

An extensive comparison of species-abundance distribution models

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Introduction

The species abundance distribution (SAD) describes the full distribution of commonness and rarity in ecological systems. It is one of the most fundamental and ubiquitous patterns in ecology, and exhibits a consistent general form with many rare species and few abundant species occurring within a community. The SAD is one of the most widely studied patterns in ecology, leading to a proliferation of models that attempt to characterize the shape of the distribution and identify potential mechanisms for the pattern (see McGill et al. 2007 for a recent review of SADs). These models range from arbitrary distributions that are chosen based on providing a good fit to the data (Fisher et al. 1943), to distributions chosen based on the most likely states of generic random systems (Frank 2011, Harte 2011, Locey and White 2013), to models based more directly on ecological processes (Tokeshi 1993, Hubbell 2001, Volkov et al. 2003, Alroy 2015).

Which model or models provide the best fit to the data, and the resulting implications for the processes structuring ecological systems, is an active area of research (e.g., McGill 2003, Volkov et al. 2003, Ulrich et al. 2010, White et al. 2012, Connolly et al. 2014). However, most comparisons of the different models: 1) use only a small subset of available models (typically two; e.g., McGill 2003, Volkov et al. 2003, White et al. 2012, Connolly et al. 2014); 2) focus on a single ecosystem or taxonomic group (e.g., McGill 2003, Volkov et al. 2003); or 3) fail to use the most appropriate statistical methods (e.g., Ulrich et al. 2010). This makes it difficult to draw general conclusions about which, if any, models provide the best empirical fit to species abundance distributions.

Here, we evaluate the performance of four of the most widely used models for the species abundance

distribution using likelihood-based model selection on data from 16,209 communities and nine major taxonomic groups. This includes data from terrestrial, aquatic, and marine ecosystems representing roughly 50 million individual organisms in total.

Methods

Data

We compiled data from citizen science projects, government surveys, and literature mining to produce a dataset with 16,209 communities, from nine taxonomic groups, representing nearly 50 million individual terrestrial, aquatic, and marine organisms. Data for trees, birds, butterflies and mammals was compiled by White et al. (2012) from six data sources: the US Forest Service Forest Inventory and Analysis (FIA; USDA Forest Service 2010), the North American Butterfly Association's North American Butterfly Count (NABC; North American Butterfly Association 2009), the Mammal Community Database (MCDB; Thibault et al. 2011), Alwyn Gentry's Forest Transect Data Set (Gentry; Phillips and Miller 2002), the Audubon Society Christmas Bird Count (CBC; Society 2002), and the US Geological Survey's North American Breeding Bird Survey (BBS; Pardieck et al. 2014). The publicly available datasets (FIA, MCDB, Gentry, and BBS) were acquired using the EcoData Retriever [Morris and White (2013); <http://ecodataretriever.org>]. Details of the treatment of these datasets can be found in Appendix A of White et al. (2012). We modified the data slightly by removing sites 102 and 179 from the Gentry data due to issues with decimal abundances appearing in raw data due to either data entry or data structure errors. Data on Actinopterygii, Reptilia, Coleoptera, Arachnida, and Amphibia, were mined from literature by Baldrige and are publicly available (Baldrige 2013).

Table 1: Details of datasets used to evaluate the form of the species abundance distribution. Datasets marked as Private were obtained through data requests to the providers.

Dataset	Dataset code	Availability	Total sites	Citation
Breeding Bird Survey	BBS	Public	2769	Pardieck et al. (2014)
Christmas Bird Count	CBC	Private	1999	Society (2002).
Alwyn Gentry's Forest Transects	Gentry	Public	220	Phillips and Miller (2002)
Forest Inventory Analysis	FIA	Public	10355	USDA Forest Service (2010)
Mammal Community Database	MCDB	Public	103	Thibault et al. (2011)
North American Butterfly Count	NABA	Private	400	North American Butterfly Association
Actinopterygii	Actinopterygii	Public	161	Baldrige (2013)
Reptilia	Reptilia	Public	129	Baldrige (2013)
Amphibia	Amphibia	Public	43	Baldrige (2013)
Coleoptera	Coleoptera	Public	5	Baldrige (2013)
Arachnida	Arachnida	Public	25	Baldrige (2013)

All abundances in the compiled datasets were counts of individuals.

Models

The majority of species abundance distributions (SADs) are constructed using counts of individuals (for discussion of alternative approaches see McGill et al. 2007 and @morlon2009). As such, the data are discrete and discrete distributions (i.e., those that only have non-zero probabilities for positive integer values of abundance) are more appropriate.

McGill et al. (2007) classified species abundance distribution models into five different families: purely statistical, branching process, population dynamics, niche partitioning, and spatial distribution of individuals. We evaluated models from each of these families, except for niche partitioning. We excluded niche partitioning models from the analysis (including both classic models like the geometric series and niche fraction models (Motomura 1932, Sugihara 1980, Tokeshi 1993) and

Alroy's [Alroy2015] new double geometric model) because these models do not have explicit likelihoods and therefore would have prevented the use of likelihood based methods for fitting and evaluating the distributions (see Analysis). We evaluated the log-series, the Poisson lognormal, the negative binomial, and the Zipf distributions. All distributions were defined to be capable of having non-zero probability at integer values from 1 to infinity.

The log-series is one of the first distributions used to describe the SAD, being derived as a purely statistical distribution by Fisher (1943). It has since been derived as the result of ecological processes, the metacommunity SAD for ecological neutral theory (Hubbell 2001, Volkov et al. 2003), and several different maximum entropy models (Pueyo et al. 2007, Harte et al. 2008).

The lognormal is one of the most commonly used distributions for describing the SAD (McGill 2003) and has been derived as a null form of the distribution resulting from the central limit theorem (May 1975), population dynamics (Engen and Lande 1996), and niche partitioning (Sugihara 1980). We use the Poisson lognormal because it is a discrete form of the distribution appropriate for fitting discrete abundance data (Bulmer 1974).

The negative binomial (which can be derived as a Gamma-distributed mixture of Poisson distributions) provides a good characterization of the SAD predictions for several different ecological neutral models for the purposes of model selection (Connolly et al. 2014). We use it to represent neutral models as a class.

The Zipf (or power law) distribution was derived based on both branching processes and as the outcome of the McGill and Collin's (2003) spatial model. It was one of the best fitting distributions in a recent meta-analysis of SADs (Ulrich et al. 2010). We use the discrete form of the distribution which is appropriate for fitting discrete abundance data (White et al. 2008).

Analysis

Following current best practices for fitting distributions to data and evaluating their fit, we used maximum likelihood estimation to fit models to the data (Clark et al. 1999, Newman 2005, White et al. 2008) and likelihood-based model selection to compare the fits of the different models (Burnham and Anderson 2002, Edwards et al. 2007). These general best practices have recently been affirmed as best practices for species abundance distributions (Connolly et al. 2014, Matthews and Whittaker 2014). This requires that likelihoods can for the models can be solved for and therefore we excluded models that lack probability mass functions and therefore likelihoods (including all niche preemption models). While methods have been proposed for comparing models without probability mass functions in this context (Alroy 2015), these methods have not been evaluated to determine how well they perform compared to the widely accepted likelihood based approaches.

For model comparison we used corrected Akaike Information Criterion (AICc) weights to compare the fits of models while correcting for differences in the number of parameters and appropriately handling the small sample sizes (i.e., numbers of species) in some communities (Burnham and Anderson 2002). The Poisson lognormal and the negative binomial each have two fitted parameters, while the log-series distribution and the Zipf distributions have one fitted parameter each. The model with the greatest AICc weight in each community was considered to be the best fitting model for that community. We also assessed the full distribution of AICc weights to evaluate the similarity of the fits of the different models.

In addition to evaluating AICc of each model, we also examined the log-likelihood values of the models directly. We did this to assess the fit of the model while ignoring corrections for the number of parameters and the influence of similarities to other models in the set of candidate models.

Model fitting, log-likelihood, and AICc calculations were performed using the macroecotools Python package <https://github.com/weecology/macroecotools> and with the R programming language (???). All of the code and all of the publicly available data necessary to replicate these analyses is available at <https://github.com/weecology/sad-comparison>. The CBC datasets and NABA datasets are not

publicly available and therefore are not included.

Results

Figure 1 shows three example sites with the empirical distribution and associated models fit to the data along with the log-likelihoods of the models. Zipf distributions tend to predict the most rare species followed by the log-series, the negative-binomial, and Poisson log-normal.

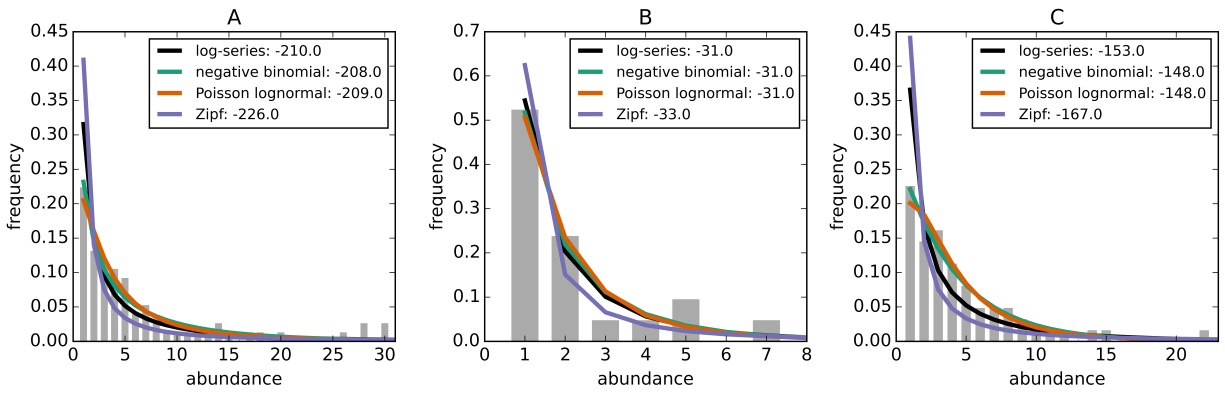


Figure 1: Example species-abundance distributions including the empirical distributions (grey bars) and the best fitting log-series (black line), negative-binomial (green line), Poisson lognormal (red line), and Zipf (purple line). Distributions are for (a) Breeding Bird Survey - Route 36 in New York, (b) Forest Inventory and Analysis ... and (c) Gentry - Araracuara High Campina site in Colombia

Across all data sets, the negative binomial and Poisson lognormal distributions had very similar average log-likelihoods (within 0.01 of one another; Figure 2). The log-likelihoods for each of these distributions averaged 0.8 units higher than for the log-series distribution and 5 units higher than for the Zipf distribution (corresponding to likelihoods that were twice as high and 140 times as high, respectively).

Although the negative binomial and Poisson lognormal distributions matched the data most closely, the likelihood provides a biased estimate of these distributions' ability to generalize to unobserved species. AICc approximately removes this bias by penalizing models with more degrees of freedom—such as the negative binomial and Poisson lognormal distributions, which have two free parameters

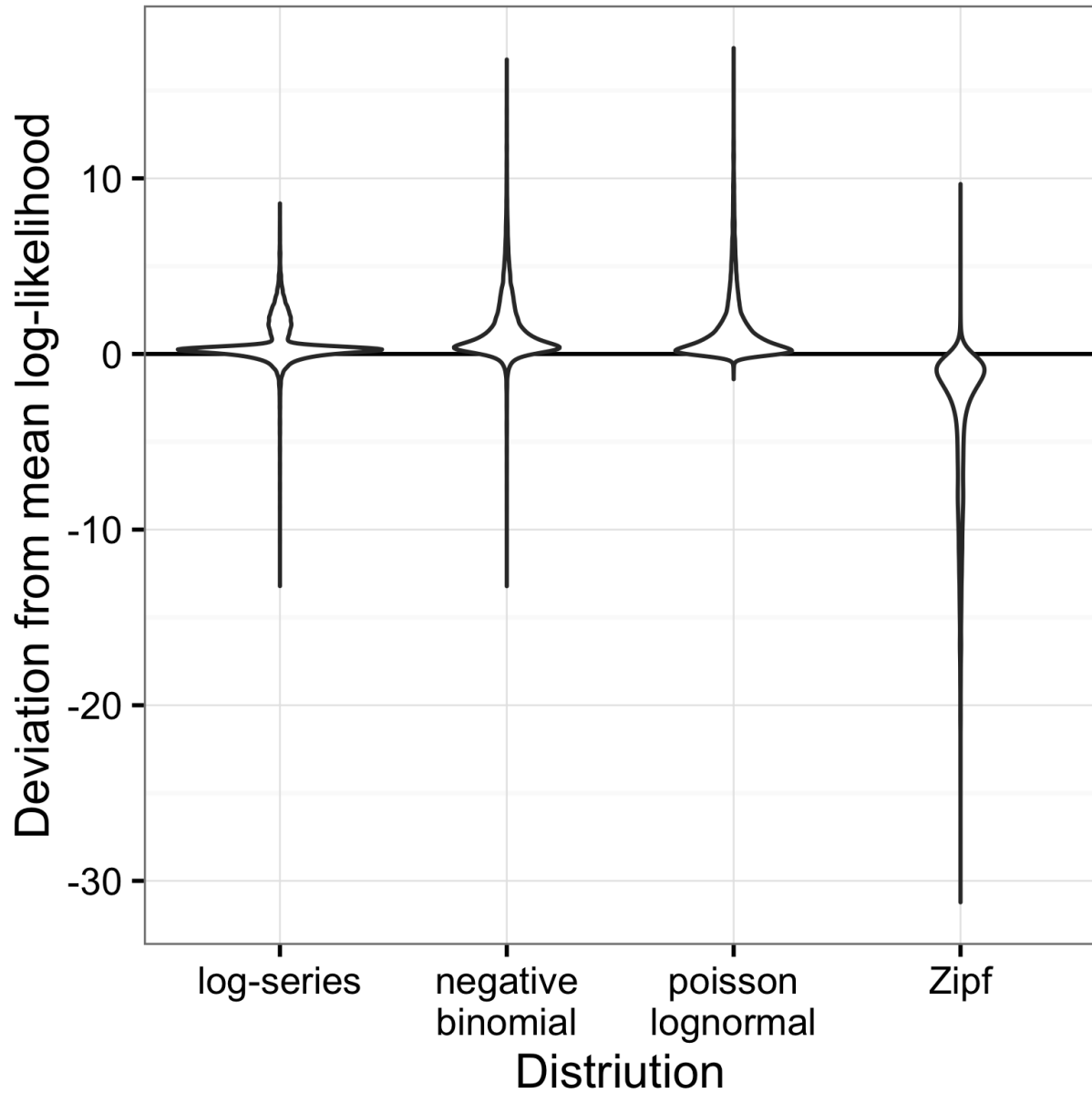


Figure 2: Violin plots of the deviation from the mean log-likelihood for each site for all datasets combined. Positive values indicate that the model fits better than the average fit across the four models.

instead of one like the log-series and Zipf distributions. After applying this penalty, the log-series distribution would be expected to make the best predictions for 69.2% of the sites. The Poisson lognormal and negative binomial distributions were each preferred in about 12% of the sites, and the Zipf distribution was preferred least often (6.0% of sites; Figure 3).

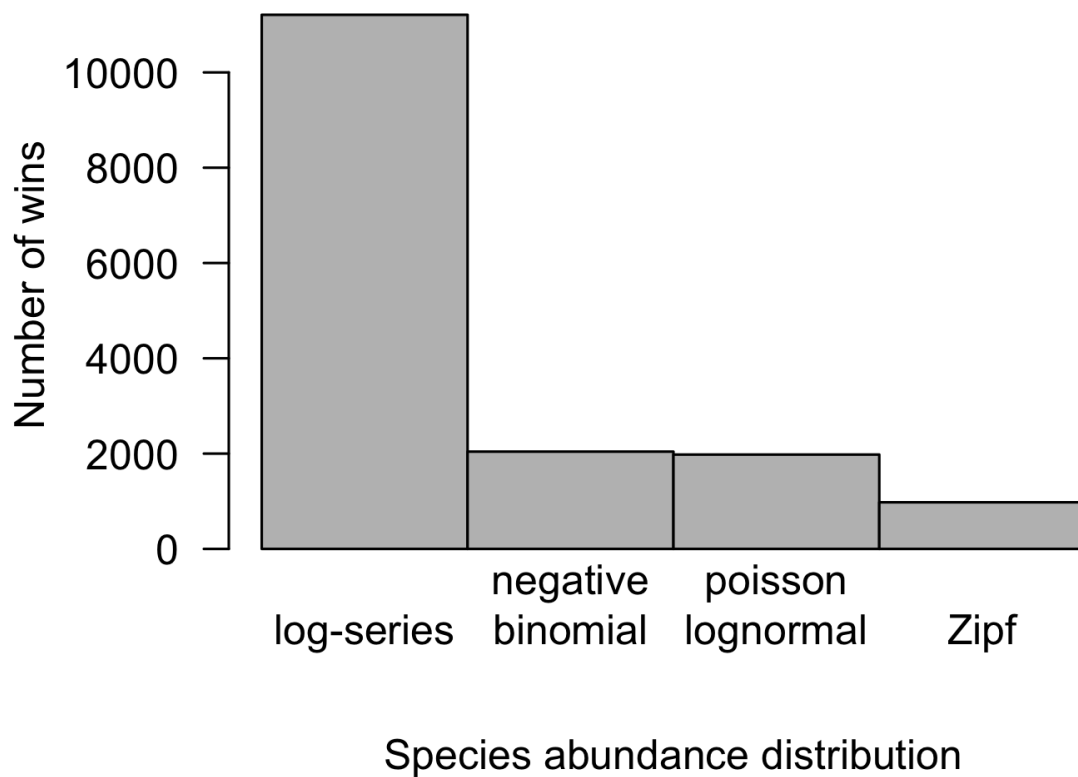


Figure 3: Number of cases where each model provided the best fit to the data based on AICc for all datasets combined.

Across all data sets and taxonomic groups, the log-series distribution had the highest AICc weights more often than any other model. The negative binomial performed well for BBS, but was almost never the best fitting model for plants (FIA and Gentry), butterflies (NABA), Acintopterygii, or Coleoptera. The Poisson lognormal performed well for the bird datasets (BBS and CBC) and the Gentry tree data, but was almost never best in the FIA and Coleoptera datasets (Figure 4). The Zipf

distribution only performed consistently well for Arachnida.

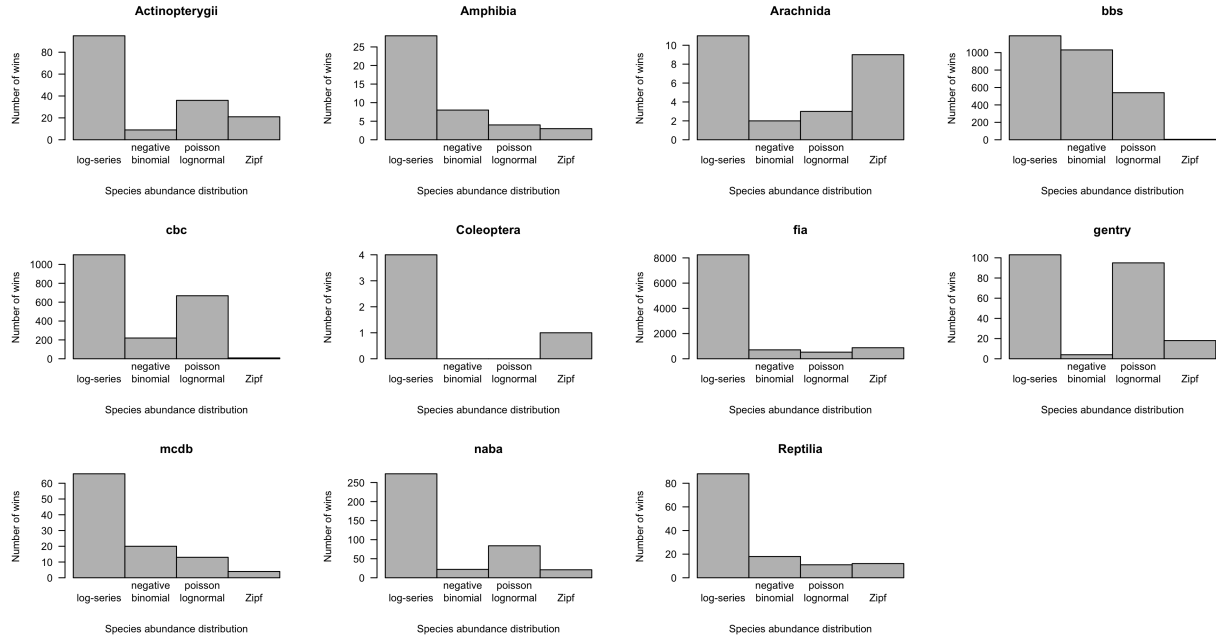


Figure 4: Number of cases where each model provided the best fit to the data based on AICc for each dataset separately.

The full distribution of AICc weights shows separation among models (Figure 5). Although the log-series distribution had the best AICc score much more often than the other models, Figure 3 shows that its lead was never decisive: across all 16,209 sites, it never had more than about 75% of the AICc weight. Most of the remaining weight was assigned to the negative binomial and Poisson lognormal distributions (each of which usually had at least 12-15% of the weight but was occasionally favored very strongly). The Zipf distribution showed a strong mode near zero, and usually had less than 7% of the weight.

Discussion

Our extensive comparison of different models for the species abundance distribution (SAD) using rigorous statistical methods demonstrates that several of the most popular existing models provide equivalently good absolute fits to empirical data. Log-series, negative-binomial, and Poisson

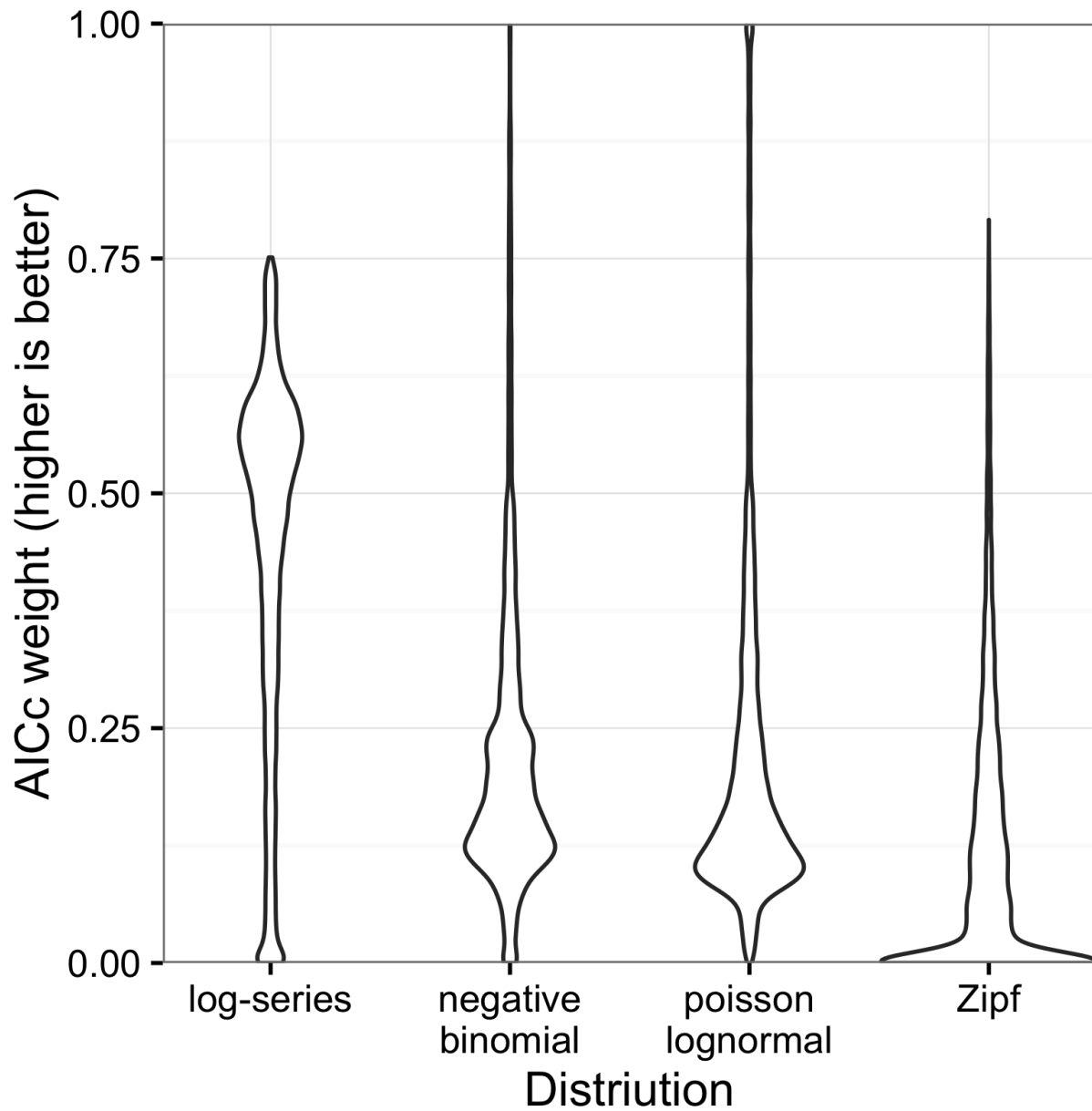


Figure 5: Violin plots of the AICc weights for each model. Weights indicate the probability that the model is the best model for the data

log-normal all had model relative likelihoods between 0.25 and 0.5 suggesting that the three distributions provide roughly equivalent fits in most cases, but with the two parameters models doing slightly better on average. Because the log-series has only a single parameter but fits the data almost as well as the two parameter models, the log-series performed better in AICc-based model selection, which penalizes model complexity. These results differ from two other recent analyses of large numbers of species abundance distributions (Ulrich et al. 2010, Connolly et al. 2014) and are generally consistent with a third recent analysis (Alroy 2015).

Ulrich et al. (2010) analyzed ~500 SADs and found support for three major forms of the SAD that changed depending on whether the community had been fully censused or not. They found that “fully censused” communities were best fit by the lognormal, and “incompletely sampled” communities, best fit by the Zipf and log-series (Ulrich et al. 2010). In contrast we find effectively no support for the Zipf across ecosystems and taxonomic groups, including a number of datasets that are incompletely sampled. Our AICc value results also do not support the conclusion that the lognormal outperforms the log-series in fully censused communities. The Gentry and FIA forest inventories, both involve large stationary organisms and were collected with the goal of including all trees above a certain stem diameter. Therefore, above the minimum stem diameter, they are as close to fully censused communities as is typically possible. In these communities the log-series provides the best fit to the data most frequently. The discrepancy between our results and those found in (Ulrich et al. 2010) are may be due to: 1) their use of binning and fitting curves to rank abundance plots, which deviates from the likelihood-based best practices (Matthews and Whittaker 2014) used in this paper; 2) the statistical methods they use to identify communities as “fully censused”, which tend to exclude communities with large numbers of singletons that would be better fit by distributions like the log-series; 3) the use of the continuous lognormal instead of the Poisson lognormal.

Connolly et al. (2014) use likelihood based methods to compare the the negative-binomial distribution (which they call the Poisson gamma) to the Poisson lognormal for a large number of

marine communities. They found that the Poisson lognormal provides a substantially better fit than the negative-binomial to empirical data and that the negative-binomial provides a better fit to communities simulated using neutral models. They conclude that these analyses of the SAD demonstrates that marine communities are structured by non-neutral processes. Our analysis differs from that in Connolly et al. (2014) in that they aggregate communities at larger spatial scales than those sampled and find the strongest results at large spatial scales. This may explain the difference between the two analyses or there may be differences between the terrestrial systems analyzed here and the marine systems analyzed by Connolly et al. (2014). The explanation for these differences is being explored elsewhere (Connolly et al. unpublished data).

Alroy (2015) compared the fits of the lognormal, log-series, Zipf, geometric series, broken stick, and a new model dubbed the “double geometric”, to over 1000 terrestrial community datasets assembled from the literature. To incorporate niche partitioning models (geometric series, broken stick, and the double geometric) this research used non-standard methods for evaluating the fits of the models to the data, however the results were generally consistent those presented here. The central Kullback-Leibler divergence statistics results show that the Zipf, geometric series, and broken stick all perform consistently worse than the other distributions, and that the double geometric, log-series, and lognormal all provide the best overall fit for at least one taxonomic group (Alroy’s tables S1, S2, and S3). We cannot directly assess the fits to the double geometric since it lacks a closed form probability mass function and therefore cannot be evaluated using likelihood, but in general Alroy’s results are consistent with ours in that they show that the lognormal and log-series both provide better fits to the data than the Zipf. While Alroy (2015) concludes that the data support the double geometric and not the other distributions, the Kullback-Leibler divergence results indicate that the lognormal provides equivalently good fits to the data (Alroy’s tables S1, S2, and S3). Alroy’s results show slightly better fits for the lognormal relative to the log-series and since the analyses did not control for differences in the number of parameters this is also consistent with our results. The double geometric is also a two parameter distribution so it is likely that if it were possible to compare its fit to that of the log-series using AICc that it would provide equivalent

or slightly worse fits to the data.

In combination, the results of these three papers suggest that in general the Zipf is a poor characterization of species-abundance distributions and that both the log-series and lognormal distributions provide reasonable fits in many cases. The differences in the performance of the log-series, lognormal, double geometric, and negative-binomial, appear to be more minor, and how they relate to differences in intensity of sampling, spatial scale, taxonomy, and ecosystem type (marine vs. terrestrial) remain open questions. Our analyses suggest that controlling for the number of parameters makes the log-series a slightly better model, at least in the terrestrial systems we studied. Neither of the other papers that include the log-series (Ulrich et al. 2010, Alroy 2015) make this correction and both show that it is still a reasonably competitive model even against those with more parameters. However many of our datasets are incompletely sampled, so if Ulrich et al.'s suggestion that the fit of these distributions depends on sampling intensity turns out to be generally correct, this result could depend on sampling intensity.]

The relatively similar fits of several commonly used distributions emphasizes the challenges of inferring the processes operating in ecological systems from the form of the abundance distribution. It is already well established that models based on different processes can yield equivalent models of the SAD, i.e., they predict distributions of exactly the same form (Cohen 1968, Pielou (1975), Boswell and Patil (1971), McGill et al. (2007)). To the extent that SADs are determined by random statistical processes, one might expect the observed distributions to be compatible with a wide variety of different process-based and process-free models (Frank 2009, Frank (2011), Locey and White (2013)). Regardless of the underlying reason that the models performed similarly, our results indicate that the SAD usually does not contain sufficient information to distinguish among the possible statistical processes—let alone biological processes—with any degree of certainty (Volkov et al. 2005), though it is possible that this result differs in marine systems (see Connolly et al. 2014). A more promising way to draw inferences about ecological processes is to evaluate each model's ability to simultaneously explain multiple macroecological patterns, rather than relying on a single

pattern like the SAD (McGill 2003, McGill et al. (2006), Newman et al. (2014), Xiao et al. (2015)). It has also been suggested that examining second-order effects, such as the scale-dependence of macroecological patterns (Blonder et al. 2014) or how the parameters of the distribution change across gradients (Mac Nally et al. 2014), can provide better inference about process from these kinds of pattern.

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