

## Multi-scale comparisons of tree composition in Amazonian terra firme forests

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**Abstract.** We explored the floristic composition of terra firme forests across Amazonia using 55 plots. Firstly, we examined the floristic patterns using both genus- and species-level data and found that the species-level analysis more clearly distinguishes among forests. Next, we compared the variation in plot floristic composition at regional- and continental-scales, and found that average among-pair floristic similarity and its decay with distance behave similarly at regional- and continental-scales. Nevertheless, geographical distance had different effects on floristic similarity within regions at distances < 100 km, where north-western and south-western Amazonian regions showed greater floristic variation than plots of central and eastern Amazonia. Finally, we quantified the role of environmental factors and geographical distance for determining variation in floristic composition. A partial Mantel test indicated that while geographical distance appeared to be more important at continental scales, soil fertility was crucial at regional scales within western Amazonia,

where areas with similar soil conditions were more likely to share a high number of species. Overall, these results suggest that regional-scale variation in floristic composition can rival continental-scale differences within Amazonian terra firme forests, and that variation in floristic composition at both scales is influenced by geographical distance and environmental factors, such as climate and soil fertility. To fully account for regional-scale variation in continental studies of floristic composition, future floristic studies should focus on forest types poorly represented at regional scales in current datasets, such as terra firme forests with high soil fertility in north-western Amazonia.

### 1 Introduction

One of the scientific challenges in tropical forest ecology is to map and understand the patterns of floristic composition and diversity (Prance et al., 2000; Phillips and Miller, 2002). Describing these patterns is important for predicting the mechanisms that determine species distributions and



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developing effective conservation strategies in the face of deforestation and climate change. Although progress is being made in assembling the large datasets that are required to understand patterns of tropical forest diversity (e.g. ter Steege et al., 2006; Pitman et al., 2008), large gaps remain, and the role of different processes determining these patterns at local, regional, and continental scales is poorly understood. It is therefore important to develop principles from existing information that can both inform current conservation policy and direct future research.

While there are practical challenges with species-based analyses in hyper-diverse Amazonian forests (e.g. Phillips et al., 2003), ideally it is preferable to study variation at the species, rather than family or genus level, because it is species that typically show restricted distributions and hence should best define floristic patterns. For example, phyto-geographic patterns of Brazilian savannah woodland were only clarified using species-level data on floristic composition (Ratter et al., 2003) and gradients in the floristic composition of plots of the Amazonian floodplain were recently resolved by species-level analysis (Wittmann et al., 2006). In addition, for a series of forest inventories in western Amazonia, Higgins and Ruokolainen (2004) showed that a reduction in taxonomic resolution, from species to genus to family level, resulted in a decrease in the mean floristic difference between sites (0.88, 0.58 and 0.32 respectively). This decline suggested that species-level analysis best resolved floristic differences between sites. However, in terms of describing the patterns of floristic variation in Amazonia, most studies have typically focused on either genus or family level comparisons (e.g. Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006). In contrast, studies at a species level have usually either focused on restricted areas in western Amazonia (e.g. Higgins and Ruokolainen, 2004; Phillips et al., 2003; Duque et al., 2009) or on a few taxa (e.g. Tuomisto et al., 2003a; Vormisto et al., 2004). Full species-level studies of floristic composition remain difficult to carry out at a continental scale in Amazonia because of the high diversity and difficulties of developing datasets with consistent identifications and nomenclature (Higgins and Ruokolainen, 2004). However, largely based on recent taxonomic publications (e.g. Vásquez, 1997; Jørgensen and León-Yáñez, 1999; Ribero et al., 1999), current ecological datasets do contain reliable species-level information for many taxa. These data could offer insights into whether results from current family- and genus-level analyses of floristic composition are likely to resemble future full species-level analyses.

A second feature of current published analyses is that they typically focus on a single spatial scale. However, understanding the relative magnitude of regional and continental variation in species composition is important for assessing the sensitivity of continental-scale compositional patterns to restricted sampling of regional floristic variation. For example, north-western Amazonia is known for its high beta diversity at a regional scale (Tuomisto et al., 2003a), but it is

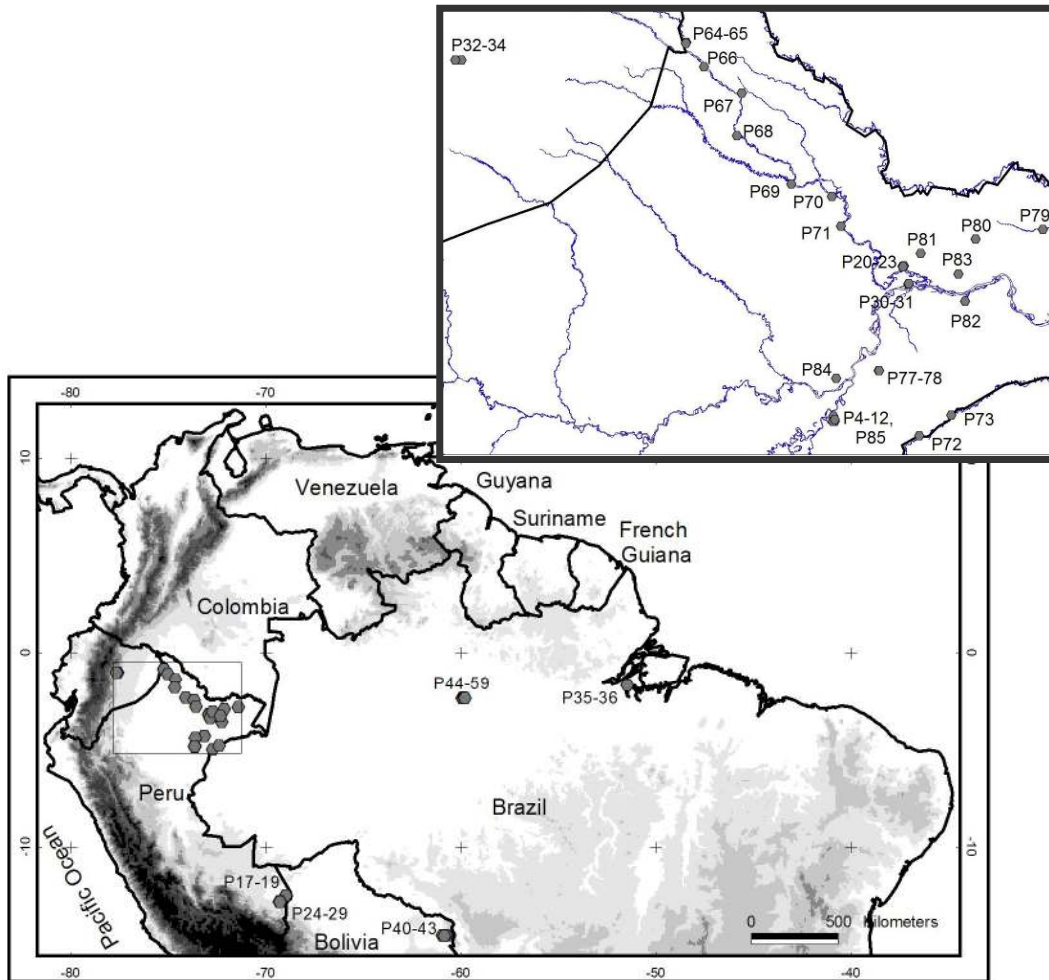
not known how this variability compares to continental-scale patterns of floristic composition, or to what extent different forests in this region resemble communities in other parts of Amazonia. It is also important to consider floristic patterns at different scales, because the mechanisms that determine these patterns may differ. For example, at a continental-scale, broad gradients in tree composition in Amazonia have been related to variation in environmental conditions such as soil fertility and dry season length (Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006). The principal gradient in floristic composition contrasts the eastern regions of Amazonia (Guiana Shield and Brazil) that are geologically older and have poorer soils, with western areas where sediments from the Andes have been deposited more recently (Quesada et al., 2009a). In addition, a second gradient in composition is associated with the gradient in climate seasonality from south-eastern (southern Bolivia and central Brazil) to north-western (Colombia, Ecuador, and northern Peru) Amazonia. However, at a regional scale within western Amazonia, floristic patterns have been related to dispersal limitation due to geographical distance, the capacity of a few groups of species to dominate large areas (“oligarchies”), large geological units, as well as fine-scale soil heterogeneity (e.g. Pitman et al., 2001; Phillips et al., 2003; Tuomisto et al., 2003a; Vormisto et al., 2004; Fine et al., 2005; Macía and Svenning, 2005; Montufar and Pintaud, 2006; Ruokolainen et al., 2007; Pitman et al., 2008; Duque et al., 2009). Different factors may well be important at different scales but the relative importance of geographical distance and environmental conditions, at both regional and continental scales, has not been studied in Amazonia.

In this study we address three questions related to floristic patterns within Amazonia terra firme forests: (1) Do genus- and species-level data give similar patterns of floristic composition? (2) Is regional- and continental-scale variation in floristic composition similar in magnitude? (3) Do environmental factors and geographical distance have a similar role in explaining floristic dissimilarity at regional and continental scales in Amazonian forests?

## 2 Materials and methods

### 2.1 Tree floristic plot data

We compiled 55 floristic tree inventories of terra firme Amazonian forests (supplementary material (<http://www.biogeosciences.net/6/2719/2009/bg-6-2719-2009-supplement.pdf>), Fig. 1), of which 30 plots are in north-western (NWA; Ecuador and Peru), 13 in south-western (SWA; Peru and Bolivia), ten in central (CA; Brazil), and two in eastern regions of Amazonia (EA; Brazil). These plots represent the broad gradients in soil fertility and dry season length across Amazonia (Sombroek, 2000; 2001). None of the plots are believed to have had



**Fig. 1.** Location of Amazonian terra firme plots in South America, high elevation areas are represented in black. Outset shows north-western Amazonian plots.

recent direct human impact (Freitas, 1996; Phillips et al., 2003; Pitman et al., 2008). Unusual formations of terra firme forest, such as white sand forest and liana forest, were excluded from these analyses. We restricted the dataset to plots that have one hectare of inventoried trees with a diameter  $\geq 10$  cm (diameter at breast height, DBH), with information on the number of individuals and species, and with voucher collections in herbaria. Prior to analysis, every scientific name was checked to validate its existence and to detect synonymy. Over 130 references including monographs, floras, checklists and revisions were used during this process.

## 2.2 Comparison of floristic analyses using genus- and species-level data

Two floristic analyses (distance matrices and floristic ordination) were used to compare patterns of floristic composition obtained using genus- and species-level data. First, a

matrix of floristic distance between sites was calculated separately for genera and species using the Bray-Curtis index based on the relative abundance of these taxa (Pitman et al., 2008). Pearson's correlation coefficient was used to examine the similarity of the two distance matrices (cf. Higgins and Ruokolainen, 2004). Next, the variation in floristic composition at the genus and species level was examined using Detrended Correspondence Analysis (DCA) with PAST version 1.82b (Hammer et al., 2001). The species-level DCA analysis was run using all species that occur in two or more plots, while the genus-level analysis used all genera that occur at one or more plots. Finally, the seven most abundant families and genera were used to examine whether the patterns of floristic composition along the main axis of the species-level DCA were consistent within different families and genera. Within each family, one genus, and within each genus, two species were selected (the genus/species with the highest abundance and the highest correlation (Kendall's tau value) between the axis 1 scores and species relative

abundance). For these two taxa within each family or genus, the direction of the correlation between the axis 1 scores and relative abundance was compared.

### 2.3 Variation of floristic composition at continental and regional scales

The average floristic similarity and the decay in floristic similarity with distance were used to compare continental- and regional- floristic patterns. As above, floristic similarity was calculated using the Bray-Curtis index based on the relative abundance of species. First, the average ( $\pm 95\%$  confidence limit) floristic similarity was calculated at a continental scale using all 55 plots and for each region using 30 plots from NWA, 13 plots from SWA and 12 plots C&E Amazonia, based on 1000 randomly selected pairs of plots within each group. The distribution of floristic similarities was compared for all plots, and separately for plots located at distances of  $<100$  or  $\geq 100$  km. Next, the decay of floristic similarity with distance was compared between regions and at a continental scale. Values of geographical distance between plots were transformed using natural log  $[\ln(x)]$  to represent the neutral theory (Hubbell, 2001), that predicts non-linear distance decay in floristic similarity. Overlapping 95% confidence limits of the intercepts and slopes of the relationship between floristic distance and  $\ln(\text{distance})$  was used to test for significant differences in the decay of floristic similarity between regions and at a continental scale.

### 2.4 Role of environmental factors and geographical distance in explaining floristic dissimilarity at regional and continental scales

Partial Mantel tests were used to test the relative influence of geographical distance and environmental factors, such as climate (dry season length - DSL) and soil fertility, as determinants of the floristic dissimilarity at continental and regional scales (Tuomisto et al., 2003a; Ruokolainen et al., 2007). The partial Mantel test involves computing the Pearson correlation coefficient or standardized Mantel statistic ( $r$ ) as a measure of the strength of relationship between two distance matrices, while controlling for correlations with a third distance matrix. Significance was assessed using a Monte Carlo randomization procedure to estimate the probability of error by comparing observed distributions of  $r$  against the distribution of random values generated by permuting one of the matrices and recalculating  $r$  999 times ( $p < 0.001$ ). The floristic dissimilarity between two plots was calculated using the Bray-Curtis index based on the relative abundance of species. Dry season length was calculated as the average number of months per year with rainfall  $<100$  mm. A variety of methods for quantifying soil fertility were used depending on the available data. First, for all plots, we used a simple classification developed by Malhi et al. (2004), in which soils were classified in eight soil fertility categories (see sup-

plementary material: <http://www.biogeosciences.net/6/2719/2009/bg-6-2719-2009-supplement.pdf>). In addition, we also used plot-level soil data from two databases, one related to plots of NWA (Pitman et al., 2008) and the other related to plots of RAINFOR (Quesada et al., 2009b). These data quantify the nutrient content of surface soils (0–20 cm) per each plot based on at least five random sampling points. Samples were analyzed at La Molina National Agrarian University, Peru (Pitman et al., 2008) or the University of Leeds, UK (Quesada et al., 2009b). Soil fertility was quantified in three ways using these data. Firstly, using the exchangeable cations ( $\text{Ca}^{++}$ ,  $\text{Mg}^{++}$ ,  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Al}^{+++}$ ) and the sum of base cations ( $\text{SB}=\text{Ca}^{++}+\text{Mg}^{++}+\text{K}^++\text{Na}^+$ ) (Huston, 1980), secondly, including only two exchangeable cations ( $\text{Ca}^{++}$  and  $\text{Mg}^{++}$ ) and thirdly using all the additional available soil data (percentage of sand, clay and silt, and pH in both databases; percentage of organic material, phosphorus, and potassium – Pitman et al., 2008, and total reserve bases, total extractable P, total P, and total N and C – Quesada et al., 2009b). Because of the differences in protocols to analyse soil fertility, the plots associated with each detailed soil database were analysed separately. Soil data were log-transformed following Phillips et al. (2003). Differences between plots were expressed in Euclidean distances computed separately for each factor.

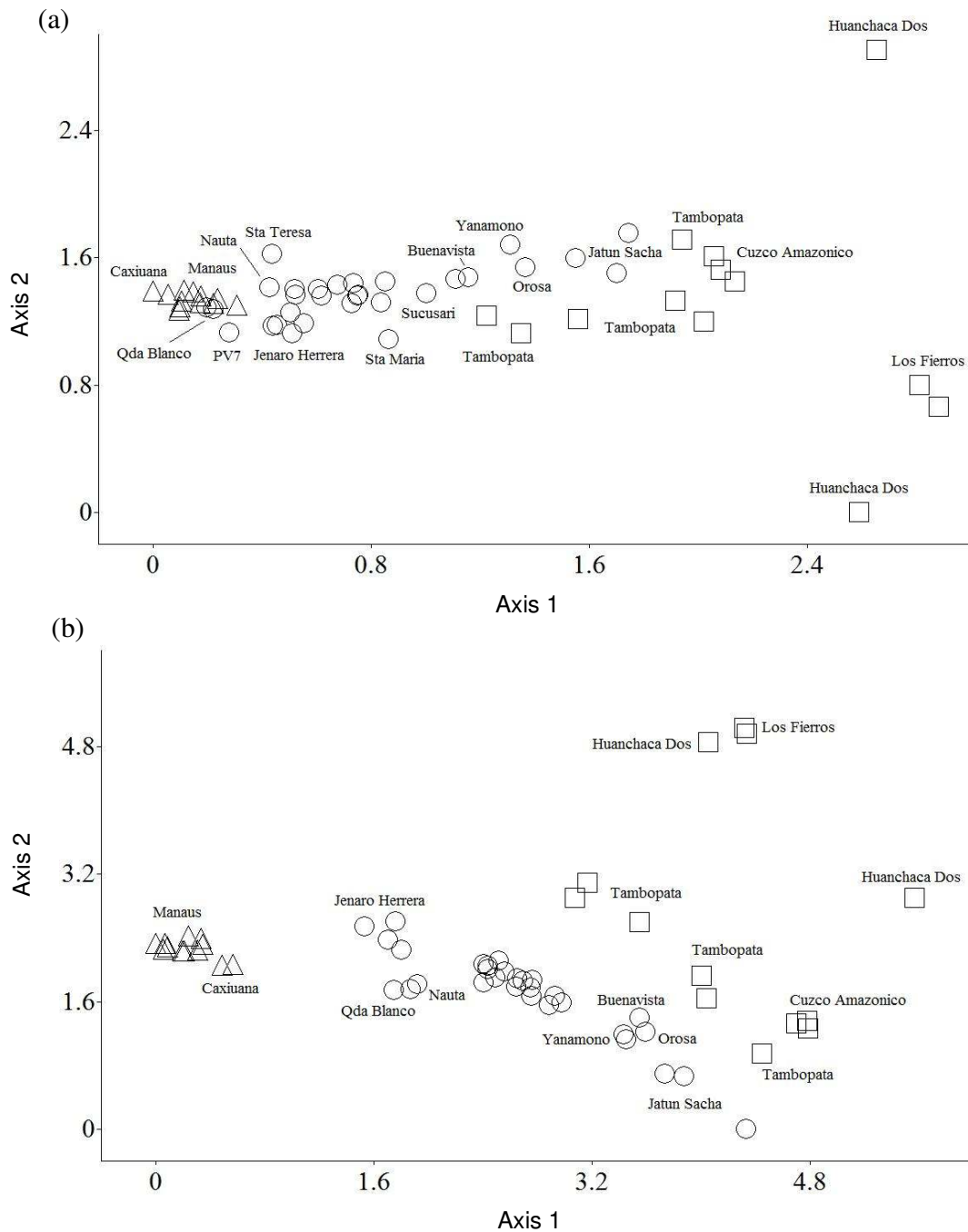
## 3 Results

### 3.1 Floristic data

The 55 floristic inventories (plots) compiled from Amazonia have a total of 32 515 trees with diameter  $\geq 10$  cm, of which 55% were from the thirty plots of north-western Amazonia (NWA), 22% from the 13 plots of south-western Amazonia (SWA) and the rest from the twelve plots of central and eastern Amazonia (C&EA). Across all the plots, on average, 99.0% of trees were identified to family, 95.8% to genus, and 73.2% to species. After the exclusion of the 26.8% of trees with no reliable species-level scientific name, 93 families, 473 genera and 1661 species remained in the entire dataset of which 512 species occurred only in one plot.

### 3.2 Comparison of floristic analyses using genus- and species-level data

The correlation between distance matrices demonstrated that only 57% of the floristic variation at the species level was explained by the genus-level data. Overall, the species-level analysis detected greater floristic differences between plots than the genus-level analysis as the average floristic difference between sites increased when the level of analysis changed from genus (0.63) to species (0.87). However, ordination using DCA showed that the affinities between plots at the genus and species level were broadly similar (Fig. 2).



**Fig. 2.** DCA ordinations of the relative abundance of (a) 473 genera, and (b) 1149 species (excluding those that occur at only one plot) occurring in 55 Amazonian terra firme plots. Symbols: ( $\Delta$ ) C and E; ( $\circ$ ) NW, and ( $\square$ ) SW Amazonia.

The relatively low correlation between species- and genus-level distance matrices was caused by a specific group of sites: plots from Manaus and Caxiuana (C&EA), Jenaro Herrera, Quebrada Blanco and some of the plots from the Napo River (NWA) were rather similar in terms of genus-level composition, and were only distinguished using species-level

analysis (Fig. 2). If these plots are excluded, the axis 1 DCA scores for the two ordinations calculated using genus and species data, were very similar and closely correlated (slope =  $1.06 \pm 0.16$ ,  $r^2 = 0.84$ ).

Additional results also suggested that the species-level data were more effective than the genus level at

distinguishing between plots. For example, in the DCA at the genus level, the first axis explained only 42.0% of the floristic variation, while at the species level, the equivalent value was 72.5%. In addition, the percentage of species with a strong correlation with the first axis (6.4% of species with  $\tau \geq 0.5$ ) was higher than the percentage of genera (3.2% of genera with  $\tau \geq 0.5$ ).

In general, along the first axis, plots were distributed according to the regions where they occurred, along an east/west axis: plots with low scores on axis 1 were found in C&E Amazonia and plots with high axis 1 scores occur in WA (Fig. 2). Lecythidaceae, Sapotaceae and Burseraceae and the genera *Eschweilera*, *Pouteria* and *Protium* increased in abundance from EA to WA, while the Moraceae and Arecaceae and their genera *Pseudolmedia* and *Iriarteia* showed the opposite trend; the only well-distributed family was the Fabaceae. The Myristicaceae and its genus *Iryanthera* were more abundant in most of the north-western Amazonian plots. While the most abundant species showed similar relationships between their relative abundance and axis 1 scores as their respective genus and family, other species, such as *Pouteria engleri* and *Inga capitata* (Fig. 3) demonstrated that rather different patterns could be found within some groups, highlighting the value of species-level analyses.

### 3.3 Variation of floristic composition at regional and continental scales

At a continental scale, floristic similarity values ranged from 0.3% (plot 41 vs. plot 78) to 70.3% (plot 42 vs. plot 43) showing that some plots contained almost entirely different species, while others were almost identical. Even though high similarity values were common between plots located closed to each other, high values were also found between plots separated by great distances. For example, a similarity value of  $17.0\% \pm 1.5$  was found between plots from Tambopata and Cuzco Amazonico in SWA, and plots from Yanamono, Buenavista, Rio Orosa and Jatun Sacha in NWA that are 930–1600 km apart. High similarity values ( $13.2\% \pm 1.2$ ) were also found between plots separated by similar long distances (approx. 1550 km), between plots from Jenaro Herrera in NWA and plots from Manaus in CA. At a regional scale, floristic similarity values ranged from 1.6% (plot 4 vs. plot 34) to 61.5% (plot 77 vs. plot 78) in NWA, from 4.8% (plot 29 vs. plot 41) to 70.3% (plot 42 vs. plot 43) in SWA, and from 13.1% (plot 35 vs. plot 54) to 57.9% (plot 56 vs. plot 57) in C&EA.

The average floristic similarity between plots at a continental scale was 0.135 – lower than the values for the different regions – 0.198 in NWA, 0.224 in SWA, and 0.366 in C&E Amazonia. However, none of these values were significantly different (95% Confidence limits: ALL=0.021–0.475; NWA=0.054–0.417; SWA=0.059–0.603; C&EA=0.138–0.562). There were greater differ-

ences when only plots less than 100 km apart were considered separately (Fig. 4). At this scale, all plots within C&EA have relatively high similarity values. In contrast, in NWA and SWA some pairs of plots were floristically very different (<10% of similarity) even at such small scales (e.g. Sucusari (plot 23) and Rio Orosa (plot 82) in Loreto and plots of Cuzco Amazonico (plots 17 and 19) and Tambopata (plot 28) in Madre de Dios).

Floristic similarity between plot pairs declined with increasing distance at continental and regional scales as a natural-log function of distance. Distance explained a lower proportion of the variation in floristic similarity in NWA than in other regions ( $r^2$ : ALL=0.662; NWA=0.274; SWA=0.577; C&EA=0.889). Nevertheless, neither the slopes nor the intercepts of the linear regressions were significantly different between any region or with the continental-scale pattern (slope  $\pm 95\%$  CI: ALL= $-0.053 \pm 0.002$ ; NWA= $-0.042 \pm 0.007$ ; SWA= $-0.046 \pm 0.009$ ; C&EA= $-0.051 \pm 0.004$ ; intercepts  $\pm 95\%$  CI: ALL= $0.834 \pm 0.026$ ; NWA= $0.704 \pm 0.081$ ; SWA= $0.759 \pm 0.102$ ; C&EA= $0.844 \pm 0.041$ ).

### 3.4 Role of environmental factors and geographical distance in explaining floristic dissimilarity at regional and continental scales

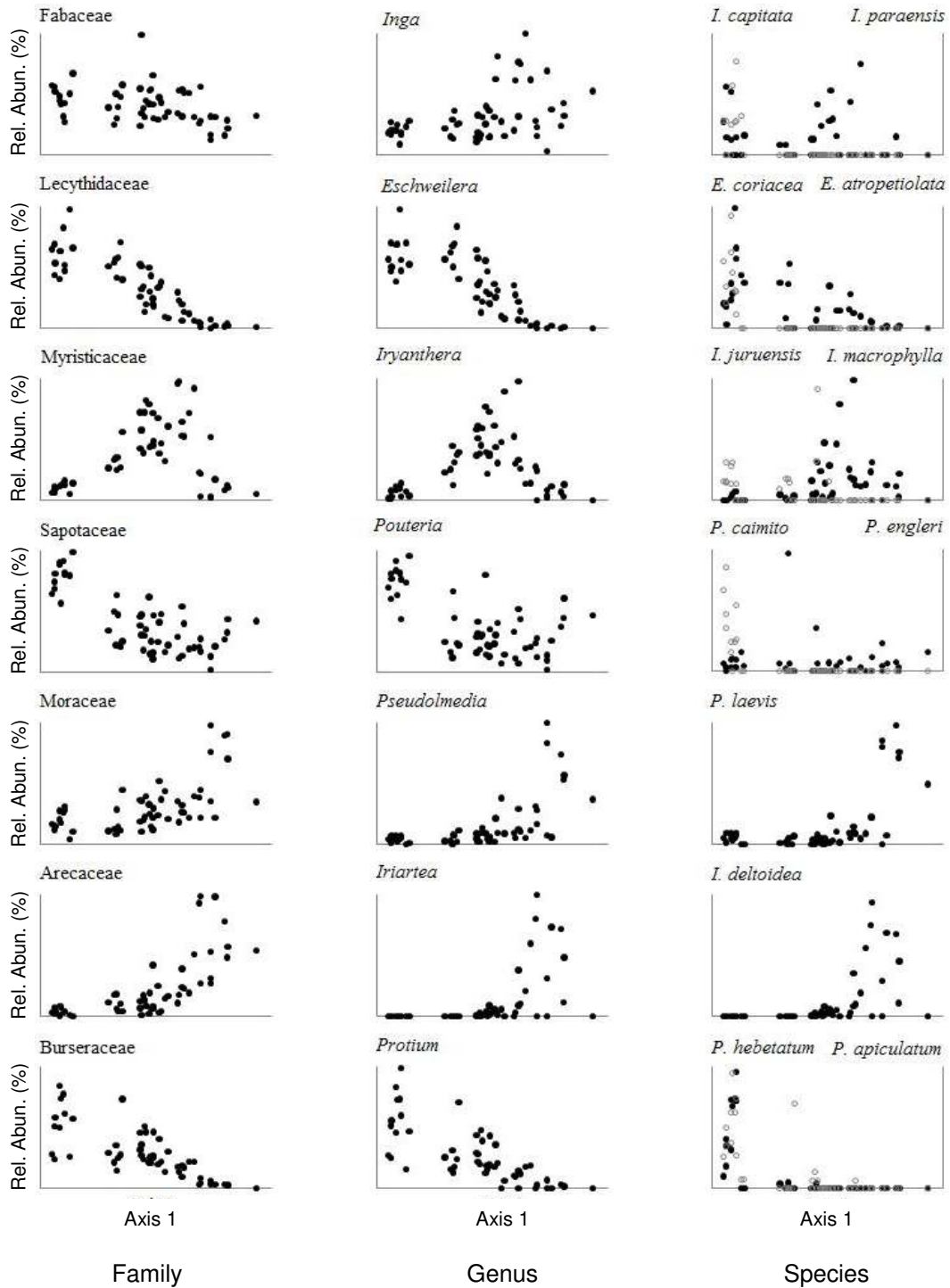
The partial Mantel test showed that geographical distance, soil fertility and climate all explained significant parts of floristic dissimilarity both at continental and regional scales. Using the soil classes as a measure of soil fertility at a continental scale, geographical distance (41.1%) explained more of the floristic dissimilarity than soils (22.9%) and climate (5.8%). A similar pattern was observed in SWA, although the contribution of climate was not significant (0.5%,  $p > 0.05$ ). In contrast, in NWA, the most important factor was soils (11.3%) followed by geographical distance (7.1%) and climate (6.7%). When plot-level soil data were used, this contrast between the relative importance of soils and distance in NWA and at a continental scale remained. However, the patterns for SWA were less robust, with a switch from a higher relative importance of distance to a higher value for soil fertility (10.3%). When only Ca and Mg were considered, the percentage of the variation explained by each factor was usually higher than when all cations or soil data were included at both scales (Table 1).

## 4 Discussion

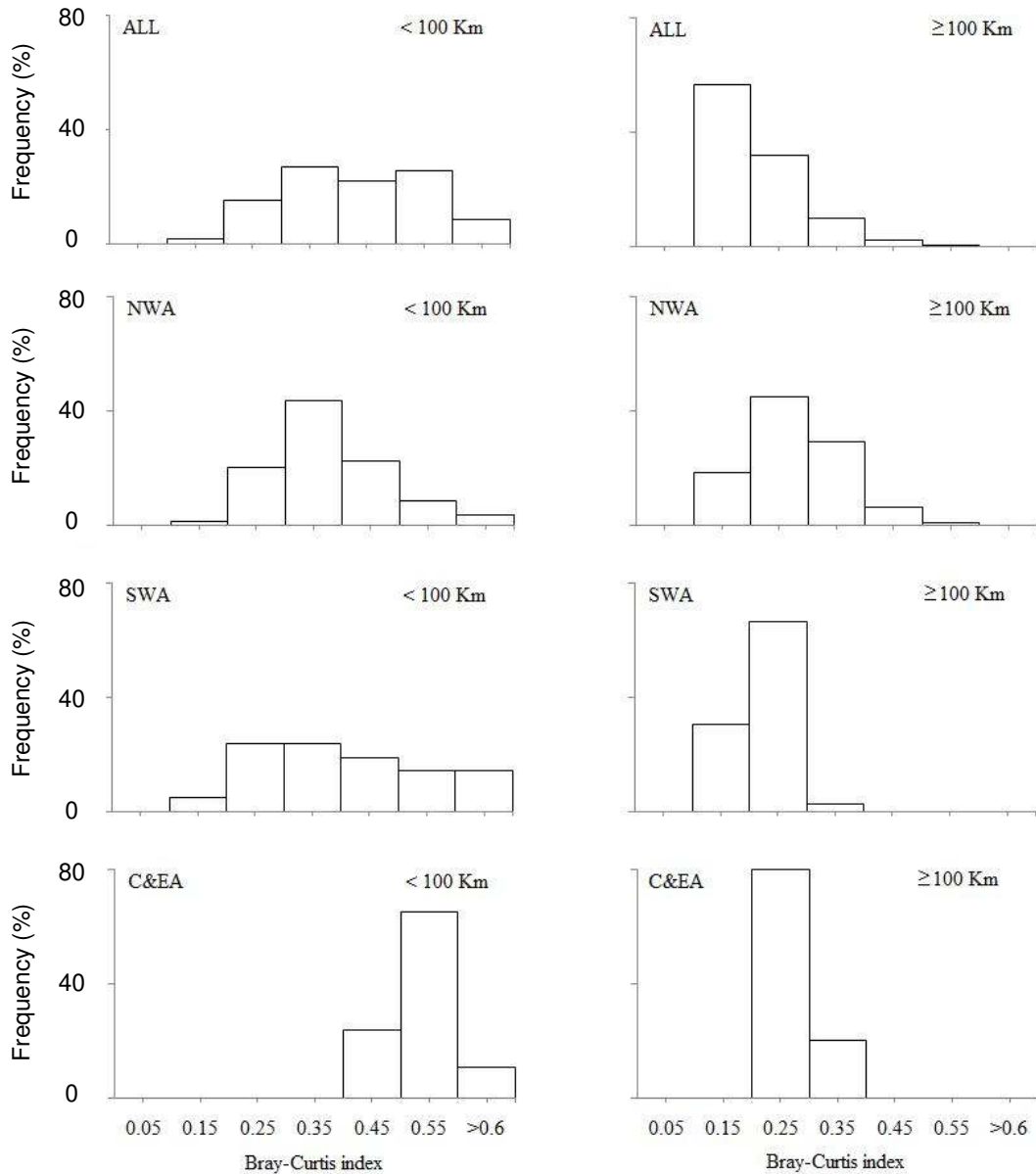
### 4.1 Do genus- and species-level data provide similar patterns of floristic composition?

Overall, genus- and species-level information produced similar floristic patterns (Fig. 2). However, the decrease in average floristic dissimilarity (0.87 to 0.63), caused by a reduction in taxonomic resolution from species to genus, clearly





**Fig. 3.** Distribution of the seven most abundant families, genera and species along the main axis of the DCA using species-level data. Species with the highest value of relative abundance within the genus are in black (left) and with the highest tau value are in grey (right). Minimum and maximum values of the vertical axes of the graphs vary as follows, starting from the top: Families (1) 3–23.7; (2) 0–23.5; (3) 0.4–19.0; (4) 0.4–16.8; (5) 1.0–21.6; (6) 0–30.8; (7) 0–17; Genera (1) 0.2–7.7; (2) 0–19.2; (3) 0–10.8; (4) 0.2–10.5; (5) 0–17.4; (6) 0–23.4; (7) 0–16.3; Species (1A) 0–0.9; (1B) 0–0.5; (2A) 0–10.5; (2B) 0–1.4; (3A) 0–6.4; (3B) 0–1; (4A) 0–4.8; (4B) 0–1.7; (5) 0–12.7; (6) 0–23.4; (7A) 0–8.1; (7B) 0–2.4.



**Fig. 4.** Frequency of similarity index for all regions and every region considering pairs of plots located less than 100 km apart and more than 100 km apart.

demonstrated that the species-level analysis was able to detect a finer level of detail in the floristic patterns. This decrease in floristic dissimilarity was very similar to that found for a series of forest inventory plots in western Amazonia that included trees  $\geq 2.5$  cm diameter (dissimilarity decreased from 0.88 to 0.58 using species- and genus-level analyses respectively; Higgins and Ruokolainen, 2004) and is consistent with the expectation that most genera should be more widely distributed than most species.

Within the overall similarity of floristic patterns at the species and genus level, there was a group of plots (Caxiuana-EA, Manaus-CA, Jenaro Herrera, Quebrada

Blanco, and some plots from the Napo River-NWA) that were floristically similar at the genus level, but clearly differentiated by their species (Fig. 2). At the genus level, their similarity emerged due to the high relative abundance of *Eschweilera* (Lecythidaceae), *Pouteria* (Sapotaceae), *Licania* (Chrysobalanaceae) and *Protium* (Burseraceae). However, at the species level, even though all of these plots shared a high abundance of *Eschweilera coriacea*, there were clear differences among the sites. For example, plots at Jenaro Herrera contain many rarely collected species of the families Sabiaceae (*Ophiocaryum heterophyllum*), Theaceae (*Gordonia fructicosa*), Styracaceae (*Styrax heteroclitus*) and



Anisophyllaceae (*Anisophyllea guianensis*; Spichiger et al., 1989, 1990). In the 55 plots assembled, these species were only present in up to four plots from the Napo River, Quebrada Blanco, Yanamono, and Sucusari in Peru and Huan-chaca Dos in Bolivia. In contrast, plots at Manaus were characterized by the high species richness of the genera *Eschweilera* and *Pouteria* (de Oliveira and Mori, 2001): at least ten new species of the family Sapotaceae have been recently described from the original collections in Manaus (Pennington, 2006).

These different floristic relationships could be an artefact of varying levels of taxonomic resolution. For example, if a species that grows in both sites, but is correctly identified in one plot (included in the analysis) but misidentified or identified to an unknown species in another plot (excluded from the analysis), this will tend to decrease the species-level floristic similarity between plots. However, both the sites at Jenaro Herrera and Manaus have a long history of botanical work and many of the same taxonomists have been involved in the identification process. In general, even though these errors may have occurred, plots established by different research teams do sometimes group together in the ordination because of the presence and high abundance of specific species (e.g. the cluster containing Jatun Sacha – D. Neill; Orosa, Buenavista – N. Pitman; Yanamono – R. Vásquez; Fig. 2b): different research teams working in high diversity forests can report very similar floristic results. Alternatively, the different patterns at the species and genus level may reflect fundamental differences in the underlying mechanisms that have determined the patterns. We suspect that the genus-level similarity may be due to the similar low fertility of the two sites, while the species-level differences may reflect a stronger role for dispersal limitation on the distribution of more recently evolved species.

#### 4.2 Is regional- and continental-scale variation in floristic composition similar in magnitude?

In this study, both the average floristic similarity and its decay with distance were not significantly different among regions or between regional and continental scales. The decay model using individuals that occur in two or more plots in this analysis decreased significantly with distance, and the distance decay was similar to that demonstrated by Condit et al. (2002) using all individuals of trees from Yasuni (Ecuador) and Manu (Peru), by Duque et al. (2009) using all individuals of trees from the Colombian Amazonia and by Tuomisto et al. (2003a) using specific taxa (Pteridophytes and Melastomataceae) in western Amazonia. Our results are consistent with a significant role for dispersal limitation, a key process that determines species turnover in space under neutral models (Hubbell, 2001; Condit et al., 2002; Duque et al., 2009).

However, the comparisons here also emphasise that very dissimilar forests can also occur nearby, and that floristically

**Table 1.** Relative importance of geographical distance, soil fertility and climate in explaining variation in floristic dissimilarity at continental and regional scales. Values from top to bottom represent the Mantel coefficient ( $r$ ), variation explained by a factor controlled by the other two factors (%) and p-value.

	Distance	Soils	Climate
<b>Continental</b>			
General soil classification N=30 plots	0.641 41.1% (0.001)	0.478 22.9% (0.001)	0.241 5.8% (0.001)
Cations and sum of bases N=18 plots <sup>a</sup>	0.554 30.6% (0.001)	0.181 3.3% (0.060)	0.266 7.1% (0.002)
Mg and Ca N=18 plots <sup>a</sup>	0.581 33.7% (0.001)	0.360 12.9% (0.001)	0.261 6.8% (0.002)
Available soil data N=18 plots <sup>a</sup>	0.543 29.5% (0.001)	0.247 6.1% (0.016)	0.311 9.7% (0.001)
<b>Regional – NWA</b>			
General soil classification N=30 plots	0.259 6.7% (0.001)	0.336 11.3% (0.001)	0.266 7.1% (0.001)
Cations and sum of bases N=14 plots <sup>b</sup>	0.240 5.7% (0.026)	0.389 15.1% (0.004)	0.068 0.5% (0.263)
Mg and Ca N=14 plots <sup>b</sup>	0.259 6.7% (0.020)	0.440 19.4% (0.001)	0.065 0.4% (0.288)
Available soil data N=14 plots <sup>b</sup>	0.163 2.7% (0.080)	0.433 18.7% (0.001)	–0.052 0.3% (0.633)
<b>Regional – SWA</b>			
General soil classification N=13 plots	0.569 32.4% (0.001)	0.337 11.4% (0.002)	–0.074 0.5% (0.769)
Cations and sum of bases N=10 plots <sup>a</sup>	0.056 0.3% (0.357)	0.223 5.0% (0.077)	0.165 2.7% (0.139)
Mg and Ca N=10 plots <sup>a</sup>	0.201 4.1% (0.104)	0.371 13.7% (0.017)	0.273 7.5% (0.045)
Available soil data N=10 plots <sup>a</sup>	0.166 2.8% (0.149)	0.321 10.3% (0.028)	0.273 7.5% (0.041)

General soil classification following Malhi et al. (2004), <sup>a</sup> Quesada et al. (2009b), <sup>b</sup> Pitman et al. (2008)

similar pairs of plots can be found much further away. In these cases, floristic similarity cannot be predicted by the distance decay model. For example, a wide range of floristic similarity was found for plots within 100 km in NWA resembling the continental-scale patterns (Fig. 4). Such high beta diversity of the north-western Amazonia region has been noted previously (Tuomisto et al., 2003a; Ruokolainen et al., 2007). Conversely, our results also supported the observation that within Amazonia, some species remained dominant at large scales and therefore distant forests can be floristically rather similar. Pitman et al. (2001) showed this pattern with *Iriartea deltoidea*, the most common tree species in both Yasuni in NWA (Ecuador) and Manu in SWA (Peru; 45–49 individuals/ha) and similar results were obtained by Macía and Svenning (2005) for a series of 0.1 ha plots in Madiidi in Bolivia and Yasuni in Ecuador. Although the identity of abundant species was often different in our set of forest plots, this pattern was very similar to our findings in terra firme forests at continental and regional scales. For example, at a continental scale, species such as *Eschweilera coriacea* (Lecythidaceae) was one of the most abundant species in Jenaro Herrera and Manaus/Caxiuana located 1550–2500 km apart, and *Iriartea deltoidea* (Arecaceae) dominates forests in Jatun Sacha and Tambopata/Cusco Amazonico, 1600 km apart. At a regional scale, regardless of the geographical distance within north-western Amazonia, distinct groups of species dominated nutrient-rich soils such as those of Yanamono, Buenavista, Rio Orosa and Jatun Sacha (*Otoba parvifolia*, *O. glycyarpa*, *Iryanthera juruensis*, *I. paraensis*), which were located 70–720 km apart and the nutrient-poor soils of Jenaro Herrera and Sucusari (*Eschweilera coriacea*, *Micropholis guyanensis*, *Minuartia guianensis* and *Osteophloeum platyspermum*), which were located 200 km apart.

#### 4.3 Do environmental factors and geographical distance have a similar role in explaining floristic dissimilarity at regional and continental scales in Amazonian forests?

The geographical distance and the environmental factors, such as soil fertility and dry season length, explained part of the floristic dissimilarity at continental and regional scales. While geographical distance appears to be more important at a continental scale, soil fertility was more important at a regional scale within western Amazonia (Table 1).

Our results are consistent with evidence that adaptation to different edaphic conditions plays a key role in determining spatial variation in floristic composition (Gentry, 1988; Tuomisto et al., 1995). In this study, we showed that the abundance of groups of species is related to the gradients in soil fertility at both regional and continental scales. Species of Lecythidaceae and Sapotaceae were characteristically found on poorer soils and species of Arecaceae and Myristicaceae were more commonly found on richer

soils. Using pteridophytes and the family Melastomataceae, Tuomisto et al. (2003a) demonstrated that environmental factors, especially soil type, were also important for species distribution and abundance patterns within terra firme forests in western Amazonia. Similar results were shown using the same taxa in a one-hectare plot in Ecuador (Poulsen et al., 2006), a 43-km long transect in northern Peru (Tuomisto et al., 2003b), palms in north-western Amazonia (Vormisto et al., 2004; Normand et al., 2006), species of trees with diameter  $\geq 10$  cm in specific areas in Colombia (Duivenvoorden, 1995), a network of 0.1 ha plots in south-western Amazonia (Phillips et al., 2003) and at a broader scale, using genera of trees from the whole of Amazonia (ter Steege et al., 2006).

Cation concentrations, and particularly  $Mg^{++}$  and  $Ca^{++}$ , may play a key role in the process of determining dominant species. For plants, magnesium plays a critical role in many physiological processes such as seed germination and the production of chlorophyll and fruits while calcium is used to regulate physiological processes that influence both growth and responses to environmental stresses (Mc Laughlin and Wimmer, 1999). Concentrations of soil cations are also associated with various aspects of forest structure and function: cations can affect seedling growth rates of tropical trees (e.g. Denslow et al., 1987) and are associated with floristic patterns and habitat preferences in Asian tropical forests (e.g. Baillie et al., 1987; Paoli et al., 2006). However, where concentrations of soil cations are low, the concentrations of aluminium may also be important: low concentrations of Mg and Ca are associated with very high aluminium contents in Amazonian soils (Quesada et al., 2009a). This might be particularly important for groups of trees, such as some genera of Melastomataceae, which are aluminium accumulators (Jansens et al., 2002). For example, Tuomisto et al. (2003a) and Ruokolainen et al. (2007) using full inventories of Melastomataceae found that Ca and Mg explained part of the floristic patterns in terra firme forests in Amazonia while aluminium concentrations correlated with species diversity and richness (Tuomisto and Ruokolainen, 2005). Further studies of soil properties, such as phosphorus fractionation, are required in order to understand more fully the role of soils in determining floristic patterns.

A large percentage of the floristic variation that we found remained unexplained by the combination of factors examined in this paper (ALL: 30–60%; NWA: 75–80%; SWA: 55–95%). Therefore it is likely that there were additional, as yet unmeasured factors that may affect the floristic patterns. These may include the effects of historical climate and geological changes on species distribution and diversification. For example, de Oliveira and Nelson (2001), using the abundance of genera in different sites in the Brazilian Amazon, showed that factors such as past disturbance history may be important in determining floristic dissimilarities. Pitman et al. (2008) discussed a range of possible historical explanations for the disjunction in species composition that occurs at the Peruvian and Ecuadorian border.

Additional work in population genetics and community phylogenetics may help differentiate the role of historical and ecological processes in determining patterns of composition and diversity. For example, population genetics could examine whether rare species are more dispersal limited compared to dominant tropical tree species. In addition, by using species-level phylogenies, it is now possible to examine the relative contribution that habitat specialisation and dispersal events have played in the plant community evolutionary process (e.g. Fine et al., 2005).

#### 4.4 Implications for biodiversity conservation

The finding that soil fertility is a good predictor of floristic patterns in Amazonia means that detailed soil maps would be required to predict the floristic composition of unsampled forests, and to direct conservation policy. For example, based on ecological inventories of a particular forest type located closed to Iquitos, the Allpahuayo-Mishana area was protected to conserve the unusual flora and fauna related to the white-sand soils (Salo and Pyhälä, 2007). Effective conservation strategies would need to include similar processes to ensure protected areas include other soil types such as those occurring in Jatun Sacha and Orosa (nutrient-rich soils) or in Jenaro Herrera and Sucusari (nutrient-poor soils).

Finally, this study also demonstrates the need to analyze floristic data to the species level to best define floristic patterns and to achieve a better understanding of the importance of environmental factors for floristic variation within Amazonia. Areas that are currently poorly represented in regional inventories, such as terra firme forests on the rare Holocene formations in north-western Amazonia or the region located between Manaus and Caxiuana in Brazil, should be included in such efforts.

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