A near half-century of temporal change in different facets of avian diversity

MARTA A. JARZYNA and WALTER JETZ

1Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, CT 06520, USA,
2Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berks SL5 7PY, UK

Abstract

Assessments of spatial patterns of biodiversity change are essential to detect a signature of anthropogenic impacts, inform monitoring and conservation programs, and evaluate implications of biodiversity loss to humans. While taxonomic diversity (TD) is the most commonly assessed attribute of biodiversity, it misses the potential functional or phylogenetic implications of species losses or gains for ecosystems. Functional diversity (FD) and phylogenetic diversity (PD) are able to capture these important trait-based and phylogenetic attributes of species, but their changes have to date only been evaluated over limited spatial and temporal extents. Employing a novel framework for addressing detectability, we here comprehensively assess a near half-century of changes in local TD, FD, and PD of breeding birds across much of North America to examine levels of congruency in changes among these biodiversity facets and their variation across spatial and environmental gradients. Time-series analysis showed significant and continuous increases in all three biodiversity attributes until ca. 2000, followed by a slow decline since. Comparison of avian diversity at the beginning and end of the temporal series revealed net increase in TD, FD, and PD, but changes in TD were larger than those in FD and PD, suggesting increasing biotic homogenization of avian assemblages throughout the United States. Changes were greatest at high elevations and latitudes – consistent with purported effects of ongoing climate change on biodiversity. Our findings highlight the potential of combining new types of data with novel statistical models to enable a more integrative monitoring and assessment of the multiple facets of biodiversity.

Keywords: biodiversity, birds, detectability, functional diversity, imperfect detection, occupancy modeling, phylogenetic diversity

Introduction

Evaluations of spatial patterns of biodiversity change and their underlying causes have been identified by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as crucial for the conservation of biodiversity, long-term human well-being, and sustainable development (Cardinale et al., 2012; Díaz et al., 2015). Spatial variation and temporal changes in biodiversity are most usually assessed for taxonomic diversity (TD), often measured as species richness (La Sorte, 2006; Dornelas et al., 2014; Newbold et al., 2015). Taxonomic diversity, however, ignores the fact that communities are composed of species with different phylogenetic positions and ecological functions, often missing information regarding ecosystem functioning (Safi et al., 2011; Cardoso et al., 2014; Gagic et al., 2015) and community evolutionary history (Redding et al., 2008; Jetz et al., 2014), and thus might underestimate implications of biodiversity change to society. Indeed, acknowledging the trait-based and phylogenetic attributes of species has become a promising avenue to better address the processes responsible for spatial and temporal dynamics of species co-occurrence (Wiens & Graham, 2005; Belmaker & Jetz, 2013; Violle et al., 2014) and is increasingly seen as vital for conservation prioritization (Faith, 1992; Devictor et al., 2010; Davies & Buckley, 2011; Jetz et al., 2014). This, paired with a rapid growth in phylogenetic trees and trait compilations, has led to a growing popularity of alternative biodiversity metrics such as functional diversity (FD, reflecting the diversity of morphological, physiological, and ecological traits and often measured as the sum of branch lengths in a dendrogram representing differences among species in terms of forms or functions; Mouchet et al., 2008; Petchey & Gaston, 2006) and phylogenetic diversity (PD; reflecting assemblage evolutionary history and often captured as the sum of the branch lengths of a phylogenetic tree connecting all species; Faith, 2006).

Trends in species richness have seen conflicting reports (Gonzalez et al., 2016), with studies documenting declines (Haines-Young et al., 2003; Konvicka et al., 2006; Wilson et al., 2007; Tingley & Beissinger, 2013), increases (Menéndez et al., 2006; Kerbiriou et al., 2009;
La Sorte et al., 2009; Keil et al., 2011; Schipper et al., 2016), and no systematic change (Petchey et al., 2007; Dornelas et al., 2014) across time. Changes in taxonomic diversity, regardless of their trend, may be accompanied by changes in functional or phylogenetic diversity. In the simplest scenario, changes in TD are accompanied by equivalent changes in FD and PD; then, increases in FD and PD are simply a result of increasing number of species. Changes in FD and PD, however, often diverge from this expectation (La Sorte & Jetz, 2010a; Barbet-Massin & Jetz, 2015) (Fig. 1). We postulate that any process that leads to biodiversity change that is nonrandom or nonuniform with regard to species local functional or phylogenetic distinctness (i.e., species’ uniqueness in relation to others in a local assemblage; Jarzyna & Jetz, 2016) will directly affect cross-assocations of changes in TD, FD, and PD. For example, if species with unique trait characteristics or phylogenetic positions are disproportionately removed from an assemblage, FD and PD might be subject to larger loss than TD (Mayfield et al., 2010) (Fig. 1). Similarly, in assemblages that harbor species with large functional or phylogenetic distinctness in relation to the regional pool (i.e., assemblages that are functionally or phylogenetically overdispersed), even random species loss might result in larger loss of FD or PD relative to TD (Fig. 1).

If the loss of functionally or phylogenetically distinct species occurs together with immigration of functionally or phylogenetically common or redundant species (i.e., those not contributing novel trait or phylogenetic positions to the community), FD and PD loss may occur as TD remains constant or increases. Moreover, colonization by redundant species might lead to smaller gains in FD and PD than expected given gain in TD. Such changes in biodiversity often signal increasing biotic homogenization (i.e., increase in species similarity in space or time) (McKinney & Lockwood, 1999; Olden et al., 2004; Olden & Rooney, 2006; Clavel et al., 2011).

Conversely, gains in FD and PD without the corresponding change in TD can arise when functionally or phylogenetically redundant species are replaced by species with novel trait values or distinct phylogenetic positions (i.e., distinct species; Fig. 1). Still, assemblages with high functional or phylogenetic redundancy might be subject to larger change in TD than FD and PD as long as species losses or gains are evenly distributed with respect to trait values and phylogenetic positions. Finally, correlated shifts in all three biodiversity components are also plausible (Petchey et al., 2007; Mayfield et al., 2010).

Evaluations of spatial patterns of changes in FD and PD and their congruence with changes in TD across multiple taxonomic groups and large spatial and temporal extents are essential to detect a signature of anthropogenic impacts, inform monitoring and conservation programs, and aid decision makers (Magurran et al., 2010). However, comprehensive assessments of concurrent temporal changes in TD, FD, and PD are

![Fig. 1 Potential consequences of temporal change in taxonomic diversity (TD) for functional or phylogenetic diversity, respectively (FD/PD), for relative change ($\Delta$, %) and beta-diversity (i.e., dissimilarity or turnover, $\beta$) for a hypothetical assemblage consisting of five birds—including four functionally-redundant species (e.g., species that are small, granivorous and lower-level foraging) and one functionally-distinct species (e.g., a woodpecker, medium-sized, insectivorous and mid-level foraging). The black dashed lines indicate no relative changes in FD/PD or in TD; red dashed line indicates the $1 : 1$ relationship; $+$ and $-$ signs indicate gains and losses of species, respectively. For example, an increase in TD (TD$_{\Delta} > 0$) could either be characterized by a gain in mostly phylogenetically or functionally redundant (medium brown) or distinct (pink) diversity. Similarly, large turnover in TD might be a result of gain and loss in phylogenetically or functionally redundant (dark brown) or distinct (green) diversity.](image-url)
currently often restricted to either plants in small-scale experimental plots (Swenson, 2011; Swenson et al., 2012) or small spatial extents in disturbance-prone regions (Monoy et al., 2016). Assessments of change in functional and phylogenetic attributes of faunal communities across sufficiently large spatial and temporal scales are scarce and rarely exceed a spatial extent of small European country or a temporal span of 25 years (Kampichler et al., 2012; Petchey et al., 2007; but see Schipper et al., 2016). Consequently, our understanding of responses of biodiversity through time is incomplete.

Changes in the different biodiversity facets will not be uniform in space because their putative environmental and ecological drivers are spatially heterogeneous and assemblage responses expected to depend on environmental context (Yang et al., 2015). Recent climate change has been shown to often locally elevate species richness (e.g., Hiddink & Ter Hofstede, 2008; La Sorte & Jetz, 2010a), but this effect is expected to increase toward higher latitudes (Chapin et al., 2000; Sala et al., 2000; Barbet-Massin & Jetz, 2015) and elevations (Forister et al., 2010; Chen et al., 2011; Pauli et al., 2012) following species range shifts in these directions. Climate change is also expected to increase species’ extinction risk (Thomas et al., 2004; Urban, 2015), although evidence for variation in extinction risks across elevational and latitudinal gradients is equivocal (Deutsch et al., 2008; Dirnbock et al., 2011). Land-use change on the other hand will be of particular importance in tropical (Chapin et al., 2000) and low-elevation regions (Bravo et al., 2008). Initial predictions suggest that functional and phylogenetic attributes of assemblages might change in congruence with taxonomic diversity along geographic and elevational gradients (e.g., Del Toro et al., 2015), but empirical support is scarce.

Here, we provide a comprehensive, continental-wide assessment of changes in avian diversity over the span of nearly five decades. Our goal was to evaluate temporal changes in taxonomic, functional, and phylogenetic diversity of breeding birds across the continental United States, examine the congruence of these changes, and evaluate their variation across spatial and environmental gradients. Specifically, we test the hypothesis that TD, FD, and PD increased over time. Because increases in species richness are often associated with increased prevalence of common species (La Sorte & Boecklen, 2005; La Sorte, 2006), we further hypothesize that changes in FD and PD were on average smaller than those in TD, signaling biotic homogenization of avian assemblages. Lastly, we test the hypothesis that assemblage changes were strongest at higher latitudes and elevations, following responses of biodiversity to recent climate change (Pauli et al., 2012; Barbet-Massin & Jetz, 2015). Based on probably the most comprehensive time series addressing multiple biodiversity facets available today, and using a novel approach to control for data biases that usually impede large-scale inference, we expect the study to advance our understanding of the spatiotemporal connections between the different facets of biodiversity change.

Materials and methods

Breeding bird survey

To evaluate changes in avian diversity, we used data from the North American Breeding Bird Survey (BBS, http://www.pwrc.usgs.gov/), an avian monitoring program tracking the status and trends of bird populations. BBS data are collected annually during the height of the avian breeding season along over 4,100 survey routes located across North America. Each survey route is approximately 40 km long and contains five segments and 50 stops at approximately 800 m intervals (Sauer & Link, 2011). At each stop, observers conduct a 3-min point count during which every bird observed or heard within an approximately 400 m radius is recorded. Data collected prior to 1995 are available for each segment of a route, but not for each point. The BBS follows a standardized monitoring protocol, allowing for sound comparison of avian diversity patterns through time.

We excluded data from 1966 to 1968 because of the limited spatial coverage at the inception of the program. To reduce spatial sampling bias and improve representation of all US regions (Lawler & O’Connor, 2004), we conducted spatial sub-sampling using Bird Conservation Regions (BCRs). We removed routes from BCRs with more than 30 routes (in order of proximity to remaining routes) until all BCRs had only 30 or fewer routes. We assessed temporal changes in avian diversity in two ways: (i) an annual analysis comparing each year between 1969 and 2013 (‘annual’), (ii) a comparison of the two extreme 4-year periods, 1969–72 and 2010–13 (‘1969–2010 comparison’). For the 1969–2010 comparison, we lumped 4 years to avoid the potential effect of unusual or abnormal years. Specifically, we combined data from 1969 to 1972 (‘1969 period’) and 2010 to 2013 (‘2010 period’). For the 1969–2010 comparison, we retained routes surveyed in both periods (447 routes were available for analysis).

Following others (Dorazio & Royle, 2005), we removed from all routes records for species that were left unidentified or are generally poorly captured by the BBS survey methodology (i.e., nocturnal and crepuscular species), resulting in 494 species analyzed. Because BBS-resulting estimates of abundance might under certain circumstances be less reliable than estimates of occurrence (Tirpak et al., 2009), we used presence–absence data. We characterized each route for its median latitude and longitude, and also for its elevation (ELEV) based on the National Elevation Dataset (http://ned.usgs.gov/) averaged over each 1 km pixel intersecting the route.

Multispecies occupancy modeling

Ignoring species’ imperfect detection in the evaluation of biodiversity dynamics might cause erroneous inference (Jarzyna
& Jetz, 2016). We used multispecies occupancy models (Kéry & Royle, 2008; Icknay et al., 2014) to account for species imperfect detection in the estimates of taxonomic, functional, and phylogenetic diversity (Jarzyna & Jetz, 2016). To discern a nondetection from a point-level absence at each location, occupancy modeling techniques rely on the repeated sampling protocol (Zipkin et al., 2009). Because the BBS monitoring program does not follow the repeated sampling protocol (i.e., each BBS survey route is visited only once during each breeding season), the five segments falling within each BBS route represented ‘repeated samples’ characterizing the route (Royle & Kéry, 2007; Bled et al., 2013; Hines et al., 2014).

To account for imperfect detection across the entire time series, we ran a total of 45 multispecies occupancy models (i.e., one for each year, 1969–2013). Observed data, \( y_{i,j,k} \) for species \( i = 1, 2, \ldots, 494 \), at site \( j = 1, 2, \ldots, j \), on sampling segment \( k = 1, 2, \ldots, 5 \), were modeled as resulting from the imperfect observation of a true occurrence state, \( z_{i,j,k} \) given a probability of detection, \( p_{i,j,k} \). Because not all BBS routes were monitored each year, \( j \) varied among years. This observation process was modeled as the Bernoulli random variable \( y_{i,j,k} \sim Bern(p_{i,j,k} \cdot z_{i,j,k}) \), where \( z_{i,j} = 1 \) if species \( i \) was truly present at site \( j \), and \( z_{i,j} = 0 \) if species \( i \) was absent at site \( j \). The true occurrence state was specified as \( z_{i,j,k} \sim Bern(\psi_{i,j}) \), where \( \psi_{i,j} \) was the probability of occurrence by species \( i \) at site \( j \). We estimated probabilities of occurrence for undetected species using data augmentation following Kéry & Royle (2008). The resulting estimates of probability of species occurrence \( \psi_{i,j} \) provided an indication of the likelihood of species presence given it went undetected.

We modeled probability of occurrence as a linear function of ELEV as follows: \( \logit(\psi_{i,j}) = \beta_{0,i} + \beta_{1,i} \cdot \text{ELEV}_j \). Probability of detection was modeled as an intercept-only as follows: \( \logit(p_{i,j}) = \beta_{0,i} \), because measurements of potential detection covariates (e.g., weather conditions) were not available for each segment of the route.

Each species was fit to all detection and occurrence parameters. To avoid instances where probability of occurrence \( \psi_{i,j} > 0 \) for species that are unlikely to be present given their ecological constraints, we further constrained the model so that only species detected within a given BCR on that year could have \( \psi_{i,j} > 0 \) at a route located within that BCR. We estimated model parameters using Bayesian analysis, using program JAGS (Just Another Gibbs Sampler; http://mcmc-jags.sourceforge.net/) via \( \kappa \) (version 3.1.2; R Development Core Team 2016) using the package rjags (https://cran.r-project.org/web/packages/rjags/index.html).

### Taxonomic, functional, and phylogenetic components of avian diversity

For each route, year, and the 1969 and 2010 periods, we calculated three diversity components: taxonomic, functional, and phylogenetic diversity. We first calculated naïve versions (TD\(_n\), FD\(_n\), PD\(_n\)) based on the raw BBS route-level presence and absence data. A species was considered present if it was detected at least once along the entire BBS route, and was otherwise considered absent. For the 1969 and 2010 periods, a species was considered present if it was detected at least once during each of the 4-year periods.

TD\(_n\) was calculated simply as the sum of all species present at a given BBS route. We based estimates of functional diversity on a compilation of function-relevant traits in Wilman et al. (2014). Four trait categories representing 15 axes were included: body size, diet (i.e., proportions of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in species’ diet), foraging niche (i.e., proportional use of water below surface, in water on surface, terrestrial ground level, understorey, mid-canopy, upper canopy, and aerial), and broad habitat types (i.e., pelagic or not). We developed a master functional dendrogram for FD\(_n\) calculations following well-established approaches (Podani, 1999; Pavoine et al., 2009; Barbet-Massin & Jetz, 2015) using Gower’s distance to calculate multivariate trait dissimilarity for each pairwise combination of the 494 species in the dataset (weighting the four trait categories equally) followed by UPGMA (Unweighted Pair Group Method with Arithmetic Mean) clustering. For each BBS route, the master functional dendrogram was pruned of branches of species absent at that route, and FD\(_n\) of the assemblage was then calculated by summing up the lengths of all remaining branches (Petchey & Gaston, 2002). The calculation of PD\(_n\) followed the same procedure, but instead of a functional dendrogram, we used 10 dendrograms sampled from full pseudoposterior distribution of phylogenetic trees assembled by Jetz et al. (2012) (http://birdtree.org/). PD\(_n\) was calculated as the total branch length of tree branches averaged over the 10 phylogenetic trees, with 10 trees thought to provide a sufficiently strong initial estimate (Schippner et al., 2016).

We then derived detection-corrected estimates of taxonomic (TD), functional (FD), and phylogenetic (PD) diversity. TD was given as summed probability of species occurrence: \( \text{TD}_d = \sum_{i,j} |\psi_{i,j}\rangle \). To derive detection-corrected assemblage FD for a route, the master functional tree was first pruned of the branches for species whose \( \psi_{i,j} = 0 \). The branch lengths of each species in the remaining functional dendrogram were then weighted by the probability of species \( i \)’s occurrence at that BBS route, \( \psi_{i,j} \), as follows: All terminal branches were multiplied by \( \psi_{i,j} \), and all intermediate branches were given the weight \( w = 1 - \prod_{i=1}^{n} (1 - \psi_{i,j}) \), where \( n \) represents all species included in the node of the intermediate branch (Barbet-Massin & Jetz, 2015). The calculation of detection-corrected PD followed the same procedure, while using the full pseudoposterior distribution of phylogenetic trees assembled by Jetz et al. (2012).

To compare the novel detection-corrected estimates of biodiversity with naïve ones, we calculated detectabilities of taxonomic, functional, and phylogenetic diversity (q\(_\text{TD}_d\), q\(_\text{FD}_d\), q\(_\text{PD}_d\), respectively; Jarzyna & Jetz, 2016). q\(_\text{TD}_d\), q\(_\text{FD}_d\), q\(_\text{PD}_d\) were given by the ratio of naïve (D\(_n\)) to detection-corrected (D) biodiversity.

### Temporal change in avian diversity

For annual analysis, for each pair of consecutive years \( m \) and \( n \), we computed the relative change in diversity estimates
Temporal trends in annual TD, FD, and PD for the 1969–2010 comparison, avian assemblages saw an average increase until ca. 2000, followed by a slowdown and decrease since the mid-2000s. Average relative annual change in TD (TD\textsubscript{r}) was \(+0.75\%\) \((5\text{th} \text{ and } 95\text{th quantiles: } -0.55\% \text{ and } +2.10\%, \text{respectively})\) with 35 years of significant increase and 7 years of significant decrease. For FD and PD, mean annual changes were +0.72\% and +0.61\%, respectively, with similar periods of significant increase (35 and 34 years) and decline (7 and 9 years).

Null models

Functional and phylogenetic diversity are closely associated with TD. We therefore generated a null model expectation for each BBS route to evaluate deviation of observed 1969–2010 comparison changes in FD and PD from those expected given in-change in TD. For the null model addressing relative change (\textit{NULL\textsubscript{r}}), we developed expected TD\textsubscript{r}, FD\textsubscript{r}, and PD\textsubscript{r} given observed TD\textsubscript{r} by randomly reshuffling values of probabilities of occurrence across the subset of species of the given assemblage, thus keeping route-level TD constant (Barbet-Massin & Jetz, 2015). For a second null model addressing temporalturnover and dissimilarity (\textit{NULL\textsubscript{TD,DIS}}), we generated a null distribution of expected FD\textsubscript{DIS}, PD\textsubscript{DIS} from the expected mean values resulting from the respective null distribution.

Results

Temporal change in avian diversity

We found significant \((P < 2 \times 10^{-6})\), Fig. 2) trends across time in the three detection-corrected biodiversity facets – TD, FD, and PD – with a continuous annual increase until ca. 2000, followed by a slowdown and decrease since the mid-2000s. Average relative annual change in TD (TD\textsubscript{r}) was +0.75\% \((5\text{th} \text{ and } 95\text{th quantiles: } -0.55\% \text{ and } +2.10\%, \text{respectively})\) with 35 years of significant increase and 7 years of significant decrease. For FD and PD, mean annual changes were +0.72\% and +0.61\%, respectively, with similar periods of significant increase (35 and 34 years) and decline (7 and 9 years).

To test for basic geographic, environmental, and biotic patterns of avian diversity change, we evaluated variation in annual and 1969–2010 diversity change along gradients of elevation, latitude, longitude, and taxonomic diversity. To test for relationships between change metrics and environmental covariates, we fit a multiple linear regression using generalized least squares with the \textit{nlme} package (https://cran.r-project.org/web/packages/nlme/index.html). We evaluated residuals of all models for spatial autocorrelation and found spatial autocorrelation to be present. We thus included a Gaussian spatial correlation structure in all models to account for spatial autocorrelation in model residuals. Partial regression coefficients provided an indication of the effect of a given environmental or biotic factor on avian diversity change. 

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similar for FD (mean $FD_{\Delta} +11\%$, quantiles $-8\%$ and $+29\%$) and PD (mean $PD_{\Delta} 10\%$, quantiles $-9\%$, $+30\%$).

Taxonomic diversity exhibited considerable turnover among years, with an average annual $TD_{\text{TUR}}$ of 0.18 and a value of 0.17 for the 1969–2010 comparison (Fig. 3). Dissimilarity of TD, $TD_{\text{DIS}}$, which is based on Sørensen dissimilarity and not independent of species richness, was 0.21 and 0.23 for the annual and 1969–2010 comparison, respectively (Fig. S1.1). $PD_{\text{TUR}} | DIS$ and $FD_{\text{TUR}} | DIS$ were overall stronger than TD with values ranging from 0.26 to 0.32 for the annual and 1969–2010 comparisons (Fig. 3). Across time, periods of TUR and DIS decrease and increase varied and showed limited consistency (Fig. S1.1).

**The effect of detectability**

As expected given the nature of the raw data and previous work (Kéry & Royle, 2008; Zipkin et al., 2012), we found that accounting for imperfect detection was critical for appropriately capturing spatial and temporal diversity trends (Appendix S2). Our study allowed extending the measurement of diversity detectabilities, $q$, to different biodiversity facets, and we found values of 0.91, 0.87, and 0.88, for $q_{TD}$, $q_{FD}$, and $q_{PD}$, respectively. This and the finding that detectability of diversity tended to be higher in high-diversity communities suggest that our approach enabled more reliable estimates and decreased potential biases (Figs S2.1 and S2.2). Temporal metrics of community change – that is, $\Delta$, TUR, and DIS – were also biased by imperfect detection, with $\Delta$ generally being overestimated and TUR and DIS being underestimated when imperfect detection was ignored, especially at sites with low levels of turnover and dissimilarity (Fig. S2.3). Estimates of temporal change in FD and PD were biased more than the estimates of change in TD (Fig. S2.3).

**Congruence among metrics and facets of change**

Both annual and 1969–2010 comparison relative changes, $\Delta$, in TD, FD, and PD were positively associated with one another (Fig. 4). However, a given change in community TD did not result in an equivalent change in FD or PD, as indicated by the slope of significantly $<1$ (Fig. 4, Appendix S3). Loss in TD was generally associated with smaller loss in FD and PD – of the 98 sites that underwent decreases in TD, 47 | 41 saw smaller and 12 | 17 saw larger absolute declines, while 39 | 30 saw increases in FD | PD despite declines in TD (Fig. 4, Appendix S3). Of sites that gained TD, 163 | 151 saw larger and 179 | 176 saw smaller gains, while 7 | 22 saw declines in FD | PD despite increases in TD (Fig. 4, Appendix S3). In almost all assemblages,
TUR and DIS of FD and PD exceeded that observed for TD, with a slightly higher discrepancies at lower levels of TD\text{\textsubscript{TUR}} and TD\text{\textsubscript{DIS}} (Fig. 4, Appendix S3). Δ declined with TUR, but showed no relationship with DIS (Appendix S3).

**Geographic variation in change**

We evaluated variation along gradients of elevation, latitude, longitude, and taxonomic diversity to test for basic geographic, environmental, and biotic patterns of avian diversity change. We found that the annual and 1969–2010 comparison Δ, TUR, and DIS in all three biodiversity facets were higher in more northerly regions (Fig. 5). Annual and 1969–2010 comparison TUR and DIS were higher at higher elevations (Fig. 5). The effect of elevation on TUR and DIS was stronger than its effect on Δ, indicating that turnover in community composition varied along elevation more than diversity loss or gain. Species-poor assemblages saw much greater Δ, TUR, and DIS in all biodiversity facets (Fig. 5), suggesting a distinct functional and phylogenetic change resilience provided by high species richness. Including Gaussian spatial correlation structure in all models removed spatial autocorrelation from model residuals (Appendix S4).

**Distinct signals of FD and PD change**

We finally asked the question of where along spatial and environmental gradients Δ, TUR, and DIS in FD and PD for the 1969–2010 comparison were indeed much outside expectations from concomitant patterns in TD. Observed FD\text{\textsubscript{Δ}} was generally lower than expected given the change in species richness (TD\text{\textsubscript{Δ}}), with these deviations greater at lower latitudes but not significantly varying with elevation (Fig. 6). In contrast, FD\text{\textsubscript{TUR}} and FD\text{\textsubscript{DIS}} were generally greater than expected from turnover and dissimilarity in species richness (Fig. 6, Appendix S5) and increased significantly toward higher latitudes (Fig. 6, see also Appendix S5). Thus, while given changes in species make-up resulted in particularly high FD losses in southern assemblages, it caused especially high turnover in FD in northern assemblages.

Observed PD\text{\textsubscript{Δ}} was in most locations substantially higher than expected from changes in species richness (TD), while PD\text{\textsubscript{TUR}} and PD\text{\textsubscript{DIS}} were on average slightly
lower than expected (Fig. 6, Appendix S5). The magnitude of PD given TD declined steeply with elevation and also with latitude (Fig. 6), indicating that many low-elevation and southerly assemblages underwent PD gains exceeding TD expectations. These same assemblages also saw smaller turnover than expected given turnover in TD (Fig. 6).

Discussion

The understanding of both the processes underpinning spatiotemporal species co-occurrence and the ecosystem consequences substantially benefits from reliable information about multiple biodiversity facets over large scales. Comprehensive evaluations of changes in the different components of biodiversity and their congruence, however, have been rare. We sought to provide such a complete assessment of changes in all three facets for the diversity of nearly 500 species and nearly five decades, made possible by a novel extension of methods addressing imperfect detection.

Declines (Konvicka et al., 2006; Wilson et al., 2007; Tingley & Beissinger, 2013), increases (Kerbirdiou et al., 2009; Keil et al., 2011; Schipper et al., 2016), and no systematic change (Petchey et al., 2007; Dornelas et al., 2014) in biodiversity across time have to date been reported. This inconsistent signal of biodiversity change might be a consequence of differences in study design, taxa, species composition, regional environmental conditions, or spatial and temporal extents and grains considered in each of the studies (Gonzalez et al., 2016). Despite an average increase in avian diversity across the conterminous United States since 1969, the changes were neither spatially homogenous nor constant across the temporal span considered in our study. Avian diversity increased steadily until the early 2000s, followed by a slowdown and decline.

Changes in land cover (Mayfield et al., 2010; Jørgensen et al., 2016), introduction of exotic species (Sax & Gaines, 2003, 2008), anthropogenic climate change (Menéndez et al., 2006; La Sorte & Jetz, 2010a; Jørgensen et al., 2016), and targeted conservation actions and federal efforts to restore critical habitats (King et al., 2006) might all have contributed to the observed increases in avian diversity. Similar increases were recently reported by Schipper et al. (2016) for a slightly shorter
version of the BBS dataset; that study, however, did not detect declines in biodiversity over the last decade. This may be due to their consideration of only pre-2010 data, use of 5-year instead of annual time intervals for diversity measurement, and also be affected by the use of raw instead of detection-controlled diversity values. The recent declines might be attributed to a number of factors, including anthropogenic climate change (Both et al., 2006, 2009; Saino et al., 2011), intensification of agricultural systems (Schaub et al., 2010), and the increased use of neonicotinoid insecticides (Hallmann et al., 2014). Whether the last decade’s avian diversity loss signals the beginning of a more drastic decline or is just an anomaly in the otherwise positive trend remains to be seen.

Large losses in taxonomic diversity were generally accompanied by disproportionately smaller losses in functional or phylogenetic diversity, indicating that on average lost species did not hold unique trait-based or phylogenetic positions relative to other species in the assemblage. However, as the absolute loss of species richness became smaller, functional and phylogenetic diversity increased – a likely result of replacement of functionally and phylogenetically redundant species with unique ones. Furthermore, small gains in taxonomic diversity were often associated with larger gains in functional or phylogenetic diversity, though as gains in taxonomic diversity became larger, we observed a decline in the corresponding gains in functional and phylogenetic diversity. Thus, the contribution of colonizing species to functional or phylogenetic attributes of the assemblage declined as number of colonizing species increased, suggesting functional and phylogenetic redundancy of species-rich assemblages (Cardoso et al., 2011; Mouillot et al., 2014; Swenson et al., 2016). Changes in functional diversity were also lower than what would have been expected given the concomitant changes in taxonomic diversity, although the same did not hold true for phylogenetic diversity. Collectively, our results indicate that – despite increasing diversity – avian assemblages across the United States underwent functional homogenization. This is in line with previous findings for birds in the United States (La Sorte & Boecklen, 2005; La Sorte et al., 2009) and as well as other regions and taxonomic groups (Menéndez et al., 2006; Kerbiriou et al., 2009; Clavel et al., 2011; Baiser et al., 2012; Magurran et al., 2015), and has been primarily attributed to environmental disturbance and introduction of exotic species (Olden et al., 2004; Olden & Rooney, 2006). Intriguingly, biodiversity change was larger in species-poor assemblages, suggesting a distinct resilience of functional and phylogenetic diversity.
Changes in assemblage composition – in terms of both species identities and their trait and phylogenetic positions – were more pronounced at higher elevations and latitudes. Global change is indeed expected to disproportionately affect biodiversity in higher latitudes (Parmesan & Yohe, 2003; La Sorte & Jetz, 2010b; Chen et al., 2011), although empirical research to date provides equivocal evidence for disparate biodiversity changes across elevational gradient (Stralberg et al., 2009; Tingley & Beissinger, 2013; Jarzyna et al., 2015). Several, not mutually exclusive, factors might be driving the geographic variation in avian diversity change. First, losses in species at high elevations and latitudes might have been replaced by upward and poleward shifts of species with different trait and phylogenetic positions, caused by changing habitat and climatic conditions. Given that land-use change in the 20th century has occurred mostly at low elevations (Bravo et al., 2008), we suggest that changes in climatic conditions, rather than land cover, were the main deterministic factor driving the compositional turnover in avian assemblages at higher elevations and latitudes. Moreover, responses to changing climatic conditions might show within-species variation. For example, species’ trends within their range might be both positive and negative (Stephens et al., 2016), causing geographic variation in the assemblage dynamics. We consider it plausible that individuals at higher latitudes responded more strongly to changing environmental conditions than those at lower latitudes, thus contributing to the observed spatial variation in change.

Alternatively, elevational and latitudinal diversity gradients – that is, decreases in species richness toward mountain tops and the poles (McCain, 2005; Mittelbach et al., 2007; Rowe, 2009; Sanders & Rahbek, 2012) – might explain observed patterns of high compositional change. Compositional change generally increases with low species richness and low abundance because small local population sizes increase the effect of demographic or environmental stochasticity (Gaublomme et al., 2014). Using a turnover index mostly independent of species richness, however, the potential bias resulting from the elevational and latitudinal diversity gradients was, at least partially, accounted for. Taken

**Fig. 6** Effects of elevation and latitude on the null-model corrected relative change (Δ, %) and turnover (TUR) in (a) functional (FD$_\Delta$ and FD$_{\text{TUR}}$) and (b) phylogenetic (PD$_\Delta$ and PD$_{\text{TUR}}$) diversity for the 1969–2010 comparison. Points show the deviations of changes at individual routes from that expected given the change in taxonomic diversity (TD), with black highlighting statistically significant deviations (P < 0.05). * indicates a significant (P < 0.05) association with the environmental gradient. For example, the assemblage circled in red underwent significantly lower and higher than expected relative change and turnover in FD, but changes in PD did not significantly differ from the expectation.

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together, our results suggest that the elevational and latitudinal gradient in temporal dissimilarity and turnover are likely a result of climate change-induced losses of high-elevation and high-latitude species and upward poleward shifts of species from lower elevations and latitudes.

Detection-related biodiversity underestimation has been demonstrated for taxonomic diversity (Zipkin et al., 2012; Tingley & Beissinger, 2013), but – beyond a conceptual exploration by Jarzyna & Jetz (2016) – never for functional or phylogenetic diversity. Here, the detectability of taxonomic diversity was higher than detectability of functional and phylogenetic diversity. Factors that might have contributed to differences in detectabilities among biodiversity attributes include different probability of detection of species with distinct or redundant trait and phylogenetic positions, functional or phylogenetic assemblage structure, spatial grain, and data resolution (Jarzyna & Jetz, 2016).

Imperfect detectability of biodiversity will result in erroneous representation of biodiversity change across both space and time. Here, the estimation bias was larger for changes in functional and phylogenetic diversity than taxonomic diversity, with biodiversity loss being overestimated and biodiversity gain and compositional changes underestimated. Species imperfect detection, when unaccounted for, will thus exert a significant and differential influence not only on different biodiversity facets but also on different metrics of biodiversity change, ultimately impeding or misleading conservation efforts. Recognizing and accounting for potential detection-related biases in studies of biodiversity dynamics should be given careful consideration, particularly if the study spans large spatial and temporal extents and encompasses a wide range of different species with varied characteristics in terms of their trait-based and phylogenetic position (Jarzyna & Jetz, 2016).

It was logistically impossible to consider in our study the entire spectrum of potential within-species trait variation (Jetz et al., 2009; Bolnick et al., 2011; Carmona et al., 2016). Moreover, functional characteristics of some species might be plastic (Rosenblatt et al., 2016), allowing species to adjust to changing environmental conditions across time. We posit, however, that variation in trait values across time or within species – and thus potential for bias – will decline with the resolution of the trait information. Given the relatively coarse resolution of trait data considered here, we find it unlikely that functional characteristics would have displayed large variation across time or within species, and thus bias our inferences and conclusions.

Our findings provide new insights into the drivers of temporal change in different avian diversity facets and have significant implications for conservation theory and practice. We found that avian diversity across the contiguous United States increased across the past nearly five decades, although the most recent decade saw declines in all three facets of biodiversity. While unclear whether the last decade’s diversity loss signals the beginning of a more drastic decline, we stress the need for active and extended monitoring and assessment to support timely management and conservation actions. Changes were the most pronounced in high-elevation and latitude regions consistent with effects of ongoing anthropogenic climate change on biodiversity. Lastly, changes in functional and phylogenetic attributes were rarely congruent with those in taxonomic diversity and expose increasing biotic homogenization of avian assemblages throughout much of the North American continent. Our findings highlight both the need and potential for more integrative monitoring and assessment of the multiple facets of biodiversity and their respective changes.

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