

## 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).
  3. This yielded 528 routes.
    1. Sometimes I subsample the 528 to get a maximum of 10 routes per bird conservation region, so that the highly-sampled BCRs don’t dominate aggregate analyses (Thibault et al. 2011). That yields 238 (I believe).
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/Catano/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).
    4. For each route in a given year, we compute total energy use, total biomass, and total abundance by summing over all individuals observed on that route in that year.
3. Comparing ISDs over time
1. Characterizing the ISD
    1. For a given route and time period, we draw the appropriate numbers of individuals of each species from their corresponding normal distributions.
  2. We use two approaches to test whether the ISD for 1988-1992 is significantly different from the one for 2014-2018
    1. Kolmogorov-Smirnov test on the vector of masses for the begin vs end time periods
    2. Bootstrap resampling of individuals (pretty sure this derives from Ernest 2005):
      1. From the pool of all individuals “observed” in both timeperiods, draw the appropriate number for each time period without replacement.
      2. KS test comparing “begin” and “end” for the reshuffled communities
      3. Repeat 500x and retain the test statistic (D) for all tests
      4. Compute the percentile and standardized effect size (???) for the test statistic for the *actual* time periods to the distribution of test statistics for the reshuffles

3. For an intuitive measure of the magnitude of change over time, we compute an overlap measure derived from (Read et al. 2018):
  1. We characterize the ISD as a smooth function by fitting a Gaussian mixture model (to logarithm of mass, up to 15 Gaussians, select best using BIC, all following Thibault et al. (2011)). We evaluate the density function of the GMM at points for a size range from 0-exp(15), which covers the range of sizes in this dataset with ample padding on each side. We then rescale the density function so the total area under the ISD is 1.
  2. We calculate the overlap between two ISDs as the sum of the minimum density at each evaluation point. This ranges from 0 (no overlap) to 1 (complete overlap).
4. Decoupling of dynamics in total abundance, biomass, and energy use over time
  1. To test whether change in the ISD results in decoupling of currencies, we can't just compare the slopes for total energy, total biomass, total abundance to each other. This is because the three different currencies are on radically different scales of measurement. We also can't rescale using the usual methods (e.g. scale to mean 0/sd 1, sqrt transform Dornelas et al. (2014); Gotelli et al. (2017)) because these destroy information about the range of variability within a single currency.
  2. Instead, we test whether the observed change in biomass or energy use differs from the change that we would expect given observed changes in community-wide abundance, but with *no change* in the ISD from beginning to end. Enter Null Model A.
  3. Simulate change in total energy and total biomass under "no change in ISD" and "observed change in ISD" scenarios
    1. We construct sampling ISDs for each time period, to characterize the probability of observing an individual of a given size in that time period. We draw individuals, fit GMMs, and characterize the probability density function as above. For this, because there is some sampling error, I draw 5 copies of the ISD and fit the GMM to the combined 5 draws. This doesn't affect anything in practice and is mostly inspired by a one-off comment from Allen Hurlbert about "sampling error" so I might drop it. We construct sampling ISDs for the "begin" and "end" time periods.
    2. We then *re draw* individuals for each time period and shuffle the ISDs to produce scenarios.
      1. First, we draw individuals for each year using the actual ISD for that time period (so the "begin" ISD for 1988-1992 and the "end" ISD for 2014-2018).
      2. Then we draw individuals for each year, but using the "begin" ISD for all years.
      3. We draw year-by-year, instead of the whole time period, because there is interannual, intratimeperiod variation in total abundance that we would like to capture. But we pool individuals within a time period to create the ISD to smooth out species accumulation.
      4. Draws from sampling ISDs like this diverge slightly from draws from the raw species counts and sds. So we run everything through this pipeline for comparability.
    3. We compute total energy use and total biomass for each year for each scenario.
    4. Again because there is some sampling error, we repeat the re-drawing of individuals 5 times and compute the mean total biomass/total energy use across draws. Again I don't think this really affects stuff in aggregate and I could be talked out of it.
  4. We use Bayesian linear models to test whether change in the "actual ISDs" vs "no change-ISDs" scenarios differs.
    1. The "no-change ISDs" scenario reflects change in total energy/biomass due simply to changes in total abundance. The "actual ISDs" scenario reflects the combined effects of change in abundance and change in the ISD.
    2. We evaluate change at the route level. I tried fitting everything within one hierarchical model, but the hierarchical model attributes a lot of variation to getting the right intercept for each route (which we don't care about) and does a really bad job estimating within-route slopes and decoupling (which is what we do care about). It's also ridiculously hard to compute for a large number of routes and I never managed to run it on the full dataset. These are challenges you don't run into if - like Dornelas et al. (2014) - you're only interested in computing one slope. We care most about the *decoupling* of slopes at the route level. The use of a Bayesian

framework helps us offset some of the issues around p-values if we were to do this many models in a frequentist setting.

3. For each currency for each route, we fit 3 models:
  1. `total_biomass ~ timeperiod * scenario, total_biomass ~ timeperiod, total_biomass ~ 1`
  2. We used LOO-crossvalidation to select the best-fitting model as the simplest model with an ELPD within 1 SE of the best-fitting model.
  3. We used `relloo` to correct for outliers.
  4. We fit as Gaussians with default priors, run for 8000 iterations. We fit as Gaussians to avoid having to deal with back-transforming the parameter estimates (and because when I coerced to other family distributions I got tons of convergence issues). Running for 8000 iterations is extremely generous for these models.
4. If the best-fitting model does not include the scenario term, it means that the change in the ISD does not ~significantly decouple the dynamics of total energy/biomass from that which is driven by changes in abundance. If there is no **timeperiod** term, it means that there's not a ~significant change begin-end.
5. We extract parameter estimates from the best-fitting model to examine the magnitude and direction of change beginning-to-end and decoupling due to change in the ISD.

## References

- Connolly, S. R., T. P. Hughes, D. R. Bellwood, and R. H. Karlson. 2005. Community Structure of Corals and Reef Fishes at Multiple Scales. *Science* 309:1363–1365.
- Cusser, S., C. Bahlai, S. M. Swinton, G. P. Robertson, and N. M. Haddad. 2020. Long-term research avoids spurious and misleading trends in sustainability attributes of no-till. *Global Change Biology* 26:3715–3725.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science* 344:296–299.
- Dornelas, M., D. A. T. Phillip, and A. E. Magurran. 2011. Abundance and dominance become less predictable as species richness decreases. *Global Ecology and Biogeography* 20:832–841.
- Ernest, S. K. M. 2005. Body size, energy use, and community structure of small mammals. *Ecology* 86:1407–1413.
- Ernest, S. K. M., E. P. White, and J. H. Brown. 2009. Changes in a tropical forest support metabolic zero-sum dynamics. *Ecology Letters* 12:507–515.
- Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010. Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography* 19:1–15.
- Fristoe, T. S. 2015. Energy use by migrants and residents in North American breeding bird communities. *Global Ecology and Biogeography* 24:406–415.
- Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: A third universal response to warming? *Trends in Ecology & Evolution* 26:285–291.
- Gotelli, N. J., H. Shimadzu, M. Dornelas, B. McGill, F. Moyes, and A. E. Magurran. 2017. Community-level regulation of temporal trends in biodiversity. *Science Advances* 3:e1700315.
- Henderson, P. A., and A. E. Magurran. 2010. Linking species abundance distributions in numerical abundance and biomass through simple assumptions about community structure. *Proceedings of the Royal Society B: Biological Sciences* 277:1561–1570.
- Hernández, L., J. W. Laundré, A. González-Romero, J. López-Portillo, and K. M. Grajales. 2011. Tale of two metrics: Density and biomass in a desert rodent community. *Journal of Mammalogy* 92:840–851.
- Holling, C. S. 1992. Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems. *Ecological Monographs* 62:447–502.
- Macgregor, C. J., J. H. Williams, J. R. Bell, and C. D. Thomas. 2019. Moth biomass increases and decreases over 50 years in Britain. *Nature Ecology & Evolution* 3:1645–1649.
- McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution* 30:104–113.
- Morlon, H., E. P. White, R. S. Etienne, J. L. Green, A. Ostling, D. Alonso, B. J. Enquist, F. He, A. Hurlbert, A. E. Magurran, B. A. Maurer, B. J. McGill, H. Olf, D. Storch, and T. Zillio. 2009. Taking species abundance distributions beyond individuals. *Ecology Letters* 12:488–501.
- Petchey, O. L., and A. Belgrano. 2010. Body-size distributions and size-spectra: Universal indicators of ecological status? *Biology Letters* 6:434–437.
- Read, Q. D., J. M. Grady, P. L. Zarnetske, S. Record, B. Baiser, J. Belmaker, M.-N. Tuanmu, A. Strecker, L. Beaudrot, and K. M. Thibault. 2018. Among-species overlap in rodent body size distributions predicts species richness along a temperature gradient. *Ecography* 41:1718–1727.
- Schmitz, O. J., C. C. Wilmers, S. J. Leroux, C. E. Doughty, T. B. Atwood, M. Galetti, A. B. Davies, and S. J. Goetz. 2018. Animals and the zoogeochemistry of the carbon cycle. *Science*.
- Smith, F. A., R. E. Elliott Smith, S. K. Lyons, and J. L. Payne. 2018. Body size downgrading of mammals over the late Quaternary. *Science* 360:310–313.

- Terry, R. C., and R. J. Rowe. 2015. Energy flow and functional compensation in Great Basin small mammals under natural and anthropogenic environmental change. *Proceedings of the National Academy of Sciences* 112:9656–9661.
- Thibault, K. M., E. P. White, A. H. Hurlbert, and S. K. M. Ernest. 2011. Multimodality in the individual size distributions of bird communities. *Global Ecology and Biogeography* 20:145–153.
- Warwick, R. M., and K. R. Clarke. 1994. Relearning the ABC: Taxonomic changes and abundance/biomass relationships in disturbed benthic communities. *Marine Biology* 118:739–744.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* 22:323–330.
- White, E. P., S. K. M. Ernest, and K. M. Thibault. 2004. Trade-offs in Community Properties through Time in a Desert Rodent Community. *The American Naturalist* 164:670–676.
- Yen, J. D. L., J. R. Thomson, J. M. Keith, D. M. Paganin, E. Fleishman, D. S. Dobkin, J. M. Bennett, and R. Mac Nally. 2017. Balancing generality and specificity in ecological gradient analysis with species abundance distributions and individual size distributions: Community distributions along environmental gradients. *Global Ecology and Biogeography* 26:318–332.
- Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47:333–358.