**Introduction**

The species abundance distribution (SAD) is one of the few ecological patterns whose shape is so consistent that it is often considered an ecological law (Lawton 1999, McGill et al 2007). Across varied ecosystems and taxa, the species abundance distribution is nearly always dominated by a few very abundant species and a larger number of increasingly rare species, generating a distinctive hollow- or J-shaped curve (Fisher 1943). Community ecologists have used the species abundance distribution to test numerous theories intended to determine which biological processes are most important for structuring assemblages of species (McGill et al 2007). However, using the species abundance distribution to distinguish amongst theories has proven frustrating because many theories predict similar shapes (McGill et al 2007), and even experimental manipulations generate little variation in the shape of the SAD (Supp and Ernest 2014). After decades of use as a theoretical benchmark, the utility of the SAD for assessing the processes structuring ecological communities is currently unclear.

Increasing evidence for statistical constraints operating on the shape of the SAD (Locey and White 2013, White et al 2012, Frank 2019) has complicated our understanding of the SAD as a *biological* pattern. Accumulating evidence suggests that statistical constraints may actually generate the most striking feature of the species abundance distribution – the hollow curve. At its core, the SAD is a representation of how the total number of individuals in a community (N) are partitioned among the number of species (S) in that community. If our implicit null expectation for such a distribution is that individuals are uniformly distributed across species (i.e. equal numbers of individuals per species), the hollow curve we see in nature is indeed surprising. However, a uniform distribution is not necessarily the appropriate baseline. Just as a Gaussian distribution emerges in the limit of many samples around a population mean, power-law or log-series distributions (i.e. ‘hollow-shaped’ curves) emerge as statistical attractors for abundance distributions (Frank 2009, 2019). Whether using statistical mechanics (i.e. the Maximum Entropy Theory of Ecology (METE); Harte et al 2008, Harte 2011) or combinatorics (i.e. ‘the feasible set’; Locey and White 2013), the random division of individuals into species can, on its own, generate realistic hollow curves. Because these statistically generated SADs are excellent empirical fits to those seen in nature (Harte et al 2011, White et al 2012, Locey and White 2013), it is reasonable to expect that statistical constraints alone may account for the widespread phenomenon of the hollow-curve SAD.

If SADs are statistically inclined to be hollow curves without requiring biological influences, it is no surprise that we have struggled to interpret the hollow curve in biological terms. However, just because the main feature of the SAD may be statistically determined, it does not necessarily follow that the SAD cannot be biologically informative. Biological processes may cause relatively subtle, but meaningful, deviations between observed SADs and their statistical expectations (Locey and White 2013, Harte and Newman 2014). We may be able to use those *deviations* to evaluate theories (Harte and Newman 2014, Xiao et al 2016) by interpreting SADs not in terms of their absolute shape, but in terms of their shape relative to what we would expect simply due to statistical processes operating within the constraints of S and N(Frank 2009, Locey and White 2013). Using SADs in this fashion depends on our capacity to detect and quantify deviations between empirical observations and randomness, which requires metrics and computational approaches that allow us to quantify and interpret whatever deviations may exist, across many different types of ecological communities.

Based on logic developed in statistical mechanics and related fields, one challenge for detecting deviations may derive from the relatively small size of sampled communities in ecology, in terms of the observed values of S and N. In general, often when a system involves very large numbers of subcomponents (individuals and species, in the case of the SAD) that can be arranged in many possible ways, nearly all of the possible arrangements share similar large-scale characteristics (Jaynes 1957, Haegeman and Loreau 2008). For such systems, an observation whose large-scale characteristics deviate even slightly from those shared by the majority of possible arrangements is unlikely to have emerged at random from the pool of possible arrangements. Such a deviation is an indication that the information and assumptions that generated the expectation do not fully account for the processes at play in the system (Jaynes 1957). For the SAD, the large-scale characteristics are the shape of the distribution as captured by how even or skewed the distribution of abundances is among species. Even small deviations between the shape of an observed SAD and the expected random outcome would suggest there are non-statistical processes at work causing the observed SAD to be more or less even or skewed than would occur at random. Crucially, expectations obtained in this way are most informative when most of the possible small-scale arrangements appear similar at large scale – i.e., when the distribution of expected outcomes is very narrowly peaked or clustered around a particular outcome, or shape for the SAD (Jaynes 1957, Haegeman and Loreau 2008). If the array of possible arrangements encompasses broader and more even variation in large-scale characteristics, the expectation is less well-resolved and less informative (Jaynes 1957). When this occurs, we have less confidence that an observation that differs from the *most* likely characteristics is inconsistent with the expectation, because the expectation itself is nonspecific (Jaynes 1957, Haegeman and Loreau 2008). Small systems may be more likely to generate relatively broad expectations, because they have fewer subcomponents and fewer possible arrangements (Haegeman and Loreau 2008). This may be particularly relevant to ecology, because ecological systems can have considerably fewer subcomponents than is usual for the systems usually studied via statistical mechanics (Haegeman and Loreau 2008). However, it is not clear whether ecological communities are affected by these small-size phenomena, and if so, which community sizes (in terms of S and N) are affected the most.

Here we build upon the combinatoric approach developed by Locey and White (2013) to establish if, and in what ways, empirical SADs deviate from a statistical expectation based on S and N. We also examine whether smaller communities indeed have less narrowly-defined statistical baselines than large ones, and whether this appears to modulate our capacity to identify deviations. For 24,500 communities of birds, mammals, trees, and miscellaneous other taxa, we use combinatorics to generate the distribution of possible states for the SAD – i.e., a statistical baseline – for each community based on its number of species and number of individuals. We then compare *observed* SADs to their corresponding statistical baselines and evaluate 1) if the shapes of observed SADs are consistently unusual given their statistical expectations, 2) how the narrowness of the statistical expectation varies over gradients of *S* and *N*, and 3) whether this variation is associated with variation in whether observations can be distinguished from the expectation.

**Methods**

*Datasets*

We use a compilation of community abundance data for trees, birds, mammals, and miscellaneous other taxa that has been used in recent macroecological explorations of the SAD (White et al 2012, Baldridge 2016, Baldridge 2015). This compilation consists of cleaned and summarized community abundance data for trees obtained from the Forest Inventory and Analysis (Woudenberg et a al 2020) 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). We filtered these data to remove exceptionally large or small communities, because characterizing the random expectation for the SAD becomes computationally intractable for very large communities, and becomes trivially uninformative for very small ones. We therefore filtered our datasets to remove communities with more than X species or X individuals, or fewer than 2 species or X individuals. We also removed communities for which N = S, because these communities have only one possible SAD. We further filtered the FIA database, which contains roughly 100,000 communities of which approximately 90,000 have fewer than 10 species. Rather than analyze all of these small communities, we randomly selected 10,000 small communities to include in the analysis. All FIA communities with more than 10 species were included in the analysis. 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. 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, with an average temporal scale of X. After filtering exceptionally large or small communities and multiple years of data collection, our final dataset consisted of 24,519 communities with S and N ranging from 2 to 250 and 3 to 40714, respectively ([Figure](#_Figure_1:_Communities)). Code detailing the filtering process can be found at X.

*Generating the statistical baseline*

We use the concept of the *feasible set* to characterize a statistical baseline for the SAD (Locey and White, 2013). For a given number of individuals *N*,there is a finite array of unique ways to partition those individuals into *S* species. The feasible set is the complete set of these unique partitions, or elements. Partitions are unique if and only if they differ in the number of species present with each abundance; neither species nor individuals are distinguishable from each other (Locey and White, 2013). Operationally, this means that for *S = 3* and *N = 9*, the vectors *(1, 3, 5)* and *(2, 2, 5)* count as distinct partitions, but *(1, 3, 5)* and *(3, 1, 5)* count as only one element of the feasible set because they contain the same numbers and differ only in the *order* of the numbers. Alternative assumptions regarding the distinguishability of species and/or individuals would effectively change the probabilities associated with various elements of the feasible set, because some partitions can be achieved via more permutations than others. However, in the absence of strongjustification for one set of assumptions over another, we adopted a simple set of assumptions that have previously been shown to generate realistic statistical baselines (Locey and White 2013).

Characterizing the feasible set can be computationally intensive, particularly for large combinations of S and N. While it is possible to list all possible partitions of a small number of individuals into a small number of species, the number of elements in the feasible set increases rapidly with S and N and renders it necessary to draw samples from the feasible set, rather than enumerating all of its elements. Unbiased sampling of large feasible sets is itself a nontrivial computational problem, and the computational resources required 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. 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 at <https://github.com/ha0ye/feasiblesads/blob/algo-vignette/vignettes/sampling_algorithm.Rmd>.

For every community in our database, we uniformly 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 to randomly draw 4000 unique samples from the feasible set, but for large communities, all 4000 are usually unique. We refer to this as the sampled feasible set.

*Comparing observed SADs to their baselines*

In the absence of any other process, an SAD with a particular S and N is likely to reflect whatever characteristics are common among the elements of its feasible set. We focus on the shape of the distribution of abundances across species as the characteristic of interest. Metrics related to this shape are frequently used in the study of community structure and have been used specifically in the context of distinguishing observed SADs from the feasible set (Locey and White 2013). We focus on two metrics to describe the shape of the SAD, skewness and Simpson’s evenness. Skewness measures the asymmetry of a distribution around its mean, and Simpson’s evenness is a commonly used metric in ecology for assessing how equitably abundance is distributed across species. By calculating these metrics for each of the unique samples in the community’s sampled feasible set (see *Generating the statistical baseline* above), we generated a distribution describing the general shape (i.e. evenness or skewness) that we expect from randomly generated SADs. Note that skewness, as implemented the R package “e1071” (Meyer et al 2019), always evaluates to 0 for distributions with only two species and cannot be computed for distributions where all values are equal, and we excluded those cases from analyses of skewness.

To assess whether the shape of an observed SAD was statistically unlikely, we calculated Simpson’s evenness and skewness for the observed SAD and compared these observed values to the distributions of evenness and skewness obtained from that community’s sampled feasible set. An observed SAD’s deviation from its feasible set was determined by assessing what percent of values in its sampled distributions for skewness and evenness were below the observed values. This percentile rank is comparable across different community sizes, allowing broad-scale assessment across wide ranges of S and N. When we compare across communities, if communities tend to reflect random draws from their feasible set, their percentile rank values should be uniformly distributed from 0 to 100. However, if observed SADs are consistently more skewed or even than their feasible sets, the percentile values will be disproportionately concentrated towards the extremes. This logic breaks down if there are very few unique values in the distribution of possible values, which can occur for small feasible sets. We excluded instances for which the distribution of possible values had fewer than 20 unique values, because in these cases, it is impossible for an observation to fall above or below the 95th or 5th percentile.

*The narrowness of the expectation*

We also used these distributions of skewness and evenness from the sampled feasible set to describe the relative narrowness or breadth of the statistical expectation over gradients of S and N, in order to assess whether there could be challenges in determining whether small communities differ from their randomly-generated expectations. We quantified the narrowness of a distribution as the ratio of the range of values encompassed within a 95% interval to the full range of values in the distribution ([Figure](#_Figure_2:_95%)). This allowed us to isolate and compare the *narrowness* of distributions that are not necessarily normally distributed and vary considerably in their actual values, means, ranges, and standard deviations. This metric corresponds qualitatively to more computationally-intensive approaches to measuring the self-similarity of the elements of feasible sets ([Supplement](https://github.com/diazrenata/scadsanalysis/blob/clean-and-tests/analysis/reports/self_similarity.md)).

**Results**

*Observed SADs compared to their feasible sets*

For four of the five datasets we analyzed – BBS, Gentry, Mammal Communities, and Misc. Abund – empirical SADs are highly skewed and highly uneven relative to their feasible sets, much more frequently than would be expected by chance ([Figure](#_Figure_3:_Overall), [Table](#_Table_1:_Percentile) ). Combined across these four datasets, 16% of observed SADs are more skewed than 95% of their feasible sets, and 31% are less even than 95% of their feasible sets. By chance we would expect only 5% of observed distributions to fall in these extremes. These outcomes contrast with the results from the FIA dataset, for which percentile scores were near-uniformly distributed for skewness (5% of observations are more skewed than 95% of the feasible set), and much noisier than any of the other datasets for evenness (9% of observations are less even).

*The narrowness of the expectation*

Over the range of communities we analyzed, the statistical expectation for both skewness and evenness narrows considerably as the size of the feasible set increases ([Figure](#_Figure_2:_95%), [Figure](#_Figure_5:_95%)). The size, or number of elements, of the feasible set increases with species richness (S), total abundance (N), and average abundance (N/S). At the extreme, for communities with relatively small feasible sets – fewer than approximately 1000 elements for skewness, and approximately 200 elements for evenness – the range of the 95% interval of values in the distribution approaches the entire range of values. Among the datasets we analyzed, the FIA database is the most dominated by communities for which the 95% interval spans nearly the entire range of values, reflecting relatively broad and nonspecific statistical expectations for the shape of the feasible set ([Figure](#_Figure_7:_Distribution)).

**Discussion**

We found widespread evidence that the shapes of the SADs for a range of real ecological communities are far more skewed and less even than we would expect given their feasible sets. These deviations may be the signature of ecological processes operating on top of statistical constraints and driving the SAD away from the shape it would assume in the absence of a dominating non-statistical process. Our results suggest that the prevailing processes structuring these communities tend to be ones that cause abundance distributions to be more uneven – rather than those that cause individuals to be spread evenly across species. These processes might be those that promote the persistence of rare species at extremely low abundances (e.g. Yenni et al 2012) –thereby lengthening the rare tail of the SAD – or processes that encourage or allow dominant species to be hyper-dominant without driving other species entirely to extinction (Chesson 2000). Although a disproportionate number of communities deviated statistically from the expected forms from their feasible set, there were many comparable communities for which we did not detect deviations. This appears consistent with the suggestion that in some cases, numerous ecological processes may operate simultaneously and with countervailing impacts on abundance distributions, resulting in no dominating net effect on the shape of the distribution beyond that imposed by fundamental constraints (Harte 2008; Harte and Newman 2014). Going forward, testing whether ecological theories or common functional approximations accurately predict this range of variation in deviations between observed SADs and their expectations may be much more fruitful than focusing only on the general form of the SAD, which may emerge from statistical constraints (McGill et al 2007; Locey and White 2013).

Unlike the other four datasets, communities in the FIA dataset showed at most weak evidence of deviations from their feasible sets. We suggest that these datasets are experiencing additional issues related to community size. The FIA communities are by far the smallest across our datasets. Community size may affect our ability to detect deviations because small communities may not have enough possible arrangements of their subcomponents, or elements in their feasible sets, to generate highly resolved distributions for the most probable shapes. Such broad distributions may not be specific enough to constitute strong statistical expectations, and the deviations – or lack thereof – that we perceive are correspondingly less informative (Jaynes 1957). When we compared the distributions of shape metrics from small communities to those for large ones, we found that samples from the feasible sets for small communities do indeed generate broader distributions of evenness, and especially skewness, than those for large communities (Figure). Moreover, if the lack of discernable deviations from the feasible set is a byproduct of FIA’s generally small community size, then we would expect similarly-sized, small, communities from other datasets to behave similarly. We identified 371 communities from other datasets with S and N matching communities in the FIA, and found no difference in the distribution of percentile scores between communities from FIA and communities from other datasets ([Figure](#_Figure_8:_Direct), [Table](#_Table_2:_Percentile)). Although this is a highly restricted subset of sites, relative to the 20,000 FIA sites we analyzed, the lack of a difference between FIA and other comparably-sized communities sites points to community size, and not biological features specific to FIA, as a likely explanation for the relatively 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 for communities with ranges of S and N that are quite common in ecological data. FIA communities, with their broad distributions of shape metrics and overall lack of detectable signal, have on the order of 10 species and 50-100 individuals. While these values do not constitute hard thresholds, they may indicate a general range of values below which we have relatively diminished power to distinguish deviation from randomness. Unless we can develop more sensitive methods for identifying deviations even for these small communities, we may stand to learn the most by focusing on SADs from relatively large communities. In the meantime, sampling the range of forms represented in the feasible set helps us identify when the distribution of shapes present is relatively broad and therefore less informative.

It is also important to recognize that there are multiple plausible approaches to the defining a statistical baseline for the SAD, of which we have taken only one (Locey and White 2013; Haegeman and Loreau 2008). The approach we used, following Locey and White (2013), reflects the random partitioning of individuals into species, and the resulting distributions are considered unique if the set of abundance values are unique regardless of the order in which the values occur. Biologically, differences in *order* would correspond to differences in *which* species contain the most or least individuals. The philosophy we take here reflects a longstanding approach in the study of abundance distributions: focusing the shape of the distribution, without regard or the species identities of the most or least abundant species (McGill 2007). However, there has never been a direct examination of either the validity or outcomes of alternative methods for generating a statistical baseline for the SAD, and there is therefore no unambiguous logical argument for one baseline over another. Other formulations for the statistical baseline may be equally valid and generate different statistical expectations, including forms that approximate exponential, Poisson, or log-series distributions (Favretti 2018, Harte et al 2008). Comparing the results that emerge from different baselines will be an important next step in this process towards reinvigorating the use of the SAD as a diagnostic tool.

Our study demonstrates both the utility, and the potential challenges, of applying tools from the study of complex systems and statistical mechanics to study ecological communities (Harte 2008, Harte and Newman 2014, Haegeman and Loreau 2008, White et al 2012)**.** 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 large systems for which these tools were originally developed (Haegeman and Loreau 2008, Jaynes 1957). If a substantial contingent of ecological systems have broad, nonspecific distributions of probable outcomes, these approaches may be less informative than we might hope – as appears to be the case for the smallest communities in our analysis. However, our application of these approaches in larger communities demonstrates that while statistical constraints have strong effects on the shape of the SAD, these constraints alone do not fully account for the extremely uneven SADs we often observe in nature – leaving an important role for ecological process. This ability to detect and diagnose the specific ways in which empirical SADs deviate from randomness can refresh our perspective on this distribution and open up new avenues for understanding how and when biological drivers affect is shape. There is, of course, still much work to do to assess 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. 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.

**Figures**

##### Figure 1: Communities by dataset, S, N

##### 

Distribution of communities from each dataset in terms of their total abundance (N) and species richness (S).

##### Figure 2: 95% ratio illustration

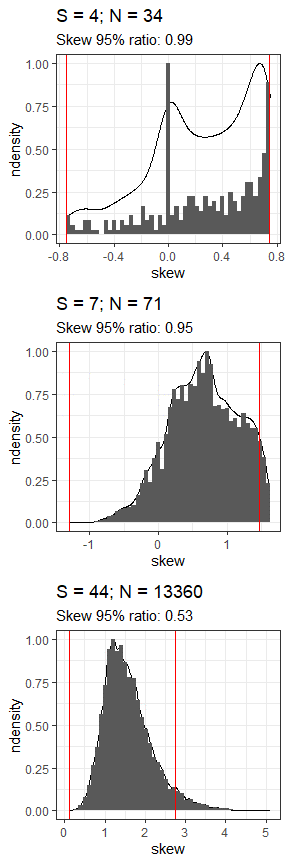
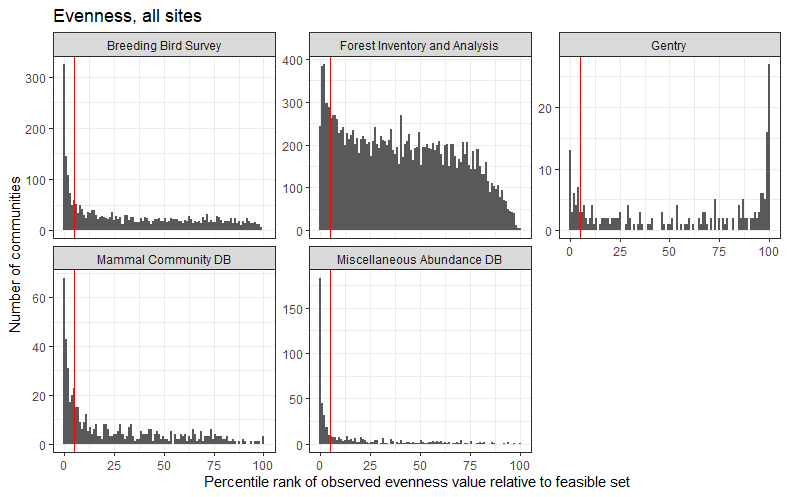


Illustration of the relationship between the feasible set and the statsitical expectation for hypothetical example communities with S = 4, 7, or 44 and N = 34, 71, or 13360 (top to bottom). Samples of unique SADs are drawn from a community’s feasible set. Feasible sets can range substantially in size, depending on the community size (e.g., a feasible set of 297 unique distributions for S=4 and N=34 vs 6.5e+70 unique distributions for S=44, N=13360). For every SAD drawn from the feasible set (left column), we calculate the skewness (color scale) or evenness (not shown). These values generate the distribution of expected statistic values from the feasible set (right column). The ratio of the range encompassed in the one-tailed 95% interval (space between red lines, right), compared to the full range of values for the statistic, describes how narrowly peaked or broad the distribution is. This ratio tends to decrease as the size of the feasible set increases and the distribution becomes more narrowly defined (top to bottom).

##### Figure 3: Overall percentile results



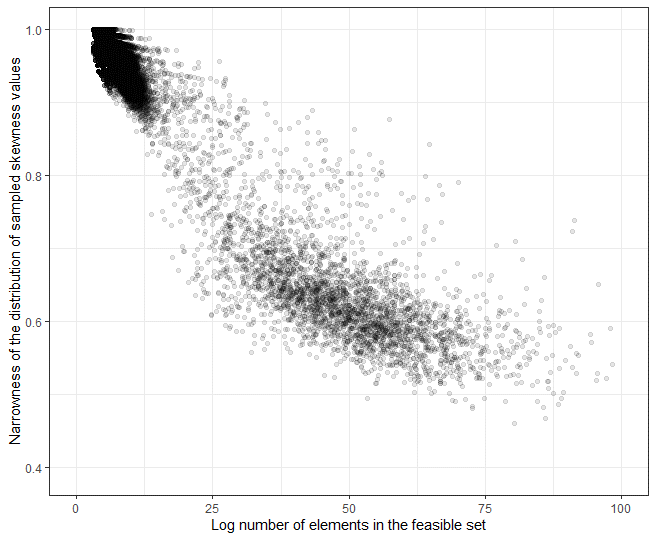
Histograms of percentile ranks for observed values of skewness (top) and evenness (bottom) relative to the distributions of values from the sampled feasible set for all communities. These plots exclude communities with fewer than 20 unique values for skewness or evenness in the sampled feasible set, and plots for skewness exclude communities with fewer than 3 species. The vertical red line marks the 95th percentile for skewness and the 5th percentile for evenness. At random, percentile ranks should be uniformly distributed from 0 to 100, and no more than 5% of values should be above or below the 95th and 5th percentiles, respectively.

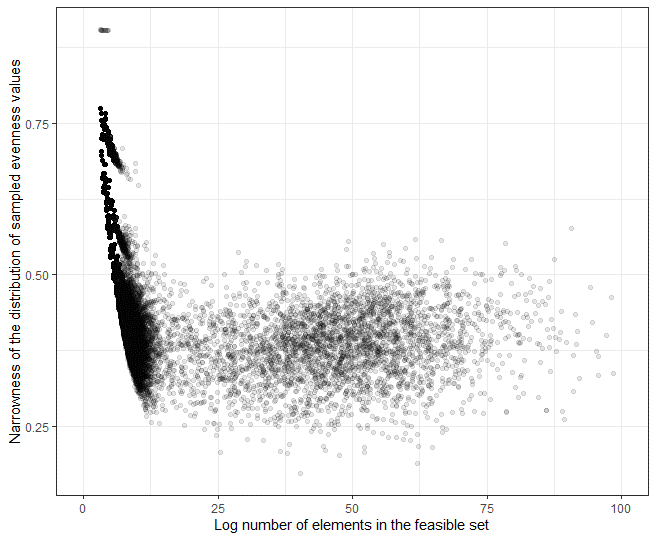
##### Table 1: Percentile results (**move to supplement)**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Dataset** | **Proportion of communities with skewness above 95th percentile** | **Number of communities analyzed for skewness** | **Proportion of communities with evenness below 5th percentile** | **Number of communities analyzed for evenness** |
| Breeding Bird Survey | 0.130184 | 2773 | 0.259647 | 2773 |
| Forest Inventory and Analysis | 0.054208 | 18300 | 0.093966 | 18113 |
| Gentry | 0.188341 | 223 | 0.151786 | 224 |
| Mammal Community DB | 0.158287 | 537 | 0.354244 | 542 |
| Miscellaneous Abundance DB | 0.345529 | 492 | 0.595918 | 490 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Dataset** | **Proportion of communities with skewness above 95th percentile** | **Number of communities analyzed for skewness** | **Proportion of communities with evenness below 5th percentile** | **Number of communities analyzed for evenness** |
| Forest Inventory and Analysis | 0.054208 | 18300 | 0.093966 | 18113 |
| Other datasets | 0.163478 | 4025 | 0.307272 | 4029 |

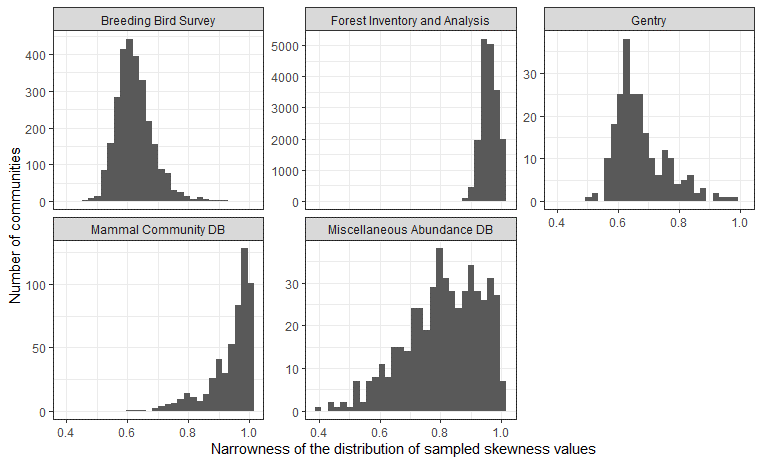
##### Figure 5: 95% intervals vs. size of feasible set **(move to supplement)**

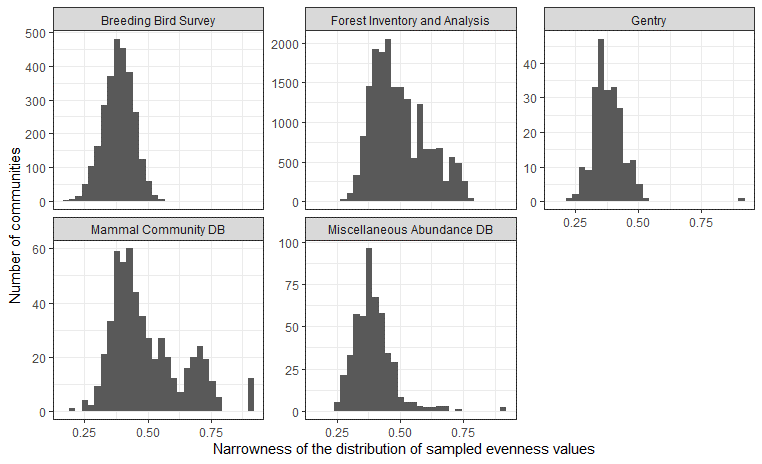




The narrowness of the distribution of skewness (top) and evenness (bottom) values from the sampled feasible set compared to the number of elements in the feasible set. The narrowness of the distribution is described as the ratio of the range of the 0-95th quantile values (for skewness), or the 5th-100th quantile values (for evenness), compared to the range of values from the entire sample. This ratio ranges from 0-1, with larger values indicating broader distributions and less-specific statistical expectations. The number of elements in the feasible set increases with increasing S, N, and average abundance (N/S). Both plots exclude feasible sets with fewer than 20 unique values for skewness or evenness, and skewness also excludes communities with S < 3.

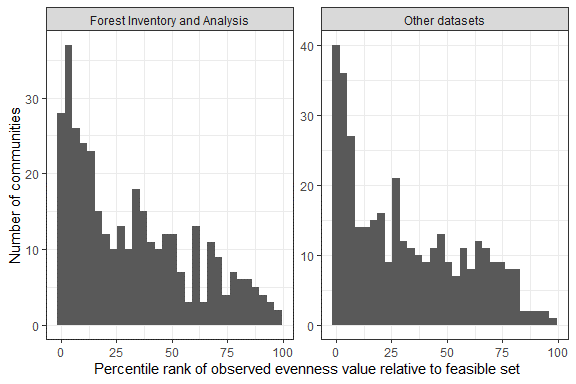
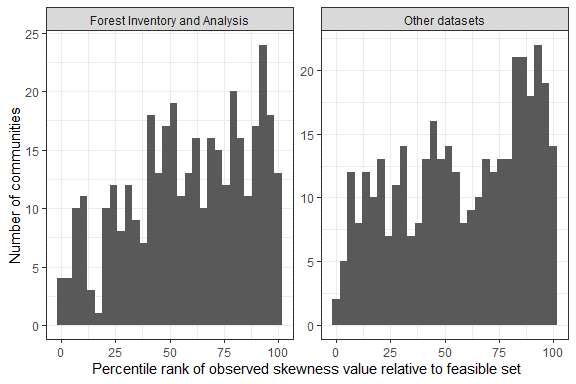
##### Figure 7: Distribution of 95% intervals by dataset





Histograms of the narrowness of the distribution of skewness (top) and evenness (bottom) values for the sampled feasible sets for communities from each dataset, excluding communities with fewer than 20 unique values for skewness or evenness and, for skewness, fewer than 3 species. The narrowness of the distribution is described as the ratio of the range of the one-tailed 95% interval to the full range of values. This value ranges from 0-1, with higher values indicating broader distributions.

##### Figure 8: Direct comparison of FIA and similarly sized sites



Histograms of percentile ranks for observed values of skewness (left) and evenness (right) relative to the distributions of values from the sampled feasible set for 371 pairs comprising a FIA community and a community from another dataset with the same S and N as the FIA community. These plots exclude communities with fewer than 20 unique values for skewness or evenness in the sampled feasible set. At random, percentile ranks should be uniformly distributed from 0 to 100.

##### Table 2: Percentile results comparing FIA to direct counterparts **(move to supplement)**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Dataset** | **Proportion of communities with skewness above 95th percentile** | **Number of communities analyzed for skewness** | **Proportion of communities with evenness below 5th percentile** | **Number of communities analyzed for evenness** |
| Forest Inventory and Analysis | 0.0808625 | 371 | 0.1780822 | 365 |
| Other datasets | 0.0862534 | 371 | 0.2109589 | 365 |

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