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No General Trend in Functional Diversity in Bird and Mammal Communities Despite Compositional Change

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ABSTRACT

Aim: Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing dissimilarity due to turnover but no overall trend in species diversity through time at the local scale. Functional diversity provides a potentially powerful alternative approach for understanding community composition by linking shifts in species identity to the characteristics that underpin ecosystem processes. Here we present the first multitaxa, multisystem analysis of functional diversity and composition through time.

Location: Global, with a North American focus.

Time Period: 1923–2014.

Major Taxa Studied: Mammals, Birds.

Methods: We paired thousands of bird and mammal assemblage time series from the BioTIME database with existing trait data representative of species' functional roles to reconstruct time series of functional diversity and composition metrics. Our dataset included 2432 time series of yearly observations from 50 studies with a maximum spatial extent of 95 km^2. Using generalised linear mixed models, we estimated general and study-level trends for those metrics.

Results: We found no overall temporal trends in functional diversity metrics. Study characteristics such as taxa, realm, biome, or protection status did not distinguish between types of change exhibited by communities. We found evidence of a temporal increase in fish consumption across all communities but no evidence to support multiple predictions for specific traits, including decreasing body size, dietary shifts or changes in bird foraging strata.

Main Conclusions: General temporal trends indicate that on the aggregate, studies do not exhibit consistent changes in functional diversity across many taxa, biomes and realms. At the study level, the majority of studies showed no temporal trends in species or functional diversity, with the remainder of the studies falling into broad categories of functional diversity change independent of species richness, functional redundancy loss (species richness declines with functional richness maintained) and increasing species richness sometimes accompanied by increasing functional richness.

1 | Introduction

Ecological communities are experiencing unprecedented changes due to anthropogenic pressures such as climate change, land use change and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (Barnosky et al. 2011) and fundamental changes in some of the most well-studied systems (e.g., coral bleaching, Sully et al. 2019). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (Brown et al. 2001; Dornelas et al. 2014; Vellend et al. 2013, 2017) and evidence of significant shifts in community composition underlying consistent species richness (Brose and Hillebrand 2016; Gotelli et al. 2017; Li et al. 2020). While communities are clearly changing, our most common species-based approaches do not fully capture the nature of that change. Still, using general trends derived from limited data as a diagnostic for the state of biodiversity is a topic of ongoing debate (Boënnec, Dakos, and Devictor 2024; Johnson et al. 2024). Global analyses have been heavily criticised for geographic biases, lack of data in the most heavily impacted areas, short time windows biased towards the present day and exclusion of individual studies' ecological context (Cardinale 2014; Cardinale et al. 2018; Gonzalez et al. 2016). Many of these criticisms reflect limitations of ecological data overall (Chapman et al. 2024), leading to a call for additional data not only to fill geographic and temporal gaps, but to fill in key characteristics of communities (Dornelas et al. 2023; Primack et al. 2018).

Functional diversity offers a powerful addition to species-based approaches for detecting and describing community change by capturing changes in the traits that underpin fundamental ecological processes (Lavorel and Garnier 2002; Mcgill et al. 2006; Streit and Bellwood 2023; Suding et al. 2008). Functional diversity metrics capture complimentary aspects of the trait space including the volume of the multidimensional space (functional diversity), how species and abundance are distributed across the space (functional evenness and divergence), and how the space maps to individual trait distributions (community-weighted trait means). Considered together, they describe the aspects of the trait space that mediate ecological process.

Trends in functional diversity across broad geographic extents are the aggregation of local-scale responses to acute pulse disturbance, persistent press disturbances and periods of relative stasis (Inamine et al. 2022). Pulse disturbances have a sudden one-time impact on the community, changing abundance distributions (functional evenness or divergence) or reducing the volume of the functional space (Boersma et al. 2016; Hillebrand and Kunze 2020; Larson et al. 2021). While press disturbances can also lead to loss of functional volume as species fail to adapt to new conditions, they can also lead to wholesale shifts in the location of the functional space as species fill in new environmental space. Rather than identifying outcomes of one of these specific processes, observational time series of functional diversity therefore capture the cumulative effects of multiple potentially competing processes.

The expectation for functional diversity change across communities is not obvious from past work and may or may not follow species richness trends (Dornelas et al. 2023; Larson et al. 2021). While loss of functional diversity is frequently cited as one of the most pressing concerns of the anthropocene (Cardinale et al. 2012; Dirzo et al. 2014; Young et al. 2016), observational trends show significant functional loss in some studies (Flynn et al. 2009) and no loss even in the most heavily impacted communities for others (Edwards et al. 2013; Larsen et al. 2018; Matuoka et al. 2020). Broad-scale observational studies are limited, but show for example functional richness increases for North American birds (Barnagaud et al. 2017; Jarzyna and Jetz 2016). We have stronger expectations for changes in the prevalence of some individual traits. For example, animal body size is expected to decrease as a result of climate change, a phenomenon that has been documented in multiple taxa empirically and experimentally (Caruso et al. 2014; Forster, Hirst, and Atkinson 2012; Huss et al. 2019; Sheridan and Bickford 2011; Tseng et al. 2018). For dietary traits, recent work documenting insect declines (Wagner et al. 2021) points to potentially profound negative impacts on insectivorous animals (Canaday 1996; Şekercioğlu et al. 2002; Tallamy and Shriver 2021). Predicted extinctions based on species-level vulnerability point to further dietary shifts, favouring increases in invertivorous species (Cooke, Eigenbrod, and Bates 2019). Some systems also show significant shifts in the prevalence of different kinds of foragers in birds, for example loss of arboreal foragers in agricultural systems (Bain et al. 2020) and loss of neotropical understory foragers even in protected areas (Pollock et al. 2022).

Here we leverage ongoing efforts to assemble functional trait data and recent computational advances to perform the first multitaxa, multirealm assessment of functional diversity and composition change through time. We focus on mammal and bird species as subsets of the world's biodiversity of particular conservation concern that is heavily impacted by anthropogenic change. While examining trends in plants, invertebrates and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (FitzJohn et al. 2014), a lack of accepted species-level means and differences in the types of traits collected. To ensure comparability across taxa in trait type and data quality, we therefore focus on mammals and birds. We include body mass, dietary, foraging and other behavioural traits that were intentionally selected to be representative of a species' Eltonian niche, thereby summarising the functional role they play in the community (Wilman et al. 2014).

We synthesise thousands of mammal and bird functional diversity time series to assess mean trends across communities. We evaluate (1) whether or not there is consistent change in the functional trait space shape (functional diversity) or location (community-weighted trait means) across communities and whether community characteristics explain variation in that change, (2) hypotheses of change for individual trait axes including: decreasing body size, decreasing insectivory, increasing invertivory, decreasing arboreal and understory foraging and (3) the implications of study-level trends for the ecology of those communities. To address these goals, we present results for general trends that aggregate across all communities, category-specific trends that aggregate across communities with similar characteristics and study-level trends.

2 | Material and Methods

2.1 | Data

We obtained mammal and bird time series from the BioTIME database, a global repository of high-quality assemblage time series collected from the literature and ongoing monitoring efforts. Data are structured such that a study comprises all data collected following consistent sampling protocols and may contain multiple site locations. Samples at each site represent full assemblages rather than populations of single species (Dornelas et al. 2018) and include both abundance and presence/absence data. Following best practices for the database (Blowes et al. 2019), studies with multiple sample locations were split into individual time series following a standardised spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see Blowes et al. 2019 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. The resulting cell size for our data was approximately 95 km^2. All samples from a study within a single cell were considered to be a single time series location, and species abundances, if available, were combined for all samples. This approach therefore sets an upper bound on the definition of local for studies with multiple locations. Our dataset included 29 single location studies (average spatial extent of ~4 km^2), and 24 multilocation studies aggregated by cell.

We used trait data from the Elton Trait Database, which consists of species-level means for traits that represent species' multifaceted role in the community (Wilman et al. 2014). Traits include body mass, diet, nocturnality, forest foraging strata and pelagic use. For categorical traits, different category levels are represented as binary or percentage use (Table 1).

TABLE 1 | Description of the traits included in the analysis broken down by categories at data type.

Trait	Category	Taxa	Data type
Diet	Invertebrate	Bird and Mammal	Percentage consumed
	Mammals and Birds		
	Reptiles		
	Fish		
	Unknown vertebrates		
	Scavenging		
	Fruit		
	Nectar		
	Seeds		
	Other plant		
Foraging strata	Below water surface	Bird	Percentage of use
	Water surface		
	Ground		
	Understory		
	> 2 m, below canopy		
	Canopy		
	Aerial		
Pelagic Specialist	Yes		Binary
	No		
Nocturnal	Yes	Bird and Mammal	
	No		
Crepuscular	Yes	Mammal	
	No		
Diurnal	yes		
	no		
Body mass	—	Bird and Mammal	Continuous, in grams

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the online database, https://doi.org/10.5066/F7KH0KBK), obtained through the taxadb R package (Norman, Chamberlain, and Boettiger 2020; R Core Team 2021). If more than one species in the assemblage data resolved to the same identifier, observations were considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies for which at least 75% of species had trait data were included. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded. Sensitivity analyses were conducted for the trait coverage threshold and duration of included time series by rerunning analyses with increasingly conservative cutoffs including 85% and 90% coverage trait coverage and durations longer than 3, 4, 5 and 10 years.

Forty-one of the 2432 time series included in our dataset had a variable number of samples within years. To account for this inconsistency in sampling effort, we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series. We made 200 rarefied samples for oversampled years and calculated diversity metrics for each sample and then took the median for each metric as the value for that year and time series. Twenty-eight of the rarefied studies required undersampling by only one sample, and only three time series required undersampling by more than ten samples. For time series with and without rarefaction, samples were pooled within each year and abundances were summed (where available).

Our final dataset included 2432 time series from 50 studies in 21 countries and 12 biomes using 7 different traits (Figure 1). Data came from both terrestrial and marine realms and five biomes (Global, Polar/Temperate, Temperate, Temperate/Tropical, Tropical). The earliest sample was in 1923 and the most recent was in 2014. While it is not possible with available data to directly assess the level of human impact occurring for each study, we include binary protection status as a coarse indicator of impact level. However, protected areas were almost exclusively from temperate terrestrial studies (with one tropical study), so results are confounded by multiple other study characteristics. For a full breakdown of studies and their characteristics, see the Supporting Information. Our final dataset reflects many of the data biases that make global synthesis work challenging, including geographic bias, a bias away from areas currently under the greatest threat and a bias towards shorter time series. We address these shortcomings and their potential impact on our results in the discussion.

2.2 | Diversity Metrics

We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate decreasing similarity. To assess for sensitivity to baseline we also calculated similarity relative to the final time step, which showed changes accumulating similarly regardless of the baseline chosen (Figure S1). We did not impose a correction for unobserved species as nonparametric estimators do not assign species identities to corrected richness values and therefore could not be propagated to the functional diversity metrics.

Functional diversity metrics were calculated using the *dbFD* function from the *FD* R package (Laliberté and Legendre 2010). Here we report functional richness (*FRic*), functional evenness (*FEve*) and functional divergence (*FDiv*) which together describe three complementary characteristics of the functional space (Hillebrand and Matthiessen 2009; Mason et al. 2005). *FRic* assesses the volume of the trait space occupied by species in the community, with higher values indicating communities with species of more extreme trait values. *FEve* describes how species are distributed across the trait space and how abundance is distributed across species. Higher values of *FEve* indicate more even spacing of species in the trait space and individuals across species. *FDiv* measures the degree to which species and their abundances maximise differences in the functional space. Higher values of *FDiv* therefore correspond to communities where many highly abundant species are on the edges of the trait space.

To assess compositional changes, we also calculated the community-weighted mean (*CWM*) of all continuous traits (diet, foraging strata, body mass) to examine changes in the distribution of each trait. Wholesale shifts in the observed trait space due to changes of trait means could occur even while the shape and dispersion of the multidimensional trait space, as defined by functional richness, evenness, and divergence, is maintained through time. *CWMs* are therefore a way to assess whether or not turnover is occurring and what the nature of the shift may be. Hereafter, we refer to results for functional metrics in two groups: functional diversity metrics (*FRic*, *FEve*, *FDiv*) and composition metrics (trait *CWMs*).

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. For variables with multiple levels, each level was included as a separate trait axis. Continuous traits were z-score scaled to give each trait equal weight in the trait space (Leps et al. 2006; Schleuter et al. 2010). In preparation for calculating diversity metrics, dbFD calculates a trait distance matrix using Gower's distance and reduces the dimensionality of that trait space by performing PCoA. We limited the number of included PCoA axes to the maximum number of traits that fulfils the criteria $s > = 2^{t}$, where s is the number of species and t is the number of traits. This restriction allows for enough axes to capture the trait space while maintaining computational feasibility (Blonder 2018). Metrics incorporated weighting based on species abundance when available.

2.3 | Null Models

To assess changes in functional diversity independent of species richness, we calculated the standardised effect size (SES)

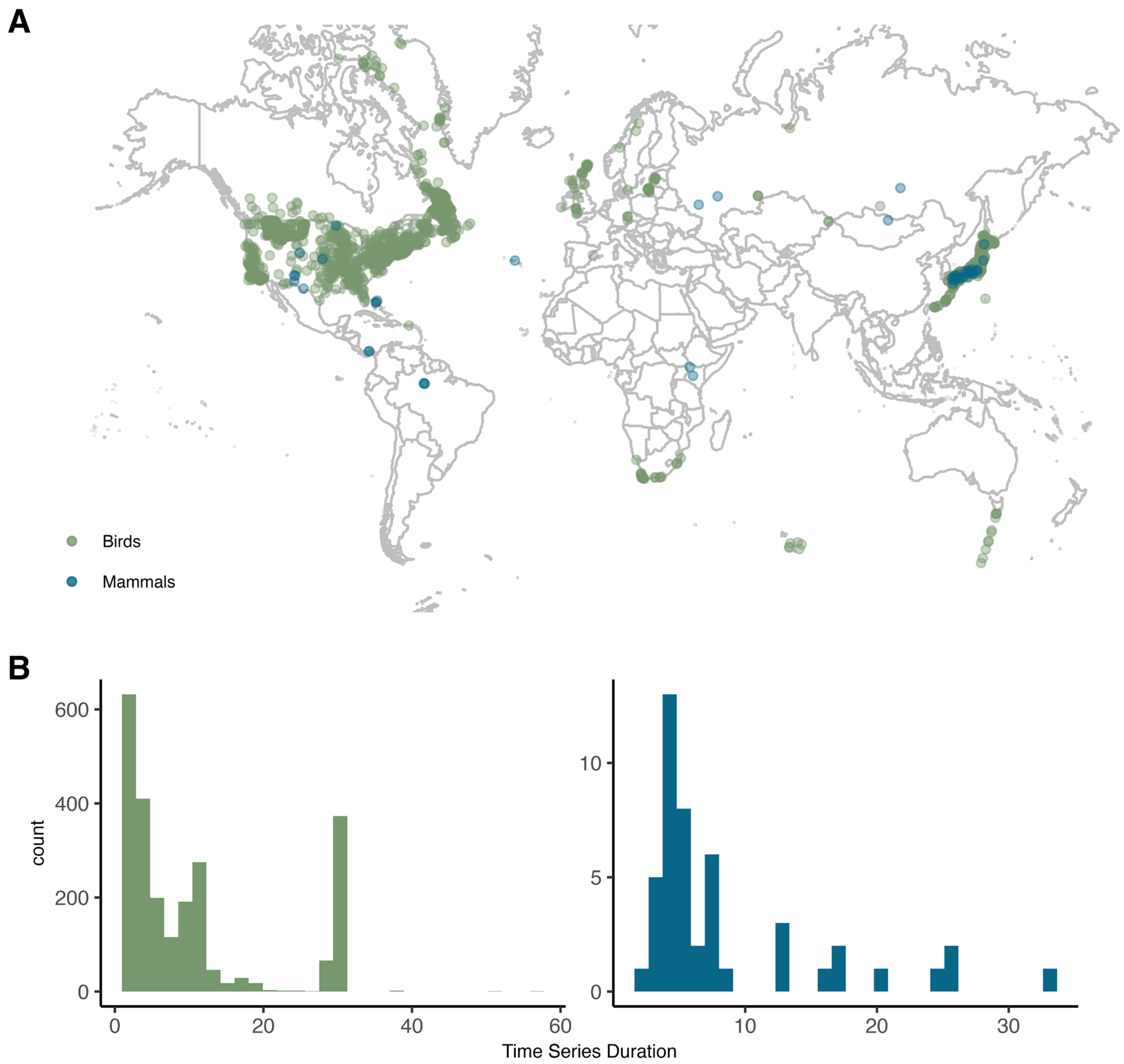

FIGURE 1 | (A) Map of time series locations with points coloured by taxa and (B) histograms of time series duration broken down by taxa.

for each of the three functional diversity metrics (*FRic*, *FEve*, *FDiv*) from null estimates (Swenson et al. 2012). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning observed abundances to species for abundance-based studies. Species pools were unique for each time series and included all species observed over the course of sampling, therefore accounting for geographic restrictions in species availability. This approach assumes the species pool is constant through time and that the species abundance distribution is conserved. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction sample for that time series. We used these values to calculate SES using the following formula: $\mathrm{SES} = \left[F_{\mathrm{obs}} - \mathrm{mean}_{(F_{\mathrm{null}})}\right] / \mathrm{SD}_{(F_{\mathrm{null}})}$. We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness. Hereafter, we refer to the *SES* as the corrected metric in comparison with the observed metric. This approach will be less accurate for shorter time series, as we likely will not have captured all available species in the true species pool, but it is impossible to know whether the mean estimate from the null model is an over- or underestimate without knowing the functional characteristics of the missing species.

2.4 | Analysis

We estimated general trends across bird and mammal communities for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each location nested within the study, methods which deal well with the inherent imbalances in our data. We fit individual models for each of the 18 CWMs calculated for continuous traits or trait categories (see diet, foraging strata and body mass traits in Table 1). All time series with data for a given trait were included in the corresponding *CWM* model. We estimated study-level trends using individual linear models. For studies with more than one location, we fit a random slope and intercept for location. Study-level models could not be fit for five studies for at least one metric due to data limitations, but those studies were still included in the general models. They represented 13 of 1350 study-level models fit for each metric. For further details, see the Supporting Information. Where appropriate, response variables were log or $\log(x+1)$ transformed to better fit model assumptions of residual normality. The log transformation was applied to all metrics except the SES-corrected functional diversity metrics, *FEve* and CWMs for invertebrate consumption, ground foraging strata and below water surface foraging strata.

We tested for category-specific trends in all diversity metrics within and between different levels of taxa, biome, realm and protection status by fitting separate models with each of those factors added as a predictor interacting with time to the original model structure. For each linear mixed effects model, we estimated within-level slopes and calculated between-level contrasts for the categorical variable using the *emmeans* package (v1.10.1, Lenth 2022). For some levels of the categorical variables, we did not have a sufficient number of studies to estimate a general trend (Global and Polar/Temperate climate categories), and we therefore only interpret results for levels with at least three studies. We assessed the impact of time series duration and start year on study-level trends using linear models with duration and start year as predictors. All models in our analysis were fit using the *lme4* (v1.1–35.3) package in R (v4.3.3), and p-values were calculated by Satterthwaite's degrees of freedom method using the *lmerTest* (v3.1–3) package with a significance level of $\alpha = 0.05$ (Bates et al. 2015; Kuznetsova, Brockhoff, and Christensen 2017; R Core Team 2023).

To correct for false positives due to multiple testing, we assess significance of temporal trends based on adjusted *p*-values. Adjusted *p*-values were calculated using the Benjamini–Hochberg procedure, which controls the false discovery rate. The procedure was implemented by the function `p.adjust` in the R package *stats* (v4.3.3).

3 | Results

We found no significant general temporal trend in species richness or functional diversity metrics including functional richness, evenness or divergence (observed or corrected) (Figure 2). We did find a significant overall decrease in Jaccard similarity, indicating accumulating changes in species composition. Nonsignificant overall temporal trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was not significantly different from zero (Figure 3). Trends by category for different taxa, biomes, realms or protection statuses were also nonsignificant for species richness and functional diversity metrics (Figure 4).

We did find significant category-specific trends for Jaccard similarity and two dietary *CWMs* (Figure 4). While Jaccard similarity was decreasing in the general trend and there were significant category-specific turnover trends for birds, terrestrial and temperate studies, there was no significant trend in Jaccard similarity for marine, mammal, tropical or temperate/tropical studies. Jaccard similarity decreased in unprotected areas only, with no trend for protected areas. We found significant dietary shifts across communities, with a significant increasing general trend in fish consumption (Figure 3), which was also reflected in increasing fish consumption trends for bird studies and unprotected studies. Vertebrate consumption significantly declined in marine studies and tropical studies. The trend for marine vertebrate consumption was significantly more negative than for terrestrial studies, and the temperate trend was significantly more negative than tropical studies (Figure 4).

At the study level, 11 of 50 studies exhibited a significant trend in species richness and 11 exhibited significant turnover. For observed functional diversity metrics, 11 of 50 studies exhibited a trend in at least one metric, and 7 of 50 studies exhibited a significant trend for at least one corrected metric (Table 2). In general, there were more significant trends for observed functional diversity metrics, with some disappearing after correction, indicating that those trends were likely due to changes in the number of species. Study-level slopes were not significantly related to start year or duration of time series for any metric.

We assessed the sensitivity of general trend results for all metrics to major data processing decision by rerunning models with increasingly conservative subsets of the data. Trends for Jaccard similarity and fish consumption were not sensitive to either time series duration or trait coverage. After excluding time series with less than 3 years, we found an increasing trend for body mass that remained after excluding time series of less than 4 and 5 years. The body size trend did however disappear after excluding time series of less than 10 years. A complete list of models run in the sensitivity analysis and their results can be found in the Supporting Information.

4 | Discussion

Our study represents the largest broad-scale multitaxa assessment of functional change through time to date, giving a first look at general, categorical and study-level local trends in functional diversity in mammal and bird communities. Our work complements efforts on a similar scale assessing temporal change in species and phylogenetic diversity across taxa (Daru et al. 2021; Dornelas et al. 2014; Li et al. 2020; Vellend et al. 2013, 2017) or functional diversity change for a single taxa (Barnagaud et al. 2017; Jarzyna and Jetz 2016; Trindade-Santos, Moyes, and Magurran 2020). We did not detect an overall trend in any functional diversity metric, corrected or observed. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by

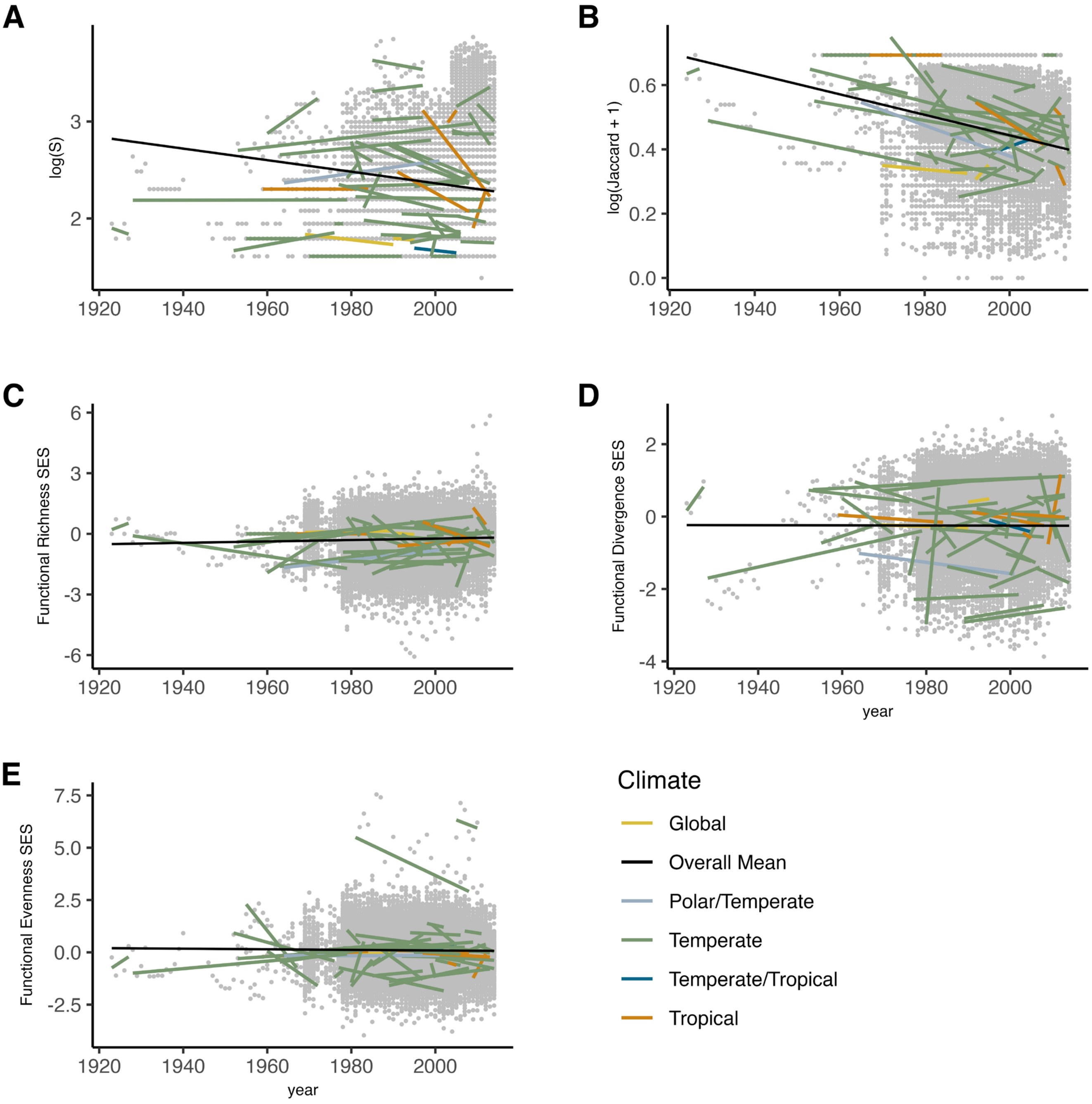

FIGURE 2 | Plots of study-level trends with line colour corresponding to climatic region, with data points in grey and the overall mean slope for a metric in black for (A) log species richness, (B) Jaccard similarity, (C) functional richness SES, (D) functional divergence SES and (E) functional evenness SES.

increasing dissimilarity through time (Dornelas et al. 2018), indicating that nonsignificant trends in functional metrics are consistent with similar well-documented species derived trends.

Category-specific trends in species turnover highlight the types of communities experiencing change in community composition. For example, we found significant turnover for many biomes, realms and taxa with the exception of marine, tropical, temperate/tropical and mammal studies. The lack of turnover in marine studies stands in contrast to other global estimates of biodiversity change that found higher turnover in marine systems than terrestrial (Blowes et al. 2019). However, previous global estimates are dominated by fish communities which we exclude here and are likely driving the overall turnover trend while disguising relative stasis in marine bird and mammal communities. We also found significant turnover for unprotected areas and no significant turnover in protected areas, indicating that in general unprotected communities are experiencing bigger shifts in community composition through time.

Surprisingly, we found no evidence for some of the strongest predictions for anthropogenic impact. For example, we found no trend

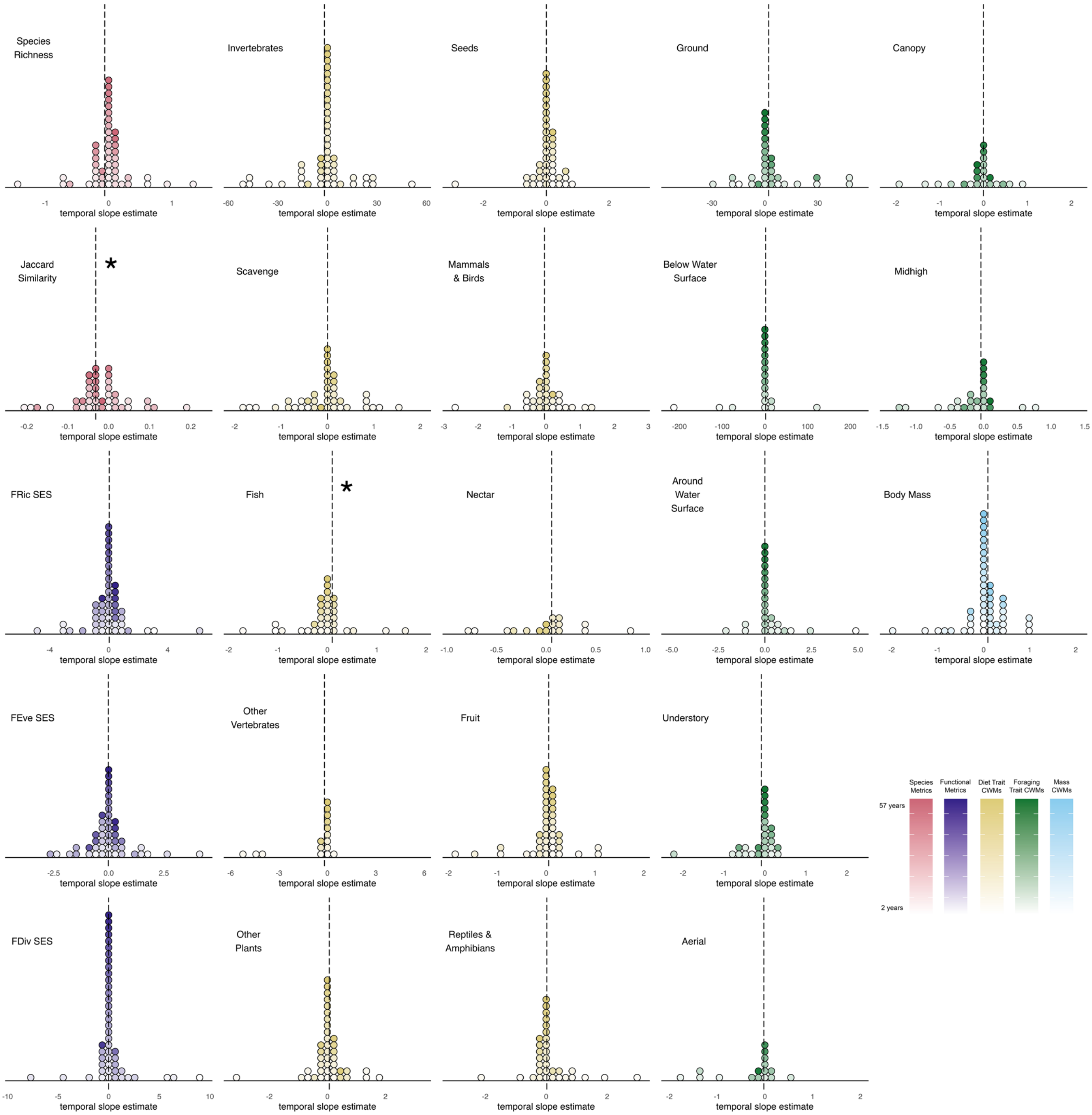

FIGURE 3 | Dotplot of study-level temporal slopes for all diversity metrics, where each dot represents a study and the dot colour value is lighter for shorter duration time series and darker for longer duration time series. Plot colour indicates the type of metric represented, with species metrics in pink, functional diversity metrics in purple, *CWM*s of the dietary trait axes in yellow, *CWM*s of the foraging strata trait axes in green and *CWM*s of body mass in light blue. The general model slope estimate (incorporating data for all studies) is denoted by the vertical dashed line. Significant general model slopes are indicated by a star.

in mean body mass in bird or mammal communities. In fact, sensitivity results indicated that after excluding the shortest time series, there is evidence of an increasing trend in body size. This result could be an indication that either body size is not changing significantly due to climate change, opposing pressures such as urbanisation or carnivore reestablishment are overshadowing climate change impacts (Hantak et al. 2021), or current shifts are happening at an intraspecific level not captured by our data. Additionally, the majority of the studies in our dataset draw from areas that may have experienced significant loss of large-bodied species before the observation window, with contemporary loss rates slowing (Fritz, Bininda-Emonds, and Purvis 2009). Trends could be significantly different for the same time periods in regions of sub-Saharan Africa, for example, which has poor representation in our dataset but where megafauna exist on the landscape and are increasingly threatened (Ripple et al. 2015).

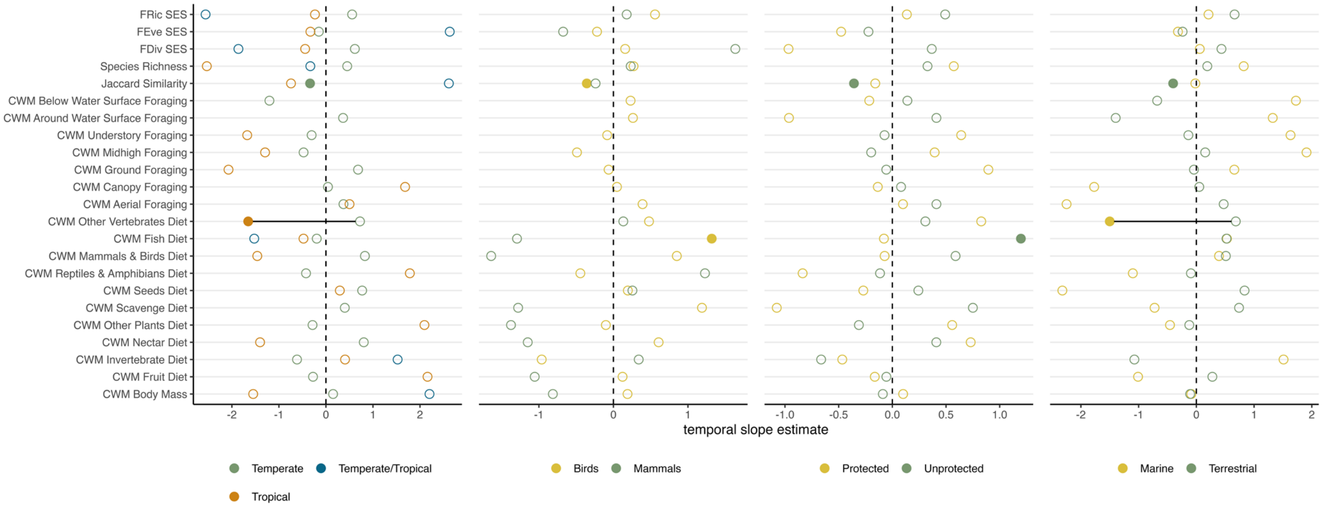

FIGURE 4 | Study-level slopes for each of the four site-level categorical variable models: Climate, taxa, protection status and realm. Dots are solid if the slope for that category and metric was significant and otherwise open. Significant pairwise differences between categories for a metric are indicated by a solid black connecting line. Slope estimates are *z*-score scaled for visualisation.

TABLE 2 | Number of studies that experienced a significant trend in each calculated metric out of 50 total studies. Both observed and corrected (SES) versions of functional metrics are included.

	Species		Functional					
	S	Jaccard similarity	FRic	FEve	FDiv	SES FRic	SES FEve	SES FDiv
+	2	0	5	3	1	4	0	1
−	9	12	2	0	3	1	1	2

We similarly did not find evidence of changes in trait distributions predicted by previous global change work. We found no changes in the prevalence of different foraging strategies, despite documented losses of understory birds in the neotropics and some evidence that agricultural incursion particularly threatens arboreal species. Those shifts may therefore be the result of specific contexts and not generalisable to bird communities across the globe. Rather than declines in insectivory and increases in invertivory predicted by changes in resource availability, we instead found changes in the degree of consumption of fish and vertebrates. Neither increasing trends for fish consumption nor decreasing trends for vertebrate consumption in marine and tropical studies are obviously consistent with known changes in those contexts and warrant further examination.

4.1 | Study-Level Functional Change

While trends aggregating across studies did not indicate one prevailing kind of change in functional diversity or functional composition (with the exception of changes in fish consumption), post hoc examination of trends for individual studies revealed four distinct change groups. These groups are categorised based on the concurrent trends in species and functional metrics and can be broadly described as no change in species or functional diversity metrics, change in functional diversity independent of species richness, loss of redundancy (species richness declines while functional richness is maintained) and increase in species richness sometimes accompanied by increasing functional richness (Table 3). The majority of studies (32 studies) exhibited no trend in any species or functional diversity metric. Contrary to the expectation due to anthropogenic and global change stressors, these communities do not show significant changes over the course of the observation window. Studies in this group span the distribution of study durations, excluding only the very longest running studies, with the longest no-change time series lasting 33 years. They also included both bird and mammal studies and only seven were located in protected areas, indicating that the lack of trend is not restricted to a specific ecological context or those communities most insulated from human impact. Across metrics, longer duration studies are distributed across the range of slope effect sizes (Figure 4).

The lack of trend could be the result of multiple possible scenarios. First, these may be communities resisting perturbations or simply not experiencing significant perturbations. Given the studies in this group come from all possible taxa, realms, biomes and protection statuses, evidence points to communities resisting perturbation. Alternatively, these may be communities that have experienced or continue to experience significant stress, but lost species or functional diversity outside the observation window. This could be true particularly for North American mammal communities where trophic downgrading and megafaunal losses occurred thousands of years ago (Estes et al. 2011). Third, these communities may be experiencing directional shifts undetectable by available data. For example, species-level trait data do not capture intraspecific shifts in the trait space, which can have significant implications for ecological processes.

TABLE 3 | Count of number of studies for different kinds of functional change, broken down into no change functional change without species richness change, loss of redundancy and increases in species richness. Trends direction is indicated by a positive or negative sign, with a 0 indicating no trend.

Type	S	Jaccard Similarity	SES FRic	SES FEve	SES FDiv	Study count
No change	0	0	0	0	0	32
Functional diversity change	0	0	0	–	0	1
	0	–	0	0	0	1
	0	–	0	0	–	1
	0	–	–	0	+	1
	0	–	+	0	0	2
	0	–	+	0	–	1
Loss of redundancy	–	0	0	0	0	5
	–	–	0	0	0	4
Increase in species richness	+	0	0	0	0	1
	+	–	+	0	0	1

The next largest group of studies (7 studies) were those with no species richness trend that showed a trend in at least one functional diversity metric. Based on a species approach alone, these communities appear to either be experiencing no change or some change in species identity, with unknown implications for conservation concern or ecological process. However, with the addition of a functional perspective we found multiple kinds of underlying change in functional diversity including increases and decreases in corrected functional richness and divergence and loss of corrected functional evenness. We therefore found evidence of both increases and decreases in the functional capacity of communities independent of species-based metrics, reinforcing the importance of moving beyond solely species-based approaches for biodiversity assessment (Hillebrand et al. 2017; Santini et al. 2017).

Nine studies showed loss of functional redundancy. These studies are characterised by a loss of species richness with no shift in functional diversity metrics, indicating the lost species were functionally similar enough to another species to not impact the overall functional diversity. Redundancy is critical for maintaining ecological processes in the face of disturbance as it ensures functional roles are maintained (Biggs et al. 2020), and a loss of functional redundancy likely reduces a community's capacity to respond to future stressors (Reich et al. 2012). These communities are actually faring better than expected looking at species-based metrics alone, but are also in a precarious position for maintaining ecological function into the future (Pimiento et al. 2020).

The final two studies showed an increase in species richness and observed functional richness, with only one showing an increase in functional richness beyond what was expected by chance (corrected functional richness). While this can be an indication of increasing functional capacity or reestablishment of previously lost species, it can also be the result of less desirable processes like the introduction of invasive species. Notably, both of these studies were from temperate, terrestrial bird communities in Scandinavian countries with a unique environment and conservation context. Still, results are consistent with other broad-scale studies of bird communities, which found loss of common, functionally general species alongside increases in rare species (Inger et al. 2015; Rosenberg et al. 2019; Schipper et al. 2016).

Study-level trends in CWMs offer insight into how the functional space might be shifting through time and how that functional turnover may or may not relate to species turnover. Every study that experienced a trend in a species or functional diversity metric (Table 3; functional diversity change, loss of redundancy and increase in species richness study types), with the exception of 3 ‘loss of redundancy’ studies, also exhibited a trend in at least one CWM. This link between CWMs and other metrics indicates that changes in the shape of the functional space, and additions or losses of species, are almost always accompanied by a functional shift. However, shifts in the functional space were not restricted to change studies, as we also found significant CWM trends in 7 of the 32 ‘no change’ studies. Functional turnover was also qualitatively divorced from species turnover, with just as many studies exhibiting functional turnover (at least one significant CWM trend) with species turnover as not. These post hoc observations give evidence that even minimal changes in species composition undetected by trends in species-based metrics can translate to significant changes to one or a few trait axes.

4.2 | Conservation Implications

While we found no overall trends in functional metrics, our results should not be interpreted as an indication that the ongoing biodiversity crisis is less severe than previously described or that there is no concern for changes in functional diversity as a result of anthropogenic impact. In fact, study-level trends indicate quite the opposite, that changes in functional diversity and composition with negative or yet unknown implications for ecosystem processes may be going undetected by common species-based approaches. For example, loss of evenness in communities with constant species richness may be a first sign of a community being impacted by environmental change, with negative implications for stability and function.

One of the biggest threats to biodiversity is the wholesale conversion of natural areas to urban or human-dominated landscapes (Tilman et al. 2017). Typical long-term monitoring data such as those included in our study stops before this conversion occurs, leaving the resultant precipitous declines in biodiversity unrecorded (Cardinale 2014). This is a known issue with the culture of long-term monitoring, and our results should not be removed from that context. Rather, this study captures communities that are likely experiencing a degree of human intervention but are still largely nature dominated.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code for the analyses in this manuscript is archived on Zenodo at https://doi.org/10.5281/zenodo.8075946. Data products are also archived on Zenodo at https://doi.org/10.5281/zenodo.12538949. Original data sources are open access and available at their respective providers.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.