Economic Valuation of Changes in the Amazon Forest Area
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Priority Areas for Biodiversity Conservation in the Brazilian Amazon

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Publisher: Centro de Sensoriamento Remoto/UFMG
Belo Horizonte
2016
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Priority Areas for Biodiversity Conservation in the Brazilian Amazon

Abstract

Biodiversity provides a wide range of ecosystem services that have important economic values. Although these economic values are difficult to measure, areas with high biodiversity, overall, contain more biological resources and thus are more valuable from an economic point of view. The objective of this study is to map biodiversity in the Brazilian Amazon under the assumption that biodiversity values for conservation are related to economic values. We used the most comprehensive dataset on biodiversity to date to identify the priority areas for biodiversity conservation in the Brazilian Amazon. Our analyses focus on composite biodiversity metrics that equally emphasize a set of biodiversity parameters, namely weight endemism, areas of endemism, and species richness. The geographical differentiation of these quantitative variables are presented in maps that account for both heterogeneity and irreplaceability measures. Our approach also includes analysis of uncertainty due to lack of knowledge about biological data. Modeling results indicate that 13% of the Brazilian Amazon is of high relevance for conservation of biodiversity. These areas may also hold higher potential economic value. Yet, vast areas still need detailed biological inventories, making it inviable to compare their relevance with those of other areas where there is more biological knowledge. Regions with high biological relevance are located in areas under deforestation pressure, making them a top conservation priority. These results are useful inputs for valuation studies of biodiversity in the Brazilian Amazon.
1. Introduction

“To value something, you first have to know what it is” [1]

This work is part of a research program aiming at expanding and improving the empirical knowledge of the local and regional-scale economic values from the Amazon rainforest and its ecosystem services, named “Economic Valuation of Changes in the Amazon Forest Area”. By mapping the changes in economic values, which result when forest cover changes across the Amazon biome, this research program aims to show how changes in the value of ecosystems services are differentiated geographically. The objective of this report is to map priority areas for biodiversity conservation across the Brazilian Amazon. These maps provide a basis to access the economic value of biodiversity across the Brazilian Amazon.

The Amazon forests contain a wide variety of resources that have an important economic value [2]. Economic values may be linked to ecological services and goods, such as timber and non-timber forest products, regulation of biogeochemical cycles, as well as the potential for new pharmaceutical products [3]. However, most ecosystem services are difficult to measure from an economic point of view. Of them, biodiversity is the most challenging one [2, 4].

Stated preference is often regarded as a feasible method for estimating the perceived aesthetic, recreational, educational and inspirational (in other words, psychological) value of an ecosystem, of which one of the attributes is biodiversity. The material benefits of an ecosystem service (food or other biological commodities, medical, genetic, and ornamental resources) are often estimated by using direct-market methods. Nevertheless, measuring the economic value of biodiversity is not trivial. To do so, there is a need to relate biodiversity both to its potential indirect use value\(^1\) (e.g. cultural ecosystem services such as recreation) and to its direct role in supporting the associated ecosystem services.

Indeed, biodiversity is associated with various ecosystem services that have economic values [5] and sites with higher biodiversity provide more ecosystem services [3, 6, 7]. These economic values can be "tangible" (directly measurable) and "non-tangible" (not directly measurable). For example, natural pharmaceutical products are directly correlated with biodiversity, the more diverse the ecosystem is, the higher is its potential for pharmaceutical product development [2]. The discovery of new drugs is often associated with new knowledge of biodiversity. Because of the paucity of knowledge about species and lineages, and consequently on the metabolic products

\(^1\) An indirect use arises from a healthy biological system, which if it is useful to humans because of its ecosystem services.
that can be extracted from these organisms, it is likely that several biological substances of chief importance for the pharmaceutical industry are yet to be discovered [8].

Pollination is an important biological ecosystem service maintained by native vegetation that has a great value to agricultural production, such as the fruits we eat (apples, oranges, etc.) and drink (coffee) [9, 10]. Tourism and recreation are also direct ways of obtaining economic value from biodiversity. Furthermore, maintaining biodiversity in natural landscapes have an indirect value associated, for example, with the prevention of infectious diseases [11-13], given that the proliferation of various tropical infectious diseases results from anthropogenic degradation of natural landscapes [12, 14]. Biodiversity losses from deforestation and habitat degradation ensue therefore economic losses [15, 16].

The mapping of conservation priority areas here is based on irreplaceability measures. Irreplaceability measures characterize places with a unique biota that, if lost, cannot be replaced from elsewhere. These measures aim to identify the extent to which a geographic location is irreplaceable in relation to species and/or lineages existing therein. Many studies have applied complementarity techniques for identifying priority areas for conservation [17, 18, 19, 20, 21], although most methodologies [17] and studies in this topic still ignore the ample shortfall in our knowledge about tropical biodiversity [18, 19]. As a result, those studies may be compromised by geographic bias in sampling species distribution, including gaps in data collection [22], producing unrealistic results, especially in tropical regions [22]. They are, thus are inefficient in orienting the protection of biodiversity [22] in vast forested areas such as the Amazon. Another problem related to mapping conservation priority areas in tropical countries is the use of taxonomic groups, such as birds, as surrogates for other groups of organisms. In temperate regions, surrogates of species and taxonomic groups have been successfully used for pinpointing biodiversity conservation priority areas [23]. However, in tropical countries, this is not the case due to the complexity of biogeographic patterns [19].

On the other hand, the composite use of a wide range of biodiversity variables such as species richness, endemism, and areas of endemism together with variables on the evolution of species, namely phylogenetic diversity, may reduce the knowledge gap on the distribution of individual species [4]. Even so, there is still a need to consider the uncertainty in sampling of biodiversity data in order to draw realistic conclusions. In this regard, it is important to acknowledge that while in some locations there are appropriate datasets that enable reliable conclusions in other locations there is still a large uncertainty due to sampling gaps. Aware of these issues, we have taken advantage of a comprehensive dataset including several taxonomic groups (see dataset description in the methods section) and used a set of biodiversity variables in order to map priority areas for conservation of biodiversity in the Brazilian Amazon. Our major set of
quantitative variables includes species richness, area of endemism, phylogenetic endemism, and endemicity. Data on species occurrence for all groups were used for estimating these variables. We selected these variables because they refer to different biodiversity aspects and thus their correlation is low (see correlation coefficient in result section). These quantitative variables were then integrated based on phylogenetic composition and species composition criteria (Figures 1 and 2). Species richness, endemism, and areas of endemism have equal weights in mapping priority for biodiversity conservation based on consensus of Species Composition and Phylogenetic Composition. Table 1 lists and defines the biological variables used in our analysis.

![Diagram of biodiversity conservation](image)

**Figure 1** - Main variables involved in modeling priority areas for biodiversity conservation.

**Table 1 - Biological variables used in our analysis.**

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Biological variables</th>
<th>Description</th>
<th>Variable Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quantitative variables</td>
<td>Areas of Endemism</td>
<td>Number of species with similar distribution (high sympatric) per unit of area</td>
<td>continuous</td>
</tr>
<tr>
<td></td>
<td>Species Richness</td>
<td>Number of species per unit of area (including all groups in our dataset)</td>
<td>continuous</td>
</tr>
<tr>
<td></td>
<td>Endemity</td>
<td>Number of species with small range of distribution (endemic) per unit of area</td>
<td>continuous</td>
</tr>
<tr>
<td></td>
<td>Phylogenetic Endemism</td>
<td>Number of evolutionary lineages with small range of distribution (endemic) per unit of area</td>
<td>continuous</td>
</tr>
<tr>
<td>Regionalization</td>
<td>Species Composition</td>
<td>Unique set of species</td>
<td>discrete</td>
</tr>
<tr>
<td></td>
<td>Phylogenetic Composition</td>
<td>Unique set of evolutionary lineages</td>
<td>discrete</td>
</tr>
</tbody>
</table>
Figure 2 - Modeling of Biodiversity conservation priorities. Quantitative variables: species richness, endemism, and areas of endemism present equal weight in model. Conservation priorities analysis consist of summing the quantitative variables (species richness, endemicity, and areas of endemism) in regionalized map (consensus of Species composition and Phylogenetic composition). All species and groups were included in the analysis.
2. Biological variables

2.1. Datasets of Species Occurrence

We compiled occurrence data on terrestrial angiosperm, arthropods, and vertebrates in the Brazilian Amazon through a partnership with several researchers as follows:


In the angiosperm groups, we included only the most speciose (with high number of species) and widely distributed families in Brazil: Asteraceae, Bromeliaceae, Fabaceae, Melastomataceae, Myrtaceae, Orchidaceae, Poaceae, and Rubiaceae. For the arthropods, we compiled data on bees, spiders, polydesmid millipedes, flies, tiger moths, dragonflies, and Orthoptera. Vertebrates include birds, mammals, and amphibians. To take full advantage of our comprehensive database, we used in the analyses the occurrence data for all the species conjointly.

We compiled occurrence data from the following online databases: GBIFii, CRIAiii, Birdlife Internationaliv, HerpNetv, Nature Servevi, and Orthoptera Species Filevii. We also compiled data from the taxonomic literature and biodiversity inventories. We checked all the data for veracity and geographic accuracy by overlaying the species maps on administrative units in which data were reportedly collected. The samples with valid names totaled 113,571 georeferenced records (Figure 3). Records missing geographic coordinates or with locational errors were georeferenced using the maps of Brazilian municipalities from IBGExiii. We reviewed all data for the validity of taxonomic names using specific catalogues and direct checking by experts on each group. All statistical analyses were performed using R softwareix.

The occurrence dataset reveals that same sampling sites are used to report occurrence of different species and groups, while there is a significant area of the Brazilian Amazon with no data for any species or groups.

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ii http://www.gbif.org
iii http://www.splink.org.br
iv http://www.birdlife.org
v http://www.herpnet.org
vi http://www.natureserve.org
vii http://www.orthoptera.speciesfile.org
viii http://mapas.ibge.gov.br
ix http://www.r-project.org
2.2. Phylogenetic Datasets

In order to identify patterns of distribution of evolutionary lineages, we compiled phylogeographic trees of taxa with geographic range limited to the Amazon rainforest. The phylogenetic trees were converted to published figures in newick format using TreeSnatcherPlus software [24]. Since branch lengths are not comparable between different trees and are sometimes not even available, we arbitrarily considered all branches length equal to one. All trees were merged into a supertree by using the recent review of tree of life [25]. In addition, we used the branches of phylogenetic trees [25] obtained through empirical studies of phylogenetic reconstruction to complement our phylogenetic sampling of taxa for the Amazon. Excluded branches were thus obtained through the taxonomic classification. For the spatialization of phylogenetic information, we also compiled all occurrence data on taxa (or populations) sampled in the source trees. Additional geographic locations for trees missing geographic coordinates were georeferenced by using maps from the original publications or from online databases*.

* http://mapas.ibge.gov.br
2.3. Species Composition

We used statistical ordination to describe the spatial variation in species composition (unique set of species). Spatial variation in species composition is usually mapped through Generalized Dissimilarity Modelling (GDM) [26], which assumes a correlation between environmental variables and species composition. Since results of GDM may be affected by sampling bias, we prefer not rely on the premises of this method. Instead, we implemented an analogous analysis by using Non-metric Multidimensional Scaling (NMDS) of species distribution interpolated on a map. This procedure, which assumes only spatial autocorrelation (how much a variable changes across the space), was performed through the following steps (Figure 4):

1) An species presence/absence matrix was assembled on a grid of 0.5 degree (=50 width) hexagonal cells laid over species distribution maps.
2) Cell-to-cell Bray-Curtis dissimilarity matrix was calculated.
3) The matrix was analyzed through NMDS with a 10,000 random starts used to find the lowest stress values and three axes.
4) The NMDS scores (for each axis) were plotted on the centroid of each hexagonal cell.
5) Interpolation from centroids using an empirical Bayesian Kriging technique, which considers that intermediate values occur proportionally to the distance between points in a normal distribution following a smooth curve [27]. In particular, this means of interpolation solves the problem of choosing the model parameters, since it automatically calculates the parameters using subsetting and Monte Carlo simulations. Empirical Bayesian kriging differs from traditional interpolation methods because it accounts for the error introduced when estimating the semivariogram, whereas other methods calculate the semivariogram from known data locations and use it to make predictions at unknown locations, assuming that the estimated semivariogram is true. By not taking the uncertainty of semivariogram estimation into account, other kriging methods thus underestimate the standard errors of prediction [27]. As a result, we obtained three surface maps (one for each axis) with interpolated NMDS scores.
6) These maps are summarized on a single RGB map, with a different color representing each NMDS axis. Grid cells with less than ten records were excluded from the analysis, since they could inflate Bray-Curtis dissimilarity, influencing the NMDS results. To verify whether our data were appropriate for this procedure, we tested the premise of our interpolation by using spatial autocorrelation analysis of the NMDS scores. The NMDS analysis was performed using the R software\(^{xi}\) package vegan\(^{xii}\) and Bayesian Kriging interpolation in ArcGIS [28].

\(^{xi}\) www.r-project.org
\(^{xii}\) http://cran.r-project.org, http://vegan.r-forge.r-project.org
Figure 4 - Steps of spatial modelling of species composition.
2.4. Phylogenetic composition

We stamped the phylogenetic composition (areas with a unique set of evolutionary lineages) on a grid of 1 degree (~100 km width) hexagons. The variation in phylogenetic composition were obtained from a matrix of phylogenetic beta diversity measured using the PhyloSor index [29]. To linearize matrix values, and then spatialize them, we transformed matrix into a three linear axes representation using NMDS analysis. The lowest stress values in the three axes of the NMDS were determined through 10,000 random starts. To spatially interpolate NMDS scores, considering the inherent data uncertainties, we used an empirical Bayesian Kriging technique. The phylogenetic beta diversity was calculated using R software package betapart\textsuperscript{xiii}.

2.5. Areas of endemism

We identified Areas of Endemism (AoEs)—regions containing species with similar distributions—using Geographic Interpolation of Endemism (GIE) [30]. In this process, species were classified into nine groups according to the distance between the centroid and their farthest distribution point: up to 50 km, 51–200 km, 201–400 km, 401–600 km, 601–800 km, 801–1,000 km, 1,001–1,500 km, 1,501–2,000 km and between 2,001 and 3,299 km. To generate the consensus AoEs, we rescaled each map to values between 0 and 1 to avoid different weights of AoEs. To check the influence of sampling effort in the results, we performed a correlation analysis with corrected degrees of freedom [31] between the kernel index of AoEs and the kernel index of interpolated density of distribution records as a surrogate for the sampling effort. As a surrogate for the sampling effort, we used the density of records (kernel interpolation). In the kernel analysis, we used as the area of influence around each distribution record the value calculated by the spatial variant of Silverman’s Rule of Thumb implemented in ArcGIS. This procedure produces an approximated Gaussian distribution for the distances from interpolated points.

2.6. Species richness

Species richness (number of species per unit area) is the biodiversity variable most influenced by the sampling effort [19]. In this way, the most direct way of estimating species richness, \textit{i.e.} summing the number of species per sampling unit (squares or hexagons), may produce unrealistic spatial patterns. As an alternative, some studies apply species distribution modeling (SDM) to estimate the distribution of species and sum the resulting distribution maps to obtain a species richness model [32, 33]. However, this approach may be biased due to the influence of the collection effort.

\textsuperscript{xiii} http://cran.r-project.org/web/packages/betapart/index.html
To resolve this problem, we applied resampling techniques to generate a uniform sampling distribution throughout the study area. Thus, reducing the effect of the collection effort on the species richness.

To create a uniform sampling, we used a fixed number of records for each hexagon. Thus, we set a minimum number of records per sample (hexagon) and we selected randomly a subsample (percentage of this minimum number of records in the samples) (Figure 5). In this way, all hexagons in the study area had the same number of records in subsamples. In each hexagon, we counted the number of species of a subsample. This procedure was repeated 1,000 times and the average of the species richness was recorded for each hexagon (Figure 4). Hence, we obtained the relative values of species richness based on a uniform sampling throughout the study area, thus largely reducing the effect of sampling effort on mapping species richness. In order to represent species richness in a continuous way, we applied the empirical Bayesian Kriging Interpolation (see details in section 2.3).

To check on how the different parameters of this resampling we conducted may affect the results, we carried out sensitivity tests of each parameter of this species richness model (figure 4). To identify the best combination of parameters, we tested the correlation between the species richness of models generated with each set of parameters and the sampling effort. The model that showed the lowest ratio between sampling effort and species richness was selected as the best and interpolated by Bayesian Kriging.

1) Test of size of sampling units: We defined hexagonal partitions as sampling units. Since the size of the hexagons can influence the analysis, we tested the effect of different sizes (1, 1.5, and 2 degrees).

2) Test of sample size: The number of records in the sample may also influence the results. To deal with this issue, we conducted tests with different sample sizes (50, 100 and 200 records per hexagon).

3) Test of size subsamples: Again, the size of the subsamples can influence the results. In order to solve this issue, we tested different sizes of subsamples (25, 50 or 75% of the hexagon sample).
In order to represent species richness in a continuous way, we applied the empirical Bayesian Kriging Interpolation (see details in section 2.4) (Figure 6).

2.7. Endemicity

To identify endemicity patterns (predominance of restricted species distribution in a specific location), we used the index of Weighted Endemism method (WE) [34]. This index yields a value to each specie that is equal to the inverse of the species' distribution area. The endemism was expressed as the sum of WE index for each cell (hexagons with 1 degree) for obtaining the general pattern of endemism. To extrapolate the index of weighted endemism onto a continuous surface, we used the empirical Bayesian kriging interpolation (2.4 section).

2.8. Phylogenetic Endemism

To identify geographic patterns of phylogenetic endemism (predominance of restricted evolutionary lineages distribution in a specific location), we used the index of Phylogenetic Weighted Endemism (PWE) method. The phylogenetic endemism was expressed as the sum of index of terminals for each cell (hexagons with 1 degree) for obtaining
the general pattern of phylogenetic endemism. To extrapolate the index of weighted endemism onto a continuous surface, we used the empirical Bayesian kriging interpolation (2.4 section).

2.9. Sampling Effort (Uncertainty inherent to data)

For mapping uncertainty, we estimated the density of records (Kernel Interpolation) as a surrogate for the sampling effort. In the Kernel analysis, we used an area of influence around each distribution record, the value calculated by the spatial variant of Silverman’s Rule of Thumb implemented in ArcGIS. This procedure provides an approximation of the Gaussian distribution of the distances from interpolated points.
3. Methods

3.1. Regionalization map

Regions may have different biota, what justifies the analysis of complementarity employed in various conservation studies. Areas with distinct biota are not comparable because each biota is irreplaceable, i.e. they cannot be found elsewhere. To overcome this problem, we used a composition of variables of species/phylogenetic to regionalize the Brazilian Amazon (Figure 2). As a result, we determined areas that contain a unique combination of species/lineages. To produce a map of biogeographic regions (places with unique composition of species/lineages) we carried out an unsupervised classification of species/phylogenetic composition. We used the maximum likelihood algorithm for the tree axes of NMDS species composition map plus the Phylogenetic composition map. To determine the ideal number of areas (classes) for performing unsupervised classification, we ran several times the classification algorithm varying the number of classes from 2 to 60. We considered as the optimal number of classes the limit beyond which the class regions do not change their shapes. To this end, we analyzed the spatial correlation between the map with $n$ classes and the map of $n + 1$ classes.

3.2. Model of biodiversity conservation priority areas

In order to map priority areas for conservation in the Brazilian Amazon, we summed three quantitative maps of biodiversity (species richness, weight endemism index and areas of endemism). To avoid that one variable would weigh more than others, all variables were rescaled between 0 and 1 (Figures 1 and 2).

To combine the quantitative variables with the biogeographic regionalization, we rescaled the of quantitative variables (scale between 0 and 1) in each area of the regionalized map. Thus, for each biogeographical unit, it was obtained an equal maximum value of priority. As a result, sites with high and low priority for conservation can be identified only within each biogeographical unit.

In order to include uncertainty into the model, we combined the results of the biological priority modeling with the map of uncertainty due to sampling effort. This allowed us to identify on the map of priority sites for conservation where the results have more empirical support based on the sampling effort (Figure 2).

To evaluate the effectiveness of using surrogates (taxonomic groups) for pointing out conservation priorities, we evaluated three models built only with data from one taxonomic group (vertebrates, arthropods or angiosperms).
3.3. Model optimization

To evaluate the effectiveness of our prioritizing conservation method, we performed five test sets to choose the model that protected more species, evolutionary lineages, phylogenetic endemism and endemism:

1 – **Threshold test**: To evaluate the effect of threshold (transformation of conservation model to binary map) we assessed four thresholds: 10, 20, 25 and 30%.

2 – **Variable test**: We removed variables to test its importance. In addition, we tested the use of only one quantitative variable (excluding others) to check the feasibility of using only one variable as an indicator of conservation priority.

3 – **Weight test**: To test the effect of the weights for combining the quantitative variables, we created models in which each quantitative variable had a weight of 1, 2 and 4.

4 – **Phylogenetic test**: To test the contribution of phylogenetic data to protecting evolutionary lineages and phylogenetic endemism, we created a model without phylogenetic data.

5 – **Group test**: To evaluate the effectiveness of using surrogates for pointing out conservation priorities, we evaluated three models, with parameters that performed best in the previous tests, built only with data from one taxonomic group (vertebrates, arthropods or angiosperms).
4. Results

4.1. Biological metrics

The biological metrics have low correlation (Table 2), except for the index of weight endemism (Figure 7) and phylogenetic endemism (Figure 8), which presents a moderate correlation with the sampling effort (Figure 16). The index of endemism (WE) identifies few regions that concentrate a large number of species of restricted geographic range; these areas coincide with the locations of greater sampling effort.

The remaining variables show low correlation with the sampling effort.

Table 2 - Correlation between variables.

<table>
<thead>
<tr>
<th></th>
<th>Areas of Endemism</th>
<th>Endemism Index</th>
<th>Species/phylogenetic composition</th>
<th>Species Richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling effort</td>
<td>0.57</td>
<td>0.65</td>
<td>-0.07</td>
<td>-0.03</td>
</tr>
<tr>
<td>Areas of Endemism</td>
<td>0.50</td>
<td></td>
<td>-0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Endemism Index</td>
<td></td>
<td>-0.18</td>
<td></td>
<td>-0.03</td>
</tr>
<tr>
<td>Species/phylogenetic composition</td>
<td></td>
<td></td>
<td></td>
<td>0.24</td>
</tr>
</tbody>
</table>

Figure 7 - Index of Weight Endemism. The blue shades indicate areas with larger number of species of restricted geographic range.
Figure 8 - Index of Phylogenetic Weight Endemism. The hot colors indicate areas with larger number of species of restricted geographic range.

The resampling procedure used for producing the species richness index has proven efficient in removing the sampling effect from this variable ($r = -0.03$). In addition, the different simulated sampling designs showed no significant differences in their results (Figure 9). Thus, we opted for interpolating the values obtained in the sampling of 50 records and 25% of subsamples due to the lower effect of sampling effort (Figure 9, 10).

Figure 9 - Correlation between different sampling design and sampling effort (density of samples).
The analyses of phylogenetic and species composition resulted in a large number of regions. These regions loosely correspond to unique species and phylogenetic compositions. The regionalization of the Amazon in biogeographic zones (consensus of species/phylogenetic composition) resulted in 50 regions based on species/lineages composition (Figures 11, 12, 13).

The number of regions is result of the stabilization of geographic patterns (aggregation and number of classes) from the maximum likelihood classification (Figure 13). The correlation between the different numbers of classes stabilizes at the fiftieth class. The analysis of the areas of endemism identified numerous areas scattered throughout the Amazon. Some of these areas hold up to 422 unique endemic species (Figure 14).

The map of sampling effort indicates large collection gaps in the Amazon. Areas with greater sampling intensity are located near urban centers and alongside rivers and roads (Figure 15). Locations shaded in the colors from red to yellow correspond to areas where there are data on species occurrence, and hence a significant sampling effort (Figure 16). Locations shaded in colors from light green to blue might also be important areas of endemism, but without data on species occurrence. In the case of variables, such as species richness and endemicity, as they tend to be autocorrelated, they can be spatially predicted by using an empirical distribution model based on Bayesian assumptions.
Figure 11 - Regions of species composition. Each region presents a unique set of species. Colors indicate similarity between areas. Lines indicate significant breaks in species composition. These breaks are based on unsupervised classification (maximum likelihood algorithm) for the tree axes of NMDS species composition map.

Figure 12 - Regions of phylogenetic composition. Each region presents a unique set of lineages. Colors indicate similarity between areas. Lines indicate significant breaks in phylogenetic composition. These breaks are based on unsupervised classification (maximum likelihood algorithm) for the tree axes of NMDS phylogentic composition map.
Figure 13 - Regions of species/lineages composition (consensus of species and phylogenetic composition). Each region presents a unique set of lineages and species.

Figure 14 - Correlation between classification maps with n classes and n+1 classes. Dashed line indicates a nonlinear trend.
Figure 15 - Consensus of areas of endemism. The pink color indicates areas of endemism with the highest number of species as well as with higher distributional congruence. The areas shaded in light blue do not have either data or it is not an area of endemism.

Figure 16 - Biological sampling effort in Brazilian Amazon.
4.2. Biodiversity conservation priorities

The optimization tests indicated that the model with threshold 25%, with all variables with equal weight with phylogenetic data and based on all groups was the model that protected more species, evolutionary lineages, phylogenetic endemism, and endemism. This conservation priority model was effective in detecting areas of high biological significance, as indicated by our specific composite metrics. Overall, the model indicates that 13% of the Amazon area (including 94% of the species under analysis) consists of areas with high biological relevance either with high or low knowledge (Figure 17). Modeling results point out that about 4% of the Brazilian Amazon consists of areas with both high biological relevance and high biological knowledge (where 88% of the analyzed species occur). The areas with high biological relevance, but where knowledge is low, occupy 9% of the Brazilian Amazon (including an additional 6% of species not included in the areas of high relevance and high knowledge). The models based in one taxonomic group (Angiosperms, Arthropods or Vertebrates) had a worse result than the model with all groups. These models protect between 80% (Angiosperms and vertebrates) and 60% (arthropods) of species. Protecting less lineages (about 10% less), and endemism (10 -20% less) that the full model also (Figure 18).

The map of biodiversity conservation priority indicates several locations with high biological value (Figure 17). These hotspots occur in areas with low biological knowledge. A vast region of the Amazon is still poorly known in terms of biodiversity, and thus insufficient for determining the level of biological relevance. Modeling results also show that all biogeographical regions present sites of high biological relevance. Some of the high relevant sites locate both in remote regions and in along the deforestation arc.
Figure 17 - Biodiversity conservation priorities (classified).

Figure 18 - Biodiversity conservation priorities (classified) based on each taxonomic group: A, Angiosperms, B, Arthropods and C, Vertebrates.
5. Discussion

Our results indicate that 8% of the Brazilian Amazon comprises areas of high biological relevance for conservation and good knowledge. These areas may also contain high potential biological resources and thus economic value. Nevertheless, vast areas still need proper biological inventories and thus their biological relevance remains uncertain. Some biologically relevant sites locate in areas under deforestation pressure, thus should be a top priority for conservation.

The model of biological relevance for the Brazilian Amazon we developed has the largest empirical support for this type of analysis to date. Previous studies of conservation priorities in the Amazon used only data from a few taxonomic groups [35, 36] or indirect inferences about biodiversity [37]. In our study, we built the most comprehensive database on species occurrence for the Brazilian Amazon with more than 100,000 records. Our results have therefore a robust empirical support. By using state of the art techniques to deal with the inherent uncertainties in data, we were able to solve at a large extent the collection bias. Hence, our result of biological relevance sites in the Amazon is one of the most realistic approaches in light of our current knowledge.

The regionalization, through the composition of species/lineages, enabled the identification of high biological relevance sites distributed throughout the Amazon. This regionalization, efficiently replaces the complementarity [38] and optimization of priority areas techniques [39] and solves potential problems related to the use of complementarity in regions with sampling deficiency like the Amazon [22]. Of the quantitative variables, species richness, despite having a smaller correlation coefficient with collection effort, shows a low richness value in some regions of southeast (Figure 10) probably due to gaps in data collection. Quantitative variables enabled the identification of the most relevant sites within each biogeographical region, optimizing the choice of the most biologically relevant areas. This stands out when we compare the proportion of species/area in our model with the percentage of protected areas in the Brazilian Amazon. Our model indicates that 8% of the Brazilian Amazon has high relevance for conservation and good knowledge (covering 92% of the analyzed species, endemism, and evolutionary lineages and 86% of phylogentic endemism). On the other hand, protected areas (excluding indigenous lands) occupy 26% of the Brazilian Amazon but protect only 31% of the analyzed species. If we consider the indigenous lands and protected areas together, the areas under protection total 54% of the Brazilian Amazon but contain only 74% of the analyzed species. Moreover, we demonstrate that the models generated with one of taxonomic group (e.g. vertebrates) is less efficient in protecting biodiversity. This highlights the need for proper planning for establishing future conservation units in the Amazon and in other biomes as well [40]. In sum, these results demonstrate the high efficiency of our modeling approach in pinpointing sites that concentrate the largest number of species in very small geographic areas.
The Amazon contains a high heterogeneity in species/lineages composition. Considering the existence of large sampling gaps in this biome [19], it is possible that this heterogeneity is even higher. Most species have restricted distribution ranges and thus are difficult to sample. In addition, high heterogeneity is supported by the large number of AoEs identified with endemic species in the Amazon. Some studies, at the local scale, have also point out a large biota heterogeneity. Heterogeneity occurs even at the smallest scales of analyses. The high heterogeneity is due to the great habitat diversity present in this biome [41-44]. As a result, the geographic distribution of species in the Brazilian Amazon is quite complex, making very challenging the design of a compressive conservation strategy. Because areas with low biological knowledge may have a high biological relevance, they also require further biological inventories to understand the values of these areas.

Conservation as well as economic valuation of the Amazon biodiversity should therefore take into account the vast gap in our knowledge about this biome [19, 45, 46]. In this respect, evidences indicate that many species are still to be discovered [19]. Thus, we should not disregard these regions poorly sampled in the analysis of conservation and valuation of biodiversity [47]. Investment in coordinated inventories in these regions is therefore the best strategy for conserving these areas.

Although our model does not valuate the products and services of biodiversity, we assume that the sites with greater biodiversity may provide more ecosystem services [3, 6, 7]. In this respect, the great heterogeneity of the Amazon biota indicates a large economic potential across vast areas of this biome. Large variation in phylogenetic composition between areas is also a good indication of diversity of biological resources. If lost, this large diversity of the Amazon biota could entail large economic losses. The eastern and southern portions of the Amazon, where deforestation has advanced deeply [48], may have already lost such a diversity of biological resources. In addition, areas of potentially high biodiversity that have limited biological knowledge are important targets for both more scientific investigation and for conservation efforts until more and better information can be gained.

Our analysis focuses on a specific composite of biodiversity metrics that equally emphasizes weight endemism, phylogenetic endemism, areas of endemism, and species richness. These results could be used to valuate biodiversity in the Amazon by studies aimed at estimating the willingness to pay to conserve such an extraordinary world heritage. But to link any metric of biodiversity to economic value, it is necessary to include how a biological resource relates to economic value. Biological metrics may have relatively different influences for bioprospecting and for recreational values, for example. These are but some issues requiring further investigation in order to connect our biodiversity modeling to economic valuation.
6. References
