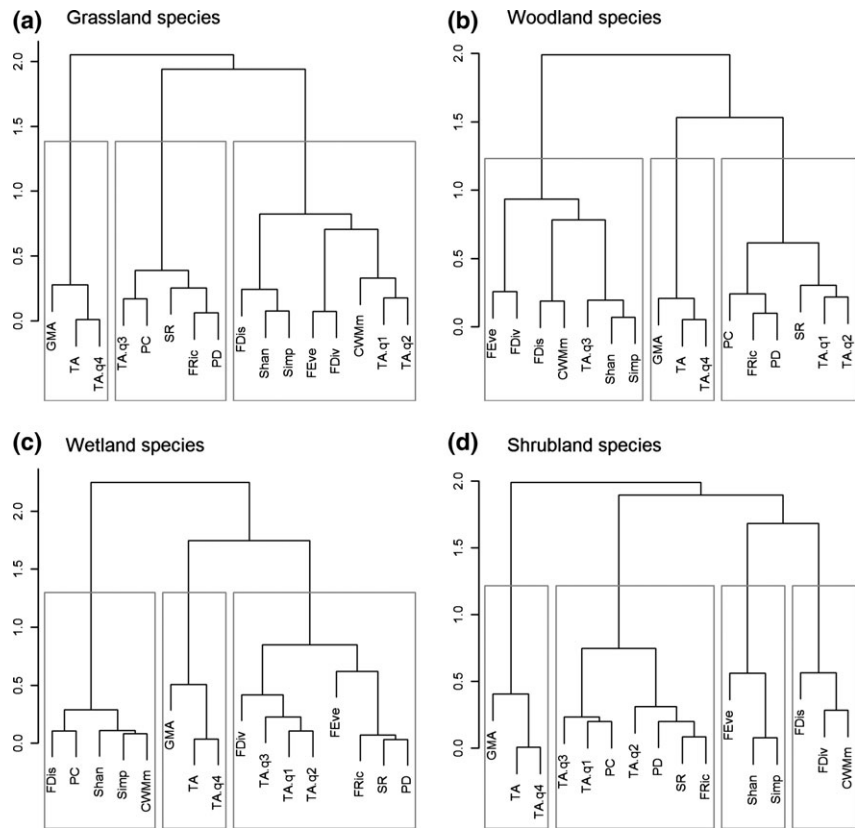


Fig. 5 Clusters of biodiversity metrics for each of the four breeding habitat groups. The number of clusters corresponds with the number of nontrivial components as identified by PCA. Full names of the metrics are provided in Table 1.

Table 2 Nonredundant key metrics best approximating the overall biodiversity changes and the corresponding cumulative proportion of variance explained. Full names of the metrics are provided in Table 1

Species group	Key metrics				Variance explained
	1	2	3	4	
All species ($n = 519$)	TA	Shan	PD	–	0.52
Species observed in all 5-year intervals ($n = 439$)	TA	Shan	PD	–	0.53
Grassland breeders	TA.q4	Shan	FRic	–	0.52
Woodland breeders	TA	Shan	FRic	–	0.54
Wetland breeders	TA	Shan	SR	–	0.56
Shrubland breeders	TA	Shan	SR	FDiv	0.58

extinctions or colonizations, changes in abundance distribution, or a combination. For the grassland birds, we observed declines in species richness and the total abundance of the common species (TA.q4), yet no changes in the Shannon or Simpson index and even increases in functional evenness and functional divergence (Fig. 2, Table 2). This illustrates how the disproportionate

decline of abundant species may yield positive trends in metrics that rely on evenness (Böhning-Gaese & Bauer, 1996). The overall increases in functional diversity and functional dispersion indicate that the declining common species are located toward the center rather than the edges of the functional trait space of the assemblages, whereas the reverse might hold for the less common species (Mouillot *et al.*, 2013). Further, the increase in community-weighted mean body mass suggests a relative increase in species with slower life histories or larger body sizes over the past decades (Reif, 2013; Inger *et al.*, 2015). Indeed, we found increases in abundance of various large-bodied species, including raptors and scavengers like hawks and vultures as well as wetland birds like geese, cranes, and cormorants (Table S1). This finding contradicts the generally positive correlation between body size and extinction risk (Gaston & Blackburn, 1995; Hilbers *et al.*, 2016) and might at least partly be explained by targeted protection and conservation measures, of which these species may have benefited in particular (Van Turnhout *et al.*, 2010, North American Bird Conservation Initiative U.S. committee, 2014). In general, richness and total abundance are more likely to be positively than negatively associated (Bock *et al.*, 2007; Hurlbert & Jetz, 2010). This seems at odds

with the opposite overall trends in richness and total abundance as we observed for all bird species together. However, the negative association between richness and total abundance breaks down when looking at particular species groups (grassland or woodland breeders; Fig. 3) or at the monitoring route scale, where richness and overall abundance turned out to represent independent (uncorrelated) dimensions (Figs 4 and 5). These findings indicate that the declines in common species and increases in less common species occurred at different locations and in response to different possible drivers (agricultural intensification versus conservation measures and forest regrowth).

To summarize, our analysis of long-term North American BBS monitoring data revealed a considerable decline in the total number of birds over the past 40 years, which coincided with stable or increasing metrics of taxonomic, functional, and phylogenetic diversity. The stable or increasing diversity metrics, including increases in mean body size and the proportion of carnivores, indicate recovery of large-bodied and carnivorous species from previously low levels ('rewilding'). Yet, the decline in total bird abundance may give rise to concern as a species' contribution to ecosystem functioning is dependent not only on its traits, but also on its numbers (Inger *et al.*, 2015). Given that the BBS is a roadside survey that covers birds only, our study does not allow to draw conclusions regarding interior habitats or other taxonomic groups. Nonetheless, our results on taxonomic diversity match three recent studies that found no net loss in local-scale taxonomic diversity based on large numbers of assemblage time series covering a variety of taxonomic groups (Vellend *et al.*, 2013; Dornelas *et al.*, 2014; Elahi *et al.*, 2015). It remains to be investigated how these results relate to biodiversity changes occurring over larger spatial scales (gamma versus alpha diversity) as well as longer time frames.

Implications for monitoring biodiversity change

The contrasting changes we observed between various diversity metrics on the one hand and the overall abundance of birds on the other hand emphasize the relevance of a multifaceted approach to monitoring biodiversity change. Our results clearly show that an exclusive focus on richness and evenness metrics might not capture all relevant aspects of biodiversity change, because these metrics might simply miss out on or even respond positively to substantial losses of individuals (Böhning-Gaese & Bauer, 1996). Thus, increasing evenness should not be considered an unambiguous indicator of greater diversity, despite it being common to do so (Magurran, 1988; Purvis & Hector, 2000; Elahi *et al.*,

2015). Our results further indicate that total abundance is more suited to capture losses of individuals than the geometric mean abundance, the latter being a composite measure of abundance and evenness and hence more sensitive to increases in the abundance or detectability of less common species.

Even a combination of metrics of total abundance, species richness, and the proportional abundance of species may not fully capture biodiversity changes, because species' replacements may go unnoticed by these metrics (Buckland *et al.*, 2005; Dornelas *et al.*, 2014). Possible solutions are to consider changes in species composition (turnover) or to include metrics of functional and phylogenetic diversity, which might be more sensitive to environmental change (Winter *et al.*, 2009; Mouillot *et al.*, 2013). Indeed, for some species groups, the set of key metrics that we identified included functional richness or phylogenetic diversity rather than species richness, indicating that the former are, in some cases, more responsive to change (Table 2). Further, our results for the wetland and shrubland breeders suggest that the community-weighted mean body mass is also indicative of changes, as this metric may change considerably even when there is little change in species richness or evenness (Figs 2 and 3). Functional diversity metrics may become even more informative if more traits are included, in particular traits that are responsive to environmental change, such as migratory behavior (Van Turnhout *et al.*, 2010). However, functional or phylogenetic diversity metrics require additional information (functional trait data, phylogenetic trees), which might be difficult to obtain in particular for taxonomic groups that are less well studied.

To summarize, we identified three main dimensions of biodiversity change (overall abundance, richness, and proportional abundance), consistent with McGill (2011), thereby observing opposing trends between overall abundance on the one hand and various diversity metrics on the other. This indicates that stable or even increasing metrics of richness or evenness may occur in parallel with substantial losses of individuals and supports the importance of population abundance as an essential biodiversity variable (Pereira *et al.*, 2013). The abundance of each species at each site is a variable that can be used to derive all possible metrics of abundance and taxonomic diversity. If this essential biodiversity variable is combined with information on the species' traits and phylogenetic positions, all other metrics used can be derived as well.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Phylogenetic diversity (PD) in relation to the number of phylogenetic trees.

Figure S2. Clusters of biodiversity metrics based on all species ($n = 519$), for different constants applied to transform the abundance data in order to calculate the geometric mean abundance.

Table S1. List of bird species and corresponding trait values.

Table S2. Mean values of the biodiversity metrics across all routes per five year interval.

Table S3. Slopes (standardized) and P -values of ordinary least squares (OLS) regression models of biodiversity metrics against time.

Table S4. Slopes (standardized) and P -values of generalized least squares (GLS) regression models of biodiversity metrics against time.

Table S5. Variance explained by the principal components, corresponding threshold values, and cumulative proportions of variance explained.