**Biogeosciences
Discussions**

Integrating regional and continental scale comparisons of tree composition in Amazonian terra firme forests

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Abstract

We contrast regional and continental-scale comparisons of the floristic composition of terra firme forest in South Amazonia, using 55 plots across Amazonia and a subset of 30 plots from northern Peru and Ecuador. Firstly, we examine the floristic patterns using both genus- or species-level data and find that the species-level analysis more clearly distinguishes different plot clusters. Secondly, we compare the patterns and causes of floristic differences at regional and continental scales. At a continental scale, ordination analysis shows that species of Lecythidaceae and Sapotaceae are gradually replaced by species of Arecaceae and Myristicaceae from eastern to western Amazonia. These floristic gradients are correlated with gradients in soil fertility and to dry season length, similar to previous studies. At a regional scale, similar patterns are found within north-western Amazonia, where differences in soil fertility distinguish plots where species of Lecythidaceae, characteristic of poor soils, are gradually replaced by species of Myristicaceae on richer soils. The main coordinate of this regional-scale ordination correlates mainly with concentrations of available calcium and magnesium. Thirdly, we ask at a regional scale within north-western Amazonia, whether soil fertility or other distance dependent processes are more important for determining variation in floristic composition. A Mantel test indicates that both soils and geographical distance have a similar and significant role in determining floristic similarity across this region. 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 dependent on a range of processes that include both habitat specialisation related to edaphic conditions and other distance-dependent processes. 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 from north-western Amazonia.

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1 Introduction

One of the scientific challenges in tropical forest ecology is to map fully and understand the patterns of floristic composition and diversity (Prance et al., 2000; Phillips and Miller, 2002). Describing these patterns is critical for predicting the mechanisms that determine species distributions and 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. Pitman et al., 2008; ter Steege et al., 2006), large gaps remain (e.g. ter Steege et al., 2006). The key is to develop useful principles from existing information that can both inform current conservation policy and direct future research.

In terms of describing the patterns of floristic variation in Amazonia, studies have typically focused on either genus or family level comparisons (ter Steege et al., 2000, 2006; Terborgh and Andresen, 1998). In contrast, studies at a species-level have usually either focused on restricted areas in western Amazonia (e.g. Phillips et al., 2003) or on a few taxa (e.g. Tuomisto et al., 2003a; Vormisto et al., 2004). Ultimately, one goal of this research area must be to undertake continental-scale, species level analyses of floristic composition as typically it is species, rather than families or genera, that show restricted distributions and hence best define floristic patterns. For example, phytogeographic patterns of the 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). Full species-level studies of floristic composition are 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. However, largely based on recent taxonomic publications (Vásquez, 1997; Ribero et al., 1999; Jorgensen and León-Yánez, 1999), current datasets do contain reliable species-level information for many taxa, and these data could offer insights into whether results from current genus-level analyses of floristic composition

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are likely to resemble future full species-level analyses.

A second feature of current published analyses is that they typically focus on a single scale: either continental or regional. 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.

In terms of explaining the underlying mechanisms that determine compositional patters in Amazonia, most studies have sought to quantify the role of environmental conditions. For example, at a continental-scale, broad gradients in tree composition in Amazonia are related to variation in 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 recently. 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. At a regional-scale within western Amazonia, floristic patterns have been related to soil heterogeneity, geological faults and other distance-related processes (Phillips et al., 2003; Montufar and Pintaud, 2006; Pitman et al., 2008; Fine et al., 2005) and the capacity of a few groups of species to dominate large areas ("oligarchies") (Pitman et al., 2001, 2008; Tuomisto et al., 2003a; Vormisto et al., 2004; Macía and Svenning, 2005). However, the relative role of environmental conditions or distance-related processes at regional- and continental-scales has not previously been studied.

In this study we therefore address three questions related to floristic patterns within Amazonia terra firme forest: (1) Does genus-level data give similar patterns of floristic composition as species-level information? (2) Is regional-scale variation

in floristic composition within north-western Amazonia similar in magnitude to patterns of continental-scale variation? (3) Do soil fertility and other distance-dependent processes have a similar role in explaining floristic similarity at both regional- and continental-scales in Amazonian forests?

2 Materials and methods

2.1 Tree floristic plot data

We compiled 55 floristic inventories of trees of terra firme Amazonian forest (Table 1), of which 30 plots are in north-western (NWA; Ecuador and Peru), 13 in south-western (SWA; Peru and Bolivia), two in central (CA; Brazil), and ten in eastern regions of Amazonia (EA; Brazil; Fig. 1). Across Amazonia, there are broad gradients in soil fertility and dry season length which increase from east to west and from northwest to southeast respectively (Sombroek, 2000, 2001). None of the plots is believed to have had recent direct human impact; either from fire or fragmentation (Pitman et al., 2008; Phillips et al., 2003; Freitas, 1996). Unusual formations of terra firme forest, such as white sand forest and liana forest, were excluded from these analyses. Priority was given to plots that have one hectare, inventoried trees with diameter ≥10 cm (diameter at breast height, DBH), with information on the number of individuals and species, and with voucher collections in herbaria.

2.2 Data analysis

Firstly, 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. The final dataset contained 93 families, 473 genera and 1661 species. Variation in floristic composition at the genus- and species-level, at continental and regional scales, was examined using Principal Coordiante Analysis

(PCoA) in PAST version 1.82b (Hammer et al., 2001). The Bray-Curtis index was used as a measure of similarity based on relative abundance of each genus or species per plot (Pitman et al., 2008). The species- and genus-level analyses were run using all species that only occur at two or more plots and all identified genera that occur at one or more plots respectively. The average of the most important families, genera, and species for each cluster of plots distinguished by the PCoA were determined using a value of Overall Relative Importance (ORI). The ORI was calculated as the sum of the relative abundance (percentage of total number of trees per plot) and the relative frequency (number of plots at which taxon occurs) for each cluster. This formula is a modification of the "important value index" used for floristic studies (e.g. Mori et al., 1983).

To assess the role of environmental factors as determinants of the floristic patterns at a continental scale, coordinates 1 and 2 of the PCoA for each plot were regressed against soil fertility category (SC) and dry season length (DSL). We followed a simple classification developed by Malhi et al. (2004), in which soils are classified in eight categories from very poor to very rich conditions, and in which DSL is calculated as the average number of months per year with a rainfall of less than 100 mm (Table 1). Additional information on the geology used to assign these plots to a category was based on the geological map from Peru (Instituto Geológico Minero y Metalúrgico, 2006). At a regional scale for the 24 plots in NWA, we used plot-level soil data (Phillips et al., 2003, 2005; Pitman et al., 2008; RAINFOR, unpublished data). 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 University, Peru (Pitman et al., 2008), the Agricultural Research Centre of Finland (Phillips et al., 2003, 2005) and the University of Leeds, UK (RAINFOR, unpublished data). The mean value of exchangeable cations (Ca^{++}, Mg^{++}, K^+, Na^+, Al^{+++}) and the sum of base cations ($SB=Ca^{++}+Mg^{++}+K^++Na^+$) were used as an estimation of soil fertility (Huston et al., 1980) and regressed against coordinates 1 and 2 of the PCoA for each plot.

The relationship between species composition and geographical distance (beta di-

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versity; Condit et al., 2002) was assessed using all 55 terra firme plots and the 30 terra firme plots from NWA. The similarity between two plots was calculated using the Sørensen's index based on the fraction of species shared (W) between pairs of plots (A and B; S=2W/A+B). Euclidean distance was estimated between sites. Values of geographical distance were transformed using natural log [ln(x)] to represent the neutral theory (Hubbell, 2001), that predicts non-linear distance decay in floristic similarity. Mantel tests were used to test the association between geographical distance and floristic composition at both a continental and regional scale, within the north-western Amazonian plots. This test involves computing the Pearson correlation coefficient or standardized Mantel statistic (r) as a measure of the strength of relationship between two distance matrices. 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 for permuting one of the matrices and recalculating r 999 times ($p<0.001$).

Finally, correlations between soil variables and floristic composition at a regional-scale within NWA were also examined using Mantel tests. Soil data was transformed using logarithm [$log_{10}(x)$] following Phillips et al. (2003). Partial Mantel tests, which control for the correlations between pairs of distance matrices whilst testing for correlations with a third matrix, were also performed to test the independence of the correlations between floristic composition, soil fertility and geographical distance within NWA.

3 Results

3.1 Floristic data

The 55 floristic inventories compiled from Amazonia have a total of 32 515 trees, ≥10 cm diameter, of which 55% were from the thirty plots of north-western Amazonia (NWA). 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

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no reliable species-level scientific name, 93 families, 473 genera and 1661 species remained in the whole dataset; and 89 families, 393 genera and 1076 species in the NWA dataset. 512 species occur at only one plot in the whole dataset and 376 species occur in only one plot in NWA.

3.2 Ordination analysis

The affinities between plots observed from the Principal Coordinate Analysis (PCoA) at different taxonomic levels (genera and species) are similar (Fig. 2) but the species-level analysis distinguishes the clusters more than the genus-level analysis. This is possibly because our analysis cannot distinguish two common cases in large datasets: 1) a well-identified species present in one plot and absent in another, and 2) a species that grows in both plots but it is well-identified in one plot (included in the analysis) but misidentified or identified to an unknown species in another plot (excluded of the analysis). Even though these mistakes may have occurred, plots established by different research teams do group together because of the presence and high abundance of specific species (e.g. the cluster containing Jatun Sacha – D. Neill; Orosa, Buenavista – N. Pitman; Yanamono – RAINFOR; Fig. 2b).

In the PCoA, the two first coordinates explain 35.6% of the tree floristic variation at the genus level (coordinate 1=22.9%, coordinate 2=12.7%) and 27.9% at the species level (coordinate 1=15.4%, coordinate 2=12.5%). Along the first axis, plots are distributed according to the regions where they occur, along an east/west axis. At the species level, plots with low scores are found in western Amazonia (WA) and plots with high scores in central and eastern Amazonia (CA and EA). The converse pattern is found in the PCoA at the genus level (Fig. 2). At genus level there are strong similarities between CA (Manaus) and EA (Caxiuana) plots and some NWA plots (Jenaro Herrera and Quebrada Blanco) and the Brazilian plots – however, at the species level the clusters of plots are more distinct.

At continental scale, the first coordinate strongly correlates with an edaphic gradient (Genus: r^2=0.52, Species: r^2=0.71, n=55, p<0.001, for both), where plots with high

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scores are found in forests on less fertile soils (CA, EA) and plots with low scores in comparatively rich soils (WA) (Fig. 2b). The second coordinate correlates with dry season length (Genus: r^2=0.81, Species: r^2=0.48, n=55, p<0.001 for both). Plots with low scores have a longer dry season (SEA) than plots with high scores (NWA). At a regional scale within NWA, the plot scores of coordinate 1 also correlate with soil fertility (sum of cations; Genus: r^2=0.10, p<0.1, Species: r^2=0.26, p<0.01, n=24 for both). For example, plots from Jenaro Herrera (high scores on axis one) have poorer soils (e.g. P12, Sum of bases = 0.24 cmol+/kg) than plots from Jatun Sacha (low scores on axis one at species level; e.g. P34, SB=13.11 cmol+/kg). In particular, coordinate 1 correlates strongly with both calcium (r^2=0.73, n=24, p<0.001) and magnesium (r^2=0.39, n=24, p<0.005) across NWA plots at species level. The r square values that correlate soil fertility and floristic composition are always stronger at the species-level rather than at the genus-level in both continental- and regional-scales comparisons.

3.3 Floristic patterns

Six main floristic groups clustered by regions were observed in the PCoA graph (Fig. 2b): one group of central Amazonian plots (44–59; CA-2) located on the highest value of axis one, followed by one group of eastern Amazonian plots (35–36; EA-1), one group of south-western Amazonian plots (17–19, 24–29, 40–43; SWA-6) with negatives coordinates, and three groups of north-western Amazonian plots. Within NWA plots, the three groups are those from Jenaro Herrera with positive coordinates along axis one (plots 4, 9, 12, 85; NWA-3), Yanomono, Jatun Sacha, Buenavista and Rio Orosa with negative coordinates on both axes (plots 30–34, 73, 82; NWA-5) and the rest of localities (NWA-4). The abundances of most important taxa within these groups differ strongly. The only family well-distributed in all groups is Fabaceae; the families Lecythidaceae, Sapotaceae and Chrysobalanaceae and the genera *Eschweilera*, *Pouteria*, *Licania*, *Protium* and *Swartzia* increase in abundance from SWA to NWA, and from WA to EA (Table 2). The families Arecaceae and Moraceae and the genera *Iriartea* and *Pseudolmedia* show the opposite trend (Table 2). The concentration

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of cations is low for the plots in group NWA-3 and higher in NWA-5; this pattern is particularly marked for calcium and magnesium (Table 3).

3.4 Beta diversity

The floristic similarity (Sørensen's index) between two plots declined with increasing distance at continental and regional scales as a natural-log function of distance (Fig. 3). Similarity values ranges from 1.3% (plot 41 vs. plot 78) to 66.9% (plot 4 vs. plot 9) showing that some plots contain almost entirely different species, whilst others are almost identical. In particular, at continental and regional scales, some pairs of terra firme forest plots that are more than 500 km apart have similarity values higher than 40%. In these cases, distance is not a good predictor of floristic similarity. For example, plots from Yanamono, Buenavista, and Rio Orosa in Peru share more species ($29.6\pm1.8\%$) with plots that are located 590–720 km away at Jatun Sacha in Ecuador, than with plots from Jenaro Herrera ($15.9\pm1.7\%$) that are much closer (140–210 km). There is also high similarity ($22.0\pm1.2\%$) between plots from Tambopata and Cuzco Amazonico in SWA, and plots from Yanamono, Buenavista, Rio Orosa and Jatun Sacha in the NWA that are 930–1600 km apart. Similar high values of similarity ($18.4\pm0.9\%$) over large distances (approx. 1550 km) are found between plots from Jenaro Herrera in NWA and plots from Manaus in CA.

These cases of high floristic similarity across large distances appear to correspond to plots with similar, either high (e.g. Yanamono/Jatun Sacha; Yanamono/Tambopata) or low (Jenaro Herrera/Manaus) soil fertility. Among NWA plots, the Mantel test shows that both geographical distance and soil fertility can predict part of the floristic similarity between sites. This test shows that there is a positive correlation between floristic composition and geographical distance ($r=0.56$, $p=0.001$), indicating that neighbouring sites have more similar floristic composition than more distant sites. A similar correlation is shown with soil variables ($r=0.51$, $p=0.001$) in which floristic composition is more similar between sites with soils with a similar concentration of exchangeable cations. While these two factors are strongly correlated to floristic composition, the

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correlation between geographical distance and soil variables is rather weak ($r=0.22$, $p=0.032$), suggesting that soil fertility and distance explain separate components of the floristic variation. This conclusion was confirmed by partial Mantel tests: controlling for geographic distance, the correlation between species composition and soil fertility remained strong and significant ($r=0.52$, $p<0.001$). Similarly, the correlation between species composition and distance remained strong when controlling for variation in soil fertility ($r=0.47$, $p<0.001$).

4 Discussion

4.1 Floristic patterns

We focus our discussion on the floristic affinities of forests in north-western Amazonia, where the majority of our plots are located. The floristic data analysis indicates that most of the plots of this region have similar floristic composition, except for two groups of plots that are either more similar to eastern (Jenaro Herrera) or south-western Amazonia (Jatun Sacha, Yanamono, Buena Vista and Rio Orosa).

The unusual nature of the flora of Jenaro Herrera has been noted previously. The flora was well-studied by Spichiger et al. (1989, 1990) who reported many rarely collected species of the families Sabiaceae (*Ophiocaryum heterophyllum*), Theaceae (*Gordonia fructicosa*), Styracaceae (*Styrax heteroclitus*) and Anisophyllaceae (*Anisophyllea guianensis*). In the 55 plots assembled, these species were only present in 0–4 plots from the Napo River, Quebrada Blanco, Yanamono, Sucusari in Peru and Huanchaca Dos in Bolivia. Two other species of the same genera were also present in Brazil (*Anisophyllea manausensis* and *Ophiocaryon manausense*). In addition, a range of new species have been recently described from the original collections in Jenaro Herrera such as *Haploclathra cordata* (Vásquez, 1993), *Pleurothyrium acuminatum* (van der Werff, 1993), *Naucleopsis herrerensis* (Berg and Franco, 1996) and *Quiina attenuata* (Schneider and Zizka, 2003) emphasising the distinctive features of

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the composition of this forest. However, the affinity of the forests in Jenaro Herrera with sites in central and eastern Amazonia has not previously been described. This similarity emerges because of the presence and high relative abundance of the association *Eschweilera coriacea* (Lecythidaceae), *Micropholis guyanensis* (Sapotaceae), *Minquartia guianensis* (Olacaceae) and *Osteophloeum platyspermum* (Myristicaceae) in Jenaro Herrera, Manaus and Caxiuana. Other analyses have also shown that the Lecythidaceae and Sapotaceae are the most abundant families in a wide range of plots from central and eastern Amazonia (ter Steege et al., 2000, 2006).

Rather different families and species are common in the floristically distinct plots at Jatun Sacha in Ecuador and Yanamono, Buena Vista and Rio Orosa in Peru. These Peruvian plots were identified by Pitman et al. (2008; plots 47, 50, 52) as sites where some Yasuni oligarchy species were present at high abundances, especially species such as *Caryodendron orinocense* (Euphorbiaceae), *Inga oerstediana* (Fabaceae), *Matisia obliquifolia* (Malvaceae), *Pentagonia amazonica* (Rubiaceae) and *Celtis schippii* (Ulmaceae). Our results show a high abundance of Arecaceae, Moraceae and Myristicaceae in these plots, typified by the high abundance of the association *Astrocaryum murumuru* (Peruvian plots), *Iriartea deltoidea* (Ecuadorian plots), *Otoba parvifolia*, *O. glycycarpa*, *Iryanthera juruensis*, *I. paraensis* and *Pseudolmedia laevis*. Similar family-level patterns of abundance are found in plots in south-western Amazonia (ter Steege et al., 2000).

The reason for these floristic differences may relate to the wide variation in soil fertility in north-western Amazonian forests. Soils in Jenaro Herrera are classified as oxisols (Spichiger et al., 1996) and are relatively poor compared to soils of Jatun Sacha, Yanamono, Buena Vista and Rio Orosa: these forests are mainly located in Holocene formations with the exception of the Ecuadorian plots that are located in Miocene formations. The differences in soil fertility are characterized in particular by significant differences in calcium and magnesium content (Table 3, see discussion below).

4.2   Beta diversity

At landscape- and regional-scales, nearby areas and areas with similar soil conditions are more likely to share a high number of species (Fig. 3, Table 3). These results show that floristic composition within Amazonian terra firme forests is dependent on a range of processes that include both habitat specializations related to edaphic conditions and other distance-dependent processes. We discuss these patterns in the context of a range of concepts and hypotheses that have been previously advanced to explain variation in the composition of Amazonian forests.

Our results are consistent with the widely documented 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 show that the abundance of a group of species is related to the gradients in soil fertility at both regional and continental scales with species of Lecythidaceae are more characteristic of poorer soils and species of Myristicaceae more common on richer soils. Using pteridophytes and the family Melastomataceae, Tuomisto et al. (2003a) demonstrated that environmental factors, especially soil type, are also important for species distribution and abundance patterns within terra firme forests in western Amazonia. Similar results have been 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 ≥ 10 cm in specific areas of north-western (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).

Our results also support the observation that within western Amazonia, a limited set of plant species, genera and families dominate distant forests with broadly similar edaphic conditions. Pitman et al. (2001) showed this pattern with *Iriartea deltoidea*, the most common tree species in both Yasuni in Ecuador and Manu in Peru (45–49 individuals/ha). Similar results were obtained by Macía and Svenning (2005)

comparing the composition of 0.1 ha plots in Madidi in Bolivia and Yasuni in Ecuador. Although the identity of abundant species is different in our set of forest plots, this pattern is very similar to our finding in terra firme forests on both rich and poor soil. In both cases, plots tend to be floristically similar regardless of the distance they are apart. For example, at continental scale, species such as *Eschweilera coriacea* (Lecythidaceae) are 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 regional scale, regardless of the geographical distance within north-western Amazonia, distinct groups of species dominate nutrient-rich soils (*Otoba parvifolia, O. glycycarpa*, *Iryanthera juruensis*, *I. paraensis*) located 70–720 km apart and nutrient-poor soils (*Eschweilera coriacea*, *Micropholis guyanensis*, *Minquartia guianensis* and *Osteophloeum platyspermum*) located 200 km apart.

Concentrations of cations and particularly Mg and Ca may have a key role in the process of determining the identity of dominant species. For plants, magnesium plays a critical role in many physiological processes such as seed germination and the production of chlorophyll and fruits whilst 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; dipterocarps in Borneo: Paoli et al., 2006). However, further studies of soil properties, such as phosphorous fractionation, are required in these plots to fully understand the potential role of the full range of elements in determining the floristic patterns.

As pointed out by Pitman et al. (2001), species oligarchies and edaphic patchiness are not mutually exclusive descriptions of forest composition. In particular, Pitman et al. (2001) emphasises that different dominant species may be found in patches with different edaphic conditions and that the size of the patches may vary. For example, close

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to the Andes, fertile soils found over very large areas are associated with dominant species that similarly occur over a very wide area. In contrast, in forests near Iquitos, edaphic patches are much smaller, resulting in the distinct sets of dominant species that we report here. However, not all the floristic patterns we describe here can be adequately explained by different suites of dominant species on soils of differing fertility. For example, there are some plots (e.g. Sucusari) where Myristicaceae dominates under poor soil conditions and a mixture of dominant species related to poorer and richer soils are present. Also, on very rich soils in north-western Amazonia, *Iriartea deltoidea* is more abundant in plots closer to the Andes in Ecuador, whilst *Astrocaryum murumuru* is most abundant in sites in Peru. Therefore, it seems that different species can have a similar role under similar environmental conditions. As a result, factors other than edaphic preference must also have influenced species composition.

One possible explanation of these additional patterns is dispersal limitation. Dispersal limitation is a key process that determines species turnover in space under neutral models that assume that species are ecologically equivalent (Hubbell, 2001; Condit et al., 2002). Evidence for the importance of this process has been suggested from independent correlations of geographical distance and floristic dissimilarity in different Amazonian regions (Phillips et al., 2003; Tuomisto et al., 2003a; Valencia et al., 2004; Vormisto et al., 2004; Normand et al., 2006). The decay with distance of floristic similarity in Amazonia at regional and continental scales of this study is similar to that demonstrated by Condit et al. (2002) for western Amazonia. It is likely this is due in part to dispersal limitation, particularly for the many rarer species that could easily have distributions more strongly influenced by dispersal limitation rather than edaphic conditions.

It also seems likely that there are additional historical factors that may affect aspects of the floristic patterns we report here, including the effects of historical climate and geological changes on species diversification rates. For example, de Oliveira and Nelson (2001), using abundance of genera in the Brazilian Amazon, showed that factors such as past history of disturbance may also be important in determining floristic dissimi-

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larities and Pitman et al. (2008) discusses a range of possible historical explanations for the disjunctions in species composition that occurs at the Peruvian and Ecuadorian border. Population genetics and community phylogenetics holds out the promise of differentiating the role that historical and ecological processes have had in determining patterns of composition and diversity. For example, at the population level it should be possible to examine whether distance is a more important correlate of relatedness in rare compared to dominant tropical tree species, and by using species-level phylogenies it is now possible to examine the role that habitat specialisation has played in the evolutionary process (e.g. Fine et al., 2005) or whether community composition has been determined by chance dispersal events.

The implications of these results for biodiversity conservation in the north-western Peruvian Amazonia are clear – that areas on nutrient-poor and -rich soils such as Jenaro Herrera/Sucusari and Orosa/Buenavista respectively merit protection for their distinct flora. Fortunately, most of these localities are partially protected by national and private institutions. For example, the Jenaro Herrera region is part of the buffer area of the Pacaya-Samiria National Reserve, a protected area that covers about 2 million hectares and is located between the Ucayali and Marañon rivers. There is a research station in Jenaro Herrera administrated by the Instituto de Investigaciones de la Amazonia Peruana that is the centre of research directed to sustainable development, forest management and the conservation of natural resources. Orosa and Sucusari have forest areas administrated by private tourist companies. Activities such as ecotourism, research and sustainable management of resources are promoted in these areas and commercial timber extraction is not allowed. In theory, therefore, a new conservation category is not necessary for these areas as they are adequately protected on paper. However, bigger protected areas must be considered to ensure species genetic variation, existing conservation regulations must be enforced and research bursaries must be guaranteed to protect this unique flora.

Finally, future floristic studies should focus on achieving a better representation of the environmental variation within western Amazonia by including areas that are cur-

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rently poorly represented in regional inventories such as terra firme forests on the rare Holocene formations in north-western Amazonia.

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Table 1. Site characteristics and references of tree inventories in Amazonian terra firme forest.

Plot	Name	Locality	Country	Region	Lat.	Long.	DSL	SC	Reference
P4	JEN-14	Jenaro Herrera	Peru	NWA-3	−4.90	−73.63	0.97	4	Freitas*
P9	JEN-13	Jenaro Herrera	Peru	NWA-3	−4.84	−73.64	0.97	5	Freitas (1996)
P12	JEN-10	Jenaro Herrera	Peru	NWA-3	−4.90	−73.65	0.97	4	Spichiger et al. (1996)
P17	CUZ-02	Cuzco Amazonico	Peru	SWA-6	−12.50	−68.97	3.46	5	RAINFOR
P18	CUZ-03	Cuzco Amazonico	Peru	SWA-6	−12.50	−68.96	3.46	5	RAINFOR
P19	CUZ-04	Cuzco Amazonico	Peru	SWA-6	−12.50	−68.96	3.46	5	RAINFOR
P20	SUC-01	Sucusari	Peru	NWA-4	−3.25	−72.91	0.54	4	RAINFOR
P22	SUC-04	Sucusari	Peru	NWA-4	−3.25	−72.89	0.54	4	RAINFOR
P23	SUC-05	Sucusari	Peru	NWA-4	−3.26	−72.90	0.54	4	RAINFOR
P24	TAM-01	Tambopata	Peru	SWA-6	−12.84	−69.29	3.46	5	RAINFOR
P25	TAM-02	Tambopata	Peru	SWA-6	−12.83	−69.29	3.46	5	RAINFOR
P26	TAM-05	Tambopata	Peru	SWA-6	−12.83	−69.27	3.46	4	RAINFOR
P27	TAM-06	Tambopata	Peru	SWA-6	−12.84	−69.30	3.46	5	RAINFOR
P28	TAM-07	Tambopata	Peru	SWA-6	−12.83	−69.26	3.46	4	RAINFOR
P29	TAM-08	Tambopata	Peru	SWA-6	−12.83	−69.27	3.46	4	RAINFOR
P30	YAN-01	Yanamono	Peru	NWA-5	−3.44	−72.85	0.54	5	RAINFOR
P31	YAN-02	Yanamono	Peru	NWA-5	−3.43	−72.84	0.54	5	RAINFOR
P32	JAS-02	Jatun Sacha	Ecuador	NWA-5	−1.07	−77.60	0.18	6	Neill*
P33	JAS-03	Jatun Sacha	Ecuador	NWA-5	−1.07	−77.67	0.18	6	Neill*
P34	JAS-05	Jatun Sacha	Ecuador	NWA-5	−1.07	−77.67	0.18	5	Neill*
P35	CAX-01	Caxiuana	Brazil	EA-1	−1.74	−51.46	3.97	2	Almeida*
P36	CAX-02	Caxiuana	Brazil	EA-1	−1.74	−51.46	3.97	2	Almeida*
P40	HCC-21	Huanchaca Dos	Bolivia	SWA-6	−14.56	−60.75	6.44	6	Killeen*
P41	HCC-22	Huanchaca Dos	Bolivia	SWA-6	−14.57	−60.75	6.44	6	Killeen*
P42	LFB-01	Los Fierros	Bolivia	SWA-6	−14.56	−60.93	6.46	3	Killeen*
P43	LFB-02	Los Fierros	Bolivia	SWA-6	−14.58	−60.83	6.46	3	Killeen*
P44	BDF-13	Manaus, BDFFP	Brazil	CA-2	−2.40	−59.91	3.05	2	Laurance and Nascimiento*

Dry season length (DSL) and soil class (SC: 2, older oxisol, 3, younger oxisol, 4, Pleistocene alluvial/ultisol, 5, Holocene alluvial, 6, inceptisol) following Malhi et al. (2004). RAINFOR database, Peacock et al. (2007).
unpublished data

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Table 1. Continued.

Plot	Name	Locality	Country	Region	Lat.	Long.	DSL	SC	Reference
P45	BDF-13	Manaus, BDFFP	Brazil	CA-2	−2.40	−59.91	3.05	2	Laurance and Nascimiento*
P52	BDF-09	Manaus, BDFFP	Brazil	CA-2	−2.39	−59.84	3.05	2	Laurance and Nascimiento*
P53	BDF-11	Manaus, BDFFP	Brazil	CA-2	−2.39	−59.84	3.05	2	Laurance and Nascimiento*
P54	BDF-12	Manaus, BDFFP	Brazil	CA-2	−2.39	−59.84	3.05	2	Laurance and Nascimiento*
P55	BDF-03	Manaus, BDFFP	Brazil	CA-2	−2.42	−59.83	3.05	2	Laurance and Nascimiento*
P56	BDF-05	Manaus, BDFFP	Brazil	CA-2	−2.42	−59.83	3.05	2	Laurance and Nascimiento*
P57	BDF-06	Manaus, BDFFP	Brazil	CA-2	−2.42	−59.83	3.05	2	Laurance and Nascimiento*
P58	BDF-07	Manaus, BDFFP	Brazil	CA-2	−2.43	−59.79	3.05	2	Laurance and Nascimiento*
P59	BDF-08	Manaus, BDFFP	Brazil	CA-2	−2.43	−59.79	3.05	2	Laurance and Nascimiento*
P64	NAP-01	PV7 terrace	Peru	NWA-4	−0.88	−75.21	0.32	4	Pitman*
P65	NAP-02	PV7 polvorín	Peru	NWA-4	−0.88	−75.21	0.32	4	Pitman*
P66	NAP-03	Vencedores	Peru	NWA-4	−1.14	−75.02	0.32	4	Pitman*
P67	NAP-04	Santa María	Peru	NWA-4	−1.42	−74.62	0.40	4	Pitman*
P68	NAP-05	Ingano Llacta	Peru	NWA-4	−1.87	−74.67	0.42	4	Pitman*
P69	NAP-06	Boca Curaray	Peru	NWA-4	−2.38	−74.09	0.48	4	Pitman*
P70	NAP-07	San José	Peru	NWA-4	−2.51	−73.66	0.50	4	Pitman*
P71	NAP-08	Santa Teresa	Peru	NWA-4	−2.83	−73.56	0.50	4	Pitman*
P72	YAR-01	Curacinha	Peru	NWA-4	−5.05	−72.73	0.90	4	Pitman*
P73	YAR-02	Buenavista	Peru	NWA-5	−4.83	−72.39	0.80	5	Pitman*
P77	QBC-01	Quebrada Blanco	Peru	NWA-4	−4.36	−73.16	0.80	4	Davila and Rios (2006)
P78	QBC-02	Quebrada Blanco	Peru	NWA-4	−4.36	−73.16	0.80	4	Davila and Rios (2006)
P79	YAG-01	Yaguas	Peru	NWA-4	−2.86	−71.42	0.45	4	Pitman*
P80	MAR-01	Maronal	Peru	NWA-4	−2.97	−72.13	0.50	4	Pitman*
P81	APY-01	Apayacu	Peru	NWA-4	−3.12	−72.71	0.54	4	Pitman*
P82	ORS-01	Río Orosa	Peru	NWA-5	−3.62	−72.24	0.54	5	Pitman*
P83	SAP-01	Sabalillo	Peru	NWA-4	−3.34	−72.31	0.54	4	Pitman*
P84	NAU-01	Nauta	Peru	NWA-4	−4.44	−73.61	0.90	4	Valderrama (2007)
P85	JEN-11	Jenaro Herrera	Peru	NWA-3	−4.88	−73.63	0.97	4	RAINFOR

Dry season length (DSL) and soil class (SC: 2, older oxisol, 3, younger oxisol, 4, Pleistocene alluvial/ultisol, 5, Holocene alluvial, 6, inceptisol) following Malhi et al. (2004). RAINFOR database, Peacock et al. (2007).
unpublished data

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Table 2. Distribution of the 20 most important families, genera, and species along an spatial gradient in 55 plots from Amazonia. Numbers represent mean relative abundance (RA, percentage of total number of trees per plot) per region. Overall relative importance (ORI) = RA_1 + $Frequency_1$. (...) indicates that some taxa were omitted to show others that had stronger patterns within the groups. EA-1: P35–36, CA-2: P44–45, 52–59, NWA3: P4, 9, 12, 85, NWA-4: P20, 22–23, 64–72, 77–81, 83–84, NWA-5: P30–34, 73, 82, SWA: P17–19, 24–29, 40–43.

			EA	CA	NWA			SWA
N°	Family	ORI	1	2	3	4	5	6
1	Fabaceae	10.8	14.0	10.9	7.9	11.2	9.7	7.1
2	Lecythidaceae	8.8	19.7	14.0	12.3	8.7	3.8	0.8
3	Myristicaceae	8.3	1.8	2.1	5.8	10.5	14.3	3.9
4	Sapotaceae	8.0	15.2	13.3	8.3	5.4	4.6	3.9
5	Moraceae	7.7	1.6	4.7	3.6	5.8	6.4	11.6
6	Arecaceae	7.6	0.1	1.3	3.1	3.4	7.6	17.0
7	Burseraceae	6.0	7.1	10.4	3.8	5.8	2.8	1.1
8	Lauraceae	5.3	3.0	4.5	5.7	5.2	2.9	3.4
9	Malvaceae	4.9	1.4	3.3	1.6	4.1	6.7	3.6
10	Euphorbiaceae	4.8	1.3	3.0	3.3	5.3	3.1	2.9
11	Chrysobalanaceae	4.5	5.5	5.4	6.2	4.1	1.1	1.2
12	Annonaceae	4.4	2.2	3.9	2.1	3.2	3.6	3.6
13	Urticaceae	3.7	1.9	1.2	2.9	2.1	2.5	4.9
14	Meliaceae	3.6	0.4	1.3	2.8	3.6	4.8	1.5
15	Rubiaceae	3.5	1.6	1.1	2.5	2.7	3.9	3.0
16	Violaceae	3.1	7.3	3.2	0.4	1.1	1.5	3.2
17	Melastomataceae	2.4	1.0	1.4	4.0	1.0	0.5	2.3
18	Elaeocarpaceae	2.4	0.7	0.9	2.3	1.4	0.5	2.2
19	Myrtaceae	2.2	0.4	1.6	1.3	1.3	1.2	1.0
20	Apocynaceae	2.0	1.6	1.1	1.8	1.0	0.5	1.1

Table 2. Continued.

|			EA	CA	NWA			SWA
N°	Genus	ORI	1	2	3	4	5	6
1	*Eschweilera*	7.5	12.1	11.8	11.7	7.6	3.0	0.5
2	*Pouteria*	5.2	9.3	8.0	4.2	3.1	3.0	2.7
3	*Protium*	5.0	5.1	9.8	3.0	4.8	2.1	0.2
4	*Iryanthera*	4.1	0.6	0.8	2.5	5.2	2.8	2.8
5	*Pseudolmedia*	3.5	0.1	0.8	0.9	1.2	1.5	7.5
6	*Virola*	3.4	0.7	1.1	2.5	4.1	2.9	1.1
7	*Inga*	3.3	1.9	1.4	1.6	2.2	4.6	2.2
8	*Licania*	3.1	3.7	3.7	2.7	2.8	0.7	0.7
9	*Pourouma*	3.1	1.5	1.1	2.6	1.6	1.3	4.2
10	*Iriartea*	3.0	0.0	0.0	0.0	0.4	4.5	7.7
11	*Guarea*	2.7	0.3	0.8	0.7	2.8	3.1	0.9
12	*Sloanea*	2.4	0.7	0.9	2.2	1.4	0.5	2.1
13	*Ocotea*	2.1	1.2	2.0	2.3	1.3	0.4	0.6
14	*Micropholis*	2.1	1.7	2.0	1.6	1.4	0.6	0.5
15	*Swartzia (...)*	2.0	2.6	1.8	1.3	1.4	0.6	0.3
16	*Oenocarpus*	1.9	0.1	0.9	2.6	1.7	0.3	0.7
17	*Miconia*	1.9	0.2	0.7	2.7	0.7	0.4	2.0
18	*Tachigali (...)*	1.8	0.1	0.5	2.1	1.0	0.4	1.4
19	*Otoba (...)*	1.3	0.0	0.0	0.0	0.1	8.1	0.1
20	*Astrocaryum*	1.2	0.0	0.0	0.1	0.7	2.2	1.1

Table 2. Continued.

N°	Species	ORI	EA 1	CA 2	NWA 3	NWA 4	NWA 5	SWA 6
1	*Iriartea deltoidea*	3.0	0.0	0.0	0.0	0.4	4.5	7.7
2	*Pseudolmedia laevis*	2.6	0.0	0.7	0.4	0.4	0.9	5.6
3	*Eschweilera coriacea*	2.0	4.3	4.0	3.6	0.3	0.8	0.4
4	*Euterpe precatoria*	1.5	0.0	0.4	0.1	0.1	0.1	3.3
5	*Virola calophylla*	1.4	0.0	0.5	0.3	1.1	0.6	0.3
6	*Leonia glycycarpa*	1.4	0.0	0.0	0.2	0.6	0.3	1.8
7	*Iryanthera juruensis*	1.4	0.0	0.2	0.1	0.6	0.9	1.6
8	*Oenocarpus bataua*	1.3	0.0	0.0	2.6	1.7	0.3	0.3
9	*Socratea exorrhiza*	1.3	0.0	0.0	0.1	0.4	0.3	2.6
10	*Virola pavonis*	1.3	0.0	0.3	0.3	1.4	0.5	0.0
11	*Iryanthera laevis*	1.2	0.0	0.1	0.0	0.6	0.7	1.1
12	*Guarea macrophylla*	1.1	0.0	0.0	0.2	1.4	0.4	0.5
13	*Pourouma minor*	1.1	0.0	0.3	0.0	0.1	0.3	2.3
14	*Osteophloeum platyspermum*	1.1	0.6	0.2	0.7	0.8	0.2	0.0
15	*Protium hebetatum*	1.1	0.0	4.4	0.2	0.0	0.0	0.0
16	*Astrocaryum murumuru (...)*	1.0	0.0	0.0	0.0	0.5	2.1	1.1
17	*Micropholis guyanensis (...)*	0.9	0.2	1.1	1.4	0.2	0.0	0.3
18	*Pouteria caimito (...)*	0.8	0.5	0.3	1.4	0.1	0.1	0.3
19	*Otoba glycycarpa (...)*	0.8	0.0	0.0	0.0	0.1	4.5	0.0
20	*Otoba parvifolia*	0.6	0.0	0.0	0.0	0.0	3.5	0.1

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**Table 3.** Mean concentration of exchangeable cations in soil per northwestern Amazonia group.

| Cations (cmol+/kg)	NWA-3 (n=2)	NWA-4 (n=15)	NWA-5 (n=7)
Ca^{++}	0.00±N.A.	0.76±0.17	3.87±1.45
Mg^{++}	0.11±N.A.	0.27±0.06	1.67±1.47
K^{+}	0.12±N.A.	0.14±0.03	0.46±0.56
Na^{+}	0.02±N.A.	0.21±0.05	0.14±0.11
Sum of Bases	0.25±N.A.	1.38±0.23	6.13±2.92
$Al^{+++} + H^{+}$	3.85±N.A.	6.00±1.14	2.43±1.40

1448
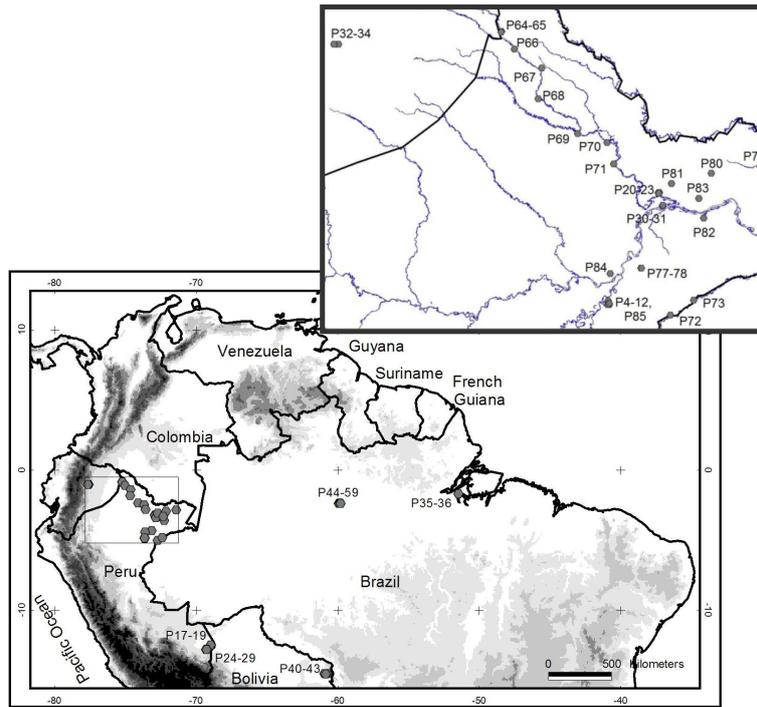
Fig. 1. Location of Amazonian terra firme plots in South America, The Andes are represented in black. Outset shows north-western Amazonian plots. See Table 1 for details of each site.

1449
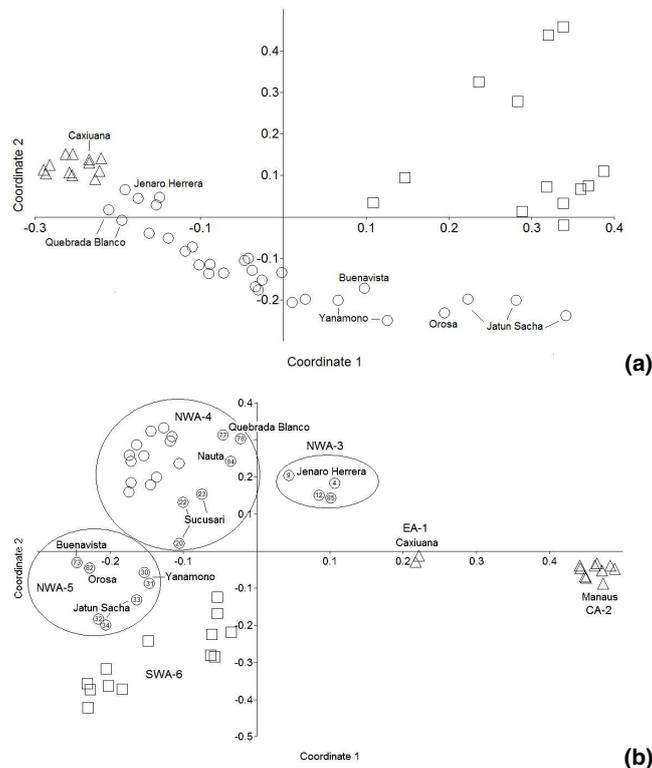
Fig. 2. PCoA graphics for relative abundance of **(a)** 473 genera, and **(b)** 1149 species (excluding those that occur at only one plot) occurring at 55 Amazonian terra firme plots. Symbols: (△) C and E; (○) NW, and (□) SW Amazonia.

1450
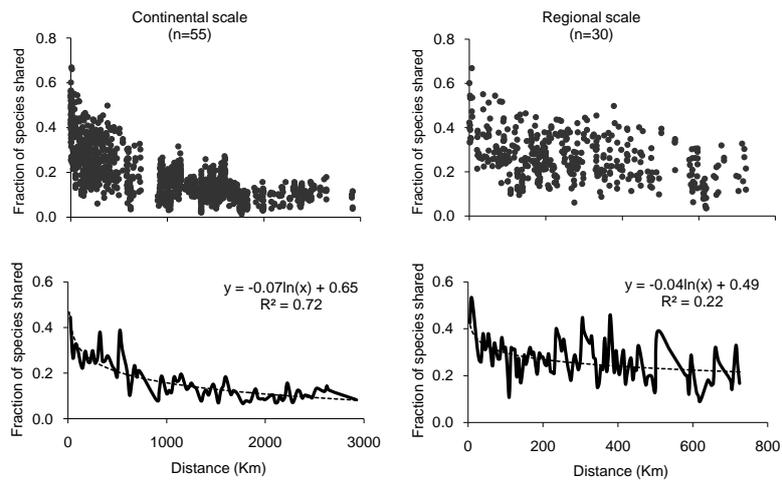
Fig. 3. Floristic similarity (fraction of species shared based on Sørensen's index) between sample pairs over geographical distance. Top: distribution of values of similarity for each pair of plots. Bottom: averages calculated over 25 km at continental scale and over 5 km at regional scale.

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