Fitting species abundance models with maximum likelihood Quick reference for sads package

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1 Introduction

Species abundance distributions (SADs) are one of the basic patterns of ecological communities (McGill et al., 2007). The empirical distributions are traditionally modeled through probability distributions. Hence, the maximum likelihood method can be used to fit and compare competing models for SADs. The package **sads** provides functions to fit the most used models to empirical SADs. The resulting objects have methods to evaluate fits and compare competing models. The package also allows the simulation of SADs expected from communities' samples, with and without aggregation of individuals of the same species.

2 Installation

The package is available on CRAN and can be installed in \mathbf{R} with the command:

```
> install.packages('sads')
```

then loaded by

```
> library(sads)
```

2.1 Developer version

The current developer version can be installed from GitHub with:

```
> library(devtools)
> install_github(repo = 'piLaboratory/sads', ref= 'dev', build_vignettes = TRUE)
```

And then load the package:

```
> library(sads)
```

3 Exploratory analyses

Throughout this document we'll use two data sets of abundances from the sads package. For more information on these data please refer to their help pages:

```
> data(moths)# William's moth data used by Fisher et al (1943)
> data(ARN82.eB.apr77)# Arntz et al. benthos data
> data(birds)# Bird census used by Preston (1948)
```

3.1 Octaves

Function octav tabulates the number of species in classes of logarithm of abundances at base 2 (Preston's octaves) and returns a data frame 1 :

```
> (moths.oc <- octav(moths))</pre>
```

Object	Object of		"octav"
octa	ave	upper	Freq
1	0	1	35
2	1	2	11
3	2	4	29
4	3	8	32
5	4	16	26
6	5	32	32
7	6	64	31
8	7	128	13
9	8	256	19
10	9	512	5
11	10	1024	6
12	11	2048	0
13	12	4096	1
14	13	8192	0

> (arn.oc <- octav(ARN82.eB.apr77))</pre>

 $^{1}\mathrm{actually}$ an object of class octav which inherits from class data frame

Object	of	class "o	cta	.v"
octa	ave	uppe	er	Freq
1	-7	7.8125e-0	03	0
2	-6	1.5625e-0	02	3
3	-5	3.1250e-0	02	5
4	-4	6.2500e-0	02	4
5	-3	1.2500e-0	01	6
6	-2	2.5000e-0	01	3
7	-1	5.0000e-0	01	5
8	0	1.0000e+	00	2
9	1	2.0000e+	00	4
10	2	4.0000e+	00	3
11	3	8.0000e+	00	1
12	4	1.6000e+	01	2
13	5	3.2000e+	01	0
14	6	6.4000e+	01	1
15	7	1.2800e+	02	1
16	8	2.5600e+	02	0

A logical argument preston allows smoothing the numbers as proposed by Preston (1948). The octave number is the upper limit of the class in log2 scale. Hence, for abundance values smaller than one (*e.g.* biomass data) the octave numbers are negative. A Preston plot is a histogram of this table, obtainable by applying the function plot to the data frame:

> plot(moths.oc)



> plot(arn.oc)



The plot method for objects of class **octav** has a logical argument **prop** that rescales the yaxis to relative frequencies of species in each octave, which can be used to compare different data sets:

```
> plot(moths.oc, prop = TRUE, border=NA, col=NA)
> lines(octav(birds), mid = FALSE, prop = TRUE, col="red")
> lines(octav(moths), mid = FALSE, prop = TRUE)
> legend("topright", c("Preston's birds", "Fisher's moths"), col=c("red", "blue"), lty=1, bty
```

3.2 Rank-abundance plots

Function rad returns a data frame of sorted abundances and their ranks ²:

```
> head(moths.rad <- rad(moths))</pre>
```

rank abund 1 1 2349 2 2 823

 $^{^2\}mathrm{actually}$ an object of class rad which inherits from class $\mathit{dataframe}$

3	3	743
4	4	604
5	5	589
6	6	572
> hea	ad(ar	n.rad <- rad(ARN82.eB.apr77))
	rank	abund
sp17	1	67.21
sp11	2	54.67
sp33	3	14.67
sp9	4	9.90
sp30	5	5.71
sp10	6	2.88

To get the rank-abundance or Whitaker's plot apply the function plot on the data frame:

> plot(moths.rad, ylab="Number of individuals")



> plot(arn.rad, ylab="Biomass")



Again, the plot method for rad has a logical argument prop rescales the y-axis to depict relative abundances:

```
> plot(moths.rad, prop = TRUE, type="n")
> lines(rad(birds), prop = TRUE, col="red")
> lines(rad(moths), prop = TRUE)
```

> legend("topright", c("Preston's birds", "Fisher's moths"), col=c("red", "blue"), lty=1, bty

4 Model fitting

The sads package provides maximum-likelihood fits of many probability distributions to empirical sads. The working horses are the functions **fitsad** for fitting species abundance distributions and **fitrad** for fitting rank-abundance distributions. The first argument of these functions is the vector of observed abundances ³ The second argument is the name of the model to be fitted. Please refer to the help page of the functions for details on the

³fitrad also accepts a rank-abundance table returned by function rad as its first argument.

models. For more information on the fitting procedure see also the vignette of the *bbmle* package, on top of which the package *sads* is built. To fit a log-series distribution use the argument **sad='ls'**:

```
> (moths.ls <- fitsad(moths,'ls'))</pre>
```

Coefficients: N alpha 15609.00000 40.24728

```
Log-likelihood: -1087.71
```

The resulting model object inherits from mle2 (Bolker & R Development Core Team, 2014), and has all usual methods for model objects, such as summaries, log-likelihood, and AIC values:

8L, 9L, 9L, 9L, 9L, 10L, 10L, 10L, 10L, 11L, 11L, 12L, 12L, 13L, 13L, 13L, 13L, 13L, 14L, 14L, 15L, 15L, 15L, 15L, 16L, 16L, 16L, 17L, 17L, 17L, 18L, 18L, 18L, 19L, 19L, 19L, 20L, 20L, 20L, 20L, 21L, 22L, 22L, 22L, 23L, 23L, 23L, 24L, 25L, 25L, 25L, 26L, 27L, 28L, 28L, 28L, 29L, 29L, 32L, 34L, 34L, 36L, 36L, 36L, 37L, 37L, 43L, 43L, 44L, 44L, 45L, 49L, 49L, 49L, 51L, 51L, 51L, 51L, 52L, 53L, 54L, 54L, 57L, 58L, 58L, 60L, 60L, 60L, 61L, 64L, 67L, 73L, 76L, 76L, 78L, 84L, 89L, 96L, 99L, 109L, 112L, 120L, 122L, 129L, 135L, 141L, 148L, 149L, 151L, 154L, 177L, 181L, 187L, 190L, 199L, 211L, 221L, 226L, 235L, 239L, 244L, 246L, 282L, 305L, 306L, 333L, 464L, 560L, 572L, 589L, 604L, 743L, 823L, 2349L)), lower = 0, upper = 240L) Coefficients: Estimate Std. Error z value Pr(z)40.247 6.961 5.7818 7.391e-09 *** alpha _ _ _ Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 Fixed parameters: Ν 15609 -2 log L: 2175.425 > coef(moths.ls) N alpha 15609.00000 40.24728 > logLik(moths.ls) 'log Lik.' -1087.713 (df=1) > AIC(moths.ls) [1] 2177.425

On the above examples, notice that the **print** method⁴ displays some statistics on the input data and fitting function used - number of species, number of individuals, truncation point

⁴Or, equivalently, the show method

for the probability distribution (when used, see below) and whether we are fitting a discrete or continuous sad or rad - while the **summary** method displays information more associated with the fitting *per se*: standard errors and significance codes for each parameter. Also, notice that the input data is displayed by both methods, but the **print** method only shows the first values, as the complete list can be quite large.

4.1 Model diagnostics

Many other diagnostic and functions are available for sad and rad models. To get likelihood profiles, likelihood intervals and confidence intervals use:

Then use plotprofmle to plot likelihood profiles at the original scale (relative negative log-likelihood) and function plot to get plots at chi-square scale (square-root of twice the relative log-likelihood):

```
> par(mfrow=c(1,2))
> plotprofmle(moths.ls.prf)# log-likelihood profile
> plot(moths.ls.prf)# z-transformed profile
> par(mfrow=c(1,1))
```





Likelihood intervals and confindence intervals: Likelihood intervals include all values of the parameters that have up to a given log-likelihood absolute difference to the maximum likelihood estimate. This difference is the log-likelihood ratio and is set with the argument ratio of function likelregions. The default value of ratio is log(8), and thus in the example above the likelihood interval encloses all values of the parameter that are up to 8 times as plausible as the estimated value of $\alpha = 40.25$.

Likelihood intervals at log(8) converge to the value of confidence intervals at 95% as sample size increases. In most cases even for moderate sample sizes the limits of confidence and likelihood intervals are very close. Discrepancies occur only when the likelihood profile is highly asymmetric or have local *minima*. But in this kind of profile usually indicates an ill-behaved fit, and so the intervals may not be meaningful anyway.

When applied on a sad model object, the function **plot** returns four diagnostic plots:

- > par(mfrow=c(2,2))
- > plot(moths.ls)
- > par(mfrow=c(1,1))



The first two plots (top right and left) are the octave and rank-abundance plots with the predicted values of number of species in each octave and of each species' abundance. The two last plots (bottom) are quantile-quantile and percentile-percentile graphs of the observed vs. predicted abundances. The straight line indicates the expected relation in case of perfect fit.

4.2 SADs vs RADs

Species-abundance models assign a probability for each abundance value. Thus, these models are probability density functions (PDFs) of abundances of species. Rank-abundance models assign a probability for each **abundance rank**. They are PDFs for rankings of species. The models are interchangeable (May, 1975), but currently only four rad models are available in package sads through the argument **rad** of function **fitrad**:

- "gs": geometric series (which is NOT geometric PDF, available in fitsad as "geom")
- "rbs": broken-stick model (MacArthur, 1957; May, 1975)
- "zipf": Zipf power-law distribution
- "mand": Zipf-Mandelbrot power-law distribution

Comparison to radfit from *vegan* package:

fits by fitsad, fitrad and radfit of *vegan* package provide similar estimates of model coefficients but not comparable likelihood values. The reason for this is the fact each function fits models that assign probability values to data in different ways. Function fitsad fits PDFs to observed abundances and fitrad fits PDFs to the ranks of the abundances. Finally, radfit of *vegan* fits a Poisson generalized linear model to the *expected abundances* deduced from rank-abundance relationships from the corresponding sads and rads models (Wilson, 1991). See also the help page of radfit. Therefore likelihoods obtained from these three functions are not comparable.

5 Model selection

It's possible to fit other models to the same data set, such as the Poisson-lognormal and a truncated lognormal:

> (moths.pl <- fitsad(x=moths, sad="poilog"))#default is zero-truncated</pre>

Maximum likelihood estimation Type: discrete species abundance distribution Species: 240 individuals: 15609

```
Call:
mle2(minuslogl = function (mu, sig)
-sum(dtrunc("poilog", x = x, coef = list(mu = mu, sig = sig),
```

```
trunc = trunc, log = TRUE)), start = list(mu = 1.99664912324681,
    sig = 2.18726037265132), data = list(x = list(1, 1, 1, 1,
    1, "etc")))
Coefficients:
      mu
              sig
1.996463 2.187131
Truncation point: 0
Log-likelihood: -1086.07
> (moths.ln <- fitsad(x=moths, sad="lnorm", trunc=0.5)) # lognormal truncated at 0.5
Maximum likelihood estimation
Type: continuous species abundance distribution
Species: 240 individuals: 15609
Call:
mle2(minuslog1 = function (meanlog, sdlog)
-sum(dtrunc("lnorm", x, coef = list(meanlog = meanlog, sdlog = sdlog),
    trunc = trunc, log = TRUE)), start = list(meanlog = 2.57905878609957,
    sdlog = 1.78235276032689), data = list(x = list(1, 1, 1,
    1. 1. "etc")))
Coefficients:
 meanlog
            sdlog
2.274346 2.039740
Truncation point: 0.5
Log-likelihood: -1086.36
moreover, the function AICtab and friends from the bbmle package can be used to get a
model selection table:
> AICtab(moths.ls, moths.pl, moths.ln, base=TRUE)
         AIC
                dAIC
                       df
moths.pl 2176.1
                   0.0 2
moths.ln 2176.7
                   0.6 2
moths.ls 2177.4
                   1.3 1
```

NOTICE that the information criterion methods do not differentiate between **fitsad** and **fitrad** methods. Because of this, it is possible to include **fitsad** and **fitrad** objects in the same IC-table without generating an error, but the result will be meaningless. To compare visually fits first get octave tables:

> head(moths.ls.oc <- octavpred(moths.ls))</pre>

	octave	upper	Freq	
1	0	1	40.14377	
2	1	2	20.02026	
3	2	4	23.27123	
4	3	8	25.12674	
5	4	16	25.86285	
6	5	32	25.67116	
>	head(mo	oths.pl	l.oc <- o	ctavpred(moths.pl))
	octave	unner	Freq	
1	00000000		27.58748	
_	-	_		
2	1	2	19.48221	
3	2	4	26.76474	
4	3	8	31.88373	
5	4	16	33.16136	
6	5	32	30.49056	
				ctavpred(moths.ln))

octave upper Freq 1 0 1 15.41886 2 1 2 22.44066 3 2 4 29.13034 4 3 8 33.72746 5 4 16 34.82976 6 5 32 32.08088

then use lines to superimpose the predicted values on the octave plot:

```
> plot(moths.oc)
> lines(moths.ls.oc, col="blue")
> lines(moths.pl.oc, col="red")
> lines(moths.ln.oc, col="green")
```





```
> head(moths.ls.rad <- radpred(moths.ls))</pre>
```

> head(moths.pl.rad <- radpred(moths.pl))</pre>

```
rank abund
     1 4348
1
2
     2 1973
3
     3 1322
4
    4 1001
5
     5
       807
6
     6
         676
> head(moths.ln.rad <- radpred(moths.ln))</pre>
 rank
           abund
     1 3524.2394
1
2
     2 1674.8603
3
    3 1148.3539
4
    4 883.6309
5
    5 720.7864
6
     6 609.2707
```

then plot observed and predicted values:



5.1 Abundance class data

For ecological communities, the representation of species abundances typically occurs through categorization. For instance, when assessing the abundance of sessile organisms, it is common practice to utilize a scale based on the coverage of sampling areas, beacause direct enumeration of individuals or estimation of biomass are are extremely laborious.

The package sads has a specific class for fitting continuous distributions for this kind of data. We will show the use of this class using the data from de Souza Vieira & Overbeck (2020), who provide the coverage class of each plant species in plots set in grasslands in Southern Brazil. The object grasslands has the data from plot 'CA8', which has the largest number of species recorded in this study.

> head(grasslands)

		class	cover	upper	mids
Andropogon	lateralis	2.0	15-25%	25	20.0

Andropogon macrothrix	0.1	<1%	1	0.5
Axonopus affinis	0.1	<1%	1	0.5
Baccharis trimera	0.1	<1%	1	0.5
Briza poaemorpha	0.1	<1%	1	0.5
Briza uniolae	0.1	<1%	1	0.5

The vector **cover** in this data frame has the cover class for each plant species, that is, the the proportion of the area of the plot covered by all individuals of each species. Coverage is expressed in a scale with 13 intervals, as defined by the breakpoints below:

> (grass.brk <- c(0,1,3,5,seq(15,100, by=10),100))
[1] 0 1 3 5 15 25 35 45 55 65 75 85 95 100</pre>

We can tally the number of species in each cover class using a histogram:

```
> grass.h <- hist(grasslands$mids, breaks = grass.brk, plot = FALSE)
```

The resulting object of the class **histogram** has the number of species in each cover class, as well as the classes midpoints:

> data.frame(midpoint = grass.h\$mids, N.spp = grass.h\$counts)

midpoint N.spp

	-	
1	0.5	16
2	2.0	9
3	4.0	1
4	10.0	1
5	20.0	1
6	30.0	1
7	40.0	0
8	50.0	0
9	60.0	0
10	70.0	0
11	80.0	0
12	90.0	0
13	97.5	0

The function fitsadC fits continuous distributions usually applied to describe this kind of data. The commands below fit all models currently available for abundance class data in the package sads. Note that the data is provided to this function through an object of the class histogram:

```
> grass.e <- fitsadC(grass.h, 'exp') # Exponential
> grass.g <- fitsadC(grass.h, 'gamma') # Pareto
> grass.l <- fitsadC(grass.h, 'lnorm') # Log-normal
> grass.p <- fitsadC(grass.h, 'pareto') # Pareto
> grass.w <- fitsadC(grass.h, 'weibull') # Weibull</pre>
```

The fitted models are of class fitsadC, for which most of the methods for diagnostics and model comparison showed in the previous sections are available. For instance, the fitted models can be compared in the usual way:

```
> AICctab(grass.e, grass.g, grass.l,
            grass.p, grass.w,
            weights = TRUE, base = TRUE)
AICc dAICc df weight
grass.p 76.6 0.0 2 0.487
grass.l 77.6 1.0 2 0.291
grass.w 78.9 2.3 2 0.155
grass.g 80.6 4.0 2 0.067
grass.e 95.2 18.6 1 <0.001</pre>
```

A histogram with observed values can plotted simply with

> plot(grass.h, main = "", xlab = "Abundance class")



By default, R plots histograms with classes of unequal size using a density scale. The function **coverpred** provides the number of species expected by a fitted model, in frequency, relative frequency and density scales.

```
> ## Predicted by each model
> grass.e.p <- coverpred(grass.e)
> grass.g.p <- coverpred(grass.g)
> grass.l.p <- coverpred(grass.l)
> grass.p.p <- coverpred(grass.p)
> grass.w.p <- coverpred(grass.w)</pre>
```

We can then use this object to add the densities values predicted by each model:

```
> ## Plot
> plot(grass.h, main = "", xlab = "Abundance class", xlim = c(0,40))
> ## Adds predicted points
```



Please refer to the man pages of fitsadC and fitsaC-class for further methods and usage.

6 Simulations

The function rsad returns random samples of a community with S species. The mean abundances of the species in the communities are independent identically distributed (*iid*)

variables that follow a given probability distribution. The sample simulates a given number of draws of a fraction a from the total number of individuals in the community. For instance, to simulate two Poisson samples of 10% of a community with 10 species that follows a lognormal distribution with parameters $\mu = 3$ and $\sigma = 1.5$ use:

```
> set.seed(42)# fix random seed to make example reproducible
```

```
zeroes=TRUE, ssize = 2))
```

```
sample species abundance
```

	~	~pooloo		
1	1	1	20	
2	1	2	4	
3	1	3	7	
4	1	4	2	
5	1	5	4	
6	1	6	1	
7	1	7	25	
8	1	8	3	
9	1	9	45	
10	1	10	1	
11	2	1	17	
12	2	2	2	
13	2	3	0	
14	2	4	3	
15	2	5	6	
16	2	6	2	
17	2	7	18	
18	2	8	0	
19	2	9	53	
20	2	10	4	

The function returns a data frame with a sample numeric label, species' numeric label and species' abundance in each sample. By default, **rsad** returns a vector of abundances of single Poisson sample with zeroes omitted:

> (samp2 <- rsad(S = 100, frac=0.1, sad="lnorm",</pre> list(meanlog=5, sdlog=2))) [1] [12]

[23]	8	51	21	1	312	42	23	20	48	12	28
[34]	14	20	40	267	5	209	36	107	93	58	1
[45]	7	39	2	7	56	70	31	3	4	305	25
[56]	15	12	3	48	8	12	101	69	255	5	51
[67]	253	4	1	2	17	49	187	121	599	3	23
[78]	12	9	16	21	10	17	3	5	2	9	5
[89]	3214	1	19	1	31						

Since this is a Poisson sample of a lognormal community, the abundances in the sample should follow a Poisson-lognormal distribution with parameters $\mu + \log a$ and σ (Grøtan & Engen, 2008). We can check this by fitting a Poisson-lognormal model to the sample:

```
> (samp2.pl <- fitsad(samp2, "poilog"))</pre>
```

```
Maximum likelihood estimation
Type: discrete species abundance distribution
Species: 93 individuals: 8759
Call:
mle2(minuslog1 = function (mu, sig)
-sum(dtrunc("poilog", x = x, coef = list(mu = mu, sig = sig),
    trunc = trunc, log = TRUE)), start = list(mu = 2.70913763997913,
    sig = 1.88422112870725), data = list(x = list(155, 697, 4,
    7, 48, "etc")))
Coefficients:
      mu
              sig
2.709138 1.884220
Truncation point: 0
Log-likelihood: -453.22
> ## checking correspondence of parameter mu
> coef(samp2.pl)[1] - log(0.1)
```

mu 5.011723

Not bad. By repeating the sampling and the fit many times it's possible to evaluate the bias and variance of the maximum likelihood estimates:

Bias is estimated as the difference between the mean of estimates and the value of parameters:

```
> ##Mean of estimates
> apply(results,2,mean)
[1] 4.967704 1.988043
> ## relative bias
> (c(5,2)-apply(results,2,mean))/c(5,2)
```

```
[1] 0.006459158 0.005978719
```

And the precision of the estimates are their standard deviations

```
> ##Mean of estimates
> apply(results,2,sd)
[1] 0.2550191 0.1852096
> ## relative precision
> apply(results,2,sd)/apply(results,2,mean)
```

[1] 0.05133541 0.09316177

Finally, a density plot with lines indicating the mean of estimates and the values of parameters:

```
> par(mfrow=c(1,2))
> plot(density(results[,1]), main=expression(paste("Density of ",mu)))
> abline(v=c(mean(results[,1]),5), col=2:3)
> plot(density(results[,2]), main=expression(paste("Density of ",sigma)))
> abline(v=c(mean(results[,2]), 2), col=2:3)
> par(mfrow=c(1,1))
```



Increasing the number of simulations improves these estimators.

7 Bugs and issues

The package project is hosted on GitHub (https://github.com/piLaboratory/sads/). Please report bugs and issues and give us your feedback at https://github.com/piLaboratory/sads/issues.

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