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Research

Peatland forests are the least diverse tree communities documented in Amazonia, but contribute to high regional beta-diversity

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Western Amazonia is known to harbour some of Earth's most diverse forests, but previous floristic analyses have excluded peatland forests which are extensive in northern Peru and are among the most environmentally extreme ecosystems in the lowland tropics. Understanding patterns of tree species diversity in these ecosystems is important both for quantifying beta-diversity in this region, and for understanding determinants of diversity more generally in tropical forests. Here we explore patterns of tree diversity and composition in two peatland forest types – palm swamps and peatland pole forests – using 26 forest plots distributed over a large area of northern Peru. We place our results in a regional context by making comparisons with three other major forest types: terra firme forests (29 plots), white-sand forests (23 plots) and seasonally-flooded forests (11 plots).

Peatland forests had extremely low (within-plot) alpha-diversity compared with the other forest types that were sampled. In particular, peatland pole forests had the lowest levels of tree diversity yet recorded in Amazonia (20 species per 500 stems, Fisher's alpha 4.57). However, peatland pole forests and palm swamps were compositionally different from each other as well as from other forest types in the region. Few species appeared to be peatland endemics. Instead, peatland forests were largely characterised by a distinctive combination of generalist species and species previously thought to be specialists of other habitats, especially white-sand forests.

We suggest that the transient nature and extreme environmental conditions of Amazonian peatland ecosystems have shaped their current patterns of tree composition and diversity. Despite their low alpha-diversity, the unique combination of species found in tree communities in Amazonian peatlands augment regional beta-diversity. This contribution, alongside their extremely high carbon storage capacity and lack of protection at national level, strengthens their status as a conservation priority.



The forests of north-western Amazonia are floristically remarkable as they include some of the most diverse tree communities on Earth (Gentry 1988a, Valencia et al. 1994, ter Steege et al. 2003), harbour communities with numerous endemic species (e.g. white-sand forest specialists [Fine et al. 2010]), and exhibit high species turnover over small spatial scales (i.e. high beta-diversity [Gentry 1988b, Tuomisto et al. 1995, 2003]). However, although there have been some studies of seasonally-flooded forests (Nebel et al. 2001, Fortunel et al. 2014), these previous comparative studies of floristic composition and diversity are largely limited to non-inundated (terra firme) forests. Compared to terra firme forests, seasonally and permanently flooded forests in Amazonia have a distinctive composition (Wittmann et al. 2006, Pitman et al. 2014) and therefore may make an important contribution to floristic beta-diversity in north-western Amazonia. In particular, permanently waterlogged peatland ecosystems, which are common in the 120 000 km² Pastaza-Marañón Foreland Basin (Lähteenoja et al. 2012, Draper et al. 2014) may have an even more distinctive composition but have been excluded from previous floristic analyses and, botanically, remain largely undescribed (but see Valderrama Sandoval 2013, Householder et al. 2015, Householder and Wittmann 2016).

The Pastaza-Marañón Foreland Basin holds a diverse range of wetland ecosystem types, several of which are peat-forming (Kalliola et al. 1991, Irion and Kalliola 2010, Lähteenoja and Page 2011, Draper et al. 2014). Some of these peatland ecosystem types, such as palm swamps, fit into existing wetland classifications (Prance 1979, Encarnación 1985, López Parodi and Freitas 1990, Kalliola et al. 1991, Junk et al. 2011): palm swamps in this region are typically less diverse than neighbouring terra firme forests (Richards 1969, Prance 1979, Dumont et al. 1990, Stropp et al. 2009, Pitman et al. 2014), and are often dominated by one or more species of arboreal palm, most commonly *Mauritia flexuosa* (Kahn and Mejia 1990, Endress et al. 2013, Pitman et al. 2014), whilst specialist swamp species account for < 10% of the remaining flora (Pitman et al. 2014).

In contrast, another ecosystem type, peatland pole forests (Lähteenoja and Page 2011, Draper et al. 2014) has only been loosely described (Lähteenoja and Roucoux 2010, García-Villacorta et al. 2011, Torres Montenegro et al. 2015, 2016), and its floristic composition remains largely unknown. These pole forests occur on raised ombrotrophic bogs (water and nutrients dominantly supplied by atmospheric deposition; Rydin and Jeglum 2006), normally on top of several meters of peat, and are characterised by their distinctive structure which consists of a dense, low stature canopy made up of many thin-stemmed trees (Draper et al. 2014). Similar raised, ombrotrophic peatland forests in Southeast Asia have a distinctive flora with numerous specialist and endemic taxa (Anderson 1963, 1983, Posa et al. 2011, Gunawan et al. 2012) but it is not known whether these characteristics are shared with Amazonian peatland pole forests.

Our first aim is therefore to describe the tree communities of Amazonian peatland forest ecosystems and explore whether peatland pole forests in north-western Amazonia contain

many endemic tree species, as in SE Asia, or whether their composition more closely reflects neighbouring forest types with just a few distinctive species, as found for Amazonian swamp forests. Secondly, we explore the contribution of these forests to beta-diversity (defined here as the turnover in species composition, or floristic dissimilarity, through space) in this region, using floristic data from all the major forest types found in north-western Amazonian lowlands.

The specific questions we address are: 1) which species are most abundant in peatland forests, and how many of these species are shared with surrounding upland and seasonally-flooded forests? 2) How floristically diverse are peatland forests, and how does their alpha-diversity compare with that of upland and seasonally-flooded forests? 3) How does floristic dissimilarity among plots within peatland ecosystems compare with those in upland and seasonally-flooded forests? 4) How does floristic dissimilarity among plots in peatland forest types vary as a function of geographic distance, and how does these patterns compare with upland and seasonally-flooded forests?

Material and methods

Forest inventories

Different data sets were used to compare the floristic composition of the five different forest types in the region. Data for 26 peatland forest plots (11 peatland pole forest and 15 palm swamp plots) are presented for the first time here, whilst data for 11 seasonally-flooded forest plots, 23 white-sand forest plots and 29 terra firme forest plots come from previously published datasets (Table 1, Fig. 1, and Supplementary material Appendix 2 [Pitman et al. 2008, Honorio Coronado et al. 2009, 2015, Fine et al. 2010]). Plots were assigned to the different forest types based on substrate character, forest structure and observed hydroperiod (Supplementary material Appendix 1 Table A1). Data for 55 out of the 89 plots used for this analysis were downloaded from the ForestPlots.net online repository (Lopez-Gonzalez et al. 2009, 2011).

Peatland forest inventories were conducted between 2008 and 2014 by FCD, EHC, TRB, LATM and EVS. A total of 26 plots were established at 11 peatland locations across the Pastaza-Marañón Foreland Basin, northeast Peru (Fig. 1). The sampling includes four peatland pole forest and seven palm swamp locations. Multiple plots were installed at several locations: the maximum number of plots in any given location was five and plots were located at least 500 m from any other plot. The 26 plots were 0.5 ha in area and were established using a modified version of the RAINFOR protocol (Phillips et al. 2009) whereby all trees with a diameter at breast height (dbh) ≥ 10 cm were measured and identified. As the peatland forests often contain many trees that are small in stature, the protocol was modified to include a 4×100 m transect in which all trees with a dbh ≥ 2 cm were measured and identified.

Table 1. Summary information for the plot dataset across five forest types showing the number, size and total plot area in each forest type, the minimum stem diameter included in the inventory, and the total number of stems and species recorded. Figures in square brackets correspond to subplots within the larger plots.

	Pole forest	Palm swamp	Terra firme	Seasonally flooded	White-sand
No. plots	11	15	28	12	24
Plot size (ha)	0.5 [0.04]	0.5 [0.04]	1	0.5 or 1	1, 0.1 or 0.025
Minimum diameter (cm)	10 [2]	10 [2]	10	10	10 or 2
Total area of plots (ha)	5.5 [0.44]	7.5 [0.6]	28	6.5	5.275
Total stems recorded	9427	4667	17311	4391	8519
Mean large (> 10 cm dbh) stem density (ha ⁻¹)	1044	532	618	682	838
Mean small (2–10 cm dbh) stem density (ha ⁻¹)	9905	1594	–	–	6103
Percentage total stems identified	97	95	64	81	86
Mean and range of total identified stems per plot	815 (418–1684)	292 (226–484)	394 (181–601)	290 (194–543)	303 (79–914)
Total identified species	99 [85] [#]	234 [201] [#]	1113	270	351

[#]refers to number of identified species found only in the 2–10 cm dbh subplots.

Of the 26 plots, 16 were permanent plots where all dbh \geq 10 cm trees were tagged and the plot corners were permanently marked. Full descriptions of plot inventories for the other forest types are provided in the Supplementary material Appendix 1.

Taxonomic standardisation

Botanical vouchers were collected and deposited in herbaria for the terra firme, seasonally-flooded and white-sand forest datasets as described in the relevant publications (Pitman

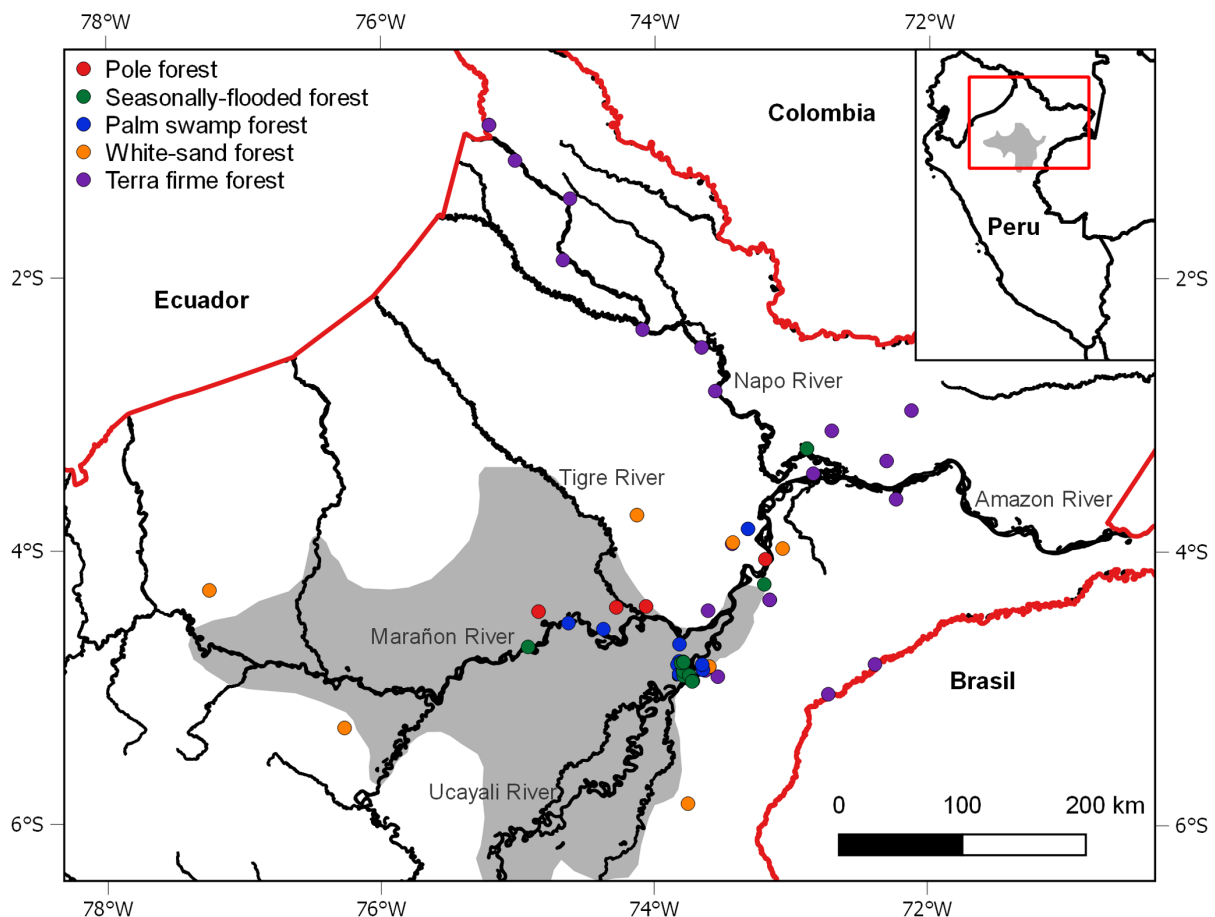


Figure 1. Location map showing all 89 forest plots, the location of the Pastaza-Marañon Foreland Basin (shaded area) within Peru (red boundary). Many locations contain several plots (median = 1, mean = 1.6, max = 11). Full details of all plots can be found in Supplementary material Appendix 2. River and country boundary was downloaded from (DIVA GIS 2014). The inset map shows the study region in relation to the rest of Peru.

et al. 2008, Honorio Coronado et al. 2009, 2015, Fine et al. 2010). The collections from peatland forests, presented here for the first time, were determined by LTM and EVS, and standardised with the previous collections of Honorio Coronado et al. (2015) as well as specimens at the Herbarium Amazonense (AMAZ) in Iquitos. The new vouchers were deposited at Herbario Herrerense (HH), digitised and are available online through the digital herbaria of the ForestPlots.net database (Baker et al. 2017). Finally, the online Taxonomic Name Resolution Service was used to remove all synonyms from the dataset using Tropicos as the source of taxonomic information (Boyle et al. 2013).

Comparing diversity and composition across datasets

In order to make comparisons of species composition and diversity among forest types it was necessary to combine datasets with different sampling protocols. Morphospecies were consistently identified within, but not among, the different datasets. Therefore, all morphospecies and individuals not identified to species level were classified as unidentified morphospecies and excluded from all subsequent analyses. As plots of different sizes contained variable numbers of stems, species richness and alpha-diversity were estimated using a standard number of 500 identified stems for each plot, derived from unified interpolated/extrapolated rarefaction curves, following the multinomial model method of Colwell et al. (2012). Full descriptions of the methods and associated implications of excluding morphospecies and using rarefaction are provided in the Supplementary material Appendix 1.

Criteria for defining ecological guilds

In order to identify specialist peatland taxa, all species found in peatland plots were split into five exclusive ecological guilds based on their occurrence in different forest types following similar definitions to those in Pitman et al. (2001, 2014). These categories were applied independently to peatland pole forest and palm swamp forest taxa. ‘Generalists’ were defined as species that occurred in the relevant peatland forest type and were common (occurred at a mean density > 1 individual ha^{-1}) in two or more other forest types. ‘Spillover’ species were defined as species that occurred in the relevant peatland forest type and were also common in one other forest type. ‘Strict specialists’ were those species that were common in the relevant peatland forest type and had over 95% of total stems within the same peatland ecosystem. ‘Functional specialists’ were those that were common in the relevant peatland forest type and had 80–95% of total stems within the same peatland ecosystem. Taxa with fewer than five individuals across all plots were considered too rare for their distribution to be characterised in this way. Taxa that did not fit the criteria for any of the above ecological guilds were grouped as ‘other’.

In addition to these qualitative thresholds we also used indicator species analysis to identify those species that were significantly ($p \leq 0.05$) indicative of peatland forest types

using the R package labdsv (Roberts 2013). Indicator species analysis provides a measure of which species are strong associated with a given forest type based on their abundance within and among forest types (Legendre and Legendre 2012). A permutation procedure is then used to compare these associations to those obtained from a random distribution for each species in order to assess significance (Dufrenoy and Legendre 1997).

Alpha-diversity analysis

Alpha-diversity was estimated for the rarefied 500 stems per plot (as outlined above) using two of the most widely used metrics, Fisher’s alpha and the exponential Shannon index (Rosenzweig 1995, Magurran 2013). These two metrics allow for easy comparison with existing studies and reflect slightly different qualities of diversity. The exponential Shannon index quantifies diversity as the effective number of species, which takes into account both species richness and the evenness of species abundances (Jost 2006). All values of species richness, Fisher’s alpha and the Shannon index were calculated using ‘estimate-S’ (Colwell 2013).

Beta-diversity analysis

To compare floristic composition among plots, floristic distance matrices were constructed using the Hellinger distance for abundance data and the Jaccard distance (1-Jaccard index) for presence/absence data (Legendre and Legendre 2012). The indices were selected as they are both asymmetric resemblance measure, and are suitable for analysing community composition data (Anderson et al. 2011). Additionally, because the Hellinger index is based on proportional abundances, it minimizes the effect of different numbers of individuals among plots (Legendre and Legendre 2012). The distance matrices were constructed in the ‘vegan’ package of R (Oksanen et al. 2013), and were used to create non-metric multidimensional scaling (NMDS) ordinations (optimized for two axes) in order to visualise floristic dissimilarity within and amongst forest types. A non-parametric permutational multivariate analysis of variance (PERMANOVA) was conducted (where the Hellinger distance matrix was the response variable) in order to test the significance of the variation in species composition among forest types (Anderson 2001). Furthermore, in order to examine the influence of variable plot size and stem number on patterns of beta-diversity, we repeated our analysis using a standardised number of 79 randomly chosen individuals from each plot.

In order to test how floristic similarity within forest types was affected by the geographic distance among plots, a distance decay approach was also used (Whittaker 1960). Here floristic similarity was calculated using the inverse Hellinger distance, which was standardised to give values ranging from zero (completely dissimilar) to one (identical) ($1 - \text{Hellinger}/\sqrt{2}$). A binomial generalised linear model (GLM) approach with a log link function was used to model

variation in species similarity as a function of geographic distance within forest types (Millar et al. 2011). This method can cope with values of zero dissimilarity and is known to be an effective method for modelling distance decay relationships (Steinbauer et al. 2012). In order to generate 95% confidence intervals, a modified bootstrap resampling procedure was adopted (Millar et al. 2011). This procedure consists of repeatedly performing the GLM outlined above with a randomly sampled subset of 4050 (the total number of unique plot pairs) paired ecological and geographical distances, 10 000 times. This sampling was conducted with replacement (i.e. bootstrapping), and samples were drawn from the lower left triangle of the similarity matrix.

A Raup–Crick null model approach was used to assess the probability that the overall beta-diversity between forest types was higher or lower than expected by chance (Raup and Crick 1979, Chase et al. 2011). For each pair of plots with a species richness of α_1 and α_2 and SS_{12} species in common, α_1 and α_2 species were randomly sampled from the total species pool, and the number of species between them (SS_{exp}) was calculated. By repeating this process 10 000 times for each plot pair, we were able to build a null distribution of (SS_{exp}) for each pair of plots. We then compare this null distribution with our observed values (SS_{obs}), and produce a metric that describes the proportion of the SS_{exp} distribution that is greater than SS_{obs} . Finally, we standardise this metric to produce a pairwise community dissimilarity metric (beta RC) ranging from -1 to 1 . Metric values approaching -1 suggest that communities are more similar than expected by chance, values approaching 0 suggest that communities are as similar as would be expected by chance, and values approaching 1 indicate greater dissimilarity than would be expected by chance.

All data manipulations and statistical analyses were conducted in the R statistical environment (R Core Team). Apart from the packages specified above, all code for resampling and data manipulation was custom-written.

Results

Floristic composition of peatland forests

Palm species accounted for approximately 50% of individuals on average in palm swamps, with four palm species in the top ten most abundant species (Supplementary material Appendix 1 Table A2). The palm species *Mauritia flexuosa* was the most abundant species, accounting for 33% of all individuals and occurring in all 15 sampled plots. Other important palms include *Mauritiella armata*, *Euterpe precatoria* and *Socratea exorrhiza*, all of which were significant palm swamp indicator species. Among dicot tree species, *Tabebuia insignis* var. *monophylla* (Bignoniaceae), *Virola pavonis* (Myristicaceae) and *Symphonia globulifera* (Clusiaceae) were also significant indicator species, and characteristic of palm swamps (Supplementary material Appendix 1 Table A2 and Supplementary material Appendix 3).

Within peatland pole forests, the seven most abundant species were all dicot trees (Supplementary material Appendix 1 Table A3). *Pachira brevipes* (Malvaceae) was the most abundant species, accounting for 29% of all peatland pole forest individual trees and occurred in nine out of 11 plots (Supplementary material Appendix 1 Table A3). Other abundant and significant indicator tree species in peatland pole forests include: *Cybianthus* cf. *reticulatus* (Primulaceae), *Tabebuia insignis* var. *monophylla*, *Platycarpum lorentensis* (Rubiaceae) and *Hevea guianensis* (Euphorbiaceae) (Supplementary material Appendix 3). Two species of palms: *Mauritia flexuosa* and *Mauritiella armata* were also abundant and widespread in peatland pole forests.

Associations between peatlands and other forest types

Few peatland pole forest or palm swamp species were strict specialists that occur almost entirely in those habitats (eleven and seven species out of a total 99 and 234 respectively; Supplementary material Appendix 1 Table A2), and they accounted for an even smaller proportion of individuals. In contrast, most species and stems were spill-over species (common in one other forest type), or habitat generalists (common in two or more forest types) (Fig. 2). Spill-over species in peatland pole forest mostly also occurred in white-sand forests. This group accounted for 16% of species and 44% of stems in the peatland pole forest plots and includes species such as *Bocageopsis canescens*, and the recently described *Platycarpum lorentensis* (Davila and Kinoshita 2016) (Fig. 2, Supplementary material Appendix 3). Within palm swamps, most species were either spill-over species or ‘too rare’ (total number of species < 5) (Fig. 2). The most important source of spill-over species in palm swamps was seasonally-flooded forest. This group accounted for 20% of species and 11% of stems in palm swamps and included species such as *Coccoloba densifrons* and *Hura crepitans* (Fig. 2). In terms of stems, spill-over species from palm swamps were also important in pole forests and vice versa, these peatland spill-over species included very common species such as *Mauritia flexuosa*.

Tree species richness and alpha-diversity

Peatland pole forests and palm swamps had lower tree species richness and alpha-diversity than all other forest types (Fig. 3 and Supplementary material Appendix 1 Fig. A1). Peatland pole forest was less species rich and less diverse than the other forest types ($p < 0.001$), and on average contained an estimated 20 species per 500 stems. In comparison, on average, palm swamps had an estimated 38 species per 500 stems (Fig. 3). Terra firme plots were always the most diverse and species rich forest type ($p < 0.001$), with an estimated 166 species per 500 stems (Fig. 3).

Beta-diversity among forest types

The five forest types defined on the basis of structural and environmental characteristics were also clearly distinct from

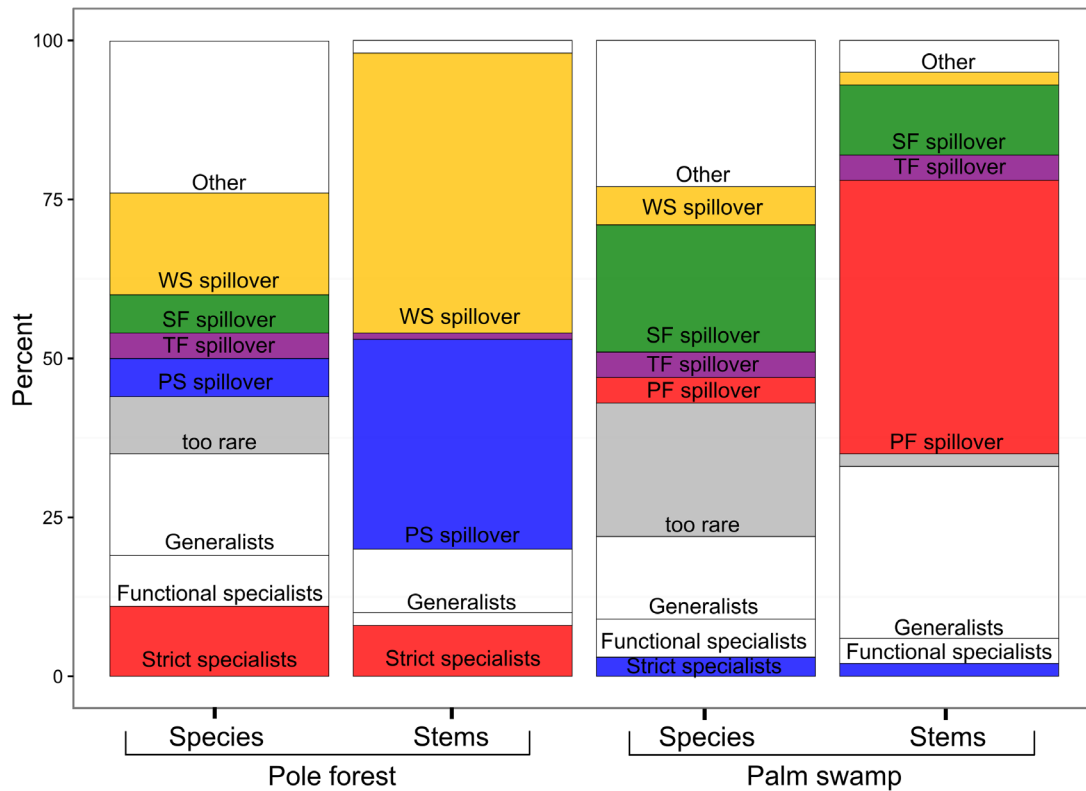


Figure 2. Percentage of species and stems in the two peat forming forest types (peatland pole forests and palm swamps) belonging to specific ecological guilds defined in the methods section. Codes refer to forest types as follows: PF (pole forest); PS (palm swamp); SF (seasonally-flooded forest); TF (terra firme forest); WS (white-sand forest).

one another in terms of their floristic composition (Fig. 4). These compositional differences among forest types were highly significant (PERMANOVA, $p < 0.001$) and persisted irrespective of whether species abundance or simply presence/absence of species were considered (Fig. 4). Furthermore, the distinctiveness of forest types cannot be attributed to the difference in stem numbers among plots, as compositional patterns were conserved when the analysis was repeated with the subset of 79 individuals per plot (Supplementary material Appendix 1 Fig. A2).

Results from the Raup–Crick null models provided further support for the significance of the floristic differences among forest types. Overall the mean beta RC values among most of the different forest types were positive and many approached one, suggesting that dissimilarity between forest types was greater than would be expected by chance (Table 2). The three beta RC values that were negative (suggesting these forest types are more similar than expected by chance) were those obtained for comparisons between peatland pole forest and palm swamp, peatland pole forest and white-sand forest, and palm swamp and seasonally-flooded forest (Table 2), consistent with the links between these forest types identified by the analysis of ecological guilds (Fig. 2).

Beta-diversity within forest types

The mean floristic similarity among plots within the two peatland forest types was higher than within any other forest type (Fig. 5). However, although peatland plots overall were usually more similar to one another than other forest types, this was not the case in all instances, and there were several pairs of peatland plots that had a very different floristic composition: the variation in floristic similarity was higher when compared with plots within other forest types (see error bars in Fig. 5).

Beta-diversity and geographic distance

Floristic similarity within forest type declined with geographic distance, but the importance of distance varied substantially among forest types. Floristic similarity decreased with geographic distance more strongly in peatland forests and seasonally-flooded forests than in upland forests (Fig. 5 and Supplementary material Appendix 1 Fig. A4). The large variability in floristic similarity observed in peatland forests seemed to be independent of distance, as high variability occurred between plots that were located both close to and far from

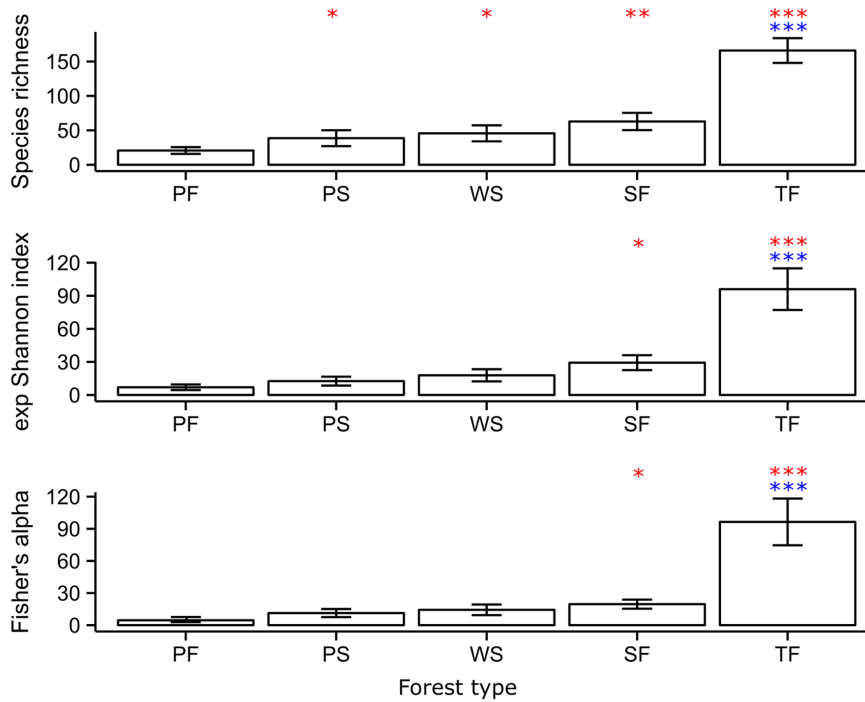


Figure 3. Estimated species richness and diversity as estimated by the exponential Shannon index and Fisher's alpha for the five forest types: peatland pole forest (PF), palm swamp (PS), white-sand forest (WS), seasonally-flooded forest (SF) and terra firme forest (TF). Estimated richness and diversity indices were calculated for 500 extrapolated individuals. Error bars are 95% confidence intervals. Asterisks indicate values significantly different from peatland pole forest (red) and palm swamp (blue), (* = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$).

one another (Fig. 5 and Supplementary material Appendix 1 Fig. A4). Again these patterns persisted when the analysis was repeated using the subset of 79 individuals, demonstrating

that our results were not dependant on the number of individuals per plot (Supplementary material Appendix 1 Fig. A3).

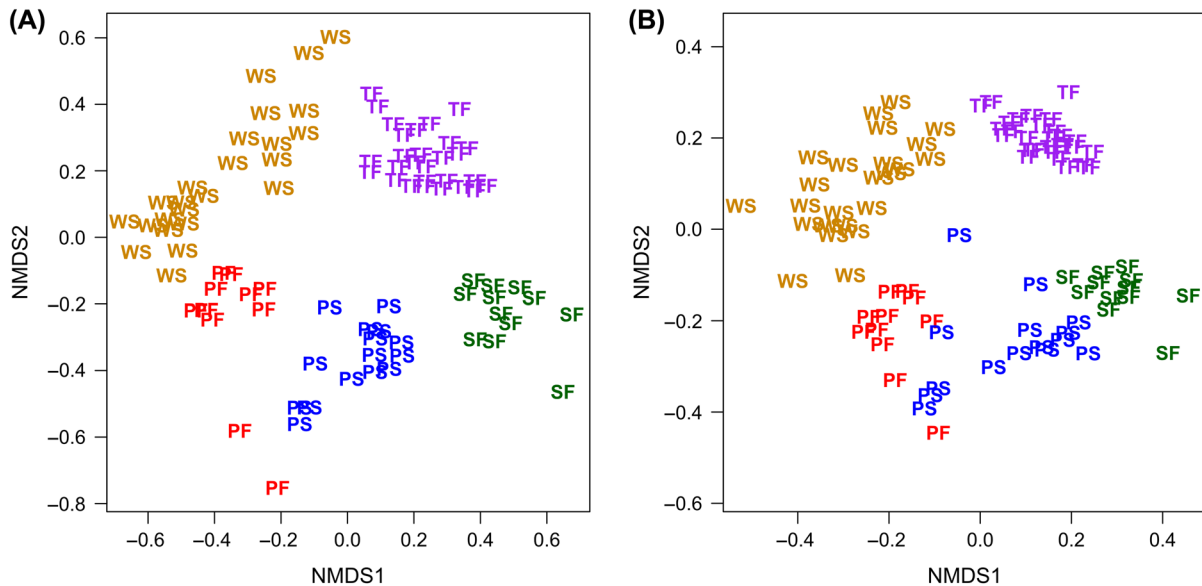


Figure 4. NMDS ordinations showing the similarity of all 89 forest plots within and among forest types. Panel (A) is an NMDS ordination based on tree species abundance data (Hellinger distance), Panel (B) is an NMDS ordination based on all tree species presence/absence data (Jaccard distance). Both ordinations were optimized for two dimensions. Labels and colours correspond to forest types: peatland pole forest (PF, red); palm swamp (PS, blue); seasonally-flooded forest (SF, green); terra firme (TF, purple); white-sand forests (WS, orange). The corresponding analyses using a subset of 79 individuals per plot are presented in the Supplementary material Appendix 1 Fig. A2.

Table 2. Mean Raup–Crick community dissimilarity. The given value indicates the degree to which the similarity between forest types is more similar, equally similar, or less similar, than would be expected by chance. The observed similarity was tested against 1000 random permutations of a null model. Values approaching zero indicate levels of similarity expected by chance, values approaching 1 indicate greater dissimilarity than expected by chance, and values approaching -1 indicate greater similarity than expected by chance.

	PF	PS	SF	WS	TF
Pole forest	-0.95	-0.52	0.46	-0.38	0.66
Palm swamp	-	-0.83	-0.31	0.50	0.61
Seasonally-flooded forest	-	-	-0.77	0.80	0.77
White-sand forest	-	-	-	-0.80	0.52
Terra firme	-	-	-	-	-0.55

Discussion

Floristic composition of peatland ecosystems

This study shows that the peatland forests of the Pastaza-Marañón Foreland Basin have a distinct floristic composition compared to the other major forest types in the region. However, unlike Amazonian white-sand forests and seasonally-flooded forests, and similar peatlands in SE Asia, the floristic distinctiveness of these peatland forests is not due to the presence of a highly specialised endemic flora (Fine et al. 2010, Posa et al. 2011, Wittmann et al. 2013). Instead, peatland forests are floristically distinctive because of the identity of their most abundant species, which are often not strict specialists. For example, although *Mauritiella armata* occurs occasionally in white-sand plots, it only forms dominant stands in peatland forests. This finding is further supported by our indicator species analysis, which shows that most significant peatland indicator species are not specialists, but instead are generalists or spill-over species (Supplementary material Appendix 1 Table A2). Such dominance or ‘oligarchic’ patterns are ubiquitous across Amazonia, in a range of

forest types (Pitman et al. 2001, 2013, 2014, ter Steege et al. 2013). A small number of peatland specialist species (e.g. *T. insignis* var. *monophylla*) also contribute to these oligarchies, and overall it is the unique combination of species forming oligarchies in peatland forests that makes the tree biodiversity of these ecosystems distinctive.

As there are apparently few specialist peatland taxa, many species that occur here are also found in other forest types. Interestingly, peatland pole forests are compositionally similar to white-sand forests as has been suggested previously (Lähteenoja et al. 2009a, García-Villacorta et al. 2011), and a number of species that had previously been considered white-sand endemics are common in peatland pole forests, such as *Platycarpum loretensis* (Davila and Kinoshita 2016). A likely explanation for this pattern is that peatland pole forests and white-sand forests share common environmental filters (Keddy 1992), including exceptionally low levels of exchangeable cations and extreme acidity (pH 3.5–4.7) (Anderson 1981, Kalliola and Flores Paitan 1998, Quesada et al. 2010, Lähteenoja and Page 2011, Adeney et al. 2016, García-Villacorta et al. 2016).

Palm swamps are floristically similar to both peatland pole forests and seasonally-flooded forests, and contain many seasonally-flooded forest spill-over taxa (Fig. 2). This is likely because palm swamps share similar environmental filters with both peatland pole forests and seasonally-flooded forests. Like peatland pole forests, palm swamps are constantly waterlogged, but typically have much higher fertility and higher pH than either peatland pole forests or white-sand forests due to fluvial mineral input (Lähteenoja and Page 2011). Palm swamps also experience extended inundation, as do seasonally-flooded forests. However, for both palm swamp and peatland pole forest it is difficult to separate the effect of environmental filters from possible dispersal limitation, as palm swamp forests are often found close to seasonally-flooded forests and peatland pole forests are most common in

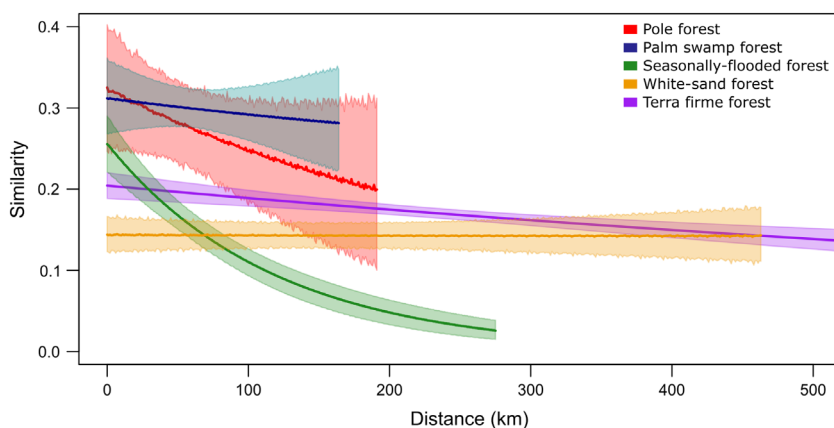


Figure 5. Floristic similarity (inverse Hellinger distance based on all tree species abundance data) between pairs of plots, within forest types, as a function of geographical distance between the plots. Solid lines show the mean similarity from the GLM models and shaded areas show the 95% confidence interval of the model fits. Individual (within forest type) model fits alongside their underlying data are presented in the Supplementary material Appendix 1 Fig. A4. The corresponding analysis using a subset of 79 individuals per plot is presented in the Supplementary material Appendix 1 Fig. A3.

the north-east of the Pastaza-Marañón Foreland Basin close to the extensive white-sand forests around the Nanay river (Fine et al. 2010, Draper et al. 2014).

Endemism in peatlands

It is remarkable that there are so few candidates for peatland endemic tree species in our study, as peatlands present a distinct combination of environmental filters compared with upland forests. We would expect this distinct environment to lead to both parapatric and allopatric speciation, as has been shown for white-sand forests in both plant and bird communities (Fine et al. 2004, 2005, 2006, 2014, Fine and Kembel 2011, Fine and Baraloto 2016). Therefore, the lack of endemism observed in the Pastaza-Marañón Foreland Basin peatlands is curious, particularly given the apparently high numbers of endemics species reported in other environmentally extreme habitats (e.g. white-sand forests in western Amazonia, 114 endemic trees species (Fine et al. 2010); Amazonian white water seasonally-flooded forests, 68 endemic tree species (Wittmann et al. 2013); SE Asian peatland forests, 172 endemic tree species (Posa et al. 2011)).

One possible explanation for this apparent low endemism is that peatlands are a relatively transient feature on the landscape in this region, and as a result there has been insufficient time for speciation to occur. Wetland swamp habitats have occurred at least intermittently in western Amazonia since the early Miocene, although their permanence on the landscape remains unclear (Hoorn 1994, Hoorn et al. 2010a, b). However, unlike in SE Asia, no peats dating to Quaternary glacial periods have yet been identified in the Pastaza-Marañón Foreland Basin (Lähteenoja et al. 2009b, 2012, Roucoux et al. 2013, Swindles et al. 2015, Watson et al. 2015). Peatlands can be exceptionally sensitive to climate dynamics, such as changes to precipitation and the flood regime (Fenner and Freeman 2011, Kelly et al. 2017). Although western Amazonia probably only experienced modest drying during glacial periods (Cheng et al. 2013), even slightly reduced rainfall may have been sufficient to cause peatlands, particularly domed ombrotrophic peatlands where pole forests are found, to disappear from the landscape for long periods (Dommain et al. 2014).

One species variety that is amongst the most common in both peatland forest types and which may be a peatland specialist is *Tabebuia insignis* var. *monophylla*. Interestingly, this variety is abundant not only in other peatland forests elsewhere in northwest Amazonia (Torres Montenegro et al. 2016), but also found in swamp forests in Guyana, Venezuela and northeastern Brazil (Gentry 1992, ter Steege et al. 1993, White et al. 2002, Van Andel 2003, Vegas-Vilarnibia et al. 2006). Understanding the evolutionary history of this unusual example of a potentially endemic Amazonian peatland tree, would be a useful future research direction in order to understand the evolution and development of peatland forests in Amazonia.

Patterns of alpha-diversity

Overall, the alpha-diversity of both peatland ecosystems, is low compared with other forest types. This finding is consistent with numerous records showing that Amazonian swamps are less diverse than terra firme forests (Dumont et al. 1990, Kahn and Mejia 1990, Pitman et al. 2014). Peatland pole forests are, in turn, much less diverse than palm swamps (estimated mean Fisher's alpha 4.57), and to our knowledge the least diverse forest type yet recorded in Amazonia. This includes comparisons with so-called 'monodominant' forests and low-diversity igapó forests, which typically contain more than twice as many species per plot than was observed here (and Supplementary material Appendix 1 Table A4) (Johnston and Gillman 1995, Nascimento et al. 1997, ter Steege et al. 2000, Marimon et al. 2001, Targhetta et al. 2015).

Why are Amazonian peatland pole forests so species-poor? One possible explanation is that the low diversity observed in the peatlands results from their strong environmental filters. However, environmental filtering alone cannot explain the disparity in diversity between peatland pole forests and white-sand forests in our data. Like peatland pole forests, white-sand forests have exceptionally nutrient-poor soils and highly acidic soils (Kalliola and Flores Paitan 1998, Quesada et al. 2010), yet they maintain much higher levels of diversity. Interestingly, SE Asian peatland pole forests, are also much more diverse (65–80 species per 0.16 ha plot; Poesie et al. 2010, Posa et al. 2011) than those we describe (7–35 species per 0.5 ha plot), despite sharing broadly equivalent environmental filters.

Another explanation is that the low diversity found in peatland pole forests results from their small area and isolated nature, which leads to enhanced dispersal limitation and increased stochastic extinctions (ter Steege et al. 2000, Stropp et al. 2009, ter Steege 2010). This explanation is consistent with neutral theory (Hubbell 2001), area-diversity theory (Rosenzweig 1995), and island biogeography theory (MacArthur and Wilson 1967). To some extent our results support this explanation, as the more diverse palm swamps occupy a greater area (27 732 km²) than the less diverse peatland pole forests (3686 km²) and occur in more continuous patches (> 50 km²) (Draper et al. 2014). However, white-sand forests also occupy a small area and have a patchy distribution in this region (Adeney et al. 2016), but are floristically more diverse than both peatland ecosystems. Furthermore, far smaller patches of palm swamp forest occurring within terra firme in western Amazonia are much more diverse than our palm swamp plots (e.g. up to 164 species ha⁻¹; Cornejo Valverde and Janovec 2006). This suggests that the tree diversity of palm swamps does not always increase with patch size, and in fact the opposite seems to be the case in this instance. This may be because small swamp patches surrounded by terra firme forest may contain many spill-over species, while larger swamp areas may effectively form their own buffer zone from surrounding vegetation types.

An alternative explanation for the low diversity observed in peatlands is that environmental dynamism over centennial timescales in peatlands may have prevented the accumulation of diversity. The oldest known peatlands in the Pastaza-Marañón Foreland Basin have been accumulating peat for 8000 yr, but the ombrotrophic conditions associated with peatland pole forest may have only developed over recent centuries (Lähteenoja et al. 2012, Kelly et al. 2017). This temporal dynamism contrasts markedly with white-sand forests which formed over six million years ago, and have probably maintained a relatively constant edaphic environment for millennia (Räsänen et al. 1987, Roddaz et al. 2005). Within this context, Amazonian peatlands may be analogous to an early successional system where species turnover in space or time is fast, but diversity at any one point is relatively low. This explanation is consistent with pollen analysis showing that peatlands in this region have undergone substantial floristic change through their development (Roucoux et al. 2013, Draper 2015, Kelly et al. 2017).

These three explanations relating to area, environment and time are not mutually exclusive, and almost certainly all three contribute to the low diversity observed in peatlands. However, we suggest it is the relative youth of Amazonian peatlands that makes them especially species-poor. A similar habitat-age explanation has been shown to determine species richness in fen-ecosystems in northern peatlands (Horsák et al. 2012). It will be important to test the importance of environmental dynamism through time in determining current diversity in these ecosystems using palaeoecological methods.

Patterns of beta-diversity

Floristic dissimilarity within peatland ecosystems is slightly lower but far more variable than that found among upland terra firme (Fig. 5). This pattern is particularly striking in the field as the high turnover in composition and abundance can occur over very short distances. For example, in one peatland pole forest plot *Pachira brevipes* accounts for ~70% of individuals, while in another peatland pole forest plot < 1 km away *Pachira brevipes* is entirely absent. Similar patterns of high tree species turnover have been found in white-sand habitats (Fine et al. 2010), and may be a product of strong fertility gradients occurring over short distances. Alternatively these beta-diversity patterns may derive from historical contingency and priority effects (Fukami 2015), whereby the species that first colonise the peatland dominate specific patches. This explanation – that the decrease in community similarity with increasing distance between peatland plots (Fig. 5), primarily reflects dispersal limitation, rather than some underlying environmental gradient – seems most likely in this case. This is because whilst there are strong environmental gradients within individual peatlands, these gradients do not appear to vary systematically across the Pastaza-Marañón Foreland Basin within peatland ecosystem types (Lähteenoja and Page 2011). The seemingly high dispersal

limitation in peatlands contrasts with other forest types: particularly in terra firme and white-sand forests, where distance appears to be a relatively poor predictor of similarity (Fig. 5), an observation consistent with other studies in this region (Condit et al. 2002, Tuomisto et al. 2003).

Limitations of our study design

Our study draws on a range of different plot datasets, including plots of different sizes and different diameter limits. The inclusion of many datasets is both a strength and a limitation of our study, as it allows us to have a large sample size across all forest types in this region, but makes comparison among sampling protocols more difficult. Although we have taken measures to standardise our dataset (e.g. through excluding morphospecies), the overall high beta-diversity among white-sand forest plots may be due, in part, to variation in sampling design, as plots varied in size from 0.025 to 1 ha, and included diameter limits of both 2 cm and 10 cm. Additionally, because we have only sampled woody stems > 2 cm, the diversity patterns that we find may not be representative of other plant groups such as herbs.

Conservation importance of peatland forests

Whilst peatland forests in the Pastaza-Marañón Foreland Basin may lack the alpha-diversity of terra firme forests and the endemism of white-sand forests, they make a substantial contribution to the regional variation in beta-diversity. As peatlands have been confirmed to harbour a number of white-sand specialist species in high abundance, they appear to provide a previously unaccounted-for link between isolated patches of white-sand forests (Lähteenoja et al. 2009a, b, García-Villacorta et al. 2011). Therefore, conserving peatlands may be an important step in conserving white-sand endemic species that have been identified as a conservation priority (Alvarez Alonso et al. 2013).

Peatland forests also harbour a number of economically important tree species. *Mauritia flexuosa* in particular is not only one of the most abundant peatland species but also the most important wild fruit-bearing plant in this region, providing a valuable resource for local communities (Manzi and Coomes 2009, Horn et al. 2012, Endress et al. 2013, Gilmore et al. 2013). Therefore, the contribution to regional beta-diversity and abundance of economically important species present a strong rationale for peatland conservation, quite apart from their value as a carbon store and potential sink (Lähteenoja et al. 2012, Draper et al. 2014, Roucoux et al. 2017).

Conclusions

The largest peatland complex in Amazonia contains two floristically distinct forest ecosystems, peatland pole forests and palm swamps. These peatland ecosystems are anomalous due to their extremely low alpha-diversity and low levels of endemism in tree species. Whilst habitat area and soil fertility

appear to contribute to this low tree species diversity, our results indicate that environmental dynamism over centennial timescales may lead to increased dispersal limitation or priority effects, resulting in the exceptionally low diversity found in peatland pole forests. The low levels of peatland endemic tree taxa in our dataset may be a result of environmental instability over longer, millennial timescales, which may have prevented speciation. Amazonian peatlands should therefore be valued as an important component of regional ecosystem diversity and not only as large carbon stores.

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Supplementary material (Appendix ECOG-03126 at <www.ecography.org/appendix/ecog-03126>). Appendix 1–3.