**Title:** Empirical abundance distributions are more uneven than expected given their statistical baseline

**Running title:** SADs deviate from statistical baselines

**Author names and affiliations:**

Renata M. Diaz\*1, Hao Ye2, S. K. Morgan Ernest3

1 School of Natural Resources and Environment, University of Florida, Gainesville, Florida, USA. [renata.diaz@weecology.org](mailto:renata.diaz@weecology.org); \*corresponding author

2 Health Science Center Libraries, University of Florida, Gainesville, Florida, USA. [haoye@ufl.edu](mailto:haoye@ufl.edu)

3 Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA. [skmorgane@ufl.edu](mailto:skmorgane@ufl.edu)

**Address for correspondence:**

Renata M. Diaz  
110 Newins-Ziegler Hall  
PO Box 110430,  
Gainesville, FL 32611-0430  
[renata.diaz@weecology.org](mailto:renata.diaz@weecology.org)  
Phone: (352) 846-0643  
Fax: (352) 392-6984

**Statement of authorship:** RMD and SKME conceived the analysis; HY devised the algorithm to sample the feasible set, reviewed the coded implementation, and wrote the explanatory vignette; RMD conducted the analyses and wrote the first draft of the manuscript; all authors contributed substantively to revisions.

**Data accessibility statement**: All data used are available publicly via Zenodo and figshare. Upon publication, all code and data will be archived and made publicly available via Zenodo. Until then, the main codebase for these analyses can be accessed at [www.github.com/diazrenata/scadsanalysis](http://www.github.com/diazrenata/scadsanalysis), while the R package for sampling from the feasible set is at [www.github.com/diazrenata/feasiblesads](http://www.github.com/diazrenata/feasiblesads).

**Keywords:** Species abundance distributions; feasible set; combinatorics; macroecology; constraints; complexity

**Conflict of interests:** The authors declare no conflicts of interest.

**Type of article**: Letter

**Word counts:**

Abstract: 147  
Main text: 4195  
No text boxes

**Number of references:** 25

**Number of figures, tables, and text boxes:** 4 figures; 1 table; 0 text boxes

**Abstract**

Incorporating the emergent properties of ecosystems as complex systems into the search for general processes to explain common ecological patterns is a promising horizon for synthesis in ecology. For example, the ubiquitous hollow-curve form of the species abundance distribution is frequently assumed to reflect ecological processes structuring communities, but can also emerge mathematically from the definition of an abundance distribution. While the hollow curve may be a statistical artefact, ecological processes may induce subtle deviations between empirical species abundance distributions and their statistically most probable forms, which may reflect biological processes operating on top of mathematical constraints and provide new avenues for developing and testing ecological theory. Examining ~22,000 communities, we found that empirical species abundance distributions are highly uneven and dominated by rare species compared their statistical baselines. However, small communities – those with few species or individuals - exhibit poorly-resolved statistical baselines, thereby reducing our statistical capacity to detect deviations. The extremely uneven nature of most empirical SADs demonstrates a path forward for leveraging complexity to understand ecological processes governing the distribution of abundance, while the issues posed by small communities illustrate the limitations of using this approach to study ecological patterns in small samples.

**Introduction**

Ecological communities are complex systems, in the technical sense: they are made up of numerous interacting entities subject to a vast array of processes operating in different contexts and at different scales (Maurer; Brown et al 2002; Nekola and Brown 2007; potentially other refs). One strategy for making sense of this inherent complexity is to identify patterns or phenomena that occur consistently across many communities, and use these general patterns to develop and test theories regarding general mechanisms that shape community structure (Brown and Maurer; Maurer; Lawton; Gaston and Blackburn). Distributions describing complex systems can have counterintuitive emergent statistical properties (Jaynes?; Nekola and Brown; Frank). Left unexamined, these phenomena can interfere with interpreting these distributions in terms of generative mechanism, but, properly understood and accounted for, they can provide leverage for detecting and identifying the processes at work in a system (Jaynes, Harte and Newman 2014). The species abundance distribution (SAD) – the distribution of how all of the individuals in a community are divided among the species in that community – is a leading example of an ecological distribution that is both commonly invoked in the search for general processes, and quite possibly subject to statistical constraints that have so far complicated efforts to use it in this way (Nekola and Brown; McGill et al; Locey and White). Investigating and accounting for these statistical considerations may open up new avenues for ecological interpretations of the SAD, in a key illustration of how embracing ecological complexity can bring us closer to ecological insight.

The shape of the SAD is one of the few ecological patterns that is so consistent that it is often considered an ecological law (Preston 1948, 1962(x2), 1980; Lawton 1999, McGill 2003. McGill et al. 2007). Across varied ecosystems and taxa, the species abundance distribution is dominated by a few very abundant species and a larger number of increasingly rare species, generating a distinctive hollow- or J-shaped curve when plotted with species rank on the x-axis and abundance on the y-axis (Fisher et al. 1943). Community ecologists have used the SAD to test numerous theories intended to determine which biological processes are most important for structuring assemblages of species, by comparing theoretical predictions for the SAD to observed SADs (McGill 2003; McGill et al. 2007). However, this approach has proven inconclusive because many theories predict similar shapes for the SAD (McGill 2003; McGill et al. 2007), and even experimental manipulations generate little variation in the shape of the SAD (Supp and Ernest 2014). Simultaneously, multiple lines of reasoning suggest that some aspects of the SAD transcend ecological processes and instead reflect mathematical properties inherent to the definition of an abundance distribution. Across linguistic, economic, information technology, and numerous other systems, empirical abundance distributions often assume hollow-curve forms similar to ecological SADs (Enquist, Nekola, Macdonald, Blackburn and Gaston (automobiles), Shockley, …), suggesting that the hollow curve is a feature of abundance distributions in general and not necessarily an ecological phenomenon. Many theoretical generative processes for abundance distributions converge to power-law or log-series distributions (i.e. hollow curves) (possibly Preston, McGill 2003, Nekola and Brown 2007, Frank 2009, Frank 2019). Dating at least as far back as Preston (1950), ecologists have suggested that the SAD may be best explained using approaches from statistical mechanics and complexity science to characterize the expected emergent shape for the distribution (McGill 2003; Nekola and Brown 2007). Indeed, recent frameworks grounded in both entropy maximization (i.e. the Maximum Entropy Theory of Ecology (METE); Harte et al. 2008, Harte 2011) and combinatorics (i.e. ‘the feasible set’; Locey and White 2013) generate realistic hollow curves via the random division of the total number of individuals in a community, *N*,into the total number of species present, *S*. If the SAD is statistically inclined to be a hollow curve because of its inherent mathematical features, the hollow-curve in itself may be of limited use for developing and testing ecological theories.

However, this does not necessarily mean that the SAD cannot be biologically informative. Biological factors may introduce subtle, but meaningful, deviations between the shapes of observed SADs and the shapes of the SADs expected due to the mathematical constraints imposed by *S* and *N,* which we hereafter refer to as the “statistical baseline” (Locey and White 2013, Harte and Newman 2014). Thus, it may be possible to use these *deviations* to detect strong ecological processes or evaluate theories (Harte and Newman 2014, Xiao et al. 2016). If the vast majority of mathematically achievable SADs for a community share a similar shape, an empirically observed SAD that deviates even slightly from this statistical baseline is unlikely to have emerged at random (Locey and White 2013). Such a deviation is therefore likely to be the signature of a non-random – i.e., biological – process operating on the relative abundances of species (Harte and Newman 2014). If, over many communities, there are consistent deviations between observed SADs and their statistical baselines, these deviations can help focus and evaluate ecological theories. For example, the high prevalence of rare species in ecological communities has attracted considerable empirical and theoretical attention (e.g. Magurran, Nee), but it is unclear how much of this phenomenon may derive from general mathematical constraints on the SAD rather than ecological processes. Taking into account the statistical baseline, if the prevalence of rare species in observed distributions consistently exceeds what would be expected to emerge from the statistical baseline, this would prompt us to look for ecological mechanisms promoting rarity. The predictions from candidate theories could then be evaluated based on how well they predict specifically the rare tails of observed distributions, not just those expected given the statistical baseline.

Successfully interpreting SADs in this fashion depends on our capacity to detect and quantify deviations between empirical observations and statistical baselines, which requires metrics and computational approaches that allow us to quantify and interpret whatever deviations may exist. Here, we build upon the combinatoric approach developed by Locey and White (2013) to define and explore the statistical baselines for SADs. For a given *N* (total number of individuals) and *S* (total number of species), there exists a finite (but potentially very large) set of possible distributions of individuals into species. Collectively, this set of possible SADs is referred to as the feasible set, with each possible SAD constituting a single element of the set. If an observed SAD is drawn at random from the set of mathematically possible SADs, it is likely to have a shape similar to the shapes most common in the feasible set. The feasible set can therefore be used as a statistical baseline for assessing whether observed SADs deviate from what is likely to occur merely due to mathematical constraints (Locey and White 2013).

The feasible set can also be used to explore how the characteristics of the statistical baseline, and the presence and nature of any deviations that occur, vary over ranges of values for S and N. Although most feasible sets are dominated by generally hollow curves, variation in S, N, and the ratio of N to S modulate more detailed attributes of the SADs in a feasible set (Locey and White 2013). For example, if the ratio of N to S is very low, all possible SADs are mathematically constrained to be fairly even (Locey and White 2013). The feasible set therefore allows us to appropriately calibrate our expectations for what types of observations would be surprising for an SAD given the specific constraints imposed by its S and N. Additionally, accounting for variation in the specificity, or vagueness, of the expectations derived from the statistical baseline is critically important for disentangling the aspects of the SAD that are likely generated by statistical constraints from those generated by other processes. If the vast majority of mathematically possible SADs are similar in shape – generating a very specific, narrowly defined statistical baseline – then even small deviations between an observed SAD and this baseline can signal the operation of ecological processes. However, if many different shapes occur with more even frequency in the feasible set, the statistical baseline is less specific and less well defined, and our sensitivity for distinguishing biological signal from statistical constraints is greatly reduced. In general, a poorly defined statistical baseline is more likely to occur when the size of the community, in terms of *S* and *N,* is small, because in such cases there may be too fewpossible SADs in the feasible set for a particular shape to emerge as the most common, and therefore most likely, shape. When this occurs, we have reduced confidence that even an observation that deviates from the statistical baseline did not emerge at random from the relatively restricted pool of possible outcomes (Jaynes 1957). This general concern has been acknowledged in efforts to comparing ecological observations to statistical baselines (Harte 2011, White et al. 2012, Locey and White 2013) but there has not yet been a quantification of these effects for the SAD or an identification of the range of community sizes most strongly affected. Because ecologists study the SAD for communities varying in size from the very small – *S* and *N* < 5 – to the enormous – *S* and *N* >> 1000 – identifying the community sizes for which we can and cannot confidently detect deviations from the statistical baseline is necessary to appropriately contextualize our interpretations.

Here we use the feasible set to define statistical baselines for empirical SADs for 22,000 communities of birds, mammals, trees, and miscellaneous other taxa. We then compare *observed* SADs to their corresponding statistical baselines and evaluate 1) if the shapes of observed SADs consistently deviate from their statistical baseline, 2) how the characteristics and specificity of the statistical baseline varies over ranges of *S* and *N*, and 3) whether this variation appears to be associated with variation in our capacity to detect deviations between observations and the corresponding baselines.

**Methods**

Data and code for all of our analyses can be accessed at [www.github.com/diazrenata/scadsanalysis](http://www.github.com/diazrenata/scadsanalysis).

*Datasets*

We used a compilation of community abundance data for trees, birds, mammals, and miscellaneous additional taxa (White et al. 2012, Baldridge 2015, Baldridge 2016, data from Baldridge 2016). This compilation consists of cleaned and summarized community abundance data for trees obtained from the Forest Inventory and Analysis (Woudenberg et a al 2010) and Gentry transects (Phillipes and Miller 2002), birds from the North American Breeding Bird Survey (Sauer et al. 2013), mammals from the Mammal Community Abundance Database (Thibault et al. 2011), and a variety of less commonly sampled taxa from the Miscellaneous Abundance Database (Baldridge 2015). Because characterizing the random expectation of the SAD is computationally intractable for very large communities, we filtered our datasets to remove communities with more than 40720 individuals, which was the largest community we successfully analyzed. This resulted in the removal of 4 communities from the Miscellaneous Abundance Database. We further filtered the FIA database. Of the 103,343 communities in FIA, 92,988 have fewer than 10 species. Rather than analyze all these small communities, we randomly selected 10,000 small communities to include in the analysis. We also included all FIA communities with more than 10 species, which added 10,355 FIA communities to the analysis and resulted in a total of 20,355 FIA communities. Finally, for sites that had repeated sampling over time, we followed White et al. (2012) and Baldridge (2016) and analyzed only a single, randomly selected, year of data, because samples taken from a single community at different time points are likely to covary. It should be noted that our analyses include data from the Mammal Community Database and Miscellaneous Abundance Database that were collected over longer timescales and cannot be disaggregated into finer units of time. Our final dataset consisted of ~22,000 communities with S and N ranging from 2 to 250 and 4 to 40714, respectively (Figure 1). Details and code for the filtering process can be found in Appendix S2 in Supporting Information.

*Accounting for empirical sampling error*

Because it is logistically impossible to exhaustively catalog all individuals present in most empirical systems, SADs derived from field sampling will inevitably be subject some degree of sampling error. Therefore, in addition to analyzing the raw SADs in our database, we employed two resampling schemes to test if, and how, different forms of observation error affect our results.

First, we explored the possibility that empirical sampling systematically undercounts the true number of rare species in a community (ref for rarefaction). Rare species may be more likely to escape detection during sampling, leading to an underestimate of both the total species richness of a community and the proportion of species in the rare tail of the SAD. We used species richness estimators to adjust for this possibility. For each community, we computed the estimated richness using the bias-correct Chao and the ACE estimators (as implemented in the R package vegan), adding one standard deviation of the estimate to each estimate, and taking the mean of the two estimates. This yields a generous estimate of the true number of species in the system. If this estimate exceeded the number of species observed for a community, we added the missing species each with abundance 1, which allowed us to explore the consequences of undersampling rare species while making the smallest possible changes to S and N.

Second, we tested the sensitivity of our results to sampling variability across the entire range of the SAD using subsampling. For each observed community, we constructed subsamples by randomly drawing 60% of the observed number of individuals from the total pool of individuals in the community, without regard to species and without replacement. This introduced substantial room for sampling error between the resampled and observed distributions, but yielded resampled communities that were not trivially small in terms of S and N. We drew 10 resampled communities for each observed community.

We ran our computational pipeline using all raw SADs and all SADs adjusted for undersampling of rare species. Because subsampling increased computational effort up to tenfold, we analyzed all subsampled communities for the Mammal Community, Miscellaneous Abundance, and Gentry databases, but on only a random subset of 300 (of 2773) communities from the Breeding Bird Survey and 2000 (of 20179) from the FIA – 1,000 with S < 10, and 1,000 with S >= 10.

*Generating the statistical baseline*

We use the concept of the “feasible set”to establish a statistical baseline for the SAD (Locey and White 2013). For a given number of individuals *N*,there is a finite number of unique ways to partition those individuals into *S* species. The complete set of these unique partitions is the feasible set. Because, in this approach, neither species nor individuals are distinguishable from each other, partitions are unique if and only if they differ in the number of species that have a particular abundance (Locey and White, 2013). Operationally, this means that for *S = 3* and *N = 9*, the species abundances *(1, 3, 5)* and *(2, 2, 5)* count as distinct partitions, but *(1, 3, 5)* and *(3, 1, 5)* are only one element of the feasible set because they each contain one species with an abundance 1, 3, and 5, respectively, and they differ only in the *order* of the numbers. In the absence of justification for additional assumptions regarding the distinguishability of species and/or individuals, we adopted this simple set of assumptions that has previously been shown to generate realistic statistical baselines (Locey and White 2013).

While it is possible to list all possible partitions in the feasible set for small *S* and *N*, the size of the feasible set increases rapidly with *S* and *N*. Therefore, characterizing the statistical properties of the feasible set for large *S* and *N* can be computationally intensive. This renders it necessary to draw samples from the feasible set, rather than enumerating all of its elements. Unbiased sampling of large feasible sets is a nontrivial computational problem that has constrained previous efforts in this vein (Locey and White 2013). We developed an algorithm to efficiently and uniformly sample feasible sets even for large values of *S* and *N*. In brief, the algorithm takes a generative approach to sampling the feasible set. Individuals are allocated one species at a time, beginning with the least abundant species. At each step, the number of individuals to allocate for the current species is determined at random, with probability based on the number of feasible sets with that specific abundance for that species, and conditional on the individuals that have already been allocated. For example, if we have 3 species and 7 individuals, the least abundant species can have an abundance of 1 or 2. Allocating 1 individual to the least abundant species allows for the SADs (1, 1, 5), (1, 2, 4), and (1, 3, 3), and allocating 2 individuals to the least abundant species means the only possible SAD is (2, 2, 3). We therefore allocate 1 individual with probability 3/4, and 2 individuals with probability 1/4. If, at the first step, we allocated 1 individual to the least abundant species, the second species can have an abundance of 1, 2 or 3 with equal probability, because there is exactly 1 possible SAD with each of these possible abundances for the first two species. This process is continued until all individuals have been allocated. We implemented this algorithm in an R package, available on GitHub at [www.github.com/diazrenata/feasiblesads](http://www.github.com/diazrenata/feasiblesads); details of the sampling methodology are available in Appendix S3.

For every community in our database, we drew 4000 samples from the feasible set to characterize the distribution of statistically probable shapes for the SAD. We filtered the 4000 samples to unique elements. For small values of S and N, it can be impossible or highly improbable for the 4000 samples from the feasible set to all be unique, but for large communities, all 4000 are usually unique. We refer to this as the sampled feasible set.

*Comparing observed SADs to their baselines*

For an overall comparison between observed SADs and their statistical baselines, we quantified the degree of dissimilarity between observed SADs and the central tendencies of their feasible sets and compared this to the degree of dissimilarity between random samples from the feasible set and the central tendency (following Locey and White, 2013). If all SADs in a feasible set are equally likely to occur in reality, then observed SADs should not be markedly less similar to the central tendency of the feasible set than random samples from the feasible set. If observed SADs are consistently more dissimilar to the central tendency than samples from the feasible set, strong processes may be at work driving observed SADs away from the central tendency. We defined the degree of dissimilarity between two SADs with the same S and N as the proportion of individuals allocated to species with different abundances between the two SADs, calculated as:

where *n1i* is the abundance at rank *i* for one SAD and *n2i* is the abundance at rank *i* for the other SAD. This value ranges from 0 to 1, with 1 being high dissimilarity. Unlike an R-squared or coefficient of determination, it is never negative and does not depend on which SAD is considered the “reference” or “comparison” sample. We used this dissimilarity score to estimate the central tendency of the feasible set, defined as the sample from that feasible set with the lowest dissimilarity to other samples. For a given sampled feasible set, we calculated the dissimilarity between every sample drawn from the feasible set and a random set of 500 other samples. We used only a subset of samples because it is computationally impractical to make all pairwise comparisons between large numbers of samples. For each focal sample, we calculated the mean dissimilarity score over the 500 comparison samples, and approximated the central tendency to be the focal sample with the lowest mean dissimilarity. To assess whether an observed SAD was dissimilar to its central tendency, and whether it was so dissimilar as to be statistically unlikely, we calculated the degree of dissimilarity between the central tendency of the corresponding feasible set and all other samples from that feasible set, and between the central tendency and the observed SAD. We then calculated the percentile rank of the observed dissimilarity score relative to the distribution of dissimilarity scores from the sampled feasible set. After aggregating across communities, if observed SADs reflect random draws from their feasible sets, their percentile rank values should be uniformly distributed from 0 to 100. However, if observed SADs are consistently highly dissimilar from their feasible sets, the percentile values will be disproportionately concentrated at high values. We used a one-tailed 95 confidence interval and tested whether the percentile values for the dissimilarity scores of observed SADs fell above 95 more than 5% of the time. Comparing percentile scores to a one-tailed 95% interval is not meaningful if there are fewer than 20 values in the sampled distribution, because in these cases, it is impossible for an observation to fall above the 95th percentile. We therefore excluded from this analysis communities with fewer than 20 unique SADs in their feasible sets, yielding a total of X communities.

While the degree of dissimilarity between SADs and the central tendency of the feasible set provides an overall sense of how large and common deviations are, it does not provide very much information about *how* observed SADs differ from their feasible set. We therefore used a set of more targeted, ecologically interpretable metrics to explore how observed SADs compare to their feasible sets in their shape and proportion of rare species. We used three metrics to describe the shape of the SAD - skewness, Simpson’s evenness, and Shannon diversity. Skewness measures the asymmetry of a distribution around its mean. Simpson’s evenness and Shannon diversity are commonly used metrics in ecology for assessing how equitably abundance is distributed across species (ref?). We also calculated the proportion of rare species (species with abundance = 1) in each SAD, because the proportion of rare species in a community is readily comparable across different community sizes and is of special interest to ecologists (Magurran, Nee, …). There exists a vast array of possible summary metrics for describing the shape of an SAD, and different metrics emphasize different aspects of the distribution. In this first effort to compare empirical distributions to a statistical baseline, we selected a suite of complementary metrics and explored whether our overall results were consistent between metrics. By calculating these metrics for each of the samples in the community’s sampled feasible set (see *Generating the statistical baseline*,above), we generated a distribution describing the shapes expected from the randomly sampled SADs.

As with the degree of dissimilarity score, to assess whether the shape of an observed SAD was statistically unlikely, we used percentile ranks to compare the values for our summary metrics for the observed SAD to the distributions of values for those metrics obtained from that community’s sampled feasible. While the actual ranges and values of summary metrics vary widely over large ranges of S and N and thus cannot be used for direct comparisons, percentile ranks are comparable across different community sizes and allow broad-scale assessment across wide ranges of *S* and *N*. We used two-tailed 95% intervals to test whether observed communities’ percentile values for each metric were disproportionately concentrated below 2.5 or above 97.5. In all cases, in testing for unusually high percentile scores, we defined the percentile score specifically as the proportion of values in the sampled distribution strictly less than the observed value, while in testing for low values, we defined it as the proportion of sampled values less than or equal to the observed value. This distinction ensured a conservative estimate of how extreme the observed values were relative to the sampled distribution, even in instances where the sampled distribution had numerous ties. Because it is impossible for an observed percentile score to be above or below the 97.5th or 2.5th percentile if there are fewer than 40 values in the sample distribution, we excluded from these analyses communities with fewer than 40 SADs in their feasible sets. Finally, note that skewness, as implemented in the R package “e1071” (Meyer et al. 2019), always evaluates to 0 for distributions with only two species, and we therefore excluded those cases from analyses of skewness (but included those communities for analyses using the remaining metrics). Our final analysis included 22,475 communities for skewness and 22,490 communities for all other shape metrics.

*The narrowness of the expectation*

of dissimilarity scores and shape metricsFor an overall sense of how tightly elements of the feasible set were clustered around the central tendency, we calculated the mean dissimilarity score between all samples from a feasible set and the approximate central tendency of that feasible set. For a more specific estimate of the narrowness of the distributions of sampled values for the shape metrics, we calculated a breadth index defined as the ratio of the range of values encompassed within a two-sided 95% density interval relative to the full range of values in the distribution (Figure 2). This breadth index for the statistical baseline ranges from 0 (a very narrow distribution and well-resolved baseline) to 1 (a very broad distribution), and is comparable across feasible sets for varying combinations of *S* and *N*. These approaches correspond qualitatively to more computationally-intensive approaches to measuring the self-similarity of the elements of feasible sets (see Appendix S4). We explored how the narrowness of the statistical baseline varies with the number of elements in the feasible set and the ratio of N to S.

**Results**

*Observed SADs compared to their feasible sets*

For four of the five datasets we analyzed – BBS, Gentry, Mammal Communities, and Misc. Abund – observed SADs are dramatically more dissimilar to the central tendencies of their feasible sets than would be expected by chance (Figure 3). Combined over these four datasets, 29% of observed SADs are more dissimilar to the central tendency than are 95% of samples from the feasible set, compared to the approximately 5% that would be expected at random (Table 1). These highly unlikely SADs have dissimilarity scores from 1.5 to 9.7 times greater than the mean dissimilarity between the central tendency and samples from the feasible set, an absolute increase ranging from .04 to .6 on a scale from 0-1. These datasets also contain highly unlikely SADs in terms of their shape metrics. At random, roughly 2.5% of observed percentile scores for these metrics should be very high (>97.5) or very low (<2.5). Instead, these four datasets contain a disproportionate number of communities with very low values for Simpson’s evenness (21%, 9.8%, 28%, and 53% of sites for the BBS, Gentry, Mammal, and Miscellaneous Abundance databases, respectively) and Shannon diversity (22%, 7.6%, 30%, and 55%), and very high skewness (8.9%, 10%, 12%, and 27%) relative to their feasible sets. The Mammal Community, and Miscellaneous Abundance databases also have high proportions of rare species (12% and 23% of sites, respectively), but this tendency is weaker for BBS (4.5%) and nonexistent for Gentry (.08%). In fact, the Gentry dataset has a high representation of sites with *low* proportions of rare species (20%). The Gentry dataset also has a disproportionate number of communities with the opposite tendencies to the other datasets for the other shape metrics– that is, an overrepresentation of communities with highSimpson’s evenness and Shannon diversity (21% and 24%), and low skewness (8%).

In contrast to the other datasets, percentile scores for sites from the FIA dataset are more uniformly distributed, and the proportions of extreme values closer to what would be expected by chance. Only 7% of FIA communities are highly dissimilar to their feasible sets (compared to a random expectation of 5%). Among the shape metrics, only 2.7% (compared to 2.5% at random) of sites have high values for skewness, 1.3% have high proportions of rare species, 5.7% have low Simpson’s evenness, and 5.4% have low Shannon diversity.

*The narrowness of the expectation*

The ability to detect deviations from the statistical baseline depends in part on the distribution of SADs in the feasible set. Overall, the SADs in a feasible set become more narrowly clustered around the central tendency of that feasible set as the size of the feasible set increases and as the ratio of the total number of individuals to the total number of species decreases. The sampled distributions for shape metrics also generally become less broad as the size of the feasible set increases. The breadth indices for small communities are highly variable and often very large – approaching 1, meaning that a 95% density interval of the values in the distribution spans nearly the entire range of values – while the breadth indices for larger communities rarely exceed ~.7 for skewness, Simpson evenness, and Shannon diversity, and ~.8 for the proportion of rare species.

*Sensitivity to sampling variability*

In almost all cases, SADs adjusted for the under-observation of rare species are even more extreme relative to their feasible sets than unadjusted SADs. For all datasets, adjusted SADs have a higher proportion of high values for skewness and the proportion of rare species, and low values for Simpson’s evenness and Shannon diversity, than unadjusted SADs. This is most pronounced for the proportion of rare species for the Breeding Bird Survey: while only 4.5% of unadjusted SADs have very high proportions of rare species, 17.5% of adjusted SADs do. Adjusting for rare species does not appreciably change the proportion of Gentry datasets that feature extremely low proportions of rare species (20% of unadjusted SADs compared to 18% of adjusted ones) and skewness (8.5% and 8%), or high values for evenness and Shannon diversity (21.5 vs 21.9%, and 24 vs 23%).

Jackknife resampling consistently reduces the proportion of extreme observations across all datasets and metrics. In most instances, the proportion of extreme observations still exceeds the proportion that would be expected by chance (i.e. ~5% for dissimilarity, and ~2.5% for all other comparisons). However, the proportion of sites with high numbers of rare species observed for the BBS and Mammal Community database drop from 4.5% to 1% and ~13% to 3.5% with resampling. For the FIA dataset, the proportions of sites with high dissimilarity, low evenness and Shannon diversity all drop from 6-8% to 2-3%. Note that, for the FIA dataset, neither the raw nor the resampled SADs have a disproportionate representation of high values for skewness or the proportion of rare species.

**Discussion**

We found widespread evidence that SADs for a range of real ecological communities deviate from the forms expected given the distribution of shapes within their feasible sets. Overall, these deviations may signal that ecological processes operate on top of statistical constraints, thereby driving the SAD away from common shapes that would be observed in the absence of a dominating non-statistical process. We also found that whether, and in which specific aspects of the distribution, we detected deviations varied among the datasets we considered. This variability may reflect statistical phenomena related the size of S and N and their ratio, or it may reflect different biological processes dominating in different contexts. Finally, we note that, althoughGoing forward, testing whether ecological theories or common functional approximations (e.g. the log-normal distribution) accurately predict this range of variation in deviations between observed SADs and their statistical baselines may be much more fruitful than focusing only on the general form of the SAD that emerges from statistical constraints (McGill et al. 2007; Locey and White 2013).

In most cases, and most pronouncedly for the Breeding Bird Survey, Mammal Community, and Miscellaneous Abundance databases, our results suggest that the prevailing processes structuring real communities tend to be those that cause abundance distributions to be highly uneven, rather than those that produce more even abundances across species. For these communities, observed SADs tended to be unusually skewed and uneven, and to have a high proportion of rare species, compared to their feasible sets. Correcting for undersampling of rare species strengthened these effects, while jackknife resampling weakened them – especially for the proportion of rare species, perhaps because subsampling is likely to miss rare species even if it otherwise recaptures the general shape of a distribution. The long rare tail of the SAD has been a consistent focus in SAD research, and our results highlight that the rare tails of observed SADs are extraordinary even among the hollow-curve shapes that dominate the feasible set. Ecological processes may lengthen the rare tail and decrease the evenness of the SAD, for example by promoting the persistence of rare species at very low abundances (e.g. Yenni et al. 2012). Or, they could drive abundant species to have larger populations that would be statistically expected, without driving other species entirely to extinction (Chesson 2000).

While the Gentry database also exhibits deviations tending towards high unevenness, it exhibits a much stronger tendency in the opposite direction: towards highly even SADs with a lower proportion of rare species than would be expected given their feasible sets. This could indicate that there are biological differences between Gentry and other datasets that result in different forms for the SAD, or that statistical characteristics of the feasible set for these communities modulate the deviations we detect. Compared to the other datasets, communities from the Gentry database tend to have high species richness and low average abundance (the ratio of N to S). Among these, the communities with high evenness and low proportions of rare species are predominately those with very high species richness and low average abundance (N/S < ~3). These extreme feasible sets constitute an unusual statistical baseline that redefines what attributes in an observed distribution are worthy of note. For example, SADs from these feasible sets have the highest proportions of rare species of any of the feasible sets in our analysis. Although observed SADs for these communities also have high proportions of rare species relative to other communities, taking the statistical baseline into account would suggest that the extraordinary thing about these SADs is actually that they do not have even morerare species. Simultaneously, there may be biological reasons why the species-rich but relatively low-abundance tropical tree communities of the Gentry database differ from those in other datasets. The same mechanisms that promote high diversity, in general, may manifest in high evenness, or ecological features particular to these forests may result in unusual SADs relative to the statistical baseline. Because no communities from our other datasets compare to these Gentry communities in S and N, we cannot disentangle statistical and biological explanations. This is an excellent opportunity to develop additional theoretical and empirical approaches to predict and explain variation in the deviations between SADs and their feasible sets, in particular for species-rich communities from different types of ecosystem.

Unlike the other four datasets, communities in the FIA dataset showed weak or no evidence of deviations from their feasible sets. These results may partially reflect statistical phenomena related to community size. The FIA communities are by far the smallest across our datasets (Figure S1). Communities with small values of S and N have smaller feasible sets. When there are relatively few possible SADs, they are not as consistently clustered around their central tendencies, and the distributions for the shape metrics are less consistently narrowly peaked, than when there are very large numbers of possible SADs. This weakens the statistical distinction between “common” and “extreme” shapes for the SAD for small, highly variable, feasible sets (Figure 1), meaning that the deviations – or lack thereof – that we perceive are less informative than for larger communities with more strongly defined statistical baselines (Jaynes 1957).

If the lack of discernable deviations from the feasible set for the FIA communities is indeed a byproduct of their generally small size, then we would expect similarly-sized communities from other datasets to have similar results. We identified 371 communities from other datasets with *S* and *N* matching communities from FIA. We found no difference in the distribution of percentile scores between communities from FIA and communities from other datasets (Figure 4; Table S6), confirmed via Kolmogorov-Smirnov tests (for evenness, *D* = 0.04 and *p* = 0.87; for skewness, *D* = 0.07 and *p* = 0.37). Although 371 communities constitute a small sample relative to the 20,355 FIA communities we analyzed, these results point to community size, and not attributes specific to FIA, as a likely explanation for the weak evidence for deviations across the full FIA dataset.

If this is indeed the case, it means that small-community considerations may affect our capacity to meaningfully distinguish signal from randomness using this approach. Because the combinations of S and N represented in our analyses are irregularly distributed among different datasets, and some ranges of possible combinations are entirely absent, we do not attempt to identify a more specific rule or threshold relating community size to statistical power. However, FIA communities have on the order of 10 species and 50-100 individuals, and these may indicate a general range of values below which we have relatively diminished power to detect deviations from the statistical baseline represented by the feasible set. To meaningfully draw inferences from deviations in these small communities, we will likely need more sensitive metrics than those used here, and/or theories that generate more specific predictions for the SAD. In the absence of such, we may stand to learn the most by focusing on SADs from relatively large communities.

It is also important to recognize that there are multiple plausible approaches to defining a statistical baseline for the SAD, of which we have taken only one (Haegeman and Loreau 2008, Locey and White 2013). Our approach follows Locey and White (2013) and reflects the random partitioning of individuals into species, with the resulting distributions considered unique if the species’ abundance values are unique, regardless of the order in which the values occur. The philosophy behind the feasible set reflects a longstanding approach in the study of abundance distributions: to focus on the shape of the distribution without regard to species’ identities (McGill 2007). Other assumptions regarding the statistical baseline may be equally valid and generate different statistical expectations, which may alter if, and in what ways, empirical distributions appear unusual. For example, incorporating differences in species order into the statistical baseline – which would imply that identifying *which* species contain the most or least individuals is important for evaluating theory – might reduce the representation of long-tailed, highly uneven SADs within the feasible set, and make the rare tail observed for real SADs appear more unlikely than it does here. Under our assumptions, the SADs (1,2,3,4) and (1, 1, 1, 8) each count as only one unique SAD. Taking species order into account would mean that (1,2,3,4) would count as 24 (4!) unique SADs, because there are 4! ways to assign the abundances to each species. However, an SAD with ties such as (1, 1, 1, 8) would only count as 4 unique SADs. For SADs, ties are likely most prevalent among rare species. If this is true, then this set of assumptions would generate feasible sets where rare-tailed SADs are relatively scarce, making observed SADs with rare tails seem even more extraordinary. Additional formulations for the statistical baseline exist, including those that approximate exponential, Poisson, or log-series distributions in the limit (Harte et al. 2008, Favretti 2018). Investigating and comparing the results that emerge from different baselines will be an important next step towards reinvigorating the use of the SAD as a diagnostic tool.

Our study demonstrates the utility, and the potential challenges, of applying tools from the study of complex systems and statistical mechanics to the study of ecological communities (Haegeman and Loreau 2008, Harte 2011, White et al. 2012, Harte and Newman 2014)**.** While concepts such as maximum entropy and the feasible set are promising new horizons for macroecology, the small size of some ecological communities may present difficulties that do not occur as often in the domains for which these tools were originally developed (Jaynes 1957, Haegeman and Loreau 2008). When the observed numbers of species and individuals are too small to generate highly resolved statistical baselines, these approaches will be less informative than we might hope – as appears to be the case for the smallest communities in our analysis. In larger communities, where mathematical constraints have stronger effects on the general form of the SAD, our results show that these constraints alone do not fully account for the extremely uneven SADs we often observe in nature – leaving an important role for ecological processes. This ability to detect and diagnose the specific ways in which empirical SADs deviate from randomness can generate new avenues for understanding how and when biological drivers affect the SAD. There are, of course, still many elements to be improved in our ability to distinguish biological signal from randomness, including assessing alternative statistical baselines and calibrating our expected power to detect deviations, especially for small communities. Indeed, more sensitive metrics could also enable identification of processes that operate through time (note that, in this analysis, we sampled only one time point for each community). Continuing to explore and account for the interplay between statistical constraint and biological process constitutes a promising and profound new approach to our understanding of this familiar, yet surprisingly mysterious, ecological pattern.

**Acknowledgements**

RMD was supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 and DGE-1842473. HY's time was supported by Gordon and Betty Moore Foundation’s Data-Driven Discovery Initiative, Grant GBMF4563, awarded to Ethan White. We thank Erica Newman, Justin Kitzes, and Ethan White for helpful and illuminating discussions.

**References**

Baldridge, E. (2015). Miscellaneous Abundance Database. figshare. Available at: <https://doi.org/10.6084/m9.figshare.95843.v4>

Baldridge, E., Harris, D.J., Xiao, X. & White, E.P. (2016). An extensive comparison of species-abundance distribution models. *PeerJ*, 4, e2823.

Baldridge, E., Harris, D.J., Xiao, X. & White, E.P. (2016). Data from *An extensive comparison of species-abundance distribution models*. Zenodo. Available at: https://zenodo.org/record/166725.

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.

Favretti, M. (2018). Remarks on the Maximum Entropy Principle with Application to the Maximum Entropy Theory of Ecology. *Entropy*, 20, 11.

Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943). The Relation Between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population. *Journal of Animal Ecology*, 12, 42–58.

Frank, S.A. (2009). The common patterns of nature. *Journal of Evolutionary Biology*, 22, 1563–1585.

Frank, S.A. (2019). The common patterns of abundance: the log series and Zipf’s law. *F1000Res*, 8, 334.

Haegeman, B. & Loreau, M. (2008). Limitations of entropy maximization in ecology. *Oikos*, 117, 1700–1710.

Harte, J. (2011). *Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and Energetics*. Oxford University Press.

Harte, J. & Newman, E.A. (2014). Maximum information entropy: a foundation for ecological theory. *Trends in Ecology & Evolution*, 29, 384–389.

Harte, J., Zillio, T., Conlisk, E. & Smith, A.B. (2008). Maximum Entropy and the State-Variable Approach to Macroecology. *Ecology*, 89, 2700–2711.

Jaynes, E.T. (1957). Information Theory and Statistical Mechanics. *Phys. Rev.*, 106, 620–630.

Lawton, J.H. (1999). Are There General Laws in Ecology? *Oikos*, 84, 177.

Locey, K.J. & White, E.P. (2013). How species richness and total abundance constrain the distribution of abundance. *Ecology Letters*, 16, 1177–1185.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., *et al.* (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol Letters*, 10, 995–1015.

Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A. & Leisch, F. (2019). *e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071),* TU Wien. R package version 1.7-4. <https://CRAN.R-project.org/package=e1071>

Phillips, O. & Miller, J.S. (2002). *Global patterns of plant diversity: Alwyn H. Gentry’s forest transect data set*. Missouri Botanical Press.

Sauer, J.R., Link, W.A., Fallon, J.E., Pardieck, K.L. & Ziolkowski, D.J. (2013). The North American Breeding Bird Survey 1966–2011: Summary Analysis and Species Accounts. *North American Fauna*, 1–32.

Supp, S.R. & Ernest, S.K.M. (2014). Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology*, 95, 1717–1723.

Thibault, K.M., Supp, S.R., Giffin, M., White, E.P. & Ernest, S.K.M. (2011). Species composition and abundance of mammalian communities. *Ecology*, 92, 2316–2316.

White, E.P., Thibault, K.M. & Xiao, X. (2012). Characterizing species abundance distributions across taxa and ecosystems using a simple maximum entropy model. *Ecology*, 93, 1772–1778.

Woudenberg, S.W., Conkling, B.L., O’Connell, B.M., LaPoint, E.B., Turner, J.A. & Waddell, K.L. (2010). The Forest Inventory and Analysis Database: Database description and users manual version 4.0 for Phase 2. *Gen. Tech. Rep. RMRS-GTR-245. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 336 p.*, 245.

Xiao, X., O’Dwyer, J.P. & White, E.P. (2016). Comparing process-based and constraint-based approaches for modeling macroecological patterns. *Ecology*, 97, 1228–1238.

Yenni, G., Adler, P.B. & Ernest, S.K.M. (2012). Strong self-limitation promotes the persistence of rare species. *Ecology*, 93, 456–461.

**Figure legends**

Figure 1. Large feasible sets may allow better detection of deviations from the statistical baseline by generating more specific, narrowly-defined baselines. We illustrate this phenomenon using 3 hypothetical communities: a small community (*S* = 4, *N* = 34; top row), an intermediate community (*S* = 7, *N* = 71; middle row), and a large community (*S*= 44, *N* = 13360; bottom row). The large communiity has approximately 6.59e+70 possible SADs in its feasible set, while the intermediate community has 60,289 and the small community has only 297. For every SAD sampled from the feasible set (left column), we calculate the skewness (color scale) and evenness (not shown). The distributions of these values (right column) constitute the statistical baseline. We define a “breadth index” as the ratio of the range encompassed in the one-tailed 95% density interval (distance between red lines, right), compared to the full range of values for the statistic (distance between the maximum and minimum values). As *S* and *N* increase, the size of the feasible set increases, resulting in a narrower statistical baseline (smaller breadth index) – thus enabling easier detection of deviations that may be the result of ecological processes affecting the SAD.

Figure 2. Many ecological communities are more skewed (left) or uneven (right) than their statistical baselines. Percentile ranks are calculated by comparing each community to its sampled feasible set, with very high or very low percentile ranks reflecting extreme values relative to statistical baselines. The vertical red line marks the 95th percentile for skewness and the 5th percentile for evenness. Species abundance distributions that are sampled at random from the feasible set will produce percentile ranks that are uniformly distributed from 0 to 100, with approximately 5% of values above or below the 95th and 5th percentiles, respectively. In contrast, most datasets have more communities that are highly skewed or uneven than would be expected by chance.

Figure 3. Breadth indices of skewness (left) and evenness (right) indicate varying ability to detect the deviations between observations and the statistical baseline. The breadth index (see Figure 1) quantifies how narrowly-defined the statistical baseline is; high values indicate broad, poorly-defined statistical baselines that may impede our ability to confidently detect deviations between observations and what is expected given the baseline. Most datasets contain a mixture of communities with broad and narrow statistical baselines, but some – particularly the skewness baseline for the Forest Inventory and Analysis – have consistently high breadth indices across all of their communities, suggesting that skewness is not an effective metric for distinguishing empirical observations from the feasible set. In general, the breadth index for evenness (right panels) indicates more narrow statistical baselines than those for skewness.

Figure 4. Small communities exhibit consistently broad statistical baselines (top), and consistently weak evidence of deviations for observed SADs (bottom), regardless of the originating dataset. For a subset of 371 communities from the Forest Inventory and Analysis with communities in other datasets with matching *S* and *N*, we generate distributions of breadth indices for skewness and evenness (top) and compute corresponding percentile ranks for the observed SADs (bottom). Visually, there is no difference between FIA (left panels) and other datasets (right panels), when they are matched in *S* and *N*. This is confirmed by Kolmogorov-Smirnov tests for the breadth indices (for evenness, *D* = 0.04 and *p* = 0.91; for skewness, *D* = 0.03 and *p* > 0.99) and percentile ranks (for evenness, *D* = 0.04 and *p* = 0.87; for skewness, *D* = 0.07 and *p* = 0.37).