

Introduction/Framing

1. Understanding the interrelated dynamics of size- and -abundance based dimensions of biodiversity is key to understanding biodiversity change in the Anthropocene.
 1. Total abundance - i.e. the total number of individual organisms present in a system - and size-based currencies, such as the total biomass or total metabolic flux (“energy use”) of a system, are intertwined, but nonequivalent, measures of biological function.
 2. Abundance is more closely tied to species-level population dynamics, while size-based metrics more directly reflect assemblage-level resource use and contributions to materials fluxes at the broader ecosystem scale (Morlon et al. 2009, Dornelas et al. 2011, Connolly et al. 2005, White et al. 2007)
 3. While these currencies are naturally linked (Ernest et al. 2009, Morlon et al. 2009), changes in size composition can decouple the dynamics of one currency from another (@dornelas2011, White et al. 2004, 2007, Henderson and Magurran 2010, Yen et al. 2017).
 4. This can mean that intuition from one currency may be misleading about others; a trend in numerical abundance might mask something else going on with biomass (White et al. 2004).
 5. Changes in size composition strong enough to decouple currencies may be symptomatic of important changes in ecosystem status
 1. E.g. abundance-biomass comparison curves (Petchey and Belgrano 2010); size-biased extinctions (Young et al. 2016, Smith et al. 2018)
 2. This underscores the need to understand how these dynamics are playing out in the Anthropocene (Fisher et al. 2010)
2. Looking at the relationship between size and abundance dynamics at the **community scale** tells us about important functional dynamics
 1. This is the scale at which ecological processes (i.e. compensatory dynamics, niche tracking, functional replacement) come into play - in contrast to population or global trends (White et al. 2007, Dornelas et al. 2014, McGill et al. 2015).
 2. To the extent that size is a proxy for other functional traits, changes or consistency in the community-level size structure over time may reflect processes related to niche structure (White et al. 2007, Petchey and Belgrano 2010)
 3. Scenarios:
 1. Strong size shifts can decouple the relationship between abundance and biomass.
 1. This is well established in aquatic systems, where changes in the scaling between abundance and biomass often signal ecosystem degradation (???, Warwick and Clarke 1994 and refs therein, Petchey and Belgrano 2010)
 2. Or, compensatory shifts in the size structure can buffer community function (in terms of biomass or energy use) against changes in abundance (Ernest et al. 2009, White et al. 2004, Terry and Rowe 2015)
 3. Or, consistency in the size structure may maintain the relationship between size- and -abundance based currencies, even as species composition, total abundance, and total biomass/total energy use fluctuate over time.
 1. Low turnover, or size-structured replacement - either of which could reflect consistency in the niche structure over time (Holling 1992)
 4. Random dynamics/drift may also contribute to the dynamics of the size spectrum
 1. Either via neutral population dynamics, or through systematic change on axes orthogonal to size.
 4. Different subsets of a community may respond in different ways.
 1. Core and transient species have different biology and respond to different cues.
3. It is important to improve our understanding of these dynamics for terrestrial animal communities in particular.

1. Terrestrial animal communities are relatively unknown in terms of size spectrum work (White et al. 2007); but see classic bugs, classic birds, (Thibault et al. 2011, Ernest 2005, Yen et al. 2017).
2. However, they:
 1. Exhibit size structure (Thibault et al. 2011, Ernest 2005)
 2. Are experiencing serious and potentially size-structured change, with implications at community, ecosystem, and global scales (Young et al. 2016, Schmitz et al. 2018)
3. Case studies have demonstrated that size shifts can decouple N from E for terrestrial animals (White et al. 2004, Yen et al. 2017) while others have them moving together (Hernández et al. 2011)
4. Establishing general commonalities regarding these dynamics has been constrained by 1) a lack of macroecological-scale timeseries data on species and size composition for terrestrial animal communities (Thibault et al. 2011, White et al. 2007), and 2) appropriate methods for working with ISDs
 1. Data requirements: A consistent sampling protocol; many communities; long temporal extent; size *AND* abundance data (for a particular taxon, often size or abundance - but not both - is the traditional unit of measure); for the community (not population or global) scale
 2. ISD challenges: the ISDs for determinate growers (mammals, birds. . .) are not simple power laws (Thibault et al. 2011, Ernest 2005). Quantifying change is not as straightforward as computing a slope. (Neither is *comparing* change across currencies.)
 3. As a result, we do not have a synthetic understanding of either 1) the extent to which changes in the size structure decouple the dynamics of abundance, biomass, and energy use in these systems, or of 2) the underlying changes in community structure that account for these effects.
5. Here, we begin to address this gap by exploring how temporal changes in species composition and the size spectrum modulate the relationship between total abundance, energy, and biomass for communities of North American breeding birds. Specifically,
 1. We used allometric scaling to estimate community size and abundance data for the North American Breeding Bird Survey, and evaluated how changes in total abundance, biomass, and energy use have co-varied from 1988-2018:
 1. How often do these currencies change together vs. have decoupled dynamics?
 2. What are the dominant directions and magnitudes of the overall change and any decoupling between the currencies?
 2. We examined how these changes differ between core species and the whole-community (i.e. including transients).

Methods

1. Bird abundance data

1. We used data from the Breeding Bird Survey to compare community attributes along each route between the 5-year periods from 1988-1992 and 2014-2018.
 1. We used a discrete time-period comparison (as opposed to continuous-time over the full time-series) to simplify comparisons between temporal turnover in species composition and the size structure - which are complex, multidimensional distributions - and changes in community-wide total abundance, biomass, and energy use.
 1. We acknowledge that a continuous-time perspective may be better equipped to detect nonlinear dynamics (Macgregor et al. 2019) and account for artefacts related to the selected beginning and ending dates (???, Cusser et al. 2020). Developing continuous-time methods for analyzing complex, multidimensional community distributions such as the size spectrum is an important and ongoing area of methodological development (e.g. Yen et al. (2017)).

2. We used 5-year periods so as to smooth out interannual variability and to account for sampling accumulation effects in characterizing the bird community in each time period (White et al. 2004).
 1. We used the same begin and end dates for all routes in the analysis so as to have a consistent window.
 2. We explored the number of routes in the dataset with complete sampling coverage for two five-year “begin” and “end” periods with start dates ranging from X to X and end dates ranging from X to X, and selected beginning and ending dates of 1988 and 2018 so as to obtain a large number of routes from diverse bird conservation regions, and span a relatively long window of time (could ref Cusser et al. (2020) there).
2. Estimated size data
1. BBS contains abundances for all species along a route in each year, but does not include measurements of individual body size. We generated body size estimates for individual birds assuming that intraspecific size distributions are normally distributed around a species’ mean body size (following Thibault et al. (2011); also recent Myers/Botero/Fristoe paper I believe).
 1. Using records of species’ mean and standard deviation body sizes from (???), we drew individuals’ body sizes from the appropriate normal distributions.
 1. For species for which there was not a standard deviation recorded in (???) ($n = ?$), we estimated the standard deviation based on an allometric scaling relationship between mean and standard deviation in body mass (also described in Thibault et al. (2011)). For species with multiple records in (???), we used the mean mean and standard deviation body sizes across all records (averaging across sexes, subspecies, and records from different locations). We performed this averaging after estimating any missing standard deviation measurements.
 2. This method does not incorporate intraspecific variation in body size across geographies or over time (???, Gardner et al. 2011).. However, it makes it possible to conduct macroecological studies of avian size distributions at a spatial and temporal scale that would otherwise be impossible (Thibault et al. 2011).
 3. For each individual bird observed, we estimated metabolic rate as (parameters) (Fristoe 2015). Change in total abundance, biomass, and energy use over time We used linear models to test for changes in total abundance, biomass, and energy use over time, and more specifically to test for coupled or contrasting changes between the different currencies. For each route, we rescaled the different currencies to a comparable order of magnitude, using a scaling method previously applied to community and population-level abundance data (Dornelas et al. 2014; Dornelas et al 2019): $\text{scaled_abundance} = \text{scale}(\sqrt{\text{abundance}})$; gives mean 0 and sd of 1 Scaling is done on each currency for each route independently. This is because the point of scaling is to get the different currencies on the same order of magnitude. For each route, we then fit a linear model of the form: $\text{value} \sim \text{time period} * \text{currency}$ and tested whether there was a significant change across time periods for any currency, and whether there was a significant interaction between time period and currency (indicating decoupling of the different currencies). Fitting independent linear models at the route scale may under-estimate p-values and would not be appropriate for estimating dataset-wide effects in a traditional framework. We adopt this approach in order to directly examine the frequency distributions of route-level effects - including trends and interactions - allowing these effects to vary freely across routes (see also Dornelas et al 2015 for the use of independent lms() to explore the frequency of different local trends). We adjusted for repeated comparisons under-estimating p-values using the false discovery rate as implemented in the R function `p.adjust`. We also calculated the ratio of the $\text{mean}(\text{rawvalue_ENDYEARS}) : \text{mean}(\text{rawvalue_STARTYEARS})$ for each currency for each route, to explore the magnitude of change over time. Change in the size structure over time Measuring change in the size structure for bird communities is not as simple as it is for the power-law size spectra generally found in aquatic, forest, and invertebrate systems (refs). The size structure for bird communities is typically multimodal

and therefore cannot be adequately summarized via a single slope (Holling 1992; Thibault et al. 2011). We characterized the size spectrum for each route in each time period using density smoothing through a Gaussian mixture model (Thibault et al. 2011). Smoothing allows us to avoid arbitrary binning decisions. Gaussian mixture models are specifically designed to work with multimodal frequency distributions and have been used previously to characterize avian ISDs. We fit a Gaussian mixture model with up to 12 Gaussians to the distribution of $\log(\text{body mass})$ of all individuals observed along each route within each time period, and selected the best-fitting model using BIC (all following Thibault et al. 2011). We characterized the size structure as the density function of the resulting GMM, evaluated at 1000 points from body mass of 1g to 15000g (corresponding to a $\log()$ body mass of 0-9.6). We used the same, very wide, range of body sizes for every route, to encompass the full range of body sizes represented in our dataset (mean body masses ranging from 2.65 to 8450g). We rescaled each density function to sum to 1. To measure change in the ISD of a given route between time periods, we used an overlap metric previously developed to compare body size distributions of mammals (Read et al 2018). This metric is calculated as: [the sum of the minimum of each scaled density function at each evaluation point]. This metric ranges from 0-1, with 1 being 100% overlap and 0 being complete dissimilarity. Change in species composition over time We calculated two metrics of taxonomic turnover for each route between the time periods. First, we calculated the taxonomic analog of the overlap metric used on the size spectrum, as: the sum over all species of [the minimum relative abundance of each species in time period 1 or 2]. This metric ranges from 0-1, again with 1 being complete overlap and 0 being complete dissimilarity. For comparability with more traditional beta-diversity metrics, we also calculated Bray-Curtis dissimilarity between the two time periods. These metrics generally vary closely with each other. Null models We used null models preserving observed dynamics in species' abundance, but randomized with respect to body size, to test for size-structured replacement or systematic size shifts. We used a null model analogous to null models used to explore patterns in taxonomic and functional beta-diversity more broadly (Swenson et al. 2011; Siefert et al. 2013; He et al. 2021). For each route, we reassigned species' trait values - mean and s.d. Body size - drawing without replacement from the species pool. We ran versions of the null model with local, regional, and continental species pools. The local species pool was defined as all species ever recorded on that route. The regional species pool was defined as all species ever recorded on a route, and all species whose resident or breeding ranges (as defined by BirdLife) overlapped that route. The continental species pool contained all ~400 species present in the dataset. For each iteration of the null model, we calculated the ISD overlap from beginning to end of the timeseries and constructed a distribution of overlap values. We ran 100 iterations. We calculated the standardized effect size (Gotelli and Graves 1996) and percentile score of the observed overlap value relative to the null distribution. We tested if the observed amount of change in the ISD is very high (reflecting a strong size shift) or very low (reflecting size structured replacement) compared to non-size-structured dynamics constrained by observed species turnover and the species pool. Results Dynamics of N, E, and M over time ~50% of the time, temporal comparison non significant When there is a trend: Usually a decrease but not a catastrophic one Usually not a significant interaction over different currencies When there is a difference... Usually an increase in size \rightarrow a less negative slope Manifests for biomass more frequently than for energy use (because of $\frac{3}{4}$ scaling) There is considerable variability in the relative change in currencies. Change in taxonomic and size structure over time Size structure consistently more conserved than species composition Null models For all species pools, SES and percentile score distributions do not differ from random expectation Discussion points Overall, a signal of ~parallel dynamics, and particularly decreases, in abundance, biomass, and energy use over time About 50% of the time, not significant. But when significant, overwhelmingly 1) a decrease and 2) changing together. This is consistent with concerns about declines in abundance, but not consistent with size-structured declines amplifying declines in function beyond abundance (Dirzo et al. 2014). Note that this study is not definitive for biodiversity monitoring Discrete vs. continuous time Geographic bias in routes Continuous-time methods for ISD work, and

case studies better targeted for biodiversity monitoring, are both next-steps Relationship usually maintained due to low taxonomic turnover, but not detectably through functional replacement Low taxonomic turnover may reflect stable niche structure over time. Absent the empirical basis for parameterizing a null model of species turnover (e.g. the necessary parameters to run neutral simulations), we cannot distinguish between random and systematic dynamics of taxonomic change. But, we observe pretty low turnover. There is no dominating signal of functional replacement conserving the size structure beyond what is expected given taxonomic turnover + the species pool. This null model is inherently conservative, with a high type-II error rate (Ulrich et al. 2017). Not deviating does not necessarily mean there's no size structured dynamics. There may be both size structured replacement and size shifts operating simultaneously, or simply weak/imperfect functional replacement. Or, birds might be less strongly size-structured than fish, trees, or rodents. There are more ways to be a 20g bird than a 20g pocket mouse. When there is a decoupling of currencies, tends to be an increase in body size \rightarrow less negative slope in biomass/energy vs abundance Contrasts with concerns about size-biased extinctions Consistent with other reports from BBS (Schipper et al. 2016) May reflect forests in ~recovery over this time period (Schipper et al. 2016) Get into some case studies here These results might or might not be borne out in other taxonomic groups or other geographic regions. BBS is on intact habitats in systems that may have been recovering - counter to global trends or trends in areas of particular concern Next steps should include specifically exploring systems that have undergone major disturbances, and/or a large degree of taxonomic turnover. And greater taxonomic coverage - comparative work between mammals and birds, for example

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