

Fisher's alpha is not a valid metric of biodiversity in tropical forests

Eric Marcon ¹

Abstract

Fisher's alpha should not be used to assess the diversity of tropical forest tree species at the local and regional scales.

Keywords

Fisher's alpha, biodiversity, tropical forests

¹AgroParisTech, Montpellier, France, 34000,

Table of contents

1	Introduction	1
2	Material and methods	1
2.1	Fisher's α fundamentals	2
2.2	Example data	2
3	Local scale	2
4	Regional scale	4
5	Conclusion	6
6	Appendix	6
6.1	Estimating α with R	6
	Point estimation ■ Likelihood maximisation	
6.2	Estimating θ by the abundant species distribution	7
6.3	Full simulation	7

1. Introduction

Tropical evergreen forests such as the Amazon host thousand of tree species that are difficult to assess (ter Steege et al., 2013). Even though their biodiversity does not reduce to trees, understanding their distribution is a necessary step to both understand the functioning of the ecosystem (Liang et al., 2016) and develop conservation policies (Strange et al., 2024).

The relation between diversity and area has long been questioned by ecologists (MacArthur and Wilson, 1967; Plotkin et al., 2000). It must be addressed according to the considered scale (Grilli et al., 2012). At the local scale, i.e. when the distribution of species can be considered as unique, species accumulation curves (SAC) are built from it with well-known statistical tools (Gotelli and Colwell, 2001; Chao et al., 2014). At regional scales, i.e. when different communities are included and beta-diversity comes into play, species-area relationships (SAR) properly speaking are derived from ecological theory (Harte et al., 1999) with empirical support (Arrhenius, 1921). Whatever the scale, the number species increases with the

area or the number of individuals, making it a challenge to correctly describe biodiversity with a number: species richness (i.e. the number of species) is the simplest candidate, but its application may be ambiguous.

Fisher's log-series (Fisher et al., 1943) was derived originally from the distribution of tropical butterflies. It is formulated as a species-abundance relationship that links the number of species to the number of individuals with a single parameter, called α . Fisher's α is thus an ideal candidate to measure diversity since it overcomes the previous issue: it is scale-independent if the actual species distribution is a log-series. After a long period of relative obscurity, α made a comeback following the development of Hubbell's neutral theory (Hubbell, 2001) since the metacommunity is distributed in log-series whose α equals θ , the fundamental number of biodiversity. Although the log-series applies neither to the local scale according to the neutral theory, it became popular (Duque et al., 2017) to describe the diversity of forest trees, probably for its simplicity. Summarizing a species distribution by a statistics that does not apply to it is questionable. The aim of this paper is to show that α actually does not measure diversity unambiguously, neither at local nor at regional scales, and should be limited to the largest metacommunity. It is organised as follows: Fisher's α fundamentals are first recalled; its use at the different scales is then discussed before concluding about its applicability.

2. Material and methods

2.1 Fisher's α fundamentals

Fisher derived the log-series distribution from a set of assumptions (Fisher et al., 1943). In his model, all species are distributed completely randomly and independently from each other, i.e. their abundance in a fixed area follows a Poisson distribution. The intensities of the Poisson distributions of all species follow in turn a gamma distribution with shape parameter (tending to) zero. Last, the number of species is infinite. Then, the number of species with non-zero abundance $S(n)$ is linked to the size of the community n through Equation 1 by a parameter named α . It is called log-series because the number of species is derived as the sum of the number of species with 1 to an infinite number of individuals: this infinite sum appears to be the Taylor series of the logarithm function.

$$S(n) = \alpha \ln \left(1 + \frac{n}{\alpha} \right). \quad (1)$$

For $n \gg \alpha$, Equation 1 can be simplified to $S(n) \approx -\alpha \ln(\alpha) + \alpha \ln(n)$, i.e. the number of observed species is linearly related to the logarithm of the sample size. The slope of the line is α and the intercept is $-\alpha \ln(\alpha)$.

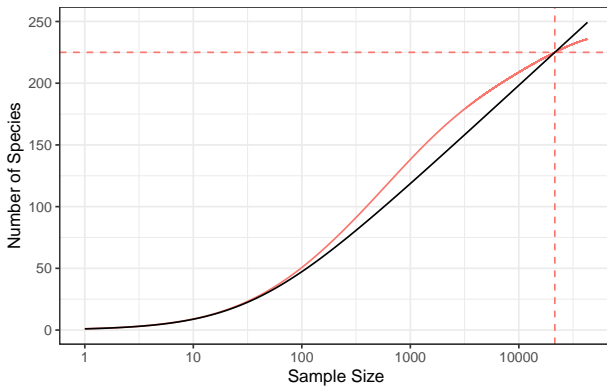


Figure 1. Accumulation curve of a log-series distribution (black) with Fisher's α equal to 35 and of BCI (red). The intersection of the dotted lines corresponds to the number of trees and of species of BCI 50-ha inventory the value of α is derived from.

Based on Equation 1, the species accumulation curve has two parts when plotted on a logarithmic x-axis: first, as n is not great enough for the approximation, it is convex, then it is linear (Figure 1).

The distribution can also be represented as a rank-

abundance curve (Figure 2). A characteristic feature of the log-series is that the abundance of species decreases linearly with their rank, except for the most abundant ones.

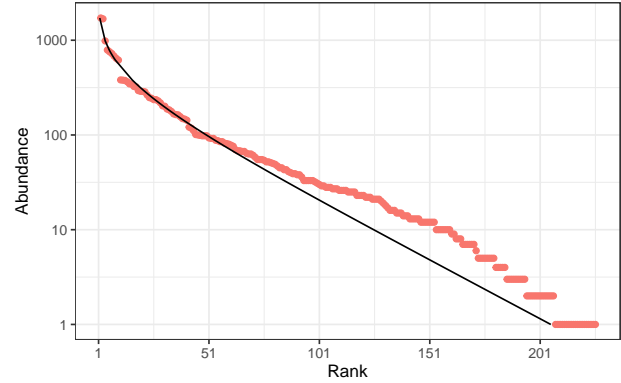


Figure 2. Rank-abundance curve of a log-series distribution (black) and of BCI (red dots). Species are ordered by decreasing abundance. The log-series is the best fit to BCI data ($\alpha = 35$).

2.2 Example data

To illustrate the estimation of Fisher's α at the local scale, the BCI data set available in the R (R Core Team, 2025) package *vegan* (Oksanen et al., 2025) will be used. It was published by Condit et al. (2002). The data consist of 50 one-hectare plots of tropical evergreen forest where all trees above 10 cm DBH (diameter at breast height) were recorded. The forest is located on Barro Colorado Island in the canal of Panama. It has been studied by many authors (Muller-Landau and Wright, 2024), allowing to compare the results of this paper to a large literature, even though the metrics of diversity may vary somehow since the forest was inventoried at different dates, including trees above 1 cm DBH. The BCI dataset used here contains 21457 trees above 10 cm DBH in 225 species.

The regional dataset is a part of the GuyaDiv network (Engel, 2015) located in French Guiana, published in Marcon et al. (2024). It contains 68 one-hectare plots located in 21 sites scattered over the territory. They were used to estimate the number of tree species in French Guiana: around 2200 in 80,000 km² of continuous, tropical evergreen forest on the north-eastern edge of the Amazon.

3. Local scale

Sampling the local community results in a species accumulation curve, studied in depth by Go-

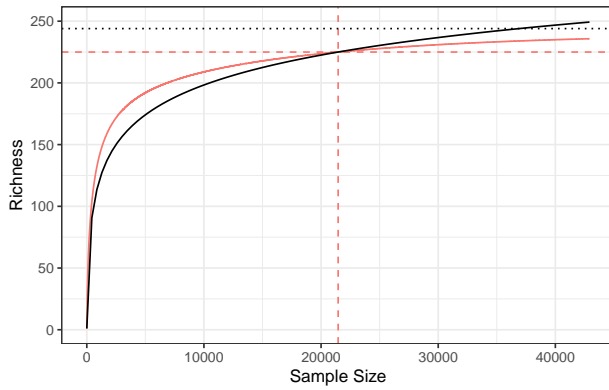


Figure 3. Species Accumulation Curve of BCI extrapolated up to twice the sample size. The dotted lines correspond to the 50-ha inventory. The horizontal, dotred line, is the estimated asymptotic number of species, calculated with the jackknife estimator of order 1 (Burnham and Overton, 1978). The black curve is the SAC of the log-series with α equal to 35.

telli and Colwell (2001). The number of species increases step by step, when the next sampled individual belongs to a new one. This stochastic *collector's curve* is of less interest than its expectation, assuming individuals are sampled independently: only that smoothed curve is called the SAC. It is actually computed by rarefaction of the distribution of the whole sample (Chao et al., 2014). It is usually plotted on continuous scales. Between sample sizes n and $n + 1$, the slope of the curve is the probability for the next individual to belong to a new species (Grabchak et al., 2017): it decreases until all species have been discovered, so it is concave.

Figure 3 shows the SAC of the Barro Colorado Island 50-ha forest plot. The number of species increases with sample size and does not reach an asymptote despite the huge sampling effort. To allow comparing diversity with other sites, two strategies are possible: estimate asymptotic diversity or standardize the sampling effort (Chao and Jost, 2012).

The asymptotic diversity here is the number of species that would be observed if the sample reached the necessary size to encompass all species of the community. In hyperdiverse ecosystems such as evergreen forests, the asymptotic community generally does not exist in the field because of environmental variations: increasing the size of the sample results in sampling in different communit-

ies. Thus, the asymptotic estimators of diversity correspond to theoretical asymptotic communities that do not necessarily exist: it is a feature of a model. This is an argument for avoiding them, but the definition of the local community is already a model (Stroud et al., 2015), in the sense that local environmental variations imply that the distribution of species varies in turn: the heterogeneity of the community considered as negligible corresponds to necessary decisions to model the reality. The estimated number of species is 244.

An alternative consists in standardizing the sample site, in general to allow comparing different communities whose inventories are not large enough to allow a reliable estimation of asymptotic diversity. Exact rarefaction formulas are available to calculate the number of tree species at any sampling level smaller than the actual sample, and estimators allow extrapolating the diversity up to a limited level, around twice the actual sample size (Chao et al., 2014). The expected number of species in one hectare of BCI, actually based on the average number of trees per hectare, is 103.

In contrast, Fisher's α does not depend on the sample size as soon as $n \gg \alpha$, which is always true in forest inventories. Thus, it appears to be an ideal, universal metric of biodiversity, allowing to compare it across sites of different sizes. The issue is that the distribution of tropical forest tree communities is not a log-series. Hubbell (2001) named it the zero-sum multinomial distribution; its mathematical derivation is due to Volkov et al. (2003). It is close to a log-normal distribution (McGill, 2003), but differs from by a greater abundance of the rarest species.

This discrepancy has two consequences: from a theoretical point of view, α is the parameter of a distribution that is not observed; from an empirical point of view, its estimation is inconsistent.

The theoretical issue does not require much more argumentation. Applying an appropriate model to describe the distribution of species is similar to trying to describe the size of a rectangle by the single length of its side, assuming it is a square.

The empirical question deserves further elaboration, based on the BCI dataset for clarity. The basic argument is that the actual distribution is not so different from a log-series that the advantages of summarizing it by α are not worth it. Several R packages allow estimating α from a vector of

abundances (see Appendix Section 6.1 for details). Most of them (such as `vegan::fisher.alpha`) just solve Equation 1, i.e. they only rely on the total abundance and number of species, ignoring the distribution. More elaborate ones (such as `sads::fitls`) find the value of α that maximizes the likelihood of the distribution assuming it is a log-series. When applied to the BCI dataset, both return the same estimation: 35. Its poor empirical fit is illustrated by Figure 3 and Figure 1.

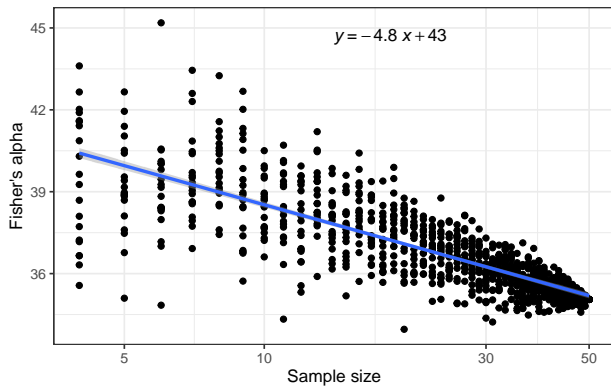


Figure 4. Estimation of Fisher's α depending on the number of 1-ha plots of BCI. The dots are random draws of plot assemblages. The line is the fit of a linear model relating α to the logarithm of the number of plots.

In contrast with the assumed advantage of α , its estimation heavily relies on the sample size. Figure 4 shows the average estimation of α based on random subsamples of BCI, from 4 to 50ha, repeated 20 times.

The estimated value of α decreases from over 40 to approximately 35, with a quite good linear relation between α and the logarithm of the sample size. Several examples can be found in the literature, e.g. Duque et al. (2017); Schulte et al. (2005), where the dependence of α to sample size is explored either with a statistical or an ecological approach.

Visually, in Figure 1, increasing α moves the log-series distribution to the right and increases its slope. Changing the sample size means changing the intersection point between the accumulation curve and the log-series curve, thus necessarily modifying α . At this stage, there is no real argument to decide whether BCI's α is 35 or 40.

A solution to this problem is to return to the neutral model theory and assume that the local community is not a log-series because of dispersal limitation, i.e. its migration parameter m is not

1. Then, the parameter to estimate is θ , the fundamental number of biodiversity in the metacommunity BCI belongs to: the metacommunity is distributed as a log-series whose parameter is θ . This is an elegant solution both theoretically (all assumptions are valid) and empirically (the estimation of α is robust).

Hubbell (2001) [page 293] proposed estimating it by adjusting the rank-abundance curve to the most frequent species in the community, arguing that these species are also the most abundant in the metacommunity. He found $\theta = 50$. The same algorithm is applied to the current BCI dataset in Appendix Section 6.2: its result is $\theta = 45$. Both θ and m can be estimated by likelihood maximization of the local distribution (Etienne, 2005) with the `untb` package (Hankin, 2007). The retained value of θ is 48. The consistency of this approach is shown in Appendix Section 6.3: θ and m are estimated from the BCI distribution, then a community of the same size is drawn with these parameters: it is very close to the actual distribution.

This faces two limits. First, as far as we know, it is not applied in the literature. Then, it does not exactly describe the diversity of the local community but that of the metacommunity: summarizing BCI by $\theta = 48$ ignores the migration parameter. Modifying m yields very different distribution, from geometric to log-series (Hubbell, 2001). In other words, θ only gives a very partial knowledge of the diversity of the local community.

4. Regional scale

The regional scale is that of Arrhenius's model (Arrhenius, 1921). Its fundamental difference with the local scale is that several communities are taken into account, involving β diversity that can't be addressed directly. Whereas the computation of the local species accumulation curve was non-parametric, based solely on statistical techniques, the regional species-area relationship follows a power model with parameters c and z ,

$$S(A) = cA^z, \quad (2)$$

where A is the surface area, c a constant that depends on the organisms taken into account and the regional diversity, and z the parameter that relates richness to area. Assuming that forest communities are saturated, i.e. $n = \rho A$ where ρ is

the number of trees per unit area, the number of individuals is proportional to the area, and, since $\ln n \gg \ln \rho$, the model can be rewritten in a linear form:

$$\ln(S(n)) = k_A + z \ln(n) \quad (3)$$

where k_A is another constant.

The regional scale is also that of the metacommunity in the neutral model. The actual size J_M of the metacommunity a local community results from is difficult to address and of little interest in the theory since the important parameter is θ , that combines both J_m and the speciation rate ν . The important fact here is that, according to the neutral model, metacommunities are distributed in log-series whose α parameter asymptotically tends to θ when their size increases (Hubbell, 2001).

Sampling the metacommunity by a large enough number of plots results in a log-series distribution. This property allowed estimating the number of species of the Amazon forest (ter Steege et al., 2013) and of all tropical forests of the world (Slik et al., 2015). Discussing the sampling issues due to the spatial structure of species (ter Steege et al., 2020) or the discrepancies between the empirical and theoretical distributions (Milton and Ostling, 2025) is not the scope of this paper: even ignoring them, the theory is very well supported empirically.

Gleason (1922) refuted Arrhenius's model, arguing that the richness would be far too high for large areas, and proposed a competing model in which the number of species, rather than its logarithm, increased with the logarithm of the area. Assuming saturation, i.e. $n = \rho A$ where ρ is the number of trees per unit area, and $\ln n \gg \ln \rho$, it can be rewritten as

$$S(n) = k_G + \alpha \ln(n), \quad (4)$$

where k_G is another constant and α the slope of the relation. This model is actually identical to Fisher's (Engen, 1977).

Arrhenius's model benefits from a long theoretical (Williamson et al., 2001; Harte et al., 1999; Preston, 1962) and empirical (Dengler, 2009; Triantis et al., 2012) support.

A simple argument against Gleason's model is contained in the neutral theory. Consider a large metacommunity and assume it is distributed as a log-series. A smaller metacommunity inside it would just be a sample of it in absence of dispersal limitation. Then both distributions would be identical, i.e. the same log-series with the same parameter α : the same Fisher's model would be valid for all subsamples of the largest metacommunity, validating Gleason's model. Yet, dispersal is limited, i.e. not all species of the largest metacommunity are present in the smaller ones: their diversity is reduced. Although they are distributed in log-series, their parameter α is smaller. Thus, the number of species decreases faster with the area than predicted by Gleason's model.

At this stage, we face an apparent paradox: the regional species area relationship follows a power model but a metacommunity is distributed in log-series. It is solved considering that the metacommunity's α parameter depends on its size. Again, a smaller metacommunity embedded in the first one does not contain all species because of dispersal limitation. When the SAR is plotted on a log-log scale, it is linear. If the y-axis is not in logarithmic scale, it becomes concave. In this representation (Figure 5), a log-series species accumulation curve is a straight line (the number of individuals is much greater than α) so α increases with area.

This theoretical result can be verified empirically with the GuyaDiv network plots in French Guiana. In Figure 6, an increasing number of plots (one per site) is randomly selected to sample the metacommunity. The estimated α are plotted against the number of plots. Clearly, α increases linearly with the logarithm of the number of plots that is a proxy of the size of the sampled metacommunity.

The metacommunity GuyaDiv is a sample of largely exceeds the borders of French Guiana. Its estimated α equals 257, implying more than 4000 tree species in the territory based on the number of trees: 627 per hectare on average multiplied by 8 million hectares. Its SAC is shown on Figure 5. The actual number of species in French Guiana was obtained by the estimation of the power model (Marcon et al., 2024): it is close to 2200. The correct estimate of α is thus only 128.

This example illustrates the impossibility to estimate α at a regional scale from sample plots,

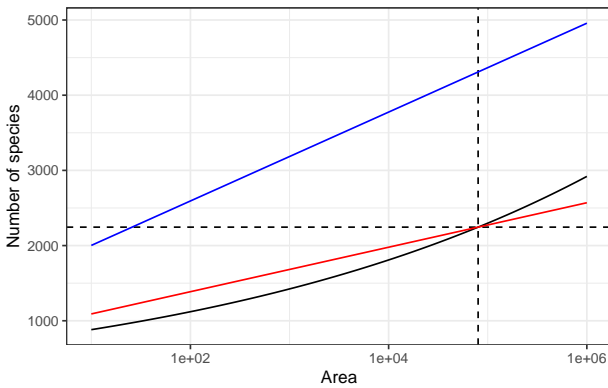


Figure 5. Number of tree species depending on the area (in square km, with density 627 trees/ha) in French Guiana, according to the Arrhenius's power model estimated by Marcon et al. (2024). The Y-axis is not in logarithm, so the relation is a convex curve instead of a straight line. The black dotted lines show the valid estimation of richness in the whole territory: around 2200 species for 80,000 km². The green line is the species accumulation curve of the log-series estimated from the GuyaDiv metacommunity assuming its area is that of French Guiana. It overestimates the regional biodiversity at all scales. The red curve is the SAC of the actual metacommunity of French Guiana, whose Fisher's α is twice smaller.

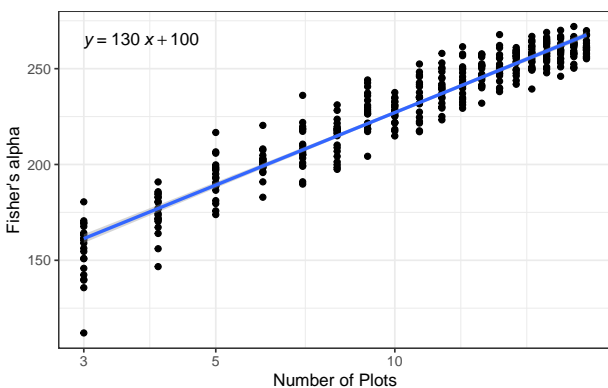


Figure 6. Estimation of the metacommunity's α as a function of the number of GuyaDiv plots used to sample it. The line is the fit of the linear model relating α to the logarithm of the number of plots.

e.g. to compare the diversity of adjacent regions. Log-series can be sampled, but the size of the metacommunities can't be controlled. Of course, this issue vanishes when the metacommunity under study is bounded, e.g. the Amazon sampled by ter Steege et al. (2013) to estimate its total number of species. In this case, adding samples necessarily leads to an asymptotic estimation of α .

5. Conclusion

Despite its popularity as an index of diversity, Fisher's α should not be applied to tropical forest communities because it is the parameter of a model that does not fit the data. According to the neutral theory, log-series communities would result from migration parameter 1, i.e. in the absence of dispersal limitation of the species of the metacommunity, which never occurs. Forcing the estimation of α in non-log-series distributions results in highly scale-dependent values that seriously question the comparisons between communities based on their α index.

At the regional scale, metacommunities do follow log-series distributions so α can be estimated from a set of scattered forest plots, even though the spatial structure of species may introduce estimation biases. Even ignoring this issue, α can't be interpreted simply because it is not possible to characterize the area of the sampled metacommunity. At this scale, the measure is correct, but the measured object is unclear.

Finally, the empirical interest of Fisher's α is limited to the distribution of clearly delimited metacommunities, such as the Amazon forest as a whole. In this context, it allowed among other results to estimate the number of tree species.

6. Appendix

6.1 Estimating α with R

Point estimation

Most implementations of the calculation of α are limited to solving the equation

$$S(n) = \alpha \ln \left(1 + \frac{n}{\alpha} \right),$$

where $S(n)$ is the number of species observed in a sample of size n . The only data required are the total number of species and the sample size.

The fifty hectares of BCI are used in the examples below.

Functions are:

- `vegan::fisher.alpha()` that relies on `vegan::fisherfit()`. The numerical resolution uses `uniroot()`.

```
library("vegan")
fisher.alpha(BCI_50ha)
```

```
[1] 35.05477
fisherfit(BCI_50ha)
```

Fisher log series model
No. of species: 225
Fisher alpha: 35.05477

- `untb::fishers.alpha()`, identical to `vegan::fisherfit()`

```
library("untb")
fishers.alpha(N = sum(BCI_50ha), S = sum(BCI_50ha > 0))
```

```
[1] 35.05477
```

Likelihood maximisation

The alternative is to adjust the observed abundance distribution to the theoretical distribution of a log series, maximising its likelihood as a function of α .

This is done by `sads::fitls()` which uses `mle2()` to maximise the likelihood of `sads::dls()` (the probability density of the log-series). The default starting value is the point estimate.

```
library("sads")
fitls(BCI_50ha) %>%
  coef()
```

N	alpha
21457.00000	35.05477

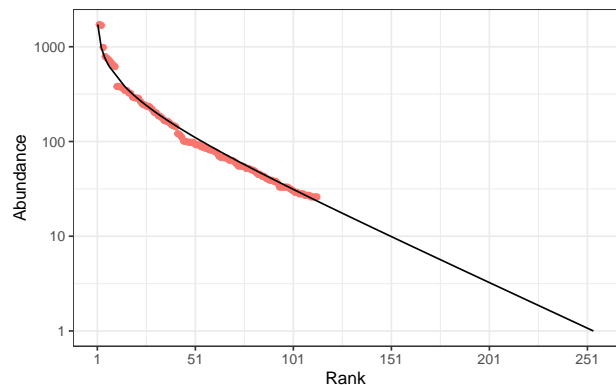
In the case of BCI, the result is the same: the likelihood calculation gives predominant weight to the most abundant species.

6.2 Estimating θ by the abundant species distribution

Hubbell (2001, page 293) proposes estimating θ by adjusting the rank-abundance curve to the most frequent species in the community, arguing that these species are also the most abundant in the metacommunity.

```
# Theoretical rank of abundances
lseries_RAC <- function(abd, alpha) {
  rank <- vapply(
    abd,
    function(x) {
      n <- x * log(1 + alpha / sum(abd))
      f <- stats::integrate(
        function(t) {exp(-t) / t},
```

```
      lower = n,
      upper = Inf
    )
    fv <- f[["value"]]
    return(alpha * fv)
  },
  FUN.VALUE = 0
)
tibble(rank, abundance = abd) |>
  arrange(rank)
}
# Fit alpha by minimizing the departure of species
# ranks from their theoretical value in a logseries
fit_alpha <- function(abd) {
  abd_decr <- sort(abd[abd > 0], decreasing = TRUE)
  optimized <- optim(
    par = vegan::fisher.alpha(abd),
    fn = function(alpha) {
      sum(abs(seq_along(abd_decr)
        - lseries_RAC(abd_decr, alpha)$rank))
    },
    method = "L-BFGS-B",
    lower = 0
  )
  optimized$par
}
BCI_50ha %>%
  sort(decreasing = TRUE) %>%
  subset(. > median(.)) ->
  BCI_abundant
BCI_theta <- fit_alpha(BCI_abundant)
library("divent")
BCI_abundant %>%
  as_abundances() %>%
  autoplot() +
  geom_line(
    data = lseries_RAC(BCI_50ha, alpha = BCI_theta),
    aes(x = rank, y = abundance)
  )
```



The estimate using Hubbell's method is 45.

6.3 Full simulation

The objective is to close the loop: using the parameters obtained from the BCI data, simulate a metacommunity and then a community of the same size as BCI. To validate the approach, the simulated distribution should be similar to the actual one.

Estimation of BCI parameters θ and m following Etienne (2005) with the `untb` package.

```
library("untb")
if (file.exists("data/BCI_logkda.RData")) {
  # Use the saved result if available to save
  # computation resources
  load("data/BCI_logkda.RData")
} else {
  BCI_50ha %>%
  # name conflict with dplyr::count()
  untb::count() %>%
  # requires pari/gp installed and in the path,
  # or use gp_binary argument
  logkda() ->
  BCI_logkda
  # Save the result
  save(BCI_logkda, file = "data/BCI_logkda.RData")
}
BCI_50ha %>%
  # name conflict with dplyr::count()
  untb::count() %>%
  # Estimate theta and m
  optimal.params(log.kda = BCI_logkda) %>%
  print() ->
  BCI_params
```

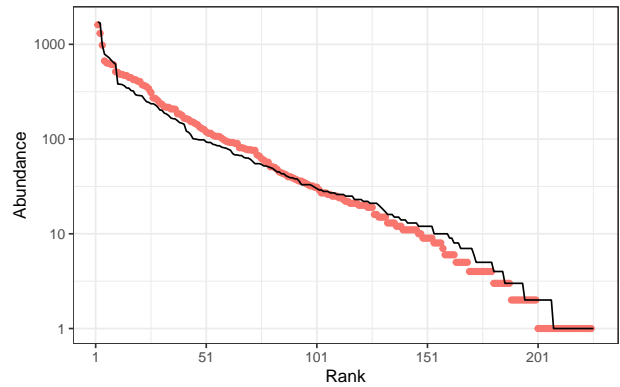
```
      theta      m
47.6001882 0.0926531
```

Simulation of a metacommunity: $J_m = 10^6$ (arbitrary), θ derived from BCI data.

```
J_m <- 1E6
theta <- BCI_params[1]
library("divent")
the_metacommunity <- rcommunity(
  1,
  size = J_m,
  distribution = "lseries",
  fisher_alpha = theta
)
```

Distribution of the local community: J from BCI and m estimated previously.

```
J <- sum(BCI)
m <- BCI_params[2]
library("sads")
# Number of species in the local community
Svolkov(theta, m, J) %>%
  # Must be integers for the simulation
  round() %>%
  # Draw the species abundances
  rvolkov(theta, m, J) %>%
  # Make it an abundances object to plot it
  as_abundances() %>%
  # Whittaker plot
  autoplot() +
  # BCI real distribution
  geom_line(
    data = {
      tibble(
        abundance = sort(
          BCI_50ha,
          decreasing = TRUE
        )
      ) %>%
      mutate(rank = seq_len(n()))
    },
    aes(x = rank, y = abundance)
  )
```



The simulated community (red dots) corresponds fairly well to the actual distribution of BCI (black line).

References

- Arrhenius, O. (1921). Species and area. *Journal of Ecology* 9(1), 95–99.
- Burnham, K. P. and W. S. Overton (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65(3), 625–633.
- Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison (2014). Rarefaction and extrapolation with hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84(1), 45–67.
- Chao, A. and L. Jost (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93(12), 2533–2547.
- Condit, R., N. Pitman, E. G. J. Leigh, J. Chave, J. Terborgh, R. B. Foster, P. Núñez, S. Aguilar, R. Valencia, G. Villa, and et al. (2002). Beta-diversity in tropical forest trees. *Science* 295(5555), 666–669.
- Dengler, J. (2009). Which function describes the species-area relationship best? a review and empirical evaluation. *Journal of Biogeography* 36(4), 728–744.
- Duque, A., H. C. Muller-Landau, R. Valencia, D. Cardenas, S. Davies, A. De Oliveira, A. J. Pérez, H. Romero-Saltos, and A. Vicentini (2017). Insights into regional patterns of amazonian forest structure, diversity, and dominance from three large terra-firme forest dynamics plots. *Biodiversity and Conservation* 26(3), 669–686.
- Engel, J. (2015). Plot networks & teams.
- Engen, S. (1977). Exponential and logarithmic species-area curves. *The American Naturalist* 111(979), 591–594.
- Etienne, R. S. (2005). A new sampling formula for neutral biodiversity. *Ecology Letters* 8(3), 253–260.
- Fisher, R. A., A. S. Corbet, and C. B. Williams (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12, 42–58.
- Gleason, H. A. (1922). On the relation between species and area. *Ecology* 3(2), 158–162.

- Gotelli, N. J. and R. K. Colwell (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4(4), 379–391.
- Grabchak, M., E. Marcon, G. Lang, and Z. Zhang (2017). The generalized simpson's entropy is a measure of biodiversity. *Plos One* 12(3), e0173305.
- Grilli, J., S. Azaele, J. R. Banavar, and A. Maritan (2012). Spatial aggregation and the species-area relationship across scales. *Journal of Theoretical Biology* 313, 87–97.
- Hankin, R. K. S. (2007). Introducing untb, an r package for simulating ecological drift under the unified neutral theory of biodiversity. *Journal of Statistical Software* 22(12), 1–15.
- Harte, J., A. Kinzig, and J. Green (1999). Self-similarity in the distribution and abundance of species. *Science* 284(5412), 334–336.
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch, and et al. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science* 354(6309), aaf8957.
- MacArthur, R. H. and E. O. Wilson (1967). *The theory of island biogeography*, Volume 1. Princeton University Press.
- Marcon, E., A. Mirabel, J.-F. Molino, and D. Sabatier (2024). Estimation of the number of tree species in french guiana by extrapolation of permanent plots richness. *Journal of Tropical Ecology* 40, e11.
- McGill, B. J. (2003). A test of the unified neutral theory of biodiversity. *Nature* 422(6934), 881–885.
- Milton, T. F. and A. Ostling (2025). Amazonian hyperdominance exceeds expectations of neutral theory. *Journal of Ecology*, 1365–2745.70174.
- Muller-Landau, H. C. and S. J. Wright (2024, Nov). *The First 100 Years of Research on Barro Colorado: Plant and Ecosystem Science (Volumes 1 and 2)*. Smithsonian Institution Scholarly Press.
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, T. Borman, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannon, M. O. Hill, L. Lahti, C. Martino, D. McGlinn, M.-H. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C. J. Ter Braak, and J. Weedon (2025). *vegan: Community Ecology Package*.
- Plotkin, J. B., M. D. Potts, N. Leslie, N. Manokaran, J. V. LaFrankie, and P. S. Ashton (2000). Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology* 207(1), 81–99.
- Preston, F. W. (1962). The canonical distribution of commonness and rarity: Part i. *Ecology* 43(2), 185–215.
- R Core Team (2025). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Schulte, R. P. O., E. A. Lantinga, and M. J. Hawkins (2005). A new family of fisher-curves estimates fisher's alpha more accurately. *Journal of Theoretical Biology* 232(3), 305–313.
- Slik, J. W. F., V. Arroyo-Rodríguez, S.-I. Aiba, P. Alvarez-Loayza, L. F. Alves, P. S. Ashton, P. Balvanera, M. L. Bastian, P. J. Bellingham, E. van den Berg, and et al. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* 112(24), 7472–7477.
- Strange, N., S. Z. Ermgassen, E. Marshall, J. W. Bull, and J. B. Jacobsen (2024). Why it matters how biodiversity is measured in environmental valuation studies compared to conservation science. *Biological Conservation* 292, 110546.
- Stroud, J. T., M. R. Bush, M. C. Ladd, R. J. Nowicki, A. A. Shantz, and J. Sweatman (2015). Is a community still a community? reviewing definitions of key terms in community ecology. *Ecology and Evolution* 5(21), 4757–4765.
- ter Steege, H., N. C. A. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J.-F. Molino, and et al. (2013). Hyperdominance in the amazonian tree flora. *Science* 342(6156), 1243092.
- ter Steege, H., P. I. Prado, R. A. F. de Lima, E. Pos, L. de Souza Coelho, D. de Andrade Lima Filho, R. P. Salomão, I. L. Amaral, F. D. de Almeida Matos, C. V. Castilho, and et al. (2020). Biased-corrected richness estimates for the amazonian tree flora. *Scientific Reports* 10(1), 10130.
- Triantis, K. A., F. Guilhaumon, and R. J. Whittaker (2012). The island species-area relationship: biology and statistics. *Journal of Biogeography* 39(2), 215–231.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan (2003). Neutral theory and relative species abundance in ecology. *Nature* 424(6952), 1035–1037.
- Williamson, M., K. J. Gaston, and W. M. Lonsdale (2001). The species-area relationship does not have an asymptote! *Journal of Biogeography* 28(7), 827–830.