

Methods

Bird abundance data

We used data from the Breeding Bird Survey (Pardieck et al. 2019) to evaluate trends in abundance, biomass, and energy use. The Breeding Bird Survey consists of roughly 40km-long survey routes distributed throughout the United States and Canada. Routes are surveyed annually during the breeding season (predominately May-June), via 50 3-minute point counts during which all birds seen or heard are identified to species (Pardieck et al. 2019). Sampling began in 1966, and routes have been added over time to a current total of roughly 3000 routes (Pardieck et al. (2019)) We explored trends in abundance, biomass, and energy use over the 30-year time period from 1989-2018. We selected these years to provide a temporal window sufficient to detect trends (Cusser et al. (2020)), while allowing for a substantial number of routes. To avoid irregularities caused by missing time steps, we restricted the main analysis to routes that had been sampled in at least 27 of 30 years in this window ($n = 739$), and compared these results to a more strict selection of routes that were sampled in every year ($n = 199$). We take the route to be the “community” scale (Thibault et al. 2011). We filtered the data to remove taxa that are poorly sampled through these methods, following Harris et al. (2018). We accessed the data, and performed this preliminary cleaning and filtering, using the R package **MATSS** (Ye et al. 2020).

Estimated size data

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)). Using records of species’ mean and standard deviation body sizes from Dunning (2008), we drew individuals’ body sizes from the appropriate normal distributions. For species for which there was not a standard deviation recorded in Dunning (2008) (185 species affected, of 421 total), we estimated the standard deviation using an allometric scaling relationship between mean and standard deviation in body mass constructed by fitting a linear model to the records in our dataset that did have mean and standard deviation measurements (resulting in the scaling relationship $\log(\text{variance}) = -5.273 + (\log(\text{mass}) * 1.995)$; model $R^2 .86$; see also Thibault et al. (2011)). For species with multiple records in Dunning (2008), 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. For each individual bird observed, we estimated metabolic rate as $10.5 * (\text{mass}^{.713})$ (Fristoe 2015, Nagy 2005, McNab 2009). 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. This method does not incorporate intraspecific variation in body size across geographies or over time (Dunning 2008, 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).

Comparing abundance- and size- based currencies

Comparing trends across different currencies is a nontrivial statistical problem. Because different currencies vary widely in their units of measure (e.g. abundance in the hundreds of individuals; total biomass in the thousands of grams), it is challenging to interpret differences in magnitude of slope across different currencies. Transformation and scaling using common approaches (such as a square-root transformation, or rescaling each currency to a mean of 0 and a standard deviation of 1) destroys information about the degree of variability within each currency that is necessary in order to make comparisons *between* currencies for the same system.

Rather than attempting to compare slopes across currencies or to transform different currencies to a common scale, we used a simple null model to compare the observed dynamics for biomass and energy use to the

dynamics that would occur in a scenario in which the species (and therefore, in this context, size) composition of the community was consistent throughout the timeseries, but in which total abundance varied over time consistent with the observed dynamics. For each route, we characterized the “observed” timeseries of total biomass and total energy use by simulating size measurements for all individuals observed in each time step and summing across individuals, using the method described above. We then created simulated timeseries for biomass and energy use incorporating observed changes in community-wide abundance over time, but under a scenario of consistent species (and therefore size) composition over time. For each community, we characterized the timeseries-wide probability of an individual drawn at random from the community belonging to a particular species ($P(s_i)$) as each species’ mean relative abundance taken across all timesteps:

$$P(s_i) = \frac{\sum_t^T \frac{n_{i,t}}{N_t}}{T}$$

where $n_{i,t}$ is the abundance of species i in timestep t , N_t is the total abundance of all species in timestep t , and T is the total number of timesteps. For each timestep t , we randomly assigned species’ identities to the observed number of individuals N_t by drawing with replacement from a multinomial distribution with probabilities weighted according to $P(s)$ for all species. We then simulated body size measurements for individuals, and calculated total energy use and total biomass, following the same procedure as for the observed community. This characterizes the dynamics for size-based currencies expected if the species (and size) composition of the community does not change over time, but incorporating observed fluctuations in total abundance. We refer to these dynamics as “abundance-driven” dynamics.

Long-term trends

For each route, we evaluated the 30-year trend in biomass (or energy use) and compared this to the trend derived from the “abundance-driven” null model using generalized linear models with a Gamma family and log link (appropriate for strictly-positive response variables such as biomass or total metabolic flux). We fit four models to characterize 1) the trend in biomass (or energy use) over time and 2) whether this trend deviates from the trend expected given only changes in abundance:

1. **biomass ~ year * dynamics**, in which “dynamics” refers to being either the “observed” or “abundance-driven” (null model) dynamics. This model fits a slope and intercept for the observed trend in biomass (or energy use) over time, and a separate slope and intercept for the trend drawn from the abundance-driven, or null model, dynamics.
2. **biomass ~ year + dynamics**. This model fits a separate intercept, but not slope, for the abundance-driven and observed dynamics. These models were never selected as the best-performing descriptions of community dynamics.
3. **biomass ~ year**. This model fits a temporal trend, but does not fit separate trends for the observed and abundance-driven dynamics.
4. **biomass ~ 1**. The intercept-only model describes no directional change over time for either the observed or abundance-driven dynamics.

We selected the best-fitting model using AICc. In instances where multiple models had AICc scores within two AICc units of the best-fitting model, we selected the simplest model within two units of the best score.

For each route’s selected model, we extracted the predicted values for the first (usually 1988) and last (usually 2018) year sampled, for both the observed and null trajectories. We calculated the magnitude of change over time as the ratio of the last (2018) to the first (1988) value, and characterized the direction of the long-term trend as increasing if this ratio was greater than one, and decreasing if it was less than one.

Relating change in community structure to decoupling between abundance and size-based dynamics

Community dissimilarity metrics are most readily interpretable when making pairwise comparisons (as opposed to repeated comparisons over a timeseries). We compared the first and last five-year intervals in

each timeseries, resulting in a “begin” and “end” comparison separated by a relatively consistent window of time across routes (usually 19-20 years). The use of five-year periods corrects for sampling effects (White (2004)), smooths out interannual variability, and, by including a relatively large proportion (1/3) of the total timeseries, partially mitigates the impact of scenarios where the start and end values do not align with the long-term trend.

We calculated three metrics to explore how changes in community composition and size structure translate into decoupling between abundance-driven and observed dynamics for biomass and energy use. First, we evaluated the change in average community-wide body size, calculated as the log ratio of mean body size in the last five years relative to the mean body size in the first five years:

$$\log\left(\frac{\bar{m}_{last5}}{\bar{m}_{first5}}\right)$$

where \bar{m}_{last5} is the mean body size of all individuals observed in the last 5 timesteps. Large changes in average body size are, by definition, expected to translate into decoupling between observed and abundance-driven dynamics.

Second, we calculated measures of turnover in the size structure and in species composition. We calculated turnover in the ISD using a measure derived from an overlap measure that has previously been applied to species body size distributions in mammalian communities (Read et al. (2018)). We characterized each “begin” or “end” ISD as a smooth probability density function by fitting a Gaussian mixture model (with up to 15 Gaussians; following Thibault et al. (2011)) to the raw distribution of body masses, and extracting the fitted probability density at 1000 evaluation points corresponding to body masses extending beyond the range of body masses present in this dataset (specifically, from 0 to 15 kilograms; mean body masses in this dataset range from 2.65 grams, for the Calliope hummingbird *Selasphorus calliope*, to 8.45 kg, for the California condor *Gymnogyps californianus*). We rescaled each density function such that the total probability density summed to 1. To calculate the degree of turnover between two ISDs, we calculated the area of overlap between the two density smooths as $\sum \min(density1_i, density2_i)$ where $density1_i$ is the probability density for the first ISD at evaluation point i , and $density2_i$ is the density smooth for the second ISD at that evaluation point. We subtracted this quantity from 1 to obtain a measure of turnover between two ISDs.

To evaluate turnover in species composition between the five-year time periods, we calculated Bray-Curtis dissimilarity between the two communities using the R package `vegan` (Pinheiro et al. 2020).

We tested whether routes whose dynamics were best-described using different syndromes of change (no trend, couple trends, or decoupled trends) differed in 1) the magnitude of change in mean body size; 2) turnover in the ISD over time; or 3) species compositional turnover over time. For change in mean body size, we fit an ordinary linear model of the form `abs(log ratio (mean body size)) ~ best fitting model type`. We used the absolute log ratio so as to focus on the magnitude, rather than the direction, of change in body size. We compared this model to an intercept-only null model of the form `abs(log ratio(mean body size)) ~ 1`. Because our metrics for turnover in the ISD and species composition are bounded from 0-1, we analyzed these metrics using binomial generalized linear models of the form `ISD turnover ~ best fitting model type` and `dissimilarity ~ best fitting model type`, and again compared these models to intercept-only null models. In instances where the model fit with `best fitting model type` outperformed the intercept-only model, we calculated model estimates and contrasts using the R package `emmeans` (Lenth 2021).

References

- 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.
- Dunning, J. B. 2008. CRC handbook of avian body masses. CRC handbook of avian body masses. 2nd ed. CRC Press, Boca Raton.
- 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.
- Harris, D. J., S. D. Taylor, and E. P. White. 2018. Forecasting biodiversity in breeding birds using best practices. *PeerJ* 6:e4278.
- Lenth, R. V. 2021. Emmeans: Estimated Marginal Means, aka Least-Squares Means.
- McNab, B. K. 2009. Ecological factors affect the level and scaling of avian BMR. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 152:22–45.
- Nagy, K. A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology* 208:1621–1625.
- Pardieck, K. L., D. J. Ziolkowski, M. Lutmerding, V. Aponte, and M.-A. Hudson. 2019. North American Breeding Bird Survey Dataset 1966 - 2018, version 2018.0. U.S. Geological Survey.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2020. Nlme: Linear and Nonlinear Mixed Effects Models.
- 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.
- 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.
- White, E. P. 2004. Two-phase speciesTime relationships in North American land birds. *Ecology Letters* 7:329–336.
- Ye, H., E. K. Bledsoe, R. Diaz, S. K. M. Ernest, J. L. Simonis, E. P. White, and G. M. Yenni. 2020, May. Macroecological Analyses of Time Series Structure. Zenodo.