**Introduction**

Monitoring the dynamics of biological abundance at the community scale is an important element of understanding how ecological systems behave over time and how they have responded to the current era of global change. The past centuries have seen unprecedented biological change, including widespread extinctions, biotic homogenization, the spread of invasive species, trophic downgrading, and declines in abundance of many animal species. Of particular concern are the apparently general trends towards declines in animal abundance, measured either in the number of individuals or the amount of biomass or energy use for a species or community. For individual species, declines in abundance can foreshadow outright extinction. At the community level, general declines in abundance, or declines in the abundance of large-bodied or trophically critical species, can result in reduced ecological function in terms of materials cycling and energetic throughput.

We do not yet have a general sense of how animal abundance has changed, at the community scale, over recent decades. Communities comprise populations of many species sharing a common spatial and temporal context and bound together by a complex network of direct and indirect interactions. Community-level attributes, such as total abundance, total energy use, or species richness, emerge from the combination of species’ population dynamics, species interactions, and exogenous pressures affecting the whole system. These community-level attributes may be sensitive to changes affecting particular species, or a combination of ecological and statistical factors may buffer community properties against fluctuations occurring at smaller levels of organization – meaning that community-scale dynamics do not necessarily mirror population-level or global trends. In this case, community-level abundance and/or energy use may not change dramatically despite population-level declines for some species. Changing biotic and abiotic conditions may drive species that were once abundant out of a system, but favor the establishment of different species that can compensate for these declines in abundance. Energy use is sometimes treated as interchangeable with the number of individuals, but systematic size shifts can decouple the dynamics of energy and individual abundance. For example, if large bodied species are replaced individual-per-individual by small bodied species, the number of individuals may change very little, but the energy use for the system will decline. Even absent strong niche shifts or competitive dynamics, the total number of individuals or energy use for all species in a system may change less than individual species because these aggregate variables result from summing numerous fluctuating variables. Or, general pressures that affect most species in similar ways may cause consistent shifts in abundance detectable at the assemblage scale.

Distinguishing between these possibilities strengthens our understanding of how dynamics propagate across levels of ecological organization and clarifies our understanding of how global change is manifesting. If declines in some species are offset by gains in others, the primary signal of change may manifest in the turnover. This may be achieved via random fluctuations, or there may be systematic trends in which size classes, species, or traits are fading out or becoming more dominant. If, however, we observe general declines in abundance and especially energy use at the community scale, we may be witnessing a widespread contraction in the resources or other ecological opportunities available to entire assemblages.

We do not yet have a general sense of how animal communities’ abundance, and especially energy use, has changed over recent decades, primarily because of a lack of data and (to a lesser extent) analytical tools for capturing signals of change. Analyzing trends in community-level abundance data reuires consistent monitoring over many years, and synthesizing the common or general trends is best done with surveys conducted with comparable methods for a large number of communities. Energy use can be estimated via metabolic scaling, but this typically relies on measurements of individuals’ body size – which is logistically challenging and rarely attempted except for certain conveniently-sized taxa, such as rodents. We used community abundance data from the North American Breeding Bird Survey, and simulated individual size data generated via allometric scaling, to study the dominant trends in the total number of individuals and total energy use for North American bird communities over the past 40 years. Specifically, we measure the net change in total abundance and energy use for each community over the course of monitoring, and the degree to which these variables have fluctuated or moved consistently over the time series. We aggregate results across the entire dataset and compare across currencies to test whether there is a consistent signal of declines in either energy use or abundance over the study period and whether the two currencies exhibit matching or divergent trends.

**Methods**

*Data*

We used community abundance data from the Breeding Bird Survey (). Following (Shawn’s paper) we treat each route as a community. Routes are approximately 50 mile transects surveyed via point and audio counts annually. For each route, we calculated total abundance as the total number of individuals of all species observed each year.

We estimated total energy use by simulating individual size measurements for every individual observed, calculating the estimated individual metabolic rate via metabolic scaling, and summing the metabolic rates of all individuals detected on each route in each year. Following Thibault (2011), we assume the body sizes of individuals of a given species are normally distributed. We obtained mean and standard deviation body sizes for each species from Dunning (200..7?). For species for which there is not a standard deviation reported in Dunning, we estimated the standard deviation based on the allometric scaling relationship between a species’ mean and standard deviation body size reported in Thibault (2011). For each species observed in each route in each year, we drew values from the corresponding normal distribution to estimate the body sizes of every individual observed. We estimated individuals’ energy use according to metabolic scaling as [scaling] (). Code to generate these estimates is available on GitHub at [www.github.com/diazrenata/BBSsize](http://www.github.com/diazrenata/BBSsize). We then summed the energy use for all individuals, regardless of species, observed for a route for a year to obtain a timeseries of the estimated energy use.

*Characterizing change over time*

We used generalized additive models (GAMs) to characterize the net change and degree of fluctuation for the timeseries of energy and abundance for each route. Unlike more traditional approaches, such as linear or segmented regression, GAMs do not require us to specify an expected functional form for a time series a priori. We used the GAM to generate a smooth, with confidence intervals, for each variable over time. We calculated the net change over time as the fitted value for the final value relative to the fitted value for the first value, with the corresponding confidence intervals. Because different time series, and especially different currencies, have widely varying absolute numbers of individuals, we summarize change as the ratio of the difference between the ending value and the beginning value compared to the beginning value, with the sign corresponding to an increase or a decrease. That is, a value of 0.25 means the ending value is 125% of the beginning value, while a value of -0.25 means the ending value is 75% of the beginning value – a 25% decrease. If the confidence interval for this value overlaps 0, there is not strong evidence for any net change from beginning to end.

This approach liberates us from the constraints and artefacts inherent to using linear models to study timeseries that may be highly nonlinear. Unlike a linear model, it allows us to detect not only “significant” change, but to see the magnitude of the change intuitively. It is not biased towards detecting “no slope” – it may detect very small changes with high sensitivity, but this is readily apparent from the magnitude.

Net change may reflect a relatively consistent direction of change over time, or may mask considerable fluctuations. The more a timeseries fluctuates above and beyond its net change, the more complex dynamics we elide by focusing only on the change from beginning to end. If a time series is highly variable, it may reduce our confidence in the ecological significance of the net change, because our perception of the net change is highly sensitive to the particular points in time that we happened to begin and end our observations. Additionally, a time series with a net change near 0 may reflect essentially no change over time, or may mask large fluctuations that cancel out over the time series. These scenarios have qualitatively different biological interpretations: the former may hint at a high degree of regulation or constraint, while the latter may reflect cyclical dynamics or oscillatory regulation at a larger scale. We calculated the variability of the time series as the ratio of the total change to the net change.

**Results**

Chart

Description automatically generated

Figure 1: Ratio of end to start for energy and abundance.

| currency | ntotal | noverzero | nincreasing | ndecreasing | ndouble | nhalf |
| --- | --- | --- | --- | --- | --- | --- |
| abundance | 100 | 13 | 36 | 51 | 8 | 8 |
| scaled\_energy | 100 | 10 | 45 | 45 | 6 | 4 |

For both abundance and energy use, the number of communities that increase are roughly balanced with communities that decrease. Slightly more communities have declines in abundance than do for energy use. For either currency, the magnitudes of these changes are not large, rarely exceeding a doubling or halving of the original values.

This is not compelling evidence, or indeed any evidence, for general declines in either abundance or energy use at the community scale. There is considerable *change* – things do not appear static - but it is not clear that there is a systematic signal of increase or decrease. While individual communities may be changing directionally for various biological reasons, we can’t rule out that each time series is fluctuating randomly and we get on average no net change.

There may be structure according to geography or habitat type that washes out at this scale.

Because these are observational data and we don’t have a measure on how the *environment* is changing, we don’t know necessarily whether increases or declines are due to a changing resource base or changes in the capacity of the species present to exploit the resources available.

Chart, scatter chart

Description automatically generated

Figure 2: Abundance vs energy

| e\_n\_compare | count |
| --- | --- |
| abund\_higher | 12 |
| abund\_lower | 35 |
| overlap | 53 |

For about 50% of communities, abundance and energy use change (on net) proportionally. For those that differ, in about 75% of cases the change in abundance is disproportionately low relative to the change in energy use (i.e., energy use increases more than abundance, or energy use *decreases* less than abundance). While neither scenario is common, it is much more common for energy use to increase while abundance declines or remains the same than for abundance to increase while energy use declines or remains the same.

Usually declines or increases in abundance correspond to declines or increases in energy, but there is considerable variation around the 1:1 line.

Energy use does not appear more static than abundance (a scenario where we would expect a high concentration of energy use towards 1 while abundance varies more broadly).

Nor do we see evidence of increases in abundance or static abundance masking dramatic declines or changes in energy use. For the first, we would see a high concentration of points below the 1:1 line in the upper right uadrant. For the second, we would see points at x = 1 with large y values. Of those we find where energy != abundance and x = 1, energy is *increasing*, meaning stable abundance is masking an *increase*.

If anything, the more common scenario is for energy to increase relatively more than abundance. Crudely, this signals an overall *increase* in the mean per capita body size and metabolic rate.

The most common outcome is for energy and abundance to increase or decrease relatively proportionately. This *may* indicate a general scaling-up or scaling-down of the available resources that does not disproportionately affect either end of the size spectrum; but this is hard to tease apart from these data because considerable variability can be masked by taking the mean.

Abundance versus energy

Abundance never increases while energy decreases. Energy often increases when abundance decreases. Most show the same sign, although with varying magnitude.