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

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

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**Data accessibility statement**: All data used are available publicly via Zenodo and figshare. 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). Upon publication, all code and data will be archived and made publicly available via Zenodo.

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**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 result from ecological processes structuring communities, but can also emerge from the mathematical constraints of an abundance distribution. Although the hollow-curve shape may be a statistical artefact, ecological processes may yet induce subtle deviations in empirical species abundance distributions. These deviations may, in turn, be informative as to which biological processes are operating on top of mathematical constraints, thereby providing a new avenue 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 to their statistical baselines. These deviations are less informative in small communities – those with few species or individuals – because these communities have less well-resolved statistical baselines. The uneven nature of 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 this approach in small samples, and that alternative methods or metrics may be needed.

**Introduction**

Ecological communities are complex systems made of numerous interacting entities subject to a vast array of processes operating in different contexts and at different scales (Levin 1992; Lawton 1999; Maurer 1999; Brown et al 2002; Nekola and Brown 2007; McGill 2019). One strategy for this complexity is to identify the patterns in community structure that are consistent, so as to distinguish among the possible theories and mechanisms that shape these common phenomena (Brown and Maurer 1989; Maurer 1999; Lawton 1999; Gaston and Blackburn 2000; McGill 2019). Some of these patterns, however, can have counterintuitive emergent statistical properties (Frank 2009; 2019). Left unexamined, these properties can confound the interpretation of observed patterns—what we interpret to be the result of generative mechanism may be an artifact of statistical constraints. However, when these properties are properly understood and accounted for, they can provide leverage for detecting and identifying the processes at work in a system (Jaynes 1957, Harte and Newman 2014).

The species abundance distribution (SAD), how all of the individuals in a community are divided among the species in that community, is a prime example of an ecological pattern that is both commonly invoked in the search for general processes, and subject to statistical constraints that have thus far complicated efforts to use it in this way (Nekola and Brown 2007; McGill et al. 2007; Locey and White 2013). Community ecologists have used the SAD to test numerous theories regarding 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). Investigating and accounting for the statistical considerations that constrain the shape of the SAD may open up new avenues for ecological interpretations.

Interpreting the ecological mechanisms underlying the SAD is a challenging prospect because the shape of the SAD is highly consistent; indeed it is one of the few ecological patterns that is so consistent that it is often considered an ecological law (Preston 1948, 1962a, 1962b, 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; McGill et al 2007). In fact, the nearly ubiquitous shape of the SAD may transcend ecological processes and instead reflect mathematical properties inherent to abundance distributions. Complex systems across multiple domains ranging from economics to information technology all exhibit empirical abundance distributions with hollow-curve forms similar to ecological SADs (Shockley 1957; Gaston et al. 1993; Nekola and Brown 2007, Blonder et al. 2014; Kiel et al. 2018). This suggests that the hollow curve is a general feature of abundance distributions and not necessarily an ecological phenomenon. Because the hollow-curve is observed in diverse systems and many theoretical generative processes converge to power-law or log-series abundance distributions (i.e. hollow curves) (Preston 1950; McGill 2003; Nekola and Brown 2007; Frank 2009; Frank 2019), approaches from statistical mechanics and complexity science may best explain the expected emergent shape for the distribution (Preston 1950; McGill 2003; Nekola and Brown 2007; Dewar and Porté 2008). 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, this shape may be of limited use for developing and testing ecological theories.

While SADs may be statistically constrained, this does not necessarily mean that they cannot be biologically informative. Biological factors may introduce subtle, but meaningful, deviations between observed SADs and the expected shapes due to mathematical constraints. These expected shapes are imposed by dividing the total number of individuals in a community, *N*, among the total number of species, *S*, and are hereafter referred to as the *statistical baseline* (Locey and White 2013, Harte and Newman 2014). If the vast majority of mathematically achievable SADs for a community of given *N* and *S* share a similar shape, then an observed SAD that deviates even slightly from this statistical baseline is unlikely to have emerged at random (Locey and White 2013), and may be inferred as the signature of a non-random – i.e., biological – process operating on the relative abundances of species (Harte and Newman 2014). Consistent deviations between observed SADs and their statistical baselines across many communities then provides a way to evaluate and refine ecological theories. For example, there is a high prevalence of rare species in ecological communities (e.g. Nee 1991; Magurran 2003), but it is unclear to what extent this phenomenon may derive from mathematical constraints on the SAD compared to ecological processes. If the prevalence of rare species in observed distributions consistently exceeds what would be expected from the statistical baseline, we would be prompted to look for ecological mechanisms promoting rarity. The candidate theories could then be evaluated based on how well their predictions of the rare tails in the SAD matched observed distributions. Thus, it is the *deviations* from the statistical baseline that enable us to detect strong ecological processes or evaluate theories (Harte and Newman 2014, Xiao et al. 2016).

Successfully interpreting SADs in this fashion depends on our capacity to detect and quantify deviations between empirical observations and statistical baselines, via metrics and computational approaches. Here, we build upon the combinatoric approach developed by Locey and White (2013) to define and explore 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 the *feasible set*, with each possible SAD constituting a single element of the set. If an observed SAD is drawn at random from the feasible set, it will be more likely to have a shape that is common in the feasible set. The feasible set therefore allows us to define the statistical baselines for assessing deviations in observed SADs and what is likely to occur merely due to mathematical constraints (Locey and White 2013).

Whether any specific metric is informative for distinguishing an observed SAD from its statistical baseline will depend on the distribution of shapes in the feasible set for the corresponding S and N. Although most feasible sets are dominated by the hollow-curve shape, different values of S, N, and the ratio of N to S will modulate the detailed attributes of the SADs in a feasible set (Locey and White 2013). For example, if the ratio of N to S is close to 1, all possible SADs are mathematically constrained to be fairly even (Locey and White 2013). Although an SAD that is very even would be highly unusual in most cases, it would be expected in this situation. Correspondingly, our ability to infer the presence of an ecological mechanism that predisposes a community to be even will thus depend on the ratio of N to S. 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.

Accounting for variation in the specificity, or vagueness, of the expectations derived from the statistical baseline will be critically important for disentangling the aspects of the SAD that can be attributed statistical constraints from those that result from other processes. If the vast majority of mathematically possible SADs are similar in shape –a 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 are common in the feasible set, then the statistical baseline is less well-defined, and our sensitivity for distinguishing biological signal from statistical constraints is 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. Statistical baselines with broad distributions will therefore impede our ability to assess whether observed deviations ecologically generated or expected to emerge randomly (Jaynes 1957). This general concern has been acknowledged (Harte 2011, White et al. 2012, Locey and White 2013) but there has not yet been a quantification of these effects. Because ecologists study the SAD for a large range of S and N, identifying the communities 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 influences 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 S1 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 to some degree of sampling error (Bonar et al. 2011). Therefore, in addition to analyzing the observed 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 (Gotelli and Colwell 2011). Rare species are 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 tail of the SAD. For each community, we computed the estimated richness using the bias-correct Chao and the ACE estimators (as implemented in the R package “vegan”; O’Hara 2005; Chiu et al 2014; Oksanen et al. 2020), 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 observed species richness, we added the missing species each with abundance 1. These adjusted SADs 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 all species in the SAD (i.e. not just rare species). For each observed community, we constructed subsamples by randomly drawing 60% of the observed individuals , without regard to species and without replacement. This introduced substantial room for sampling error, but yielded resampled communities that were not trivially small in terms of S and N. We generated 10 resampled communities for each observed community.

We ran our computational pipeline using all observed SADs and all SADs adjusted for undersampling of rare species. Because the resampling approach increased computational effort approximately tenfold, we only analyzed some of the communities using this method: all communities for the Mammal Community, Miscellaneous Abundance, and Gentry databases, but 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 are a finite number of unique ways to partition those individuals into *S* species. The complete set of these unique partitions is the feasible set. In this approach, neither species nor individuals are distinguishable from each other; thus, 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 SADs *(1, 3, 5)* and *(2, 2, 5)* count as distinct partitions, but *(1, 3, 5)* and *(3, 1, 5)* do not, because they each contain one species with an abundance 1, 3, and 5, respectively, and 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, an exhaustive characterization of the statistical properties of the feasible set for large *S* and *N* quickly becomes computationally intractable. This renders it necessary to draw samples from the feasible set, rather than enumerating all of its elements. Previous efforts in this vein (Locey and White 2013) have been constrained by the problem of unbiased sampling of large feasible sets.

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 sample the feasible set for a given combination of *S* and *N*, based on recurrence relations used to calculate the size of the feasible set. Let f(S, N) be the number of possible partitions of N individuals into exactly S species, i.e. the size of the feasible set for the given values of S and N. Computation of f(S, N) can be achieved without enumerating the entire feasible set through the recurrence relation f(S, N) = f(S-1, N-1) + f(S, N-S) (originally documented in a 1742 letter from Euler to Bernoulli; 1862). For example, consider the feasible set with S = 3 and N = 7. For all possible partitions, either (a) at least one species has an abundance equal to 1, or (b) all of the species have abundance greater than 1. In the case of (a), removing one species with abundance equal to 1 must result in a partition of 6 individuals into 2 species. In fact, all of the unique partitions in (a) must have a corresponding unique partition in the feasible set for S = 2 and N = 6, and vice versa. In the case of (b), removing 1 individual from each species must result in a partition from the feasible set with S = 3 and N = 4. Here, all the partitions in (b) must have a corresponding unique partition in the feasible set with S = 3 and N = 4, and vice-versa. Therefore, f(3,7) = f(2,6) + f(3,4). By storing the values in a lookup table, f(S, N) can be calculated for increasing values of S and N through summation.

This recurrence relation also makes it possible to draw random samples from the feasible set without enumerating all possible partitions of N into S. For the example of S = 3 and N = 7, there are a total of 4 possible partitions (i.e. f(S, N) = 4). Because f(2, 6) = 3 and f(3, 4) = 1, we know that (a) 3 of the 4 partitions must correspond to a partition of the feasible set with S = 2 and N = 6 (but with a species of abundance equal to 1 removed), and (b) 1 of the 4 partitions must correspond to a partition of the feasible set with S = 3 and N = 4 (but with 1 individual removed from each species). Thus, we can determine the probability that a partition drawn at random from the feasible set for S = 3 and N = 4 is in case (a) – probability ¾ - or case (b) – probability ¼. To generate a partition in case (a), we sample a partition for S = 2 and N = 6 and then add a species with abundance equal to 1; for case (b), we sample a partition for S = 3 and N = 4 and then add 1 individual to each species. In this way, we use the recurrence relation to transform the problem of sampling from a large feasible set into the problem of sampling from a smaller, different feasible set. This procedure continues until a partition is uniquely determined, after which some back-transformation yields a unique partition for the feasible set of interest. A detailed description of the algorithm we use, based on a slightly different recurrence relation, is available in Appendix S2 and is implemented in the R package feasiblesads available on GitHub at [www.github.com/diazrenata/feasiblesads](http://www.github.com/diazrenata/feasiblesads).

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 statistical baselines*

We compared SADs to their statistical baselines using several metrics, including a general measure of dissimilarity, as well as skewness, Simpson’s evenness, Shannon’s index, and the proportion of rare species (species with abundance = 1). These metrics represent just a few of the vast array of possible summary metrics that describe the shape of an SAD or 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 the community’s sampled feasible set (see *Generating the statistical baseline*,above), we generated a portfolio of measures describing the shapes expected from randomly sampled SADs.

First, as a general characterization of whether observed SADs occupy rare or common shapes, we computed a dissimilarity rank, relative to the central tendency of an SAD’s feasible set (following Locey and White, 2013). We started by defining the degree of dissimilarity between two SADs with the same S and N as the proportion of individuals allocated to species with different abundances, 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. The range of values for this index is 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 computed the central tendency of a feasible set as the SAD with the lowest mean dissimilarity to the rest of the SADs in the feasible set. However, because it is computationally impractical to make all pairwise comparisons between large numbers of samples, we only computed dissimilarity between each SAD in the sampled feasible set and a random set of 500 other SADs.

Although dissimilarity is scaled from 0 to 1, the distribution of values will be different depending on the feasible set, and the relative dissimilarity of SADs from the central tendency. We therefore calculated the percentile rank of the observed dissimilarity score relative to the distribution of dissimilarity scores among the feasible set, relative to its central tendency. For example, a percentile score of 95 for an observed SAD indicates that there is a 5% chance that a randomly drawn SAD from the feasible set will be more dissimilar, relative to the central tendency.

After aggregating across communities, we can examine the distribution of percentile ranks. If all SADs in a feasible set are equally likely to occur, then the distribution of percentile ranks for observed SADs will be similar to that for random samples from the feasible set (i.e. a uniform distribution from 0 to 100). However, if observed SADs are, on average, more dissimilar than expected at random, then strong processes may be at work driving SADs away from the central tendency—if observed SADs are consistently highly dissimilar, 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. We note that it is impossible for an observation to fall above the 95th percentile if there are fewer than 20 values in the sampling distribution. We therefore excluded from this analysis communities with fewer than 20 unique SADs in their feasible sets, yielding a total of 22,490 communities. Finally, note that, if the observed dissimilarity scores for individual communities are not systematically higher than the distributions of dissimilarity scores from the corresponding feasible sets, increasing the number of *communities* in the analysis will not increase the frequency of extreme percentile scores.

While the degree of dissimilarity between SADs and the central tendency of the feasible set provides an overall sense of deviations among possible SADs, it does not describe *how* observed SADs may differ from their feasible set. We therefore used a set of more targeted, ecologically interpretable metrics to explore deviations in SAD shape and the proportion of rare species. We examined three metrics for the shape of the SAD - skewness, Simpson’s evenness (1-D), and Shannon’s index. Skewness measures the asymmetry of a distribution around its mean. The Simpson and Shannon indices assess how equitably abundance is distributed across species (Maurer and McGill 2011). 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.

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 the observed SAD to the distributions of values for that community’s sampled feasible set. While the actual ranges and values of summary metrics vary widely over the ranges of S and N among our data and thus cannot be directly compared, percentile ranks are comparable across different community sizes, thereby enabling broad-scale assessment across our entire dataset. We used two-tailed 95% intervals to test whether 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, in the event of ties in the sampled distribution. 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 21,395 communities for skewness and 21,403 communities for all other shape metrics.

*The narrowness of the expectation*

of dissimilarity scores and shape metricsquantifywhen For 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 its central tendency. 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 S3). We explored how the narrowness of the statistical baseline varies with the size of the feasible set and the ratio of N to S.

**Results**

*Comparing observed SADs to their statistical baselines*

For four of the five datasets we analyzed – BBS, Gentry, Mammal Communities, and Misc. Abund – observed SADs are more dissimilar from their statistical baselines than would be expected by chance (Figure 3). Over these four datasets, 29% of observed SADs are in the 5% tail of dissimilarity from the central tendency. If observed SADs were simply random draws from the feasible set, we would expect only 5% to be that dissimilar (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 (Figure S4).

These datasets also contain highly unlikely observed SADs in terms of their shape metrics. At random, roughly 2.5% of percentile scores should be very high (>97.5) or very low (<2.5). Relative to their feasible sets, these four datasets contain a disproportionate number of communities with very low values for Simpson’s evenness and Shannon diversity, and very high skewness (Table 1). The Mammal Community, and Miscellaneous Abundance databases also have high proportions of rare species, but this tendency is weaker for BBS and nonexistent for Gentry – in fact, the Gentry dataset has a high representation of sites with *low* proportions of rare species (20% of sites; Table S5). 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, and low skewness.

In contrast to the other datasets, percentile scores for sites from the FIA dataset are more uniformly distributed, and the proportions of extreme values are closer to what would be expected by chance (Table 1). 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, as the size of the feasible set increases, the SADs in a feasible set become more narrowly clustered around the central tendency of that feasible set (Figure 4). The sampled distributions for shape metrics also generally become less broad as the size of the feasible set increases. In small communities (N < X), the breadth indices are highly variable and approach 1, meaning that a 95% density interval of 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. Among our datasets, the FIA and Mammal Community databases have the smallest communities, in terms of S and N, and tend to have the most feasible sets with high breadth indices (Figure S6).

*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 (Figure 5; see appendix A7 for complete results of resampling). For all datasets, adjusted SADs show more 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 and skewness and high values for evenness and Shannon diversity.

Jackknife resampling consistently reduces the proportion of extreme observations across all datasets and metrics (Figure 5; Appendix A7). In most instances, the proportion of extreme observations still exceeds the proportion that would be expected by chance. 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 generated by purely statistical processes. We also found that the mangitude and form of deviation varied among the datasets we considered. This variability may reflect statistical phenomena related to the size of S and N and their ratio, or it may reflect different biological processes dominating in different contexts. Finally, we note that, althoughThis does not imply the absence of certain ecological processes operating in these communities! One possible explanation is ing, Going forward, testing whether ecological theories or common functional approximations (e.g. the log-normal distribution) accurately predict the 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. An attempt to account for undersampling of rare species strengthened these effects, while subsampling weakened them. This effect was especially noticeable 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 tail of rare species in the SAD has been a consistent 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 than would be statistically expected, without also 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 the detected deviations are modulated by statistical characteristics of the feasible set. Compared to the other datasets, communities from the Gentry database tend to have high species richness and low average abundance (i.e. a low ratio of N to S) (Figure 1). 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) (see Appendix A8). 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, the statistical baseline includes even more rare species than observed in the data. 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 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 are comparable 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 across ecosystems.

Unlike the other four datasets, communities in the FIA dataset showed weak or no evidence of deviations from their feasible sets. We entertained two general classes of explanation for why the FIA dataset differs from the others in our analysis: first, that biological attributes of the FIA communities mean that the SADs for these communities differ from the others in our database, and second, that statistical phenomena related to S and N, and specifically community size, may modulate the capacity to detect deviations for these communities. To distinguish between possible biological drivers causing FIA to differ from the other datasets, and factors intrinsic to S and N, we compared a subset of ~300 FIA communities to communities from other datasets with directly comparable S and N. did not find differences in thefor any metrics datasets, conAppendix A9300statistical phenomenadifferences in results between and the other datasets

A second possibility is that these differences reflect statistical phenomena related to community size in terms of S, N, and as a result, the number of possible SADs in a community’s feasible set. The FIA communities are by far the smallest across our datasets (Figure 1), and communities with small values of S and N have smaller feasible sets. When there are relatively few possible SADs, they may be less tightly clustered around their central tendencies, and the distributions for the shape metrics less consistently narrowly peaked, than when there are very large numbers of possible SADs. This variability within the feasible set weakens the statistical distinction between “common” and “extreme” shapes for small, highly variable, feasible sets (Figure 2). Under these circumstances, any deviations – or lack thereof – that we perceive may be less informative than for communities with more strongly defined statistical baselines (Jaynes 1957). The average dissimilarity to the central tendency among elements of the feasible set, and the distributions of breath indices for specific metrics, broadly align with this principle. Across the range of community sizes represented across our datasets, small feasible sets are more highly variable, with broader shapes compared to larger feasible sets (Figure 4). More specifically, very small communities – for example, those with fewer than 2000 possible SADs in their feasible sets, or S ~ 20 and N ~ 40 – have higher variability among SADs and with less consistent deviations than larger communities (Figure 6; Appendix A10). Of our datasets, FIA is most dominated by small communities (68% of communities have fewer than 2000 possible SADs), and these small-community phenomena may therefore have the greatest impact on results aggregated over the FIA dataset.

If it is true that the highly variable feasible sets associated with small communities contribute to the weak evidence of deviations observed for the FIA dataset, such considerations may affect our capacity to use this approach to distinguish signal from noise for a substantial contingent of ecological communities. Because the combinations of S and N represented in our analyses are irregularly distributed among different datasets (Figure 1), and because there is a great deal of variation in our breadth indices not accounted for by the size of the feasible set (Figure 4), we do not interpret these results as showing a threshold for defining problematically small communities. A more systematic exploration of the S and N state space, possibly combined with more nuanced metrics for characterizing the variability of the feasible set, could clarify and refine the relationship between S and N, the size of the feasible set, and statistical power. However, FIA and other small, highly variable communities have on the order of 10-20 species and 30-60 individuals, and these may indicate a general range of values below which we have diminished power to detect deviations from the statistical baseline represented by the feasible set. Communities with on the order of 5 species, or 100s to 1000s of individuals, have previously been identified as “small” in this context (Preston 1948; McGill et al. 2007). To meaningfully draw inferences using deviations in these small communities, we will 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 containing species with equal abundances, such as (1, 1, 1, 8), would only count as 4 unique SADs. For SADs, equal abundances 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.

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