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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Temporal changes in bird functional diversity across the United States

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Abstract Global changes are modifying the structure of species assemblages, but the generality of resulting diversity patterns and of their drivers is poorly understood. Any such changes can be detected and explained by comparing temporal trends in taxonomic and functional diversity over broad spatial extents. In this study, we addressed three complementary questions: How did bird taxonomic and functional diversity change over the past 40 years in the conterminous United States? Are these trends non-linear? Can temporal variations in functional diversity be explained by broad-scale changes in climate and vegetation productivity?

We quantified changes in taxonomic and functional diversity for 807 bird assemblages over the past four decades (1970–2011) considering a suite of 16 ecological traits for 435 species. We found increases in local bird species richness and taxonomic equitability that plateaued in the early 2000's while total abundance declined over the whole period. Functional richness, the total range of traits in an assemblage, increased due to the rising prevalence of species with atypical life-history strategies and under-represented habitat or trophic preferences. However, these species did not trigger major changes in the functional composition of bird assemblages. Inter-annual variations in climate and primary productivity explained the richness of bird life-history traits in local assemblages, suggesting that these traits are influenced by broad-scale environmental factors, while others respond more to more local drivers. Our results highlight that a comparative analysis of the multiple facets of functional diversity can raise novel insights on processes underlying temporal trends in biodiversity.

Keywords Breeding bird survey · Climate · Community dynamics · Ecological traits · NDVI · Non-linear trends

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Introduction

The past two decades have seen an upsurge in biodiversity monitoring programs in response to increasing awareness of the ecological consequences of global changes (Pereira and David Cooper 2006; Cardinale et al. 2012; Hooper et al. 2012). The proliferation of these long-term datasets across locations and over multiple spatial extents has opened a debate on the generality of biodiversity declines across spatial and temporal scales (Dornelas et al. 2014; Gonzalez et al. 2016). However, the fact that biodiversity may vary

non-linearly over time and with strong scale-dependency complicates estimates of large-scale ecological changes (Dornelas et al. 2012; McGill et al. 2015) and renders the identification of the underlying environmental drivers especially challenging (Korhonen et al. 2010). Adding to this complexity, the multiple facets of biodiversity often vary asynchronously. Comparing variations of the taxonomic, functional and phylogenetic definitions of diversity over large spatial extents and long time frames has emerged as a fruitful opportunity to overcome these challenges (Monnet et al. 2014; Jarzyna and Jetz 2016a). How and why the multiple facets of biodiversity change across time and space therefore deserves comparative assessments across multiple taxa and locations.

Whether or not anthropogenic disturbances result in widespread declines in biodiversity depends on the taxa of interest and the scale of observation (McGill et al. 2015). A global analysis of biodiversity trends across a range of taxonomic groups found that taxa substitutions within local assemblages were more common than systematic losses in diversity (Dornelas et al. 2014). However, the extent to which these substitutions involved species that share redundant functional traits (sensu largo, any phenotypic characteristic corresponding to species' response and/or species' impact on their environment, Violle et al. 2007) remained unclear in this study. This question is critical to assess whether biodiversity changes are associated with modifications of ecosystem functions (Schleuning et al. 2015), and suggests the need to complement taxonomic diversity (species richness in its rawest version) with measures of functional diversity (Petchey and Gaston 2006; Cadotte et al. 2011).

In recent years, a wide array of functional diversity indices has been developed to quantify either the total range of traits within assemblages, their dispersion, or the evenness of individual or species distributions in a functional space (Carmona et al. 2016). Beyond the challenge of interpreting patterns of variations in these multiple indices, a fundamental issue lies in choosing a suitable set of functional traits (Petchey and Gaston 2006; Villéger et al. 2008). A first approach has been to accumulate a comprehensive matrix of traits that measure the different facets of species' niches so that functional diversity provides a holistic picture of the variety of the ecological strategies that co-occur in an assemblage (e.g., Devictor et al. 2010; Monnet et al. 2014). This approach is useful in generating integrative indices for purposes of monitoring or measuring community-level changes in biodiversity. Unfortunately, such holistic indices are impaired by their indirect biological interpretability and non-causal correlations among traits. Alternatively, focusing on a selected number of traits that reflect well-defined components of the niche—such as trophic or habitat preferences—improves interpretability at the cost of generality

and increased subjectivity (Petchey and Gaston 2006). Identifying congruencies and discrepancies in functional diversity indices based on all or a priori defined components of the niche may be especially helpful to identify which aspects of species' ecology underpin changes in the composition of species assemblages over space or time (Cisneros et al. 2015).

The dynamics of species assemblages are driven by an interaction between environmental factors and variability in species' functional characteristics (Violle et al. 2007; Soininen 2010). Comparing variations in functional and taxonomic diversity, therefore, improves both our understanding and ability to predict diversity dynamics as it reflects the extent to which assemblages are dominated by deterministic or stochastic processes (Purschke et al. 2013; Lamanna et al. 2014). Most studies that addressed incongruences of taxonomic and functional diversity over broad geographic scales have investigated spatial patterns (e.g., Devictor et al. 2010; Keil et al. 2015), but their results may not easily be transferable to temporal trends (Soininen 2010; Magurran et al. 2010). This limitation has been repeatedly pointed out and has been used as a central justification to claim for more broad-scale quantifications of temporal functional diversity trends and of their relations with human-induced global changes (Lavorel and Garnier 2002; Mc Gill et al. 2006; Cadotte 2011), Nevertheless, such assessments remain scant due to the lack of suitable temporal datasets and limitations in modeling (Magurran et al. 2010). This is a major research gap as quantifying temporal functional diversity trends is critical to assess the dynamics of ecological processes over time and inform stakeholders on the impacts of increasing anthropogenic influences on biodiversity (Magurran and Dornelas 2010). Furthermore, temporal trends may permit more direct inference on processes underlying species assemblages than spatial patterns (Dornelas et al. 2012).

Over 10 years ago, a continental-level assessment of 35-year trends in the taxonomic composition of local bird assemblages in the United States revealed an increase in species richness, coupled with a tendency towards less taxonomically even assemblages (La Sorte and Boecklen 2005). These temporal trends exhibited spatial patterns, suggesting influences of local habitat and climatic gradients (La Sorte and Boecklen 2005; Stegen et al. 2013). Recently, this study was updated and taxonomic trends were compared with their functional counterparts (Jarzyna and Jetz 2016b; Schipper et al. 2016). Schipper et al. (2016) found continent-wide linear increases or stability in species richness mirrored by diet- and habitat-based assessment of functional diversity in North American Birds. However, they did not explore other niche dimensions (such as breeding strategies and migratory status), non-linear trends and their spatial heterogeneity. Jarzyna and Jetz (2016b) showed that taxonomic and functional bird diversity trends were congruent and non-linear over the

last four decades, with a first period of increase followed with a stabilization or decline in the 1990s. This study also showed that these trends were heterogeneous across geographic and topographic gradients. Yet, they did not compare them with temporal variations in environmental correlates. Species' responses to environmental dynamics and the resulting changes in diversity are ultimately driven by local processes. The broad-scale temporal variability of climate, vegetation productivity or other factors influence may synchronize changes in species assemblages over time through effects on population dynamics (Blenckner and Hillebrand 2002; Jones et al. 2003). In this new comparative study on US bird assemblages, we question whether these broad-scale sources of environmental variation can be invoked to explain congruencies and discrepancies in the temporal changes of bird taxonomic and functional diversity.

Our over-reaching aim was to quantify recent (1970–2011) trends in several complementary measures of bird taxonomic and functional diversity in the US and to investigate their broad-scale environmental correlates across time. We addressed four specific questions:

1. How have the multiple facets of bird taxonomic and functional diversity changed over the past 40 years? We predicted increases of the trait range (functional richness), spread (functional dispersion) and regularity (functional evenness) within the functional space of local assemblages, associated with previously observed increases in species richness and taxonomic evenness (La Sorte and Boecklen 2005; Schipper et al. 2016).

2. Are these trends non-linear? We expected to find that both taxonomic and functional diversities would level-off since the 1990s as reported by Jarzyna and Jetz (2016b), and explored the consistency of this pattern across indices. Furthermore, we investigated the existence of breakpoints to find out whether extreme events (e.g., abnormally warm summers or cold winters) could have left a signature in bird diversity trends (Jiguet et al. 2011).

3. Are these patterns consistent across ecological, life-history and reproductive traits? These groups of traits correspond to different dimensions of the niche which may not be associated with the same environmental changes (Cisneros et al. 2015). In particular, we expected a decrease in the diversity and evenness of traits related to habitat and resource use as a broad-scale signal of increased anthropogenic disturbance (Devictor et al. 2008; Flynn et al. 2009).

4. To what extent do continental-level variations in climate and vegetation productivity explain temporal variations in functional diversity? Continent-scale changes in temperature, precipitation, seasonality and primary productivity, either due to recent climate changes or natural climatic variability, modify species' distributions and the resulting species assemblages (Blenckner and Hillebrand 2002; Evans et al. 2006). We especially expected that the diversity of traits related to life-history and reproduction (migratory strategy, body mass, brood size and clutch size) would be correlated to large-scale variations in temperature and precipitations. We also expected that variations in primary productivity would better explain diversity in birds' habitat and dietary preferences.

Materials and methods

A graphical overview of the methodological workflow is provided in Supplementary Material 1.

Study area

We compiled data from the USGS North American Breeding Bird Survey (BBS), a long-term volunteer-based program aimed at monitoring the population dynamics of common breeding birds along randomly selected routes over a continental extent (Sauer et al. 2011, data and protocol at http://www.pwrc.usgs.gov/bbs/). We excluded Alaska due to weak BBS coverage and because the Alaskan bird assemblage differs markedly from that of conterminous United States. Although the BBS started in 1966, we removed the first 4 years due to insufficient sample size and spatial coverage. We ended our time window in 2011 as sample size decreased markedly in subsequent years. We removed first-year observer effects by excluding the first survey performed by a given observer on a given route (following Kendall et al. 1996). Finally, we restricted our analyses to the 807 routes that were monitored at least 8 years and once every 5 years over 1970–2011 (Fig. 1). Thus, in spite of missing data (mean = 4 missing years per route ± 3 SD, 5% of the 807 roads had more than 11 missing years, 104 had no missing years), we ensured that the temporal coverage of each route was sufficient for estimating temporal trends. The number of routes peaked to 775 in 1973 and remained roughly constant until the end of the 1990s, then declined down to 646 in 2011. However, variation in sample size across years should have limited effects on continental trends as geographic coverage remained constant over the time span (Supplementary Material 2).

Bird sampling

In the BBS, local bird assemblages are surveyed within 24.5-miles route sections on which point counts evenly spaced by 0.5 miles are monitored by trained observers once per year in June. At each point, all individual birds seen or heard in
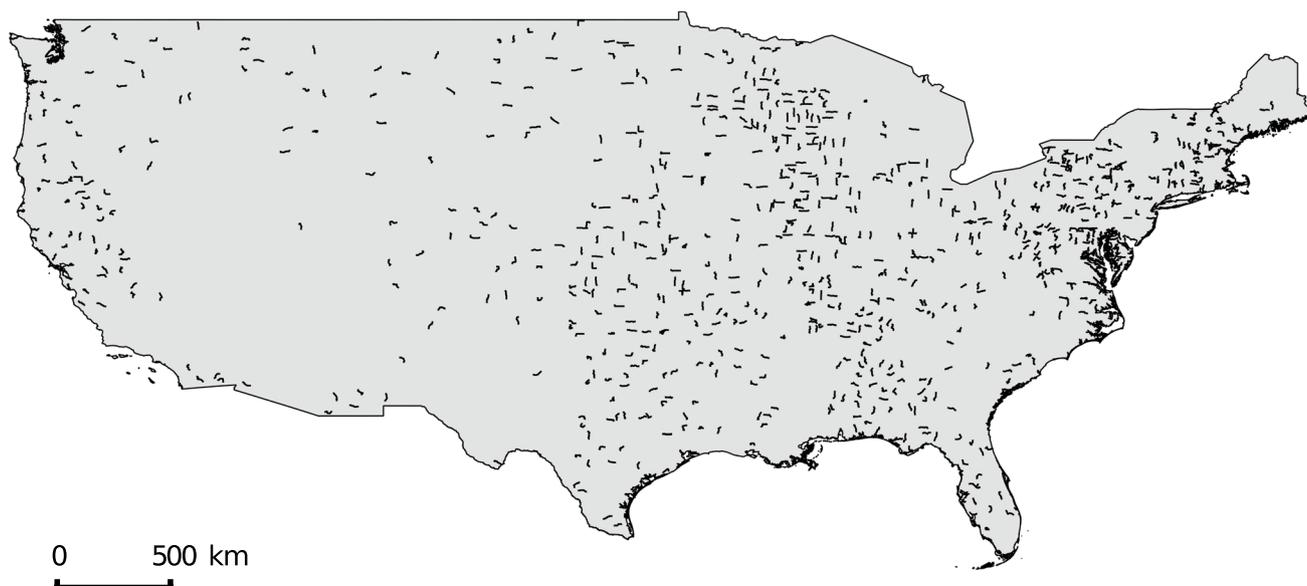
Fig. 1 The breeding bird survey routes used in our study (*n* = 807)

a 400 m radius have to be recorded during a 3-min point count and the whole route has to be sampled in about 5 h in the early morning while avoiding adverse weather. A total of 435 bird species were sampled on the 807 routes during the 42 survey years, after excluding 87 coastal, pelagic and species which accounted together for less than 1% of the records (list of routes and species in Supplementary Material 3).

We used species-level bird counts as an index of local bird abundance. We acknowledge that detection error may lead to underestimating the true diversity of an assemblage, especially if detectability is non-random relative to species' traits or phylogeny (Jarzyna and Jetz 2016a). Although bird counts are sensitive to detection error (Royle and Dorazio 2008), they cannot be properly corrected in the temporal frame of our study without making the unreasonable assumption that point counts or segments along a BBS route are replicates of a closed, spatially homogeneous bird assemblage. In a previous study, using occupancy models to account for imperfect detection increased noise, but did not substantially change estimates of temporal trends in functional diversity (Jarzyna and Jetz 2016b). Therefore, we relied on the assumption that the temporal variation in species' abundances within a route and the resulting diversity changes are correctly reflected by raw counts, which sounds reasonable over the continental extent of our study.

Environmental covariates

We retrieved climatic data from an interpolated 4 × 4 km grid calibrated on weather stations from the PRISM Climate Group (Oregon State University, http://www.prism.oregonstate.edu/). We computed the annual mean temperatures and cumulated precipitations over the breeding season and the annual temperature and precipitation seasonality (April–July) for the study extent (dismo R package, Hijmans et al. 2017). We also retrieved the growing season Normalized Difference Vegetation Index (Time Integrated NDVI from http://phenology.cr.usgs.gov) as a measure of annual variations in vegetation productivity at a continental level. We used these variables as proxies of the multiple environmental processes that may influence trends in local bird diversity across a continent, such as consistent and synchronic changes in climate, habitat suitability, resource availability and phenology. Therefore, we averaged these variables each year across the conterminous United States, and used them as covariates in the subsequent statistical modeling. Temperature, precipitations, their seasonality and NDVI exhibited low collinearity according to Pearson's correlations (maximum = 0.29 between temperature and precipitations). We discarded several other possible covariates (minimum and maximum temperatures) due to their high correlation (> 0.7) with temperature or NDVI.

Taxonomic diversity

We monitored temporal changes in taxonomic diversity with three complementary indices classically used in similar studies (e.g., La Sorte and Boecklen 2005): species richness (total number of species recorded on a route and year), total abundance (total count of individuals per route and year, log-transformed for normalization) and Pielou's taxonomic

evenness (Shannon's index relative to its maximum theoretical value, Legendre and Legendre 2012).

Ecological traits

We compiled 16 ecological and life-history traits for the 435 species from the Encyclopedia Of Life (http://www.eol.org), the Animal Diversity Web (http://www.animaldiversity.org) and the field guide to North American birds (Sibley 2014). The full species × trait matrix is provided in Supplementary Material 3. We grouped these traits into three categories:

- Ecological traits (primary habitat, nest location, foraging strategy, main diet): these traits reflect the extent to which species overlap in their use of habitat and food resources;
- Life-history traits (territoriality, migration, developmental mode, log-transformed body mass, wingspan, body length): these traits separate sedentary species with large body sizes and large home ranges from smaller, usually migratory species with smaller territories;
- Reproductive traits (number of broods per year, clutch size, mating, chick-rearing mode, maximum lifespan): these traits are related to breeding performances and duration of life cycle.

Functional diversity indices

We first summarized the 16 traits in a Principal Coordinates Analysis (PCOA) based on a species x species Gower's dissimilarity matrix (Laliberté and Legendre 2010). The distances between species pairs on the eight first components of this ordination were sufficient to provide an unbiased representation of the initial distance (Supplementary Material 4; Maire et al. 2015). We used species' coordinates on these eight components to build an eight-dimensional convex hull from which we computed three complementary functional diversity indices for each BBS route and year (Villéger et al. 2008; Laliberté and Legendre 2010):

- Functional richness (FRic) is the amount of the functional space filled by a given bird assemblage on a given year irrespective of species' abundances, and as such represents the rawest possible multivariate measure of functional diversity;
- Functional dispersion (FDis) is an abundance-weighted complement to FRic which quantifies the spread of species relative to the centroid of the functional space;
- Functional evenness (FEve) quantifies the regularity of species' abundance distribution in the functional space, as a trait-based equivalent to taxonomic evenness.

We computed these three indices from the complete matrix of 435 × 16 traits (hereafter "generic functional diversity") as well as separately for ecological, life-history and reproductive traits.

Temporal trends in taxonomic and functional diversity

We modeled bird diversity trends over the 1970–2011 time-frame in search of possible non-linearities or breakpoints common to taxonomic and functional indices. We considered 12 response variables: three taxonomic diversity indices: species richness, log(total abundance), evenness; nine functional diversity indices: FRic, FDis and FEve for all traits, ecological traits, life-history traits and reproductive traits. We scaled all these response variables to null mean and unit standard deviation prior to modeling in order to facilitate direct comparisons among them.

We first used generalized additive mixed models (GAMM, Wood 2006) assuming a gaussian distribution for all response variables. In these models, trends were quantified by a continuous penalized spline with a degree of smoothness estimated by generalized cross validation (constrained to a maximum of 4 to avoid unjustified complexity). Exploratory analyses showed that splines were systematically better than linear or quadratic models based on Akaike's Information Criterion (AIC). We further added scaled species richness as a spline covariate in all models with FRic, FDis or FEve as the response variable to correct statistically the sampling-mediated positive relationship between the number of species and the trait range in an assemblage (although it is less stringent for FDis, Laliberté et al. 2010). We added a random "route" effect on the intercept to account for count replication across years within each BBS route, and controlled residual spatial autocorrelation with an unconstrained two-dimensional (latitude, longitude) spline. Eventually, we controlled for temporal autocorrelation in response variables among successive years with a first-order autoregressive structure, selected over more complex structures (ARMA and higher orders) on the basis of AIC and graphical checks (Zuur 2011). Note that these models accommodate missing data (i.e., missing bird records on a given route, a given year), which should furthermore have a limited influence on our results as we ensured that extant data were homogeneously spread over the period on each route.

We supplemented this first analysis with piecewise regression models (Muggeo 2008) to identify the possible temporal breakpoints in diversity trends. To this aim, we had to simplify the models substantially as compared with GAMMs because the current implementations of piecewise regressions do not incorporate random effects and error correlation structures. We, therefore, fitted a piecewise regression model

for each response variable against a linear "year" covariate with no a priori assumption on the number of breakpoints, and used Davies test to assess the significance of estimated breakpoints at a 0.05 error risk (Davies 1987).

Statistical relationships with environmental covariates

We tested how temporal changes in broad-scale environmental variables influenced all facets of bird taxonomic and functional diversity. We restricted this analysis to the 1989–2011 period as NDVI data were not available in earlier years. We used the same GAMM structure as for temporal trends, but added linear effects for four environmental variables: mean temperature, precipitations, temperature and precipitation seasonality and NDVI, all scaled to zero mean and unit standard deviation to facilitate parameter comparisons. Quadratic effects and splines on environmental variables increased AIC, and were thus not used in the final analyses. Also note that random slopes should be added to account for between-route heterogeneities in the relationships between bird diversity and environmental covariates, but they revealed to be non-estimable with our data set.

Results

Trends in taxonomic diversity

Species richness increased from an average of 44 ± 11 species per route in 1970 (uncertainties in SD units unless otherwise specified) to a maximum of 50 ± 11 species per route in 2005 (Table 1). Our GAMM showed that the increase plateaued in the late 1990s and may even have been reversing since the mid-2000s (Fig. 2a, estimated degree of freedom e$df = 2.95$, $p < 0.0001$, $F = 326.22$, $n = 30,405$ for all models; all the trend estimates can be found in Supplementary Material 5), with a significant estimated breakpoint in 2001 [95% confidence interval CI (1998, 2004), Davies' tests significant at the $p = 0.0001$ risk for all reported breakpoints unless otherwise specified]. Meanwhile, total abundance decreased monotonically from 1973 to 2011 (Table 1, Fig. 2b, e$df = 2.78$, $F = 35.31$, $p < 0.0001$). In contrast to species richness, however, the abundance trend strengthened in the last decade with a breakpoint in 2002 [1998, 2006]. Taxonomic evenness showed a marginal, yet significant, non-linear increase from close to 0.54 in the first decade to 0.56 in the last decade (Table 1), suggesting a light trend towards a more even distribution of species' abundances among species within local assemblages (Fig. 2c, e$df = 2.61$, $F = 267.79$, $p < 0.0001$). The piecewise regression for evenness showed a significant breakpoint in 1993, but with a wide 95% CI [1986, 1999], suggesting no abrupt change in the trend during the period.

Trends in generic functional diversity

We report raw variation in all functional diversity indices in Table 1. Even after accounting for species richness, FRic exhibited a non-linear increase (Fig. 3a, e$df = 2.9$, $F = 160.9$, $p < 0.0001$), with a slightly earlier breakpoint in 1997 [1993, 2001], suggesting that the total trait range

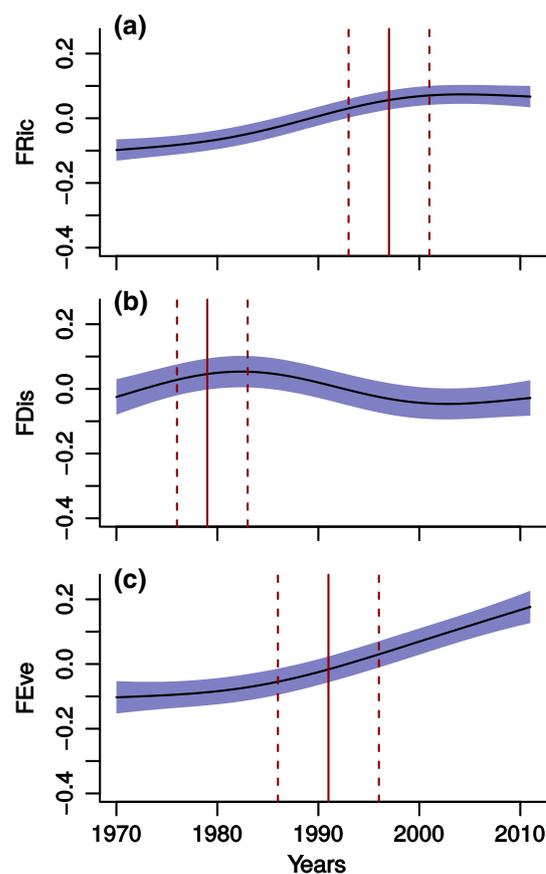**Table 1** Descriptive summary of temporal variations in US bird taxonomic and functional diversities

Indices		Mean $\pm$ SD (1970–2011)	Min (year)	Max (year)
Taxonomic diversity	Species richness	47.671 ± 2.068	44.343 (1971)	50.468 (2005)
	Total abundance	761.930 ± 23.533	691.522 (2011)	801.467 (1972)
	Taxonomic evenness	0.549 ± 0.008	0.535 (1972)	0.560 (2008)
Functional diversity	Functional richness	0.021 ± 0.004	0.015 (1972)	0.027 (2008)
	Functional dispersion	0.275 ± 0.001	0.273 (1972)	0.278 (1988)
	Functional evenness	0.591 ± 0.004	0.584 (1977)	0.600 (2008)
	Functional richness—ecological traits	0.111 ± 0.009	0.096 (1978)	0.124 (2001)
	Functional dispersion—ecological traits	0.493 ± 0.002	0.490 (1972)	0.496 (2005)
	Functional evenness—ecological traits	0.493 ± 0.005	0.485 (1977)	0.502 (2010)
	Functional richness—life-history traits	0.056 ± 0.012	0.034 (1972)	0.081 (2011)
	Functional dispersion—life-history traits	0.238 ± 0.002	0.232 (1975)	0.244 (1988)
	Functional evenness—life-history traits	0.409 ± 0.003	0.402 (1982)	0.415 (1989)
	Functional richness—reproductive traits	0.369 ± 0.031	0.325 (1978)	0.410 (2008)
	Functional dispersion—reproductive traits	0.249 ± 0.003	0.242 (2010)	0.255 (1970)
	Functional evenness—reproductive traits	0.490 ± 0.004	0.484 (2007)	0.500 (1970)

The table shows inter-annual variations of raw indices, averaged over 807 Breeding Bird Survey routes
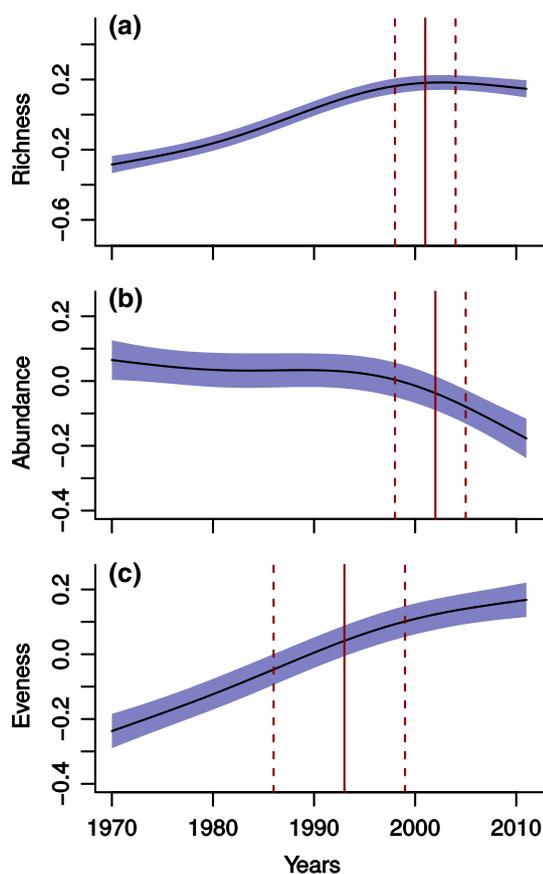
Fig. 2 Temporal trends in bird taxonomic diversity (1970–2011). The smoothed curve and confidence interval are fitted with a generalized additive model. Red lines indicate significant breakpoints in the trends (if any) estimated with piecewise regressions. Diversity indices were scaled to mean = 0 and SD = 1 to ease comparisons, and abundance was log-transformed prior to modeling. All models include a 2-dimensional spline spatial smoother, a random "route" effect and a first-order temporal autoregressive structure (color figure online)

Fig. 3 Temporal trends in three indices of bird functional diversity (1970–2011), quantified with 16 traits reflecting multiple facets of birds' ecological preferences and life history. The smoothed curve and confidence interval are fitted with a generalized additive model. Red lines indicate significant breakpoints in the trends (if any) estimated with piecewise regressions. Diversity indices were scaled to mean = 0 and SD = 1 prior to modeling to ease comparisons (color figure online)

of local bird assemblages increased during the period. However, this increase is mainly attributable to the addition of a few functionally distinct species, as FDis (the abundance-weighted dispersion of traits around the centroid of the functional space, structurally less impacted by outliers) exhibited little variation during the 40 years (Table 1) although the edf of the temporal trend controlled with species richness was significant [Fig. 3b, $edf = 2.90$, $F = 17.73$, $p < 0.0001$; shallow breakpoint in 1979 (1976, 1983), $p < 0.001$] as an effect of a small local maximum. FEve exhibited a clearer, non-linear increase (Fig. 3c, $edf = 2.42$, $F = 93.21$, $p < 0.0001$) which sharpened after 1991 [1986, 1996]. Overall, bird assemblages appeared to become more functionally even over the period, owing to the addition of original trait combinations departing from the average dispersion of their functional space.

Trends in ecological, life-history and reproductive functional diversities

As expected, there were marked discrepancies in functional diversity trends based on the three considered trait subsets (Fig. 4), except for FDis which remained roughly steady over the period for all trait subsets. Ecological trait FRic increased during the period (Table 1), but this trend disappeared once accounting for species richness [Fig. 4a, $edf = 2.90$, $F = 18.28$, $p < 0.0001$, breakpoint in 1993 (1988, 1997)]. Similar to generic FRic, the FRic of life-history strategies increased linearly (Fig. 4b, $edf = 1.00$, $F = 1103.71$, $p < 0.0001$) and the FRic of reproductive strategies increased non-linearly with an S-shape [Fig. 4c, $edf = 2.98$, $F = 242.14$, $p < 0.0001$, breakpoint in 2001 (1997, 2005)]. The increase in generic FEve was consistent with an increase in the FEve of ecological traits [Fig. 4g,
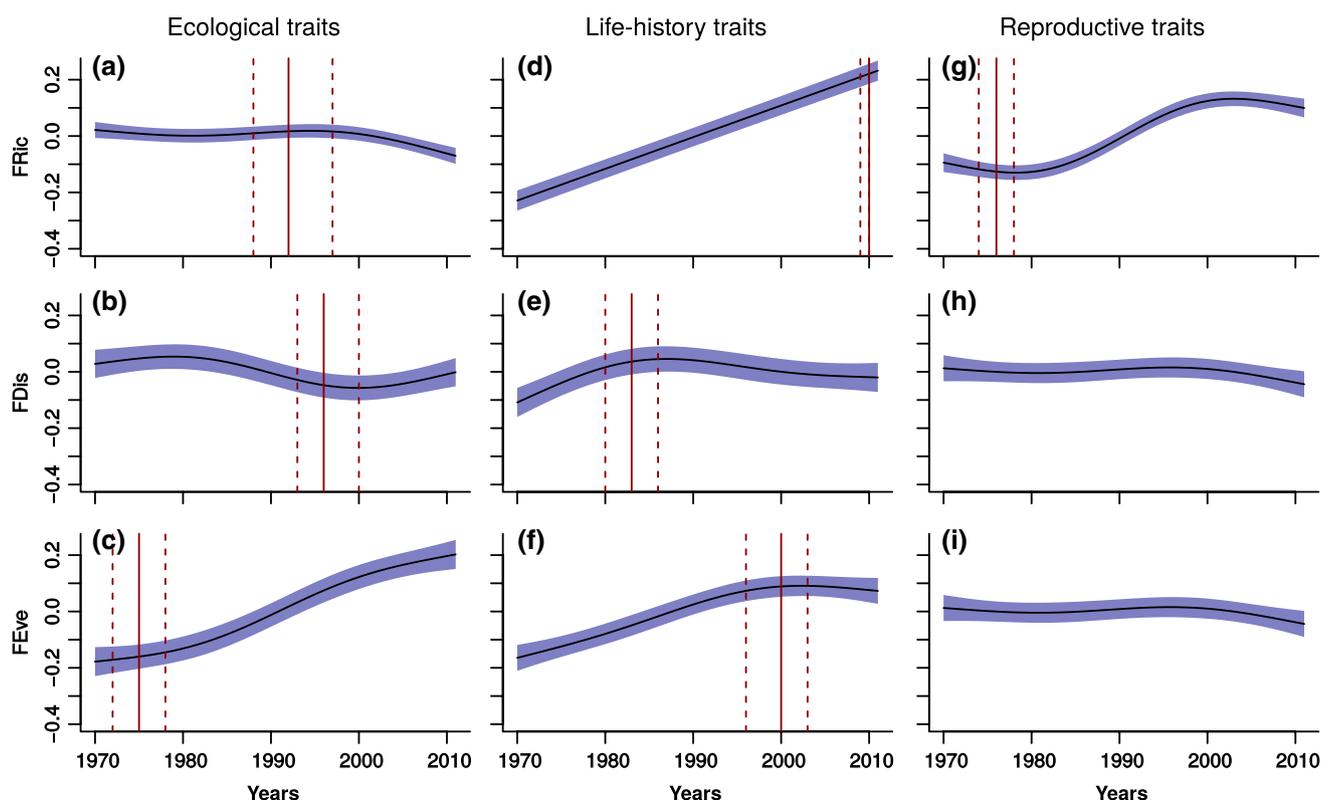
Fig. 4 Temporal trends in three indices of bird functional diversity (1970–2011) for several sets of traits that quantify, respectively, birds' ecological preferences, mobility and reproduction strategies. The smoothed curve and confidence interval are fitted with a general-ized additive model. Red lines indicate significant breakpoints in the trends (if any) estimated with piecewise regressions. Diversity indices were scaled to mean = 0 and SD = 1 prior to modeling to ease comparisons (color figure online)

edf = 2.80, F = 190.63, $p < 0.0001$, breakpoint in 1975 (1971, 1978), $p = 0.006$] and life-history traits [Fig. 4h, edf = 2.77, F = 91.79, $p < 0.0001$, breakpoint in 2000 (1996, 2003)], without any associated change in the FEve of reproductive strategies (Fig. 4i, non-significant year effect).

Effect of continental trends in climate and primary productivity

No clear pattern emerged from models with environmental covariates as most parameter estimates did not depart signifi-cantly from zero (Fig. 5, Supplementary Material 6). Spurious correlations due to multiple testing could not be ruled out for the few significant relationships (such as, e.g., the negative effect of spring temperature on generic FRic, Fig. 5a, or the positive effect of NDVI on ecological traits, Fig. 5e). Nota-bly, however, all environmental variables had an effect on the FRic of life-history traits with a stronger magnitude than any other reported relationship. Specifically, the FRic of life-his-tory traits decreased with rising spring temperature (Fig. 5a),

precipitation (Fig. 5b) and NDVI (Fig. 5e) and increased with higher seasonality (Fig. 5c, d).

Discussion

Overview of the results

The taxonomic and functional diversity of local bird assem-blages changed non-linearly in the past 40 years across the conterminous US. Species richness and taxonomic evenness increased synchronously with an increase in FRic and FEve without an accompanying change in FDis. This pattern was sustained by the addition of species with new life-history and reproductive strategies in local assemblages without accompanying changes in the diversity of dietary or habitat strategies. Furthermore, climate and primary productivity influenced inter-annual variations of the FRic of life-his-tory traits. Our results expand beyond previous research on trends in US bird diversity (La Sorte and Boecklen 2005; Jarzyna and Jetz 2016b; Schipper et al. 2016) by raising
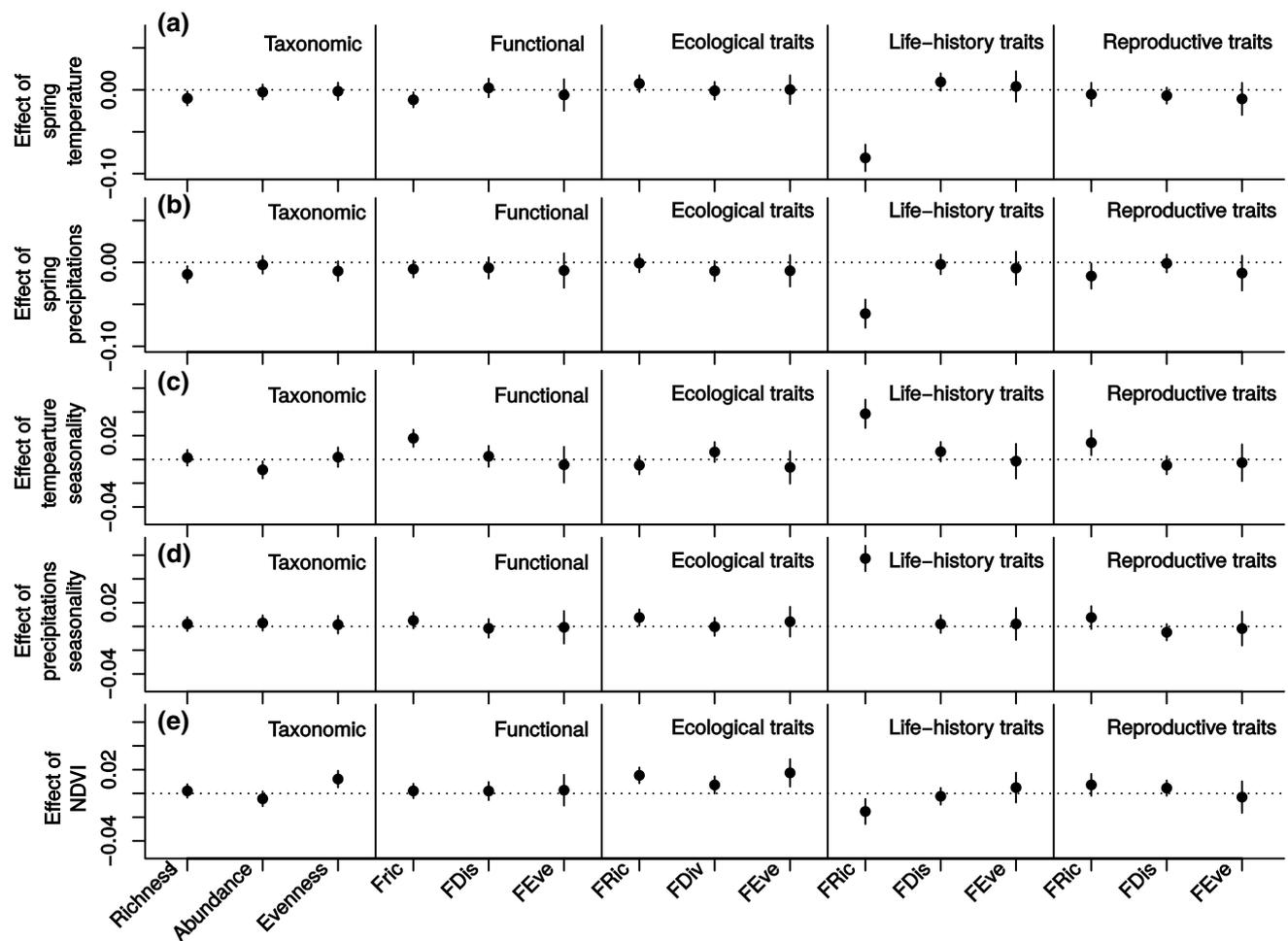
Fig. 5 Effect of environmental variables on bird taxonomic and functional diversity, estimated as linear coefficients (± 95% confidence intervals) from generalized additive mixed models. Abundance was log-transformed, and all diversity indices and environmental covariates were scaled to mean = 0 and SD = 1 prior to modeling to ease comparisons. *FRic* functional richness, *FDis* functional dispersion, *FEve* functional evenness

complementary insights on the broad-scale dynamics and determinants of bird assemblages over time.

Trends in bird taxonomic and functional diversity

While the total bird count per BBS route decreased, species richness and taxonomic evenness and their functional counterparts increased between 1970 and 2011. These trends come in contrast with previous work (La Sorte and Boecklen 2005) but are coherent with a similar analysis on a comparable spatial extent and time frame in which the functional diversity was restricted to trophic and foraging traits (Schipper et al. 2016). Hence, decreasing bird abundances were not associated with a taxonomic or functional homogenization of local bird assemblages, unlike patterns usually observed or assumed in anthropogenic landscapes (Mc Kinney and Lockwood 1999; Devictor et al. 2008). Multiple factors can promote local decreases in bird diversity (such as land-use

intensification, pesticides, climate change or species invasions, Cardinale et al. 2012; Gonzalez et al. 2016). However, these processes are likely too geographically heterogeneous to trigger a consistent continent-wide pattern (Korhonen et al. 2010; Vellend et al. 2013; Dornelas et al. 2014). Multi-scale studies incorporating trends in regional diversity or fine-grained spatial turnover, which were beyond our aim of providing a continental-level picture of bird diversity trends, would probably help in explaining the apparent discrepancies among studies (White et al. 2010; McGill et al. 2015).

The decline in total bird counts reflects a generalized decline in North American bird species' abundances (Sauer et al. 2011) which might counter diversity increases, especially if they are triggered by a small number of range-expanding species (Mc Kinney and Lockwood 1999). Consistently, most diversity trends were non-linear and several of them involved a flattening in recent years concurrent with a rapid decrease of total bird counts per route. We failed to

find thresholds suggesting that a single environmental event, such as a heat wave or drought, could explain these recent dynamics (Jiguet et al. 2011). Furthermore, although these non-linearities may be temporary (Jarzyna and Jetz 2016b), a 10-year hiatus in species richness and FRic is unlikely to be purely stochastic. So far, our results therefore only suggest changes in bird assemblage dynamics that deserve a specific focus in future monitoring and studies in the prospect of identifying possible changes in underlying diversity drivers.

Trait responses to large-scale environmental variation

Comparing functional diversity measures based on different underlying trait sets is especially relevant to assess the relative contributions of multiple facets of species' ecology to diversity trends (Calba et al. 2014). In our study, the increase in generic FRic in spite of a relatively stable FDis suggests that species bearing novel trait combinations colonized local assemblages without changing the average dispersion of species in the functional space (Villéger et al. 2008; Laliberté and Legendre 2010). Interestingly, "ecological traits" (those related to resource and habitat use) varied consistently with generic FEve but not FRic. Consequently, our results suggest that species richness increased over time due to colonizing species with habitat and dietary preferences that were previously under-represented in local assemblages, which may arise under range expansions resulting from land-use or climate change (Zuckerberg et al. 2009; Sohl 2014; Princé and Zuckerberg 2015), partly consistent with Schipper et al. (2016) who found an increase in an FDis measure based only on dietary and foraging traits.

We found that the increase in FRic was related to an accumulation of novel combinations of migration strategies, developmental modes and body sizes, suggesting that bird diversity dynamics is primarily linked to traits coupled to broad-scale environmental conditions rather than to traits related to resource use. Consistently, the FRic of life-history traits decreased with increasing temperature, precipitation, NDVI and increased with seasonality. Migratory species are more specialized than residents and hence more sensitive to small variations of weather, resource availability and phenology during the breeding period (Pearce-Higgins and Green 2014). This interpretation needs further support as we cannot fully rule out an effect of phenological adjustments in abnormally warm and wet springs which lowers the detectability of sedentary species and increases that of late migrants during the survey period (Bas et al. 2008). This particular result, therefore, raises two non-mutually exclusive hypotheses that are worthy of further investigation: either phenology influences variations in functional diversity through variability in detectability or trait choice influences the sensitivity of FRic to environmental changes (Calba et al. 2014). Whatever the explanation, it appears that a functional diversity measure based on traits related to mobility and body size is the most sensitive to broad-scale environmental forcings (partly in line with Jiguet et al. 2007). We failed to explain other changes in diversity indices with variations in temperature, precipitation, seasonality and primary productivity, in contrast with previous studies (Korhonen et al. 2010; Stegen et al. 2013) but consistent with the absence of a consistent climate change signal on North American birds (Currie and Venne 2017). Importantly, primary productivity did not explain diversity changes, while it accounted for substantial variation in bird spatial and temporal turnover (Chase 2010; Stegen et al. 2013). These inconsistencies suggest that the processes influencing one facet of functional diversity may not be transferable to another (McGill et al. 2015). One explanation could be that environmental constraints on regional species pools interact with local drivers such as land-use changes (Mittelbach and Schemske 2015), resulting in spatially heterogeneous changes in species assemblages that cannot be easily accounted for by environmental variability at a continental scale.

Conclusion

Our results showed that the simultaneous investigation of multiple facets of taxonomic and functional diversity yields insights on the possible factors that structure their temporal trends. Extending the time span towards deeper into historical times will be needed to investigate whether contemporary trends in diversity are transient or the result of longer term dynamics originating before the onset of the Anthropocene (Barnosky et al. 2011). Most importantly, models allowing spatially explicit diversity trends will be critical for further advances in exploring the consistency of diversity trends across species, regions, and periods of rapid environmental change.

References

Barnosky AD, Matzke N, Tomiya S et al (2011) Has the Earth's sixth mass extinction already arrived? Nature 471:51–57

Bas Y, Devictor V, Moussus JP, Jiguet F (2008) Accounting for weather and time-of-day parameters when analysing count data from monitoring programs. Biodivers Conserv 17:3403–3416

Blenckner T, Hillebrand H (2002) North Atlantic oscillation signatures in aquatic and terrestrial ecosystems—a meta-analysis. Glob Change Biol 8:203–212

Cadotte MW (2011) The new diversity: management gains through insights into the functional diversity of communities. J Appl Ecol 48:1067–1069

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087

Calba S, Maris V, Devictor V (2014) Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices. Glob Ecol Biogeogr 23:669–678. doi:10.1111/geb.12148

Cardinale BJ, Duffy JE, Gonzalez A et al (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. doi:10.1038/nature11148

Carmona CP, de Bello F, Mason NWH, Leps J (2016) Traits without borders: integrating functional diversity across scales. Trends Ecol Evol 31:382–394. doi:10.1016/j.tree.2016.02.003

Chase JM (2010) Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391. doi:10.1126/science.1187820

Cisneros LM, Fagan ME, Willig MR (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. Divers Distrib 21:523–533. doi:10.1111/ddi.12277

Currie DJ, Venne S (2017) Climate change is not a major driver of shifts in the geographical distributions of North American birds. Glob Ecol Biogeogr 26:333–346. doi:10.1111/geb.12538

Davies RB (1987) Hypothesis testing when a nuisance parameter is present only under the alternatives. Biometrika 74:33–43. doi:10.2307/2336019

Devictor V, Julliard R, Clavel J et al (2008) Functional biotic homogenization of bird communities in disturbed landscapes. Glob Ecol Biogeogr 17:252–261

Devictor V, Mouillot D, Meynard C et al (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol Lett 13:1030–1040

Dornelas M, Magurran AE, Buckland ST et al (2012) Quantifying temporal change in biodiversity: challenges and opportunities. Proc R Soc B. doi:10.1098/rspb.2012.1931

Dornelas M, Gotelli NJ, McGill B et al (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science 344:296–299. doi:10.1126/science.1248484

Evans KL, James NA, Gaston KJ (2006) Abundance, species richness and energy availability in the North American avifauna. Glob Ecol Biogeogr 15:372–385. doi:10.1111/j.1466-822X.2006.00228.x

Flynn DFB, Gogol-Prokurat M, Nogeire T et al (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33. doi:10.1111/j.1461-0248.2008.01255.x

Gonzalez A, Cardinale BJ, Allington GRH et al (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology 97:1949–1960. doi:10.1890/15-1759.1

Hijmans RJ, Phillips S, Leathwick J et al (2017) Package 'dismo'. Available online at:http://cran.r-project.org/web/packages/dismo/index.html

Hooper DU, Adair EC, Cardinale BJ et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108. doi:10.1038/nature11118

Jarzyna MA, Jetz W (2016a) Detecting the multiple facets of biodiversity. Trends Ecol Evol 31:527–538. doi:10.1016/j.tree.2016.04.002

Jarzyna MA, Jetz W (2016b) A near half-century of temporal change in different facets of avian diversity. Glob Change Biol. doi:10.1111/gcb.13571

Jiguet F, Gadot AS, Julliard R et al (2007) Climate envelope, life history traits and the resilience of birds facing global change. Glob Change Biol 13:1672–1684

Jiguet F, Brotons L, Devictor V (2011) Community responses to extreme climatic conditions. Curr Zool 57:406–413

Jones J, Doran PJ, Holmes RT (2003) Climate and food synchronize regional forest bird abundances. Ecology 84:3024–3032. doi:10.1890/02-0639

Keil P, Storch D, Jetz W (2015) On the decline of biodiversity due to area loss. Nat Commun 6:8837. doi:10.1038/ncomms9837

Kendall WL, Peterjohn BG, Sauer JR (1996) First-time observer effects in the North American breeding bird survey. Auk 113:823–829

Korhonen JJ, Soininen J, Hillebrand H (2010) A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91:508–517. doi:10.1890/09-0392.1

La Sorte FA, Boecklen WJ (2005) Changes in the diversity structure of avian assemblages in North America. Glob Ecol Biogeogr 14:367–378. doi:10.1111/j.1466-822X.2005.00160.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. doi:10.1890/08-2244.1

Laliberté E, Wells JA, DeClerck F et al (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol Lett 13:76–86. doi:10.1111/j.1461-0248.2009.01403.x

Lamanna C, Blonder B, Violle C et al (2014) Functional trait space and the latitudinal diversity gradient. Proc Natl Acad Sci 111:13745–13750. doi:10.1073/pnas.1317722111

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556

Legendre P, Legendre LFJ (2012) Numerical ecology, vol 24, 3rd edn. Elsevier, Amsterdam

Magurran AE, Dornelas M (2010) Biological diversity in a changing world. Philos Trans R Soc B Biol Sci 365:3593–3597

Magurran AE, Baillie SR, Buckland ST et al (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol Evol 25:574–582. doi:10.1016/j.tree.2010.06.016

Maire E, Grenouillet G, Brosse S, Villéger S (2015) How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Glob Ecol Biogeogr 24:728–740. doi:10.1111/geb.12299

Mc Gill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185

Mc Kinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol Evol 30:104–113. doi:10.1016/j.tree.2014.11.006

Mittelbach GG, Schemske DW (2015) Ecological and evolutionary perspectives on community assembly. Trends Ecol Evol 30:241–247. doi:10.1016/j.tree.2015.02.008

Monnet A-C, Jiguet F, Meynard CN et al (2014) Asynchrony of taxonomic, functional and phylogenetic diversity in birds. Glob Ecol Biogeogr 23:780–788. doi:10.1111/geb.12179

Muggeo V (2008) segmented: an R package to fit regression models with broken-line relationships. R News 8:20–25

Pearce-Higgins JW, Green RE (2014) Birds and climate change: impacts and conservation responses, 1st edn. Cambridge University Press, Cambridge

Pereira HM, David Cooper H (2006) Towards the global monitoring of biodiversity change. Trends Ecol Evol 21:123–129

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9:741–758. doi:10.1111/j.1461-0248.2006.00924.x

Princé K, Zuckerberg B (2015) Climate change in our backyards: the reshuffling of North America's winter bird communities. Glob Change Biol 21:572–585. doi:10.1111/gcb.12740

Purschke O, Schmid BC, Sykes MT et al (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. J Ecol 101:857–866. doi:10.1111/1365-2745.12098

Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology. Academic Press, London

Sauer JR, Hines JE, Fallon JE et al (2011) The north american breeding bird survey, results and analysis 1966–2010, Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD

Schipper AM, Belmaker J, de Miranda MD et al (2016) Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. Glob Change Biol 22:3948–3959. doi:10.1111/gcb.13292

Schleuning M, Fründ J, García D (2015) Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. Ecography 38:380–392. doi:10.1111/ecog.00983

Sibley DA (2014) The sibley guide to birds, 2nd edn. Knopf, New York

Sohl TL (2014) The relative impacts of climate and land-use change on conterminous united states bird species from 2001 to 2075. PLoS One 9:e112251. doi:10.1371/journal.pone.0112251

Soininen J (2010) Species turnover along abiotic and biotic gradients: patterns in space equal patterns in time? Bioscience 60:433–439. doi:10.1525/bio.2010.60.6.7

Stegen JC, Freestone AL, Crist TO et al (2013) Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. Glob Ecol Biogeogr 22:202–212. doi:10.1111/j.1466-8238.2012.00780.x

Vellend M, Baeten L, Myers-Smith IH et al (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proc Natl Acad Sci 110:19456–19459. doi:10.1073/pnas.1312779110

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. doi:10.1890/07-1206.1

Violle C, Navas M-L, Vile D et al (2007) Let the concept of trait be functional! Oikos 116:882–892

White EP, Ernest SKM, Adler PB et al (2010) Integrating spatial and temporal approaches to understanding species richness. Philos Trans R Soc B Biol Sci 365:3633–3643. doi:10.1098/rstb.2010.0280

Wood SN (2006) Generalized additive models. An introduction with R. Chapman & Hall/CRC, London

Zuckerberg B, Woods AM, Porter WF (2009) Poleward shifts in breeding bird distributions in New York State. Glob Change Biol 15:1866–1883. doi:10.1111/j.1365-2486.2009.01878.x

Zuur A (2011) Mixed effects models and extensions in ecology with R, Softcover reprint of hardcover, 1st edn. Springer, New York