**Introduction**

How abundance is distributed over the range of body sizes in a community (the individual size distribution, ISD) is a key dimension of community structure. To the extent body size is a proxy for a host of functional traits, the ISD reflects the functional composition of a community. The ISD also links individual species’ abundances to ecological function in terms of community-level total biomass and total metabolic flux. Changes in the ISD over time can signal shifts in functional composition, and can decouple the dynamics of abundance, biomass, and energy use. Alternatively, the ISD may remain stable over time, even as the species composition of a community changes, if species of similar body sizes systematically replace each other (size-structured replacement).

In the first macroecological study of the temporal dynamics of terrestrial vertebrate ISDs, we evaluated the change in the ISDs of North American breeding bird communities from 1988-2018, and the consequences for the dynamics of total abundance, biomass, and energy use. Because changes to vertebrate ISDs are intrinsically intertwined with species turnover, we also compared the observed dynamics of ISDs to a null model preserving the observed patterns of species turnover without respect to body size.

**Methods**

*Data*

We used route-level species abundance data for the ~500 routes from the Breeding Bird Survey with records in all of the years in the five year windows from 1988-1993 and 2014-2018 - 10 years total. This time period was chosen to cover a relatively long period of time (30 years) while capturing a large number of routes and bird conservation regions. For bird conservation regions with > 10 routes, we randomly selected 10 routes to use so as not to over-weight these BCRs in aggregate analyses, yielding a final set of ~300 routes.We removed species poorly sampled by the BBS protocols (following [others]). We performed analyses on all species observed, and on only core species (defined for each route as species present in at least ⅔ of all time samples for that route). Results are qualitatively the same, and here we present results for core species.

*Simulating the individual size distribution*

Following Thibault et al. (2011), we simulated the individual size distributions for each route in each 5 year period by drawing the observed numbers of individuals of each species from normal distributions with each species’ mean and standard deviation body size. Mean and standard deviation data were accessed from Dunning (2007). For species without standard deviation data available, we estimated the standard deviation allometrically from the mean. We pooled the individuals observed over all 5 years in each 5 year period, to account for species accumulation due to repeated sampling through time and to smooth out inter-annual variability (White two phase).

*Measuring change in the ISD*

We used an overlap metric to measure the degree of similarity or dissimilarity of two ISDs. First, we characterized each ISD as a smooth density function fit via a Gaussian mixture model. Smoothing allows us to avoid arbitrary binning decisions, and Gaussian mixture models are specifically designed to work with multimodal frequency distributions and have been used previously to characterize avian ISDs. We computed the overlap between the density functions for two ISDs as [the sum of the minimum of each density function at each evaluation point]. This metric ranges from 0-1, with 1 being 100% overlap and 0 being complete dissimilarity.

*Community-level attributes*

We calculated total abundance of all individual, total biomass (as the sum of the estimated body sizes of all individuals), total metabolic flux (as the sum of estimated individual metabolic rates, calculated as pars \* body size ^ pars (Fristoe 2015)), and mean per capita body size for each community in each 5 year period. For each metric, we compared the beginning and end time periods using the log ratio: log(val\_end / val\_end). Values > 0 indicate that the end value is greater than the start value; values <0 indicate a decrease over time. The log ratio provides a direct and intuitive measure of the *magnitude* of change between the two time periods.

*Null model*

Because the ISDs for communities of determinate growers are strongly linked to species composition, we evaluated the degree to which change or consistency in the ISD deviated from that which would be expected given a null model of species turnover without respect to body size. This approach is analogous to studies of functional and taxonomic beta diversity. We randomly reassigned body size values and species labels across all species present in our dataset and computed the change in community-level attributes and ISDs for each route given the shuffled species trait-identity pairings. We repeated this process 1000 times to obtain a null distribution of change metrics (log ratios and overlap values) for each community. To test whether observed dynamics exhibit strong size-structured shifts or size-structured replacement, we calculated the percentile rank for each observed metric relative to the distribution of simulated metrics. Strong size-structured shifts would manifest as low overlap values relative to the null, while size-structured replacement would manifest as high overlap relative to the null.

This null model preserves observed dynamics of species composition and spatial occupancy, but simulates change in the size structure as if species’ dynamics over time were not structured according to their body size. Similar null models have been used to understand community assembly and functional diversity more broadly (Swenson papers). We note that they are intrinsically conservative, with a high type 2 error rate (Narcissus effect paper), and sensitive to the trait composition of the overall species pool. To calibrate our interpretation of the model, we explored the behavior of this model applied to ISDs using a well-studied, experimentally manipulated system (Box 1). We also explored null scenarios using strictly local species pools (shuffling species identities among all species observed only on a single route) and [regional species pools (defined as all species observed in a random sample of 10 routes within Xkm of a focal route)], with qualitatively the same results.

**Results**

*Observed change in the ISD and community attributes*

Overall, avian ISDs have been highly conserved over the 30-year window. ISDs from the two time periods had a median overlap score of .8 (95% interval .63-.88). Total energy and total abundance have both increased in more communities than they have decreased, although the magnitudes of these changes are small. Mean body size has increased more often than it has decreased, but again, the magnitude is small. The degree of overlap in the ISD is consistently greater than, but strongly predicted by, overlap in species composition. Change in total E is strongly predicted by change in total N.

*Null model*

We did not detect a dominating singal of either size-structured replacement or shifts operating above and beyond the dynamics of species turnover. Percentile ranks for observed values of overlap in the ISD, change in total E, and change in mean body size relative to those generated by the null model were essentially uniformly distributed from 0-1.

*Testing the null model (Box 1)*

Using long-term data on desert rodents from the Portal Project, we explored the behavior of this null model under two scenarios corresponding to documented shifts in the rodent community and changes induced via experimental manipulations. The Portal Project includes sets of control plots and partial exclosure plots, from which the 3 largest rodent species are removed. Over time, the site has undergone habitat shifts and changes in the local species pool, which have had documented effects on the degree of functional replacement observed between control and exclosure communities. We compared the ISDs on control and exclosure plots in two time periods corresponding to different scenarios of size-structured shifts and replacement.

For the first 20 years of the study (from 1977-1996), no species were present at the site that were capable of substituting for the large species removed on exclosure plots. During this time, the experimental manipulation essentially induced a powerful size-structured shift between control and exclosure plots. This is confirmed via the null model; the overlap between exclosures and controls in this time period is very low compared to the null distribution. From 1996-2010, a species similar in size to the removed species colonized the site and substituted for these species on exclosure plots. Based on the natural history of these species, this is a real-world example of imperfect, but compelling, size-structured replacement. This change does *not* manifest as a deviation from the null model, possibly because size-shifts and replacement are occurring simultaneously in this scenario, or because the replacement species is not sufficiently similar in size to the original species. Indeed, in a third, hypothetical scenario in which the replacement species is more similar in size to the original species, these dynamics do manifest as a deviation towards high overlap relative to the null.

This exercise demonstrates that, while this null model helps identify cases of strong size shifts or size-structured replacement, weak or messy size-structured processes may obliterate any detectable signal. Therefore, we interpret a lack of deviations from this null model with caution.