Inferring macro-ecological patterns from local species' occurrences

Anna Tovo[1]*, Marco Formentin[2]+, Samir Suweis[1], Samuele Stivanello[2], Sandro Azaele[3], Amos Maritan[1]

[1] *Dipartimento di Fisica e Astronomia "Galileo Galilei", Istituto Nazionale di Fisica Nucleare, Università di Padova, Via Marzolo 8, 35131 Padova, Italy*

[2] *Dipartimento di Matematica "Tullio Levi-Civita", Università di Padova, Via Trieste 63, 35121 Padova, Italy*

[3] *Department of Applied Mathematics, School of Mathematics, University of Leeds, Leeds LS2 9JT, UK.*

***Corresponding author**: anna.tovo@unipd.it*

+***Corresponding author**: marco.formentin@unipd.it*

Summary

1. Biodiversity provides support for life, vital provisions, regulating services and has positive cultural impacts. It is therefore important to have accurate methods to measure biodiversity, in order to safeguard it when we discover it to be threatened. For practical reasons, biodiversity is usually measured at fine scales whereas diversity issues (e.g. conservation) interest regional or global scales. Moreover, biodiversity may change across spatial scales. It is therefore a key challenge to be able to translate local information on biodiversity into global patterns.

2. Many databases give no information about the abundances of a species within an area, but only its occurrence in each of the surveyed plots. In this paper, we introduce an analytical framework to infer species richness and abundances at large spatial scales in biodiversity-rich ecosystems when species presence/absence information is available on various scattered samples (i.e. upscaling).

3. This framework, derived from first principles on the basis of biological processes, is based on the scale-invariance property of the negative binomial distribution. Our approach allows to infer and link within a unique framework important and well-known biodiversity patterns of ecological theory, such as the Species Accumulation Curve (SAC) and the Relative Species Abundance (RSA) as well as a new emergent pattern, which is the Relative Species Occupancy (RSO).

4. Our estimates are robust and accurate, as confirmed by tests performed on both in silico-generated and real forests. We demonstrate the accuracy of our predictions using data from two well-studied forest stands. Moreover, we compared our results with other popular methods proposed in the literature to infer species richness from presence-absence data and we showed that our framework gives better estimates. It has thus important applications to biodiversity research and conservation practice.

Keywords: biodiversity patterns, species-abundance distribution, species-area relationship, upscaling biodiversity patterns, spatial ecology

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Introduction

The problem of inferring total biodiversity when only scattered samples are observed is a long-standing problem. In the 1940s, the British chemist and naturalist A. S. Corbet spent two years in Malaya to trap butterflies [1]. For every species he saw, he noted down how many individuals of that species he trapped. When Corbet returned to England, he showed the table to its colleague R. A. Fisher and asked him how many new species he would trap if he returned to Malaya for another couple of years. The father of statistics was only the first to tackle the problem of species estimation [2], which since then has found large applications in different scientific fields, from ecology [3, 4, 5] to bioscience [6, 7, 8], leading to the development of a myriad of estimators [9, 10, 11].

Indeed, although ecological drivers crucial for conservations act at large scales, biodiversity is typically monitored at limited spatial scales [12, 13]. Extrapolating species richness from the local to the whole forest scale is not straightforward, because it is not additive as a function of the area. As a result, a huge number of biodiversity estimators have been proposed in ecological literature [4, 14, 15, 16, 17, 18, 19, 20, 21]. Their commonest limitation is to have a limited application range (local/regional-scale extrapolations), and to be sensitive to the trees' spatial distribution [22, 23, 24], sample coverage and sampling methods [25].

Recently, analytical methods have been proposed to upscale species richness using as input the local Relative Species Abundance distribution (RSA) [26, 27, 28, 29] ,i.e. the list of the species present at a that spatial scale along with the proportion of individuals belonging to each of them. These methods have been proved to typically perform better than non-parametric estimators of biodiversity [30]. In contrast with the former, these latter methods make no assumption on the RSA distribution and they thus perform no fit of empirical patterns, rather they only take into account rare species, which are intuitively assumed to carry all the needed information on the undetected species in a sample.

Nevertheless, all the aforementioned methods need abundance data in order to infer biodiversity at larger scale. However, in many open-access databases (e.g. species abundance data obtained from metagenomics [31]) this information is highly imprecise, if available at all. Indeed, there are lots of datasets which give only information about the presence or absence of a species in different surveyed plots, without specifying the number of individuals within them. Some non-parametric approaches have been generalized to infer species richness from this presence-absence data [30, 11]. Table 2 summarizes the most popular estimators and for each one details the predicted biodiversity as a function of the input data. However, most of them have the strong limitation that they do not have an explicit dependence on the observation scale, leading to poor estimates of the number of species at the global scales (see Results). The only estimator which takes into account the ratio between the surveyed area and the global one is the one introduced by Chao [30, 25, 11] and denoted here as $Chao_\text{wor}$ (see Table 2). This method takes into account the number of species detected in one sample only and those detected in exactly two samples observed at the sample scale to infer the total species richness at the whole forest scale. However, it has been shown that Chao's method, although giving reliable species estimates, it does not properly capture the empirical Species Accumulation Curve (SAC) [29], which describes how the number of species changes across spatial scales. In absence of spatial correlation, it is equivalent to another macro-ecological pattern of interest which is the Species Area Relation (SAR).

Moreover, both parametric and non-parametric methods proposed in the literature do not give any insights on the species abundance at both local or larger scales. Indeed the problem of relating occupancy data with information on species abundance is a relevant issue in theoretical ecology [32, 33, 34]. In particular, given the information on the presence or absence of a species in different scattered plots, one would like to infer its population size or, more generally, the RSA distribution of the forest.

In this paper, we present a general analytical framework to extrapolate species richness and other relevant biodiversity patterns (e.g. RSA, SAC) at the whole forest scale from local information on species presence/absence. Our framework exploits the *form-invariance* property of the Negative Binomial (NB) distribution, derived as the steady-state RSA of a birth and death stochastic dynamics, accounting for effective immigration and/or intraspecific interactions [35, 24, 29]. Crucially, the functional form of a negative binomial does not change when sampling different fractions of areas. This property allows for an analytical expression for how parameters of the distribution change across scales. Form-invariance under different sampling efforts is at the core of the present work, however our method can applied any time the dependence on the distribution on the size of the sampled area can be calculated exactly. We will find an analytical relation

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between the NB RSA at a given spatial scale and the SAC. Thanks to this function, starting from the empirical SAC constructed at the sample scale from the local presence-absence data (see Eq. 12), we will be able to:

1. infer species richness at larger scales, thus the SAC up to the whole forest scale;

2. obtain information on species abundances in order to construct the RSA at both local and global scales;

3. infer the Relative Species Occupancy (RSO), i.e. the distribution of the occurrences (number of occupied cells) across species, at both local and global scales.

We tested our framework on *in-silico* generated forests and on the two well-studied tropical forests of Barro Colorado Island and Pasoh. We finally compared the global estimates with the abundance-based method proposed in [29].

1. Materials and Methods

1.1. Theoretical Framework

We denote as $P(n|1)$ the relative species abundance, – i.e. the probability that a species has exactly n individuals – at the whole forest scale (here 1 refers to the whole forest). Note that $P(n|1)$ should be defined only for $n \geq 1$, because S is the total number of species actually present in the forest, assuming that the area was exhaustively surveyed with no missing species.

Here the RSA is postulated to have a negative binomial functional form (NB) [36, 37, 29], $\mathcal{P}(n|r,\xi)$ with parameters (r,ξ) (r is known as the clustering coefficient):

$$P(n|1) = c(r,\xi)\mathcal{P}(n|r,\xi) \tag{1}$$

with

$$\mathcal{P}(n|r,\xi) = \binom{n+r-1}{n}\xi^n(1-\xi)^r, \qquad c(r,\xi) = \frac{1}{1-(1-\xi)^r},$$

where $c(r,\xi)$ is the normalisation constant taking into account only species with non-zero abundance, which is different from the usual NB normalization.

Let us consider a sub-sample of area a of the whole forest and define $p = a/A$ the sample scale. Assuming that the local RSA is not affected by spatial correlations due to both inter-specific and intra-specific interactions and strong environmental gradients, the conditional probability that a species has k individuals in the smaller area $a = pA$, given that it has total abundance n in the whole forest of area A is given by the binomial distribution

$$\mathcal{P}_{binom}(k|n,p) = \binom{n}{k}p^k(1-p)^{n-k}, \qquad k = 0, \dots, n.$$

This distribution helps us linking the distribution at the global scale with the one at the sample scale. It can be proved (see [29], Supplementary Materials) that, under the hypotheses that the RSA is described by a negative binomial and that no strong spatial correlations affect the individuals' locations, the RSA at scale p, $\mathcal{P}_{sub}(k|p)$, is again a negative binomial, for $k \geq 1$, with rescaled parameter $\hat{\xi}_p$ and the same r:

$$\mathcal{P}_{sub}(k|p) = \begin{cases} c(r,\xi) \cdot \mathcal{P}(k|r, \hat{\xi}_p) & k \geq 1 \\ 1 - c(r,\xi)/c(r, \hat{\xi}_p) & k = 0 \end{cases}$$

with

$$\hat{\xi}_p = \frac{p\xi}{1 - \xi(1-p)}. \tag{2}$$

A RSA with the property of having the same functional form at different scales is said to be *form-invariant*.

Given the parameters r and $\hat{\xi}_{p^*}$ of the RSA at the sampling scale p^*, we can get the value of ξ by inverting (2):

$$\xi = \frac{\hat{\xi}_{p^*}}{p^* + \hat{\xi}_{p^*}(1 - p^*)}. \tag{3}$$

Using (2) to eliminate ξ from the last equation, one gets the following relation for the parameter ξ at the two scales p and p^*

$$\hat{\xi}_p = \frac{p\hat{\xi}_{p^*}}{p^* + \hat{\xi}_{p^*}(p - p^*)} \equiv U(p|p^*, \hat{\xi}_{p^*}). \tag{4}$$

from which, of course, one can recover both (2), (3) where one has to use that $\xi \equiv \hat{\xi}_{p=1}$.

Let now determine the relation between the total number of species at the whole scale $p = 1$, S, and the total number of species surveyed at a local scale p, S_p. For the sampling scale p^*, in the following, we will use the notation $S^* \equiv S_{p^*}$. Note that, denoting with $S^*(k)$ the number of species having k individuals at the scale p^*, one has

$$\mathcal{P}_{sub}(k = 0|p^*) = (S - S^*)/S \tag{5}$$
$$\mathcal{P}_{sub}(k|p^*) = S^*(k)/S. \tag{6}$$

Thus, the total number of species in the whole forest, in terms of the data on the surveyed sub-plot is given by

$$\begin{aligned} S &= \frac{S^*}{1 - \mathcal{P}_{sub}(k = 0|p^*)} \\ &= S^* \frac{1 - (1-\xi)^r}{1 - (1 - \hat{\xi}_{p^*})^r}, \end{aligned} \tag{7}$$

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where ξ is given by (3).

In general, given two scales p and p^*, one has the following relation between the number of species at the scale p, the one at p^* and the RSA parameters (r, ξ_{p^*}) at the scale p^*:

$$S_p = S^* \frac{1 - (1 - U(p|p^*, \xi_{p^*}))^r}{1 - (1 - \xi_{p^*})^r} \tag{8}$$

In order to reduce the number of parameters to fit from three to two (see (7)), we rescale the setting, by assuming that the global scale $p = 1$ is actually the one where we have data, i.e. the sampling scale $p^* = na/A$. Then, for any sub-sampling scale $p_k = ka/A$, $k = 1, \ldots, n$, one has that the SAC up to p^* is given by

$$S_{p_k} = S^* \frac{1 - (1 - U(\tilde{p}_k|1, \xi_{p^*}))^r}{1 - (1 - \xi_{p^*})^r}, \tag{9}$$

where $\tilde{p}_k$ is the fraction of sub-sampling area with respect to a: $\tilde{p}_k = p_k/p^* = k/n$. One can therefore use (9) to fit the empirical SAC obtained through (13) to get the parameters r and ξ_{p^*} shaping the RSA at the sample scale p^*. From these, one can estimate the ξ parameter by using eq. (3) to predict both the number of species at the global scale S via (7), the RSA through (1) and the SAC by using (8).

Another important pattern which we can predict with our framework is the relative species occurrence, $Q(v|M, 1)$, which gives the probability that a species occupies v cells at the global scale, given that the forest can be tiled in M equal-sized cells of area a.

In order to find an expression for it, we firstly need the probability, $Q_{occ}(v|n, M, 1)$, that a species occupies v over M cells at the global scale, given that is has abundance n. Under the mean field hypothesis, this is given by an hyper-geometric distribution

$$Q_{occ}(v|n, M, 1) = \frac{\binom{M}{v}\binom{n-1}{v-1}}{\binom{n+M-1}{M-1}}. \tag{10}$$

The RSO distribution $Q(v|M, 1)$ can thus be obtained by marginalizing with respect to the abundance n:

$$Q(v|M, 1) = \sum_{n=1}^{\infty} Q_{occ}(v|n, M, 1)P(n|1), \tag{11}$$

where $P(n|1)$ is the global RSA given by eq. (1).

1.2. Implementation of the Framework

Our analytical framework consists of the following steps (see Figure 1).

- First, given a set of scattered samples, list the species in it.

  In formulae, sample $C = \{c_1, \ldots, c_n\}$, $n \geq 2$, cells covering a fraction p^* of the whole forest in which S^* species are observed. To each cell c_i, associate a vector $\Omega(c_i) = \{\omega_1^i, \ldots, \omega_{S^*}^i\}$, with $\omega_s^i \in \{0, 1\}$, $s \in \{1, \ldots, S^*\}$, $i \in \{1, \ldots, n\}$. The entry ω_s^i of vector $\Omega(c_i)$ gives information on the presence/absence of the species s in the cell c_i – i.e. $\omega_s^i = 1$ if species i is present in cell c_i, $\omega_s^i = 0$ otherwise.

- Compute the empirical species-area relationship as follows. From now on, let us suppose that all cells are of equal size a. This assumption does not affect the general framework but it simplifies the computation of the SAC. Call A the area of the whole forest, so that $p^* = na/A$. At each sub-sampling scale $p_k = ka/A$, with $k \in \{1, \ldots, n\}$, compute the average number of observed species as

$$S_{\text{emp}}(p_k) = \frac{1}{\binom{n}{k}} \sum_{\substack{I \subseteq \{1, \ldots, n\} \\ |I| = k}} \sum_{s=1}^{S^*} \mathbb{1}\left(\sum_{i \in I} \omega_s^i \geq 1\right), \qquad (12)$$

  where $\mathbb{1}(\mathcal{P})$ is the indicator function, which equals one when the random event $\mathcal{P}$ happens and it is zero otherwise.

  In words: for every scale p_k, we compute the empirical average of the species observed in all subsets of k cells.

- Fit the empirical species-area relationship with the theoretical equation

$$S(p_k) = S^* \frac{1 - (1 - U(\tilde{p}_k|1, \xi_{p^*}))^r}{1 - (1 - \xi_{p^*})^r} \qquad (13)$$

  and obtain the parameters (r, ξ_{p^*}) which best describe the empirical curve $S_{\text{emp}}(p_k)$. These are the parameters of the NB relative species abundance distribution at the sample scale p^*. This protocol allows us to capture some spatial effects in the effective parameters.

- As showed in [29], under the hypotheses of absence of strong spatial correlations due to both inter-specific or intra-specific interactions, strong environmental gradients and abundances distributed according to a negative binomial at the whole forest scale, the RSA distributions at different scales have the same functional form of the RSA at the scale p^*, and only the values of the parameter ξ changes as a function of the scale. Thus we obtain an analytical form of the upscaled RSA at any scale p given we know it at scale p^* in term of the equation $\xi(p|\xi_{p^*}) = U(p|p^*, \xi_{p^*})$, relating $\xi_p = \xi(p)$ to p, p^* and $\xi_{p^*} = \xi(p^*)$. Therefore, using the RSA parameters at scale p^* and the upscaling equations (see below), we can predict the total number of species, S, at the whole forest scale, $p = 1$.

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- The key feature of the method is the possibility, given only presence/absence data, to connect and infer different biodiversity patterns at the global scale. Indeed, we can predict, in addition to the SAC, the RSO, the cell occupancy distribution, and the RSA, the abundance proportions of the S species present at $p = 1$.
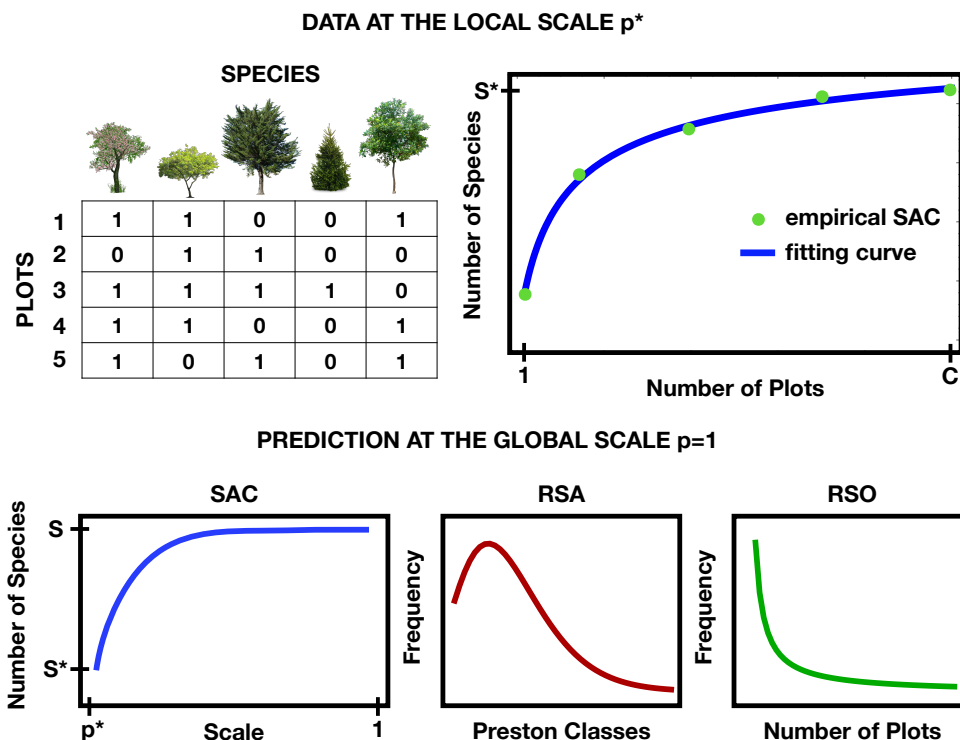

Figure 1: **Schematic presentation of our theoretical upscaling framework.** It consists of three steps. (A) We start from a dataset in the form of a binary matrix giving information on the presence or absence of S^* species within each of the C surveyed plots. (B) We perform the best fit of the empirically SAC computed via 12. (C) Using the best-fit parameters obtained in (B) and using our upscaling Eqs. 7, 8 and 11, we predict the species richness S of the whole forest and three important macro-ecological patterns: the SAC, the RSA and the RSO.

2. Results

2.1. Tests on in-silico databases

We test our presence/absence upscaling method on four computer generated forests without and with spatial correlations. Indeed, we expect that in the first case our framework will give more accurate estimates, and we wish to test how the introduction of correlations affect the reliability of our results.

As RSA we choose a negative binomial (NB forest) of parameters $r = 0.8$ and $\xi = 0.999$ and a log-normal (LN forest) with parameters $\mu = 5$ and $\sigma = 1$. Once generated the abundance of every species ($S = 4974$ for the NB forest and 5000 for the LN forest), we distribute the individuals within the forest area, here set equal to a square of 4900×4900 units, according to two different processes: at random or according to a Thomas process [38, 29, 39] with a clustering radius of 15 units.

We then divide each forest generated as described above into 98×98 units cells and compute the $C \times S$ presence/absence matrix, thus forgetting the information about the species distribution. Finally, we sub-sample the 5% of the cells (corresponding to a fraction $p = 0.05$ of the total forest area) and apply our method to infer the total number of species in each of the four *in-silico* forests.

We also compared our results to those obtained by accounting for the data on species populations with an abundance-based upscaling framework developed and tested in [29]. In the case of the NB forest, the two methods performed very well for both the random and the clumped distribution with an average prediction error below 1% in absolute value (see Table1). In the Thomas distributed forests, the error increased, although remaining around 3% for the presence/absence method and around 7.5% for the abundance-based one (using maximum likelihood methods. The latter percentage error can be improved using calibrated statistical method for the single fit). Thus, with respect to the degree of individuals' clustering, the new framework seems to give more robust estimates than the second one. This is due to two main reasons: 1) For the presence-absence case, we fit the empirical SAC, which has a very smooth functional shape, and it is easy to describe through our analytical SAC. On the other hand, the RSA displays a more complex and variable shape and thus fitting it with the NB is a more delicate task (indeed we find sensible differences on the accuracy using different statistical methods for the fit); 2) Binary data on which the empirical SAC is based are less sensitive to sampling fluctuations.

2.2. Tests on real databases

We finally test our method on sub-samples taken from two empirical forest data for which we have informations on both species occurrence and abundances. In particular we extract abundances of tree species observed in 50ha of rainforests from Pasoh (Malaysia) and Barro Colorado Island (Panama) together with the spatial locations of each of their individual.

Firstly, we divide both forest data into a grid consisting of $C = 800$ equal-sized cells of area 625 m^2 and we derive the $C \times S^*$ presence/absence matrix for the S^* observed species ($S^* = 927$ for Pasoh forest and 301 for BCI). We then sub-sample species occurrence for different fractions $0 < p < p^*$ of the cells and apply our

Table 1: Predictive error for three generated forest (characterized by a log-normal and a negative binomial RSA) having individuals distributed according to a high clustering Thomas process and at random. Tests were performed by sampling a fraction $p = 0.05$ of each forest and by applying our framework (P/A columns) and the abundance-based method (RSA columns) to predict the true number of species S (5000 for the LN forest and 4974 for the NB forest). For each estimated S_{pred}, the average relative percentage error $(S_{\mathrm{pred}} - S)/S \cdot 100$ between the true number of species and the predicted one is shown together with the corresponding standard deviation. Results are relative to 100 iterations.

| | Spatial Distribution | | | |
| Forest RSA | Random | | Thomas | |
	P/A	RSA	P/A	RSA
Log-normal	3.1 ± 0.51	7.6 ± 0.52	2.5 ± 1.8	7.2 ± 3.1
Negative binomial	-0.50 ± 0.34	-0.52 ± 0.28	-0.81 ± 1.6	-0.60 ± 1.7

framework to infer the number of species and other biodiversity patterns (RSA, RSO and SAC) at the corresponding largest empirically-observable scale p^*, for which we know the ground truth.

We compared our results on species richness obtained only from presence-absence data with the most popular non-parametric indicators proposed in the literature [30, 11], which are summarized in Table2. We found that our method outperforms all the others for both BCI and Pasoh forests. We also remark that all these methods have the further limitation that they can only infer the total species richness, without allowing for an estimate of the abundances' and occurrences' distributions, i.e the shape of the RSA and the RSO.

Indeed, as shown in Figure 3, from the local presence-absence data, we can reconstruct, among the SAC and RSO, the RSA at the whole tropical forest scale, thus relating species occurrence data with information on the abundances. In particular we can see that the inferred RSA are statistically comparable with the empirical ones obtained by using all the information on species' abundances which we deleted before applying our method.

Another biodiversity pattern that we can infer from our framework is the RSO. As shown in Figure 3, we find that, as for the RSA, this pattern seems to have a universal form which can be well described and correctly inferred through our neutral approach.

We highlight that the SAC (green line), the RSA (red line) and RSO (blue line) predicted patterns in Figure 3 have not been obtained through the fit of some pa-

Table 2: Summary table of the most popular biodiversity estimators for presence/absence data.

| Estimator	Predicted S	Details
NB	$S^* \dfrac{1-(1-\xi)^r}{1-(1-\hat{\xi}_{p^*})^r}$	$(\xi,\, r)$ NB parameters at $p=1$ $(\hat{\xi}_{p^*},\, r)$ NB parameters at p^*
Chao$_2$	$S^* + \begin{cases} \dfrac{C-1}{C}\dfrac{Q_1^2}{2Q_2} & Q_2 > 0 \\[2ex] \dfrac{C-1}{C}\dfrac{Q_1(Q_1-1)}{2} & Q_2 = 0 \end{cases}$	$Q_i = \#$ of species detected in i plots at the scale p^*
iChao$_{i2}$	$S_{Chao_2} + \dfrac{C-3}{4C}\dfrac{Q_3}{Q_4}\max\left(Q_1 - \dfrac{(C-3)Q_2 Q_3}{2(C-1)Q_4},\, 0 \right)$	$S_{Chao_1} = S$ predicted by $Chao_1$ method
Chao$_{wor}$	$S^* + \dfrac{Q_1^2}{\frac{C}{C-1}2Q_2 + \frac{p^*}{1-p^*}Q_1}$	
Jacknife$_1$	$S^* + \dfrac{C-1}{C}Q_1$	
Jacknife$_2$	$S^* + \dfrac{2C-3}{C}Q_1 - \dfrac{(C-2)^2}{C(C-1)}Q_2$	
Turing	$S^*_{abun} + \dfrac{S^*_{rare}}{\hat{C}_{rare}}$	$S^*_{abun} = \sum_{n>10} Q_n$ $S^*_{rare} = \sum_{n=1}^{10} Q_n$ $\hat{C}_{rare} = 1 - Q_1/\sum_{n=1}^{10} nQ_n$
ICE	$S_{Turing} + \dfrac{Q_1}{\hat{C}_{rare}}\hat{\gamma}^2_{rare}$	$\hat{\gamma}^2_{rare} = \max\{\gamma - 1, 0\}$, where $\gamma = \dfrac{S^*_{rare}C_{rare}}{\hat{C}_{rare}(C_{rare}-1)}\dfrac{\sum_{n=1}^{10} n(n-1)Q_n}{(\sum_{n=1}^{10} nQ_n)(\sum_{n=1}^{10} nQ_n - 1)}$ $C_{rare} = \#$ of samples containing at least one rare species
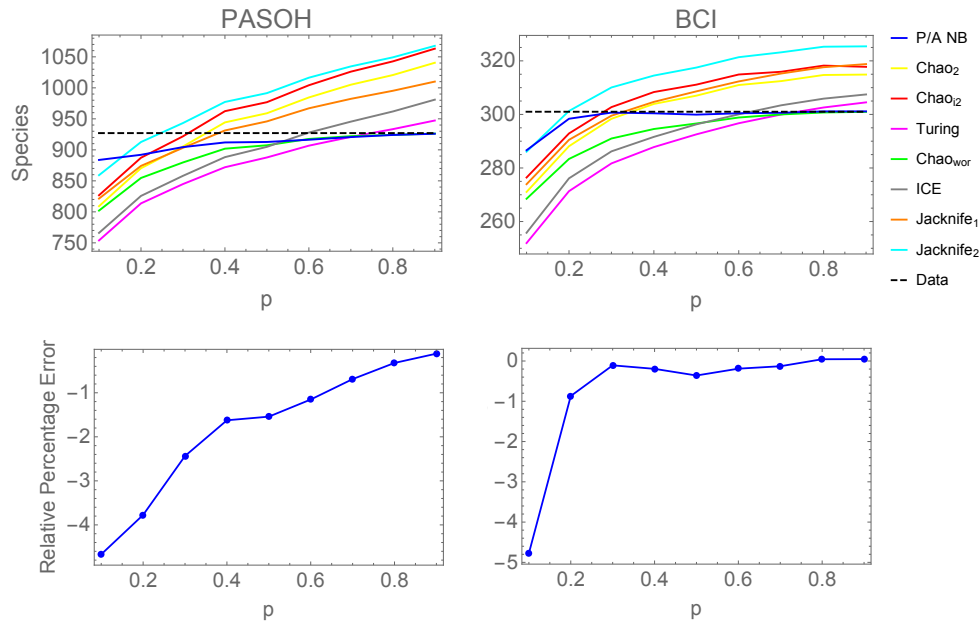
Figure 2: **Test from different scales for Pasoh and BCI.** For each forest we sub-sample a fraction $0 < p < p^* = 1$ of the available spatial cells and apply different popular upscaling methods based on presence/absence data (see Table 2) and our method to predict the true number of species, S^*, observed in our data. While our (P/A NB) and Chao_{wor} methods do converge at S_{p^*} as p goes to p^*, all the others have a monotonically increasing behaviour due to the independence, in their predictions, of the scale p. We can see that for both rainforest, our method outperforms all the others. Bottom panels show the relative percentage error $(S_{\text{pred}} - S^*)/S^* \cdot 100$ obtained with our framework between the predicted number of species S_{pred} and S^*. We find that the method underestimated the true number of species of at most 5%. The larger the sample area, the smaller the relative error.

rameters, but they have been analytically predicted through our upscaling equations 1118. The only fitting occurs at the scale $p = 0.1p^*$ using the empirical SAC to parametrize eq. 12. In other words, by fitting species occurrence data at the sample scale, our framework allows to estimate: 1) The RSA at the sample scale; 2) The SAC, the RSA and the RSO at larger scales. We provide an open source R code that perform the above estimates giving as input only the presence-absence matrix data.

After testing our model on controlled computer generated data and real forest sub-samples, we apply our framework to predict the species richness of the two tropical forests. Moreover, we compare our results to those obtained with the upscaling framework based on RSA pattern previously developed and tested in [29] by our group.

We therefore predict, through the presence/absence method, the species richness
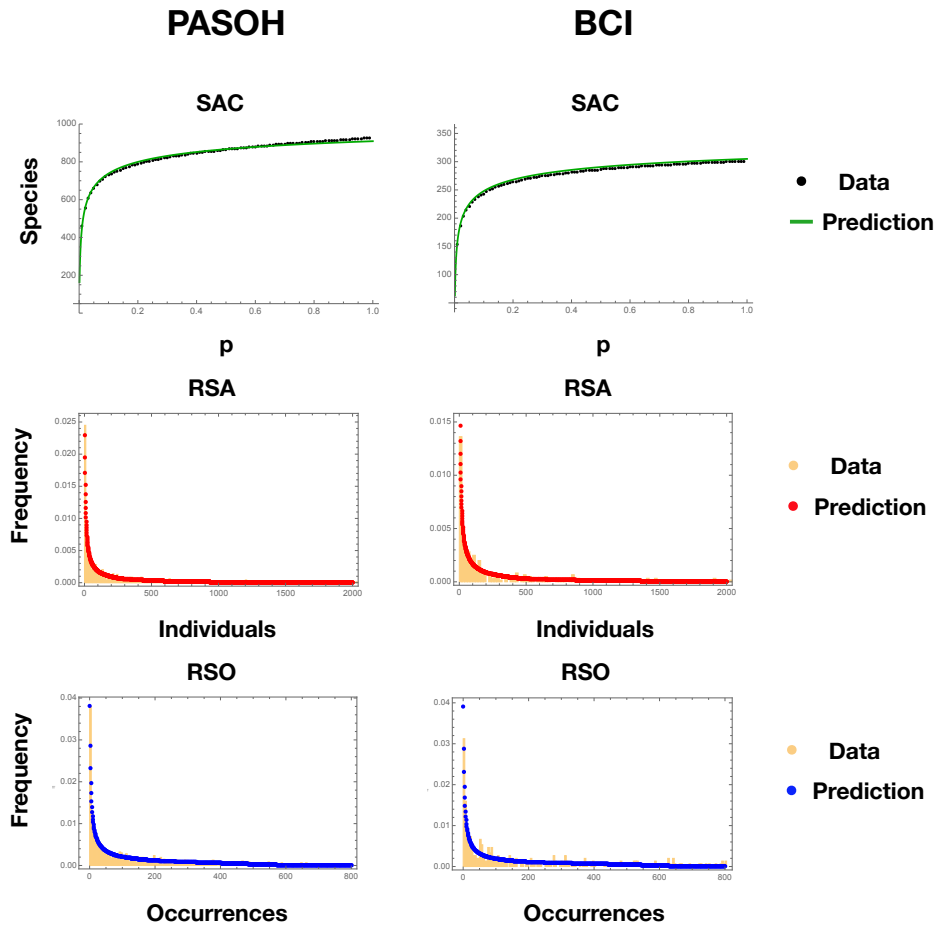
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Figure 3: **Test on ecological macro-patterns for Pasoh and BCI.** For each forest we sub-sample a fraction $p = 0.1$ of the available spatial cells and apply our framework to predict three important ecological pattern at the largest scale at which we have information, p^*. In the first row we see the prediction for the SAC curve, which describes how the number of observed species increases with the sampled area, from $p = 0.1$ to 1, corresponding to p^* in these tests. In the second row we plot the empirical RSA, the distribution of abundances across species against the framework prediction. Finally, in the third row we compare the ability of the model to capture the empirical RSO, i.e. the distribution of the occurrences (number of occupied cells) across species. For both forests, all the three patterns are well described by our framework.

at the whole forest scale ($p = 1$) for BCI and Pasoh tropical forests. Figure 4) shows the prediction of the overall (and unknown) SAC for a scale ranging from 50 to 14000 hectares for the Pasoh ($p^* \approx 0.0036$) and to 1560 for the BCI ($p^* \approx 0.032$). The blue curves represent the prediction obtained only using presence-absence data whereas red curves are the SAC inferred by exploiting also the information about species' population through the abundance-based method (see [29]).

We find that the two methods give comparable results for both the databases, a
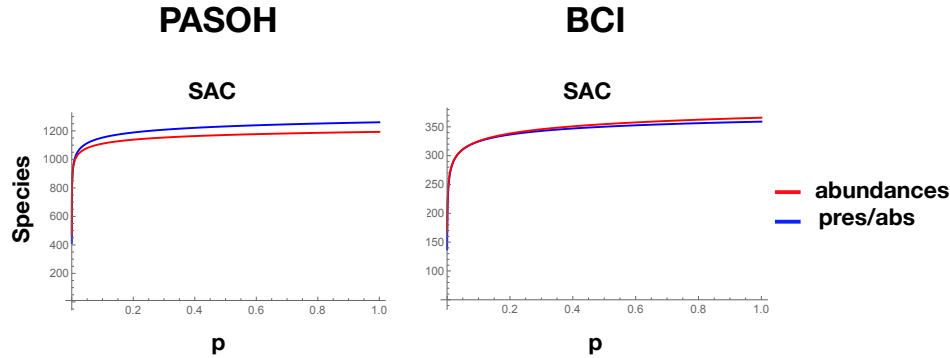
PASOH   **BCI**

Figure 4: **SAC predicted for Pasoh and BCI using abundance method versus presence/absence method.** Using all the available data for both tropical forest, we compare the prediction for the SAC curve obtained by the abundance method [29] with the results obtained with the presence/absence framework presented here. At the whole forests' scale $p = 1$, the two predictions are 3σ compatible ($S_{\text{Pasoh}}^{\text{abund}} = 1193 \pm 36$, $S_{\text{Pasoh}}^{\text{p/a}} = 1260 \pm 22$, $S_{\text{BCI}}^{\text{abund}} = 366 \pm 15$, $S_{\text{BCI}}^{\text{p/a}} = 359 \pm 2$).

confirm of the robustness of the theoretical framework.

3. Discussion

In this work we proposed and tested a novel rigorous statistical framework to upscale ecological biodiversity patterns from local information on species occurrence data. Different upscaling approaches have been proposed in ecological literature [26, 28, 40, 4, 9, 10, 11, 18, 41, 40]. However, to the best of our knowledge, they have not been generalized to the case of binary data. Our framework not only provides a generalization of the method recently proposed in [29] when only presence-absence information are available, but also allows to extract abundance distributions from species occurrence data. The underlying hypothesis that we need to do in order to perform these estimates is that the RSA at a given scale is a negative binomial distribution, a RSA that arises naturally as the steady-state species abundance distributions for ecosystems undergoing simple birth and death dynamics [42, 24]. The negative binomial is a simple and versatile distribution that depending on its parameters can display an interior mode or log-series like behaviour, i.e. it can accommodate different RSA shapes. Therefore we can use the same RSA function to reproduce different ecosystems' RSA, as those typically observed in real ecosystems [43, 44, 45, 35, 46, 47, 48, 49, 24]. Even more generally, by using mixtures of negative binomials - a case for which our framework still works - we can fit more complex RSA shapes (see [29]).

Furthermore, we introduce a new descriptor of biodiversity within an ecological community, the RSO, which describes the distribution of species occurrences in scattered plots. The RSO distribution displays a fat tail, indicating that many species typically occupies only few scattered plots, while only very few species are pervasive and are found in most of the plot. Our prediction is that this property is not particular for the dataset here considered, rather it is another emergent patterns [50, 24] pervasive in highly biodiverse ecosystems. Our framework gives directly all parameters of the RSO by solely fitting the SAR curve, through which one can obtain the r and ξ parameters, which well describe both the RSA and the RSO distributions at all spatial scales of interest.

Expanding the ability to upscale species richness and obtain abundance distributions from presence-absence data is of fundamental importance in many contexts, where abundance information are not available or trustable. This is particularly true for microbial or marine (e.g. plankton) ecological data obtained from metagenomics [51] and 16S ribosomal gene sequences [52]. The use of sequence-based taxonomic classification of environmental microbes has exploded in recent years [52, 53, 51, 31] and these approaches are becoming a standard method for characterizing the biodiversity of both prokaryotes and eukaryotes [53]. Thanks to advance in high throughput sequencing we begin to be able quantifying the vast number of microbes in our environments, expanding our knowledge on microbial diversity [31]. However, large fractions of the sequence reads remain unclassified [51] and also species abundance estimated have a very high uncertainty [31]. Thus, being able to estimated species richness and abundance distributions from species occurrence data may lead to a big step-forward in the taxonomic classification of microbial ecosystems.

To summarize, this flexible analytical method provides, from local presence/absence information, robust estimates of species richness and important macro-ecological patterns of biodiversity (SAC, RSA, RSO), as tested in both *in-silico* generated and two rainforests. The method may be applied to any database in the form of a binary matrix, where presence/absence features (tree species in our case) are detected across different samples.

Data Availability

All data are publicly available. The Pasoh and Barro Colorado Island datasets are provided by the Center of Tropical Research Science of the Smithsonian Tropical Research Institute (http://www.ctfs.si.edu/site).

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