# Estimation of the number of tree species in French Guiana by extrapolation of permanent plots richness

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**Abstract**

The biodiversity of tropical rainforest is difficult to assess. Yet, its estimation is necessary for conservation purposes, to evaluate our level of knowledge and the risks faced by the forest in relation to global change. Our contribution is to estimate the regional richness of tree species from local but widely spread inventories. GuyaDiv is a network of forest plots installed over the whole territory of French Guiana, where trees over 10 cm DBH are identified. We use its information (1315 species censused in 68 one-hectare plots) to estimate the exponent of the species-area relationship, assuming Arrhenius's power law. We can then extrapolate the number of species from a local, wide inventory (118.75 ha in Paracou research station). We evaluate the number of tree species around 2200 over the territory.

Biodiversity, Tropical Forest, Self Similarity, French Guiana

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## Contents

## 1.  Introduction

Biodiversity assessment in tropical moist forests is a practical challenge but a major goal considering they are the most diverse terrestrial ecosystems. Estimating the number of tree species is made possible by the long-term effort of sampling resulting in thousands of forest plots organized in various networks. In French Guiana, the GuyaDiv network consists of close to 250 plots across the whole forest. Based on similar datasets, the diversity of tree species has been estimated in Amazonia (ter Steege et al., 2013, 2020) and at the world scale (Slik et al., 2015). The methods used in those studies are not appropriate to estimate regional diversity, i.e. at a smaller scale where dispersal limitation is critical. The contribution of this paper is to estimate the number of tree species at the regional scale, in French Guiana (8 million hectares of tropical moist forest with no ecological boundary to distinguish them from the rest of Amazonia) and demonstrate which method is valid to do so. We build on Harte's self similarity model (Harte et al., 1999) that implies the power-law relatioship of Arrhenius (1921) and provides a technique to evaluate its parameters (Harte et al., 1999), previously applied by Krishnamani et al. (2004) in the Western Ghats, India. We show that the log-series model underlying the work of ter Steege et al. (2013) does not apply at the regional scale.

## 2.  Methods

Self-similarity (Harte et al., 1999) is a property based on scale invariance. Consider a species $s$ that is present in an area $A_0$, say French Guiana. The probability to find it in half the whole area, denoted $A_1$ is $h_s$. Then, if it is present $A_1$, the probability to find it in turn in half $A_1$, denoted $A_2$, is also $h_s$, and so on. The probability to find the species in $A_n$ is thus $h_s^n$. In other words, the conditional probability to find a species in a sub-area, given that it is present in the area containing it, only depends on the relative size of the sub-area (half the parent area here for simplicity): it does not depend on the observation scale.

Arrenhius's power law (Arrhenius, 1921) is a consequence (Harte et al., 1999) of the self-similarity property. The number of species $S(A)$ observed in an area $A$ is

$$S(A) = cA^z \qquad (1)$$

where $z$ is the power parameter and $c$ is the number of species in an area of size 1. This is a classical relation in macroecology, with long empirical and theoretical support (Williamson et al., 2001; Gárcia Martín and Goldenfeld, 2006).

If $z$ is known, the inventory of a reasonably large area $a$ allows computing $c = a^z/S(a)$. Then, $S(A)$ can be calculated for any value of $A$.

Harte et al. (1999) showed that under the assumption of self-similarity, $z$ can be inferred from the dissimilarity between small and distant plots distributed across the area. The Sørensen (1948) similarity between two plots is

$$\chi = 2(S_1 \cap S_2)/(S_1 + S_2) \qquad (2)$$

where $S_1$ (respectively $S_2$) is the number of species in plot 1 (resp. plot 2) and $S_1 \cap S_2$ is the number of common species.

Applied to plots of the same size separated by distance $d$, Sørensen's similarity decreases with distance following the relation $\chi \sim d^{-2z}$ (Harte et al., 1999) that can be estimated by the linear model

$$\log(\chi) \sim \log(d). \qquad (3)$$

The logarithm of the Sørensen dissimilarity between pairs of plots can be regressed against the logarithm of the distance between the plots: the slope of the regression is $-2z$.

The relation (3) holds at the same scale as the power law, i.e. at the regional scale (Grilli et al., 2012). Krishnamani et al. (2004) estimated $z \approx 0.12$ with a very good fit to the linear model at distances up from 1 km but not below. Our data confirm that.

A large enough inventory, provided by a permanent forest facility, is necessary along with a set of small, widely spread forest plots.

The Paracou research station (Gourlet-Fleury et al., 2004) is located at latitude 5°18'N and longitude 52°53'W. It contains fifteen 6.25-ha and one 25-ha plots of primary rainforest summing up a 1.1875-km$^2$ inventory. It is included in a 3.5-km$^2$ convex envelope.

We obtained the abundances of 697 species from the Paracou database (https://paracoudata.cirad.fr/) after eliminating undetermined trees (with a botanical confidence level below 2, i.e. either not identified by a botanist or not identify at the genus level). We extrapolated richness up to the size of the envelope following Colwell et al. (2012), assuming the number of trees per area identical to that of the inventory. We found 764 species.
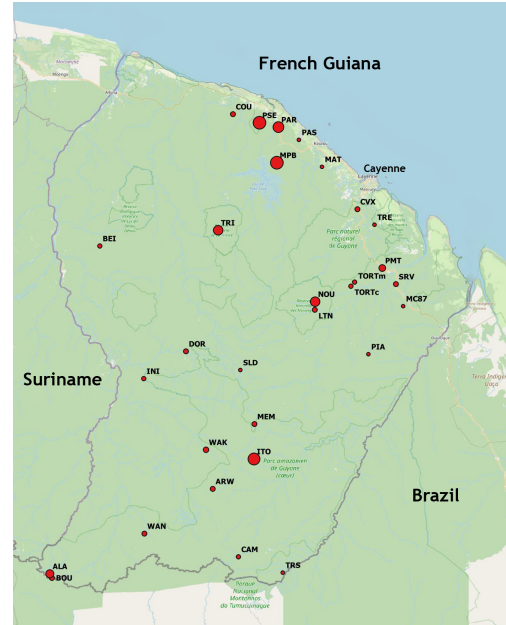


**Figure 1.** The GuyaDiv network.

**Decription of GuyaDiv here**

We took into account the 68 one-hectare plots of the network. They are located in 21 locations that allow a quite good coverage of the variability of the forest in French Guiana (figure 1). The number of plots varies across locations so the estimation of $z$ must be made with care. We sampled one random plot at each location to obtain $21 \times 20/2 = 210$ pairs of plots. We calculated the Sørensen dissimilarity $\chi$ and the geographic distance $d$ between each pair of plots. We estimated $z$ as half the coefficient of the distance variable in the linear model $\log(\chi) \sim \log(d)$. We repeated these steps 1000 times to obtain a distribution of estimated $z$ values depending on the plots drawn in each location. $z$ was estimated as the empirical mean of the distribution and its 95% confidence interval was obtained by eliminating the 2.5% extreme values on both tails.

All analyses were made with R (R Core Team, 2022) v. 4.1.2.

## 3. Results

The estimated value of $z$ is 0.103 with a 95% confidence interval between 0.089 and 0.121.

The number of species per squared kilometer, $c$, is 671.

Finally, the estimated number of species is 2156. Taking into account the uncertainty about $z$, its 95% confidence interval is between 1824 and 2619.

## 4. Discussion

The self-similarity model allows estimating the number of species of tropical forests at a regional scale. It requires a network of plots at a wide range of distances from each other to estimate Arrhenius's power

law parameter. It should be completed by a continuous inventory whose size is consistent with the smallest scale of the power law. These constraints explain why the method has not been widely applied, beyond Krishnamani et al. (2004) and this paper.

At smaller scales, i.e. inside a single community, the relation between area and number of species is described by species accumulation curves (SAC: Gotelli and Colwell, 2001). It is driven by statistical models that address incomplete sampling (Shen et al., 2003; Béguinot, 2015). After replacing the sampled area by the number of individuals it contains, well-known estimators of richness such as Chao's (Chao, 2004) or the jackknife (Burnham and Overton, 1978) apply.

At the scale of the metacommunity, defined as of the neutral model of biogeography, the species distribution is in log-series (Hubbell, 2001; Volkov et al., 2003). ter Steege et al. (2013) fitted a log-series to data provided by a network of plots to estimate the number of species in Amazonia. We applied the same method to our data in appendix 5.2. Its estimation is close to 4000 species in French Guiana: a very unlikely result according to the current expert knowledge and the recent checklist (Molino et al., 2022). The regional species pool does not follow a log-series distribution because of dispersal limitation (Grilli et al., 2012). In other words, the regional community is not a sample of the metacommunity: many of the metacommunity's species are not present. As a consequence, the log-series estimation of the richness of a regional species pool leads to severe overestimation. For the sames reason, hyperdominance is less pronounced: 5% of the species contain half the trees (apendix 5.3), compared to 1.4% in Amazonia as a whole (ter Steege et al., 2013).

The estimated number of tree species in the 8-million-hectare forest of French Guiana is close to 2200, with a quite wide confidence interval due to the variability in the estimation of the power-law parameter. As shown in figure 2, the fit of the linear model is not perfect. The theory does not address habitat variation, that is well-described in French Guiana (Guitet et al., 2015). The dissimilarity between plot pairs is thus explained by distance and habitat dissimilarity, the latter ignored in the model. Yet, the estimation of $z$ is quite robust because the GuyaDiv network covers a wide range of habitats, allowing to cancel out local variability. Its value 0.103 is in line with that of Krishnamani et al. (2004) in another tropical forest: it is very small compared to the classical 0.25 of Arrhenius (1921) or 0.263 of Preston (1962). This was discussed by MacArthur and Wilson (1967), chapter 2. The power law applies to embedded scales of the same ecosystem here, in contrast to the usual sets of isolated islands providing the data (Triantis et al., 2012): in our case, the number of species increases less with the area, leading to smaller $z$ values.

Another issue of the estimation is due to its unique starting point, i.e. Paracou field station, that is not
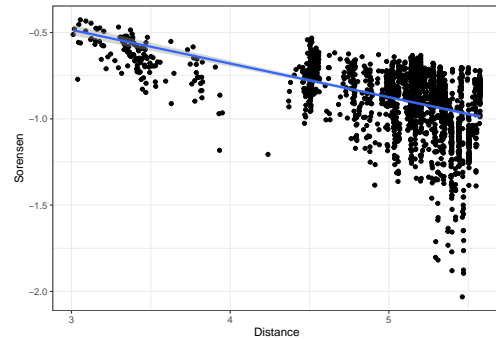


**Figure 2.** Relation between Sørensen's similarity and the distance between pairs of plots. Both axes are in base-10 logarithms, distances are in meters. Each point is a pair of plots more than 800m apart, up to 377km. A linear model is fitted: the slope of the regression is $-2z$.

representative of the whole French Guiana. Actually, it is located at the edge of the forest, close to the coast. Again, the self-similarity model assumes that $c$, the number of species per squared kilometer, is the same everywhere. Local, observed values must be understood as variations around the real $c$, that should be estimated by replicating inventories across the whole region. This is of course impossible due to the huge resources needed to settle a single one so Paracou's local richness adjusted to 1 km$^2$ must be considered as the best available estimator of $c$. Its uncertainty cannot be evaluated because of the lack of replication. Its effect on the number of estimated species is proportional.

2156 species are a very likely estimation according to the current knowledge > **JF**.

## 5. Appendix

### 5.1 Similarity distance decay
The relation between Sørensen's similarity and distance is presented in figure 2. All pairs of plots more than 800 meters apart (the scale of Paracou's 0.625-km$^2$ inventory) are shown. The estimation of $z$ is not made this way because some locations contain more plots than others so their weight is increased. The technique used in the text of the paper consists of drawing a random plot in each location to estimate $z$, and repeat this process a large number of times to estimate the expectation of $z$.

### 5.2 Log-series estimation of the number of species
Assuming that the plots are samples of a metacommunity that follows a log-series distribution, the rank-abundance curve can be extrapolated (figure 3) following ter Steege et al. (2013).

First, the total number of trees is estimated by extrapolation of the average number of trees per plot. There are close to 260 million trees in French Guiana.

The probability for one of these trees to belong to a given species is obtained by averaging the probability of the species among plots. Each plot is a sample
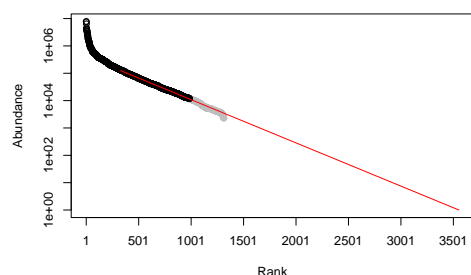
**Figure 3.** Extrapolation of the rank-abundance curve built from the GuyaDiv plots. Extrapolated abundances (in log scale) of observed species are plotted against the rank of their species. The abundances of unobserved species (the red curve) is extrapolated linearly from the center 50% of the distribution of the observed species. The rarest 25%, ignored for the extrapolation, are plotted as grey points.

of a local community whose composition is not completely known: for example, many rare species are not in the sample. The observed frequency of a species in a plot is not the probability of the species in the community: frequencies sum up to 1 while the sum of the actual probabilities of observed species, called the sample coverage (Good, 1953), sums up to 1 minus that of the unobserved species. The actual probabilities of observed species can be estimated following Chao and Jost (2015), with the *entropart* package (Marcon and Hérault, 2015).

The most abundant tree species is *Eperua falcata* with around 8 million trees.

The estimated number of species according to this model is 3554. This is undoubtedly a severe overestimation, see the discussion section of the paper.

### 5.3 Hyperdominance

Hyperdominance is a characteristic of many distributions of species. Figure 4 shows the accumulation of individuals from the most adundant to the rarest species.

Only 90 species, i.e. 4% of their estimated number, contain half the number of trees.
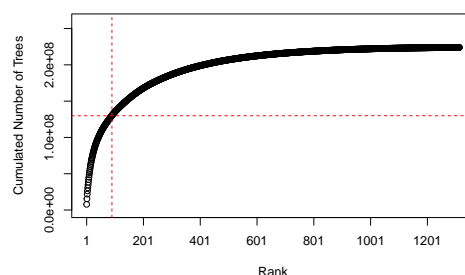
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**Figure 4.** Accumulation of the number of individuals from the most abundant to the rarest species. The horizontal line corresponds to half the individuals. The vertical line allows reading the corresponding rank of the species.

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