# Pilot manuscript

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## Introduction

[10,000 ft view/why dynamics/why change over time]

Classical approaches to studying ecological communities have focused on identifying stable or equilibrium states, rather than on the signatures of change over time. Recently, macroecology has begun to incorporate explicitly temporal perspectives – rather than employing time-averaging or assuming that a single observation period captures a stable or representative arrangement for a community. This is especially important now, given that over the past century, ecological communities have endured a period of unprecedented changes brought about via anthropogenic impacts. We set out in search of a more developed macroecological view of how community-scale properties change over time, and particularly whether they have changed directionally in recent decades.

[the state-variable, cross-community view]

We adopt a specifically macroecological perspective on community dynamics. We relinquish a focus on the rise and fall of individual species and instead use a set of aggregate characteristics, or “state variables”: the total number of individuals (*N*) and the total amounts of biomass (*M*) and/or energy use (*E*) present for a community at a moment in time. These state variables are directly comparable across communities comprising different sets of species or even representing different taxa or ecosystem types. While we sacrifice the details of which species are thriving and where, we gain the power to synthesize across numerous communities and identify prevailing trends in which kinds of dynamics tend to occur most frequently and in what general contexts. These three state variables capture related, but not identical, dimensions of community abundance, including direct measures of ecological function. Because they are *aggregate* variables, summed over the diversity of species and individuals that make up a community at any time point, they may be less variable and idiosyncratic than their component time series. While individual species maybe highly variable for countless reasons, shifts that propagate to the aggregate scale may be more reflective of consistent and systematic processes affecting the community.

[how things might change]

We have two centers-of-thought around how community-level abundance, defined generally, mightvary over time. Especially in theoretical exercises, *abundance* – variously measured in *N*, *E, M*, or even species richness – is often taken to be static or even as a hard constraint on species dynamics. This is, for example, one of the key elements of the classic formulation for neutral theory. In contrast, the weight of literature on the fate of ecosystems in the Anthropocene suggests that we are in an era of unprecedented biological loss, potentially across all currencies. Reports of declines in species richness, population sizes of individual intensively-studied species, and size-biased declines in large-bodied taxa all point towards the expectation of systematic declines in abundance. There are at least two additional, less popular and more complicated, general types of dynamics we might observe. First, communities might pass through multiple regimes or eras where one type of dynamics – no change, or systematic directional change – are dominant, only to be replaced by another trend in a later time period. The net effect could be overall trends, or in a time series that appears not to change *overall* despite considerable, nonrandom, variability. Second, the trajectory could be highly variable – not static – but without detectable temporal structure, even with the option of breaking into disjoint regimes.

[but we don’t know about the **community** scale]

Despite these assumptions and expectations, we do not have a well-resolved empirical picture of how abundance changes at the community scale. The community-scale question differs somewhat from theoretical conventions and population-level assessments. The theoretical assumption of fixed abundance is a mathematical convenience, not an assertion about reality. The trajectories of individual populations do not necessarily reflect the overall aggregate trajectory; even if *most* species in a community have an overall positive slope to their populations, if the few most abundant species are declining, the overall signal will be of decline. Because changing species composition can result in shifts in the average body size of a community, the trajectory of the number of individuals also does not necessarily track the trajectory of total energy use or total biomass. For example, body-size shifts may cause an apparent lack of change or even increase in the number of individuals to mask declines in overall energy use, if small species are becoming more abundant while large species disappear.

[why we don’t know about communities: data]

Documenting the dynamics of community-level abundance in these three currencies requires a type and amount of data that is challenging to collect, especially for terrestrial animals, and therefore rare. Community-wide population censuses, conducted consistently over time, are rare enough for terrestrial animals. Of those that exist, it would usually be impractical to also collect highly detailed size data for the full range of species observed (with the notable exception of small mammal communities). Recently, the combination of large databases of ecological timeseries and trait data, and greatly expanded computational capacity, have made it possible for us to fill in this gap and generate realistic estimates for timeseries of *N*, *E*, and *M* for large numbers of ecological communities.

[capturing (some degree of) nuance in dynamics]

Given newly available data streams, we have the opportunity to for the first time document community-level state variable trajectories for the three currencies. We set out to distinguish among broad classes of dynamics for the state variables, and document which types of dynamics occur most commonly among the communities in our database. We also set out to test whether different kinds of dynamics are more typical for the different currencies.

We define four classes of dynamics that might reflect qualitatively different histories for a community. First, a time series may be best-described by a simple linear model with little to no slope. This can reflect a fairly static trajectory over time, especially if the variation around the mean is low across the time series. It may also signal highly variable fluctuations with respect to time verging on noise. Second, it may be well-described via either a single slope, or as multiple eras with varying slopes that accelerate or decelerate but maintain a monotonic trend, resulting in a net increase or decline over the observation period. Either of these variations points to a systematic change in abundance over time. While these first two classes feature consistent dynamics across the course of the time series, it is also possible that the observation period encompasses multiple segments with contrasting trends. These differ from random fluctuations, in that the trendswithin segments are internally consistent, and detectably different from the trends in adjacent segments. In these cases, the best *linear* description of the time series is an oversimplification that can mask or distort complex, systematic dynamics. The third class of dynamics describes multi-segment time series with at least one change in direction, but resulting in no net change in abundance from beginning to end. While the average, and often the best-fit linear, slope for these time series may be near zero, conflating them with either static or essentially noisy dynamics (as in the first class) would elide multiple periods of systematic change that happen to cancel each other out over the observation period. The final class is for multi-segment time series that change direction but maintain a net increase or decline over the study period. This is a more complex scenario than a monotonic trend (even one that accelerates or decelerates). The net change that results from a non-monotonic trajectory is perhaps weaker evidence of a directional shift than change that is more consistent over time.

[implications of which classes dominate abundance generally]

Which of these classes dominate community abundance timeseries has implications for how we understand biodiversity trends in the Anthropocene, and for how we approach analyzing these time series in greater detail. If the majority of time series are well-described via simple linear, or monotonic, trends, we may be able to proceed with the relatively straightforward interpretation that the distribution of slopes for these trends reflects the prevailing trends, and that these trends are relatively likely to hold for the immediate future. If most of these slopes are concentrated around zero, we may be witnessing relatively little change in abundance at the *community* scale despite considerable evidence of change to individual species and populations – perhaps because communities are buffered, in aggregate, against the fluctuations of their component parts. If we find large contingents of positive or negative slopes, these may signal systematic trends in abundance over the past half-century. Especially if we were to find mostly negativeslopes, it would signal systematic declines in abundance that echo alarm calls about defaunation. However, if many or most community abundance timeseries are better described via multiple segments with changes in direction, we may need additional analytical tools to disentangle systematic, but complex, *trends* from complex, trend-agnostic dynamics. The net or average change for these timeseries may reflect genuine trends or patterned dynamics on longer timescales, but may not be an adequate summary of the most important underlying dynamics or a reliable indicator for future dynamics.

[implications of different classes for different currencies]

Energy != nind

Energy may be more buffered than nind

Energy may more directly reflect function than nind

If energy == nind……. Interesting?

## Methods

### Data

We analyzed energy and total-individuals timeseries for 108 communities from the North American Breeding Bird Survey (). Because this is a preliminary analysis, we used the first 100 that come up alphabetically by the “rt\_rg” designation as implemented via MATSS, and an additional 8 communities selected because of personal significance. They are not at all random spatially and are probably not representative of the dynamics in the database as a whole.

We constructed the total-individuals timeseries as the total number of individuals observed for each year sampled. We constructed the energy timeseries via estimations based on scaling relationships (metabolic theory, Thibault). First, following Thibault et al (2011), we estimated the body size for every individual observed, based on species’ mean and standard deviation body size documented in Dunning (2007). For species with no recorded standard deviation, we estimated the standard deviation based on the scaling relationship between species’ mean and standard deviation body size documented in Thibault et al (2011). We then estimated individual’s metabolic rates via metabolic scaling (), and summed the metabolic rates of all individuals observed at each time point to obtain the total energy use at that time point.

### Categorizing dynamics

For every time series of a community’s energy use or total number of individuals, we summarized the dynamics using a combination of segmented linear regression (also known as breakpoint regression, piecewise linear regression, broken-stick regression, and others) and simple linear regression.

We fit simple linear regression models with only the intercept (i.e. no slope) and with slope and intercept terms, and segmented linear regression models with intercept-only and with slope and intercept terms. We allowed the segmented regressions to be discontinuous, such that the model prediction for the first observation in one segment need not be continuous with the last observation in the preceding segment. This allows fits to faithfully describe sudden jumps and step functions, which occur in these time series. We did not specify the number of segments *a priori* but did constrain them such that every segment must contain a minimum of 4 observations (approximately 10-20% of the observations in most of our timeseries). We implemented segmented regression models using the *strucchange* package for R, and OLS models using the base R lm() function. We then selected the best-fitting model – segmented or not, slope or not – using BIC. It may be more appropriate to use a crossvalidation or training/test split, and to develop some way to describe whether multiple models fit similarly-well. We did not make any effort to detect or account for autocorrelation or non-normality in the data.

We used the fitted values derived from the best-fitting model to determine whether a timeseries’ dynamics were best described as monotonic or changing direction. If all of the timestep-to-timestep differences in the fitted values were of the same sign, or 0, we designated the timeseries as monotonic; if there were both positive and negative differences in the same timeseries, we designated it as changing direction. All one-segment (OLS) models describe monotonic dynamics. Multi-segment models may be monotonic or changing direction.

We tried several approaches to detect and measure the net trend in a timeseries. First, we fit a one-segment linear model and tested whether the slope term was statistically significant. For one-segment models, this is equivalent to the best-fitting model; for multi-segment models, the strictly-linear fit can elide considerable variation. We describe the overall change as the ratio of the model prediction for the last observation to the prediction for the first observation. If the slope is 0, this ratio is 1. Second, we compared the value observed for the first five observations to the last five observations. We tested for significant differences using t-tests and Wilcoxon tests; in no instance did the different tests disagree. We described the overall change as the ratio of the mean of the last five to the mean of the first five. This approach is less susceptible than the one-segment linear model to missing a trend due to highly nonlinear dynamics in the middle of the timeseries, but it is highly sensitive to the choice of the number of observations to include (in this case, 5 was chosen because it accounts for approximately 1/4-1/8 of the observations most timeseries). Third, we calculated the ratio of the fitted value from the best-fitting model (above) for the last observation to the fitted value for the first observation. If this ratio was 1, it reflects no net change; otherwise, there is some net change predicted over the course of the time series. In reality, any model with a slope term or multiple segments results in some net change from the first to the last observation according to this metric.

For timeseries that were best described via a one-segment linear model with no slope term, we calculated the coefficient of variation to help describe whether that timeseries hews closely to its mean or fluctuates widely over time.

### Summarizing dominant dynamics

We tallied the number of timeseries falling into the following categories:

* Monotonic without a statistically significant net change
* Monotonic with a statistically significant net change
* Changing direction without a significant net change
* Changing direction with a significant net change

We report the distribution of net change (described as the ratio of the end:beginning of the time series) broken out according to monotonic and changing-direction. For timeseries without a statistically significant net change, this ratio is reported as 1.

We report results using both of our approaches to detecting and describing net change.

For timeseries that were best-described as monotonic without a statistically significant net change, we also report the coefficient of variation to describe the variability around the mean over the course of the observation period.

## Results

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Currency | Monotonic + net change  Caps (linear model) | Monotonic + no net change | Change in direction + net change | Change in direction + no net change |
| Abundance | 16 (20) | 27 (23) | 28 (30) | 37 (35) |
| Energy | 15 (18) | 32 (29) | 13 (18) | 47 (43) |

For abundance, 65 sites were best-described with models that changed direction, and 43 were best-described with a monotonic fit.

Of the 43 monotonic sites, 27 (62%) did not differ from the first 5 to the last 5 years, and 23 (53%) had a linear fit with 0 slope. Of the 20 sites with a significant slope, 6 were increasing and 14 were decreasing; of the 16 sites with a significant difference from start to end, 4 increased and 12 decreased.

Of the 65 sites that changed direction, 37 (56%) did not differ from the first to the last 5 years, and 35 (53%) had a linear fit with 0 slope. Of the 30 that that had a nonzero slope, 9 were increasing and 21 were decreasing. Of the 27 that changed from beginning to end, 11 increased and 16 decreased.

For energy, 61 sites changed direction, and 47 were monotonic.

Of the 47 monotonic sites, 32 (68%) did not change from beginning to end and 29 (61%) had a linear fit with 0 slope. Of the 18 with a slope, 8 increased and 10 decreased; of the 15 that changed from beginning to end, 7 increased and 8 decreased.

Of the 61 sites that changed direction, 48 (78%) did not change from beginning to end, and 43 (70%) had a 0 slope. Of the 18 that had a nonzero slope, 6 increased and 12 decreased; of the 13 that changed from beginning to end, 4 increased and 9 decreased.

For both energy and abundance, the coefficient of variation for timeseries best-described via a monotonic fit with no net change – potentially the most static timeseries – was often high, comparable to the distribution of c.v. for sites best-described with trends resulting in net change, or changes in direction resulting in no net change.

## Discussion

[on directional trends]

At least half, and, for energy, closer to 60-70%, of timeseries did not have statistically significant change from beginning to end or a nonzero slope. When we did detect a significant change over the course of the timeseries, the change is more often decreasing than increasing. For the 16-20 sites that were best-described via a monotonic fit that had a significant trend, 2/3 of sites were decreasing.

Declines similarly dominate other categories, but we interpret the net change for more complex timeseries with more caution.

[on regulation/static trajectories]

A substantial proportion of timeseries were best-described via a monotonic fit with no net change or slope. This could signal a fixed or static trajectory, where the variable hews close to a long-term mean, or it could betray a lack of temporal structure that would provide the traction for a more complex model. If these monotonic, non-changing time series were bounded or regulated, we would expect the coefficient of variation to be low. In contrast, the coefficient of variation for these timeseries is often comparable to that for timeseries that have statistically detectable temporal structure in the form of multiple sections or directional trends. This suggests that these timeseries are hardly less variable than those that feature systematic change, but that their variability is not easily described via the temporal models we have available here. This could mean that they are random noise, or that the dynamics are more subtle or complex than our models can account for.

[on more complex dynamics]

Many if not most of the timeseries we analyzed are not well-described via monotonic trends: either they span multiple time periods with distinct temporal trends, or they are highly variable over the course of the timeseries but lack strong temporal structure.

* There may be more complex dynamics than these models account for
  + E.g. cyclical dynamics at time scales that do not mesh well with the breakpoints. If the cycles are too short, they may not be easily described via segments of a minimum of 4 observations. If the cycles are long, they may not be apparent in a 20-to-40-year time series.
* The processes or conditions that determine total abundance may have changed substantively over the observation period. Trying to synthesize over time periods when the system was in a qualitatively different state may not be a faithful representation of the different periods.
* A net trend, or lack thereof, may be misleading, and we are considerably less confident that the net outcome summarizing over complex dynamics is a reasonable indicator of the probable trajectory in the future than we are for timeseries that change in consistent, if nonlinear, ways.
* If the general conditions of the Anthropocene are driving systematic changes at the community scale, these changes are not smooth or straightforward.
* This points to a need for more nuanced methods for describing complex, nonlinear dynamics in community timeseries, and ways these changes in ways that are faithful to the underlying behaviors but that allow us to synthesize across communities.

[on abundance vs. energy]

Timeseries for energy had similar, but less systematic dynamics, than individuals. A larger proportion of energy timeseries had no net change over time, and of those that did change, there was a more even representation of increasing vs decreasing trajectories.