One sixth of Amazonian tree diversity is dependent on river floodplains

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Amazonia's floodplain system is the largest and most biodiverse on Earth. Although forests are crucial to the ecological integrity of floodplains, our understanding of their species composition and how this may differ from surrounding forest types is still far too limited, particularly as changing inundation regimes begin to reshape floodplain tree communities and the critical ecosystem functions they underpin. Here we address this gap by taking a spatially explicit look at Amazonia-wide patterns of tree-species turnover and ecological specialization of the region's floodplain forests. We show that the majority of Amazonian tree species can inhabit floodplains, and about a sixth of Amazonian tree diversity is ecologically specialized on floodplains. The degree of specialization in floodplain communities is driven by regional flood patterns, with the most compositionally differentiated floodplain forests located centrally within the fluvial network and contingent on the most extraordinary flood magnitudes regionally. Our results provide a spatially explicit view of ecological specialization of floodplain forest communities and expose the need for whole-basin hydrological integrity to protect the Amazon's tree diversity and its function.

Amazonia's floodplain forests border the rivers that collectively make up our planet's largest fluvial system and underpin crucial aspects of floodplain ecosystem function[1]. But how and why are the Amazon's floodplain tree communities distinct from surrounding forests? These questions have long intrigued ecologists because they get to the heart of what floodplain forests mean for the maintenance of tree diversity[2–4], population regulation[5,6] and speciation[7–10]. These questions are vital for conservation planning too. Natural flood regimes are a principal driver of growth, phenology and life cycles of floodplain trees[1] but are becoming increasingly altered by proliferating hydroelectric dams, changing rainfall patterns and deforestation[11–13]. These changes threaten to reshape floodplain tree assemblies in ways that imperil both biodiversity and fundamental ecosystem functions[14–16]. For example, compositional changes to floodplain forests are expected to affect crucial fish–tree interactions that sustain aquatic trophic webs, with unknown consequences for productive fisheries on which the livelihoods of Amazonian peoples depend[17]. Given the evidence that human interventions in the Amazon's hydrological system are disruptive to floodplain tree communities and propagate over large spatial scales[11–13], our understanding of the species composition of floodplain forests and the extent to which they differ from surrounding forest types is still too fragmented[18], coming mostly from studies with limited spatial extents (but see refs. 7,9,19). Amid the growing pace and scope of hydrological threats, there is a pressing need for an integrated, system-wide approach that can guide floodplain conservation strategies and identify potential vulnerabilities in spatially explicit ways.

Central to this aim are two concepts that together capture essential information about linkages between species and their environment. The first is habitat specialization, which measures the restriction of a tree species' distribution to particular environments (here, to floodplains). It sheds light on species adaptation and ecological function and can be a key indicator of species vulnerability to environmental change[20]. The second is species turnover—here as a measure of the level of compositional differentiation between floodplain and adjacent terra firme forest—which reflects the extent to which species distributions are constrained by habitat, and thus how tree diversity is spatially organized on landscapes[21]. Because both concepts link species to their environment and capture the component of forest diversity that is unique to floodplains, they offer key insights into how floodplains regulate species populations and maintain tree diversity on Amazonian

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landscapes as well as related challenges for floodplain conservation[21]. Our understanding of the geographic and environmental patterning of habitat specialization and species turnover remains inadequate in the context of floodplain forests, but it will be a crucial feature of our ability to safeguard the biodiversity of future floodplain ecosystems and ensure their ecological functioning amid growing hydrological risks.

Dataset and approach

We examined Amazon-wide patterns of floodplain tree specialization and species turnover by analysing a uniquely suited dataset of 1,705 mostly 1 ha tree inventory plots, with information on species composition and abundances, from the Amazon Tree Diversity Network (ATDN)[22]. This includes both floodplain (n = 455) and terra firme (n = 1,250) sites, extending across most of the Amazon region and enabling us to assess species turnover and specialization across greater spatial, environmental and floristic heterogeneity than previously possible. We first used a spatially explicit approach to examine Amazon-wide patterns of tree species turnover between seasonal floodplain forests and surrounding, non-flooded terra firme. We found clear geographic patterning and subsequently considered a suspected driver, regional differences in flooding[7,9,23,24]. Second, we assessed species-specific habitat patterns with tests of floodplain specialization for over 1,600 tree species, examining the local abundance patterns of floodplain specialists. Finally, we considered how our findings contribute to discussions of floodplain biodiversity conservation in the face of systemic hydrological change.

Results and discussion

Geographic patterning of species turnover

To assess spatial variation in species turnover between floodplain and terra firme forests, we first used plot data (Extended Data Fig. 1 and Supplementary Table 1) to produce separate 1° compositional grids for three habitats: (1) terra firme is the predominant Amazonian forest type, without seasonal river flooding; (2) *várzea* is seasonally flooded forest that borders white-water rivers, characterized by their laterally migrating channels, high sediment loads and relatively fertile substrates of Andean origin[25]; and (3) *igapó* is seasonally flooded forest that lines black- and clear-water rivers with relatively stable channels, low sediment loads and nutrient-poor substrates[25]. The two floodplain classes capture important differences in limnology and chemistry that can strongly influence forest composition and therefore species turnover with adjacent terra firme[25]. The distinction of floodplains is recognizable in the field by the colour of the river water, and we used the reported field designations of ATDN data contributors. We populated cell compositional data for each habitat grid by spatially interpolating habitat-specific species densities (with distance decay) from inventories located within a ~300 km circular window. Spatially continuous maps of landscape-scale species turnover for *várzea*–terra firme and *igapó*–terra firme comparisons were then produced by measuring differences in tree species compositions at analogous cells of overlapping floodplain and terra firme compositional grids (Extended Data Fig. 2).

The resulting maps reveal striking spatial patterning, with a distinctive nucleus of high species turnover emerging in central Amazonia (Fig. 1a). The high species turnover implies that populations of tree species are more strongly constrained by habitat in this central region than elsewhere. Outside this core region, *várzea*s have a secondary concentration of high species turnover in the west, although most other peripheral regions tend to show lower levels of species turnover that suggest a greater degree of species spillover across floodplain and terra firme habitats that homogenizes their tree communities to a larger extent.

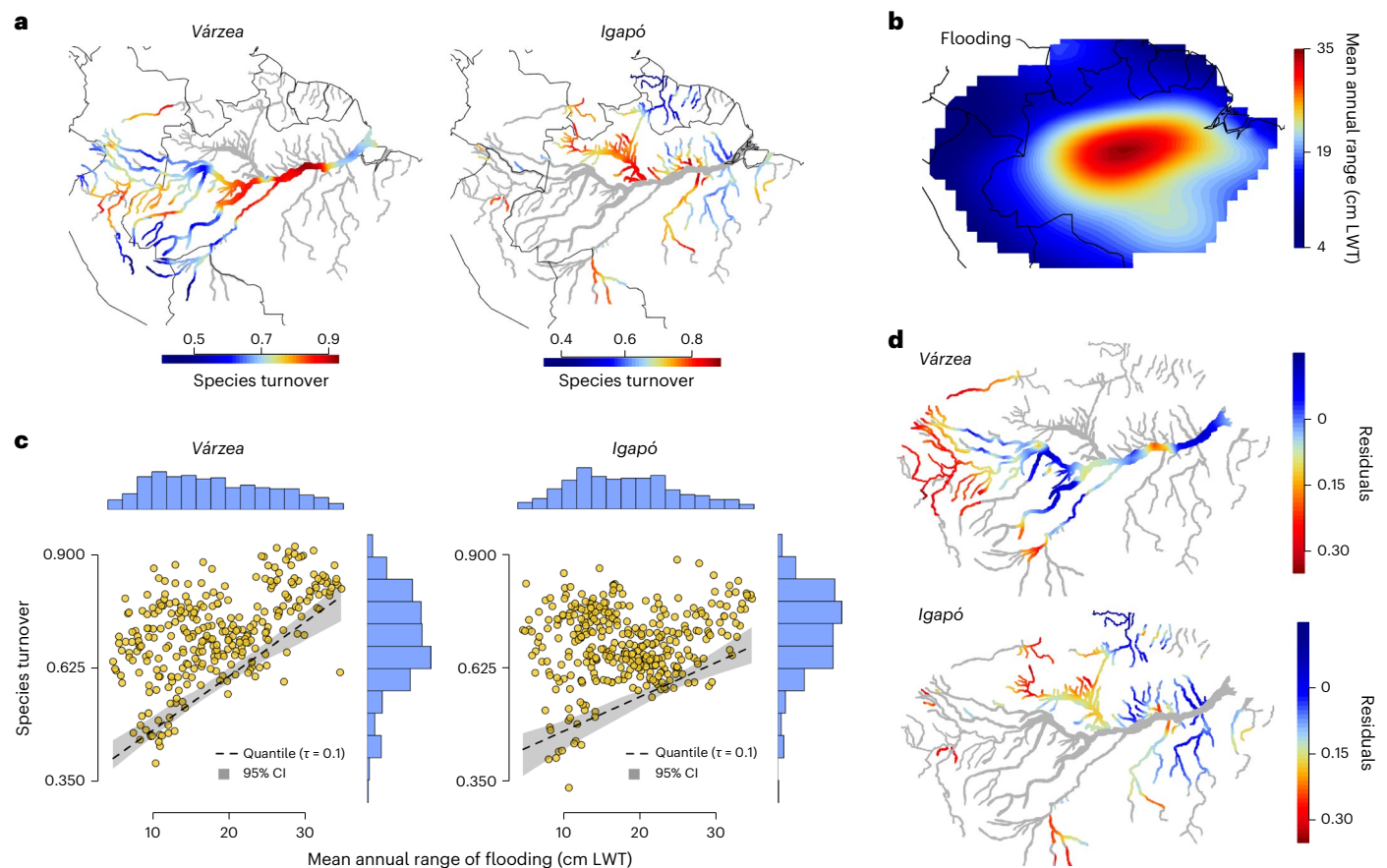### Patterning of species turnover with the Amazon flood wave

Flooding is a principal driver of environmental heterogeneity with important implications for forest composition[1,7,18]. The magnitude of flooding at local scales is strongly governed by the position of floodplains along the Amazon flood wave—a seasonal, moving mass of water that initiates as orographic rainfall feeding headwater rivers with short and sporadic flooding; propagates towards major collecting channels with larger-amplitude, unimodal flood pulses; and finally dissipates further downstream into the tidally influenced river estuary region[1]. We described the flood wave using spatiotemporal data on Terrestrial Water Storage (TWS) from NASA's GRACE Tellus (GRC-Tellus) satellite[26], estimating at every grid cell the mean annual magnitude of seasonal changes in the mass of surface flood waters (cm of land water thickness), averaged over a 15-year period (2002–2017) (Fig. 1b). Central Amazonian floodplain forests positioned at the peak of this flood wave annually experience severe seasonal flood amplitudes surpassing 8 m and inundation periods lasting for most of the year. Floodplains peripheral to this central region are located at low positions on the flood wave and tend to experience seasonal flooding that is less severe.

We found that both *várzea* and *igapó* floodplains located at the peak of the flood wave (those experiencing larger flood magnitudes) always had high species turnover with surrounding terra firme, suggesting that flooding is the primary factor limiting the level of compositional overlap with terra firme. However, floodplains with lower flooding did not always have low species turnover; indeed, many maintained high species turnover (Fig. 1c). The resulting triangular pattern suggested that while flooding may set the minimum level of species turnover, above these minima other (unmeasured) factors may interact with flooding to maintain compositional differences. With potentially many interacting factors, standard regression methods are not capable of detecting appropriate relationships[27], so we employed quantile regression to model the lower bounds of species turnover (the tenth percentile of species turnover conditional on flooding). An added benefit is that by describing the lower bounds of species turnover, model residuals more appropriately reflect the summed effect of possible interacting factors, permitting us to investigate their geographic patterns without prior knowledge of what they might be[27,28].

We found that the lower bounds of species turnover with flooding were statistically indistinguishable for both *várzea* and *igapó* floodplains, suggesting that the effect of flooding on species turnover is similar in both floodplain habitats (*várzea* slope ± 95% confidence interval (CI), $1.21 \times 10^{-2} \pm 2.48 \times 10^{-3}$; t = 9.57; n = 301; P < 0.001) (*igapó* slope ± 95% CI, $1.05 \times 10^{-2} \pm 2.60 \times 10^{-3}$; t = 7.86; n = 347; P < 0.001). Some residual spatial autocorrelation in both the *várzea* and *igapó* models (assessed with Moran's I at P < 0.01) raised questions about the robustness of the observed relationships. This was expected because of the spatial dependencies built into the compositional response variable from interpolating species abundances, so we double-checked the observed relationships between flooding and species turnover using an alternative procedure for populating grid cells with plausible communities that did not involve spatial interpolation. Rather, we pooled species abundance information for each cell only from plot inventories directly located within that cell. This alternative procedure retains only well-sampled cells containing multiple floodplain and terra firme inventories but ensures cell-wise spatial independence of species abundance data. Despite the methodological differences, the relationships between species turnover and flooding were similar (*várzea*, $1.29 \times 10^{-2} \pm 1.21 \times 10^{-2}$, t = 2.20, n = 25, P = 0.038; *igapó*, $1.54 \times 10^{-2} \pm 1.19 \times 10^{-2}$, t = 2.66, n = 22, P = 0.015) (Extended Data Fig. 3). The patterns of species turnover with flooding therefore appear robust among methodological choices and similar across the two major floodplain types.

Geographic patterns of model residuals spotlighted a large area of northwestern Amazonia (particularly for *várzea*) with elevated residuals, implying that species turnover with surrounding terra firme was higher than expected given the region's limited flooding and peripheral position far from the peak of the flood wave (Fig. 1d). High compositional differences may be maintained by one or more unmeasured

Fig. 1 | Broad-scale geographic and environmental patterning of species turnover across floodplain and adjacent terra firme forest habitats, for *várzea*–terra firme and *igapó*–terra firme comparisons. a, Spatial patterns of species turnover for *várzea* and *igapó*, showing a concentration of high species turnover located centrally within the fluvial network. Grey rivers are masked out because they either correspond to a different floodplain habitat or did not meet minimum sampling criteria for analysis. **b**, Regional differences in seasonal flooding are described as an annual flood wave that originates in Andean headwaters, peaks in central Amazonia and dissipates near the Amazon mouth.

Floodplains positioned at the peak of this flood wave are seasonally inundated by the highest-amplitude and longest-lasting floods. LWT, land water thickness. **c**, Patterning of species turnover of *várzea* and *igapó* with surrounding terra firme along the flood wave. The black dashed line shows the lower bound of species turnover with flooding, assessed with quantile regression at $\tau = 0.1$. **d**, Mapped residuals from quantile regression modelling for *várzea* and *igapó*. Throughout much of western Amazonia, species turnover is relatively higher than expected given the lower flooding implied by its headwater position on the flood wave.

factors that interact with flooding, or, alternatively, our estimate of the broad-scale flood wave failed to capture local but nonetheless important patterns of flooding that contribute to species turnover. For example, rivers in this area drain vast catchments exposed to some of the highest annual precipitation rates in Amazonia, which may influence local flooding patterns in ways that maintain compositional differences with surrounding terra firme (we explore this further in Supplementary Discussion 1, Supplementary Fig. 1 and Supplementary Table 2).

Identifying floodplain specialist tree species

Differences in composition between floodplain and terra firme forests imply that many species may have narrow preferences for one or the other habitat. To better identify these specialized species, we employed association tests, which measure the strength of habitat preference for each species independently. We ran tests for a subset of 1,666 relatively well-sampled tree species (those with at least 20 occurrences in the plot network) using species-specific abundance information from plot inventories to test for non-random habitat selection for floodplains or terra firme. Specifically, we used a correlation index because absences outside a target habitat are also taken into account[29], permitting us to categorize each species as a floodplain specialist, a terra firme specialist or a habitat generalist and subsequently examine each group's relative abundance and richness in relation to species turnover.

Of the 1,666 species, a clear majority (1,450 species, 87%) occurred in floodplains at least once, and all had at least one occurrence in terra firme. Many tree species can therefore inhabit floodplains at least sporadically. Association tests revealed a smaller group of 301 species (18% of 1,666) that occurred in floodplains more often than random expectation ($P < 0.05$) and were therefore considered floodplain specialists (Supplementary Table 3). The majority of floodplain specialists had a clear preference for one type of floodplain habitat or another (*várzea*, 51%, 154 species; *igapó*, 38%, 115 species), while relatively few floodplain specialists were associated with both floodplain habitats (11%, 32 species). False positives due to multiple testing are expected for about 15 species (5% of 301 species), so we estimate the overall percentage of floodplain specialist tree species to be 17% of the 1,666 species tested. Terra firme specialists accounted for 700 species (42% of 1,666), and the remaining 665 species (40%) had no clear habitat association and were therefore considered generalists.

By cross-referencing the names of the 1,666 tested species with each floodplain composition grid, we were able to examine the cell-wise relative abundance and richness of floodplain specialists (301 species), habitat generalists and terra firme specialists (that is, spillover from terra firme) in floodplains. As expected, the relative abundance and richness of floodplain specialists increased with species turnover. More surprising were the upper limits of floodplain
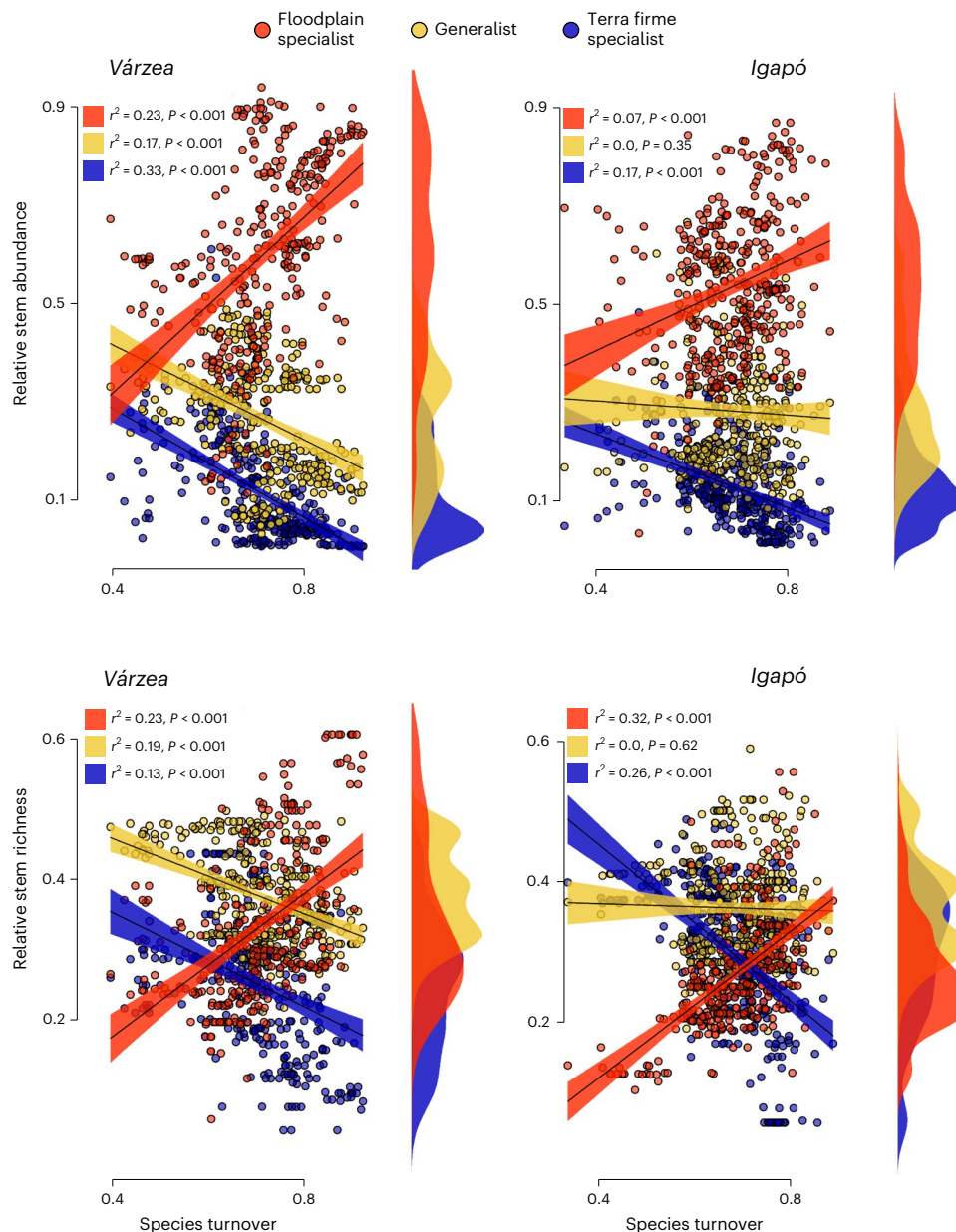
Fig. 2 | Relationships between species turnover and the relative abundance and richness of floodplain specialists, habitat generalists and spillover from terra firme (terra firme specialists) in *várzea* and *igapó*. With increasing levels of species turnover, floodplain specialists become more dominant, while spillover from terra firme species decreases. The proportions are derived from interpolated compositional grids of *várzea* and *igapó* after cross-referencing with the names of the 1,666 species tested for habitat association. The relationships with species turnover are derived from simple least squares models. The coloured boxes indicate the proportion of explained variance (r^2) and P values. The trend lines (black) are bounded by coloured bands showing the 95% CIs. Density plots for the relative abundance and richness of each species group are shown in the right margins.

specialist rates—in areas of high species turnover, floodplain forests are decidedly specialist-dominated, with nearly half of floodplain cell richness and a majority (>70%) of floodplain stems pertaining to specialist species (Fig. 2). At low levels of species turnover, generalist species and spillover species from terra firme (terra firme specialists) together accounted for the majority of species and stems in floodplains. However, even at low levels of species turnover, floodplain specialists still account for about a third of stems and 20% of tree species richness. For any floodplain anywhere, therefore, a considerable complement of its local tree diversity is strongly circumscribed to its flooded habitat. Habitat generalists, particularly in *igapó*, can remain an important component of floodplain forests regardless of the level of species turnover. Our lower range of relative richness for habitat specialists in floodplains is remarkably similar to our previous estimate for *várzea*[7],

but our upper range (about 60%) is nearly twice as large, undoubtedly reflecting the greater amount of quantitative abundance information available in our current database.

Optimizing conservation benefits for biodiversity

Our results suggest that although floodplains cumulatively account for only about a fifth of the regional surface area, they contain most of Amazonian tree diversity. Assuming that our sample of 1,666 species can be taken as representative of the tree flora at large, then nearly 9 of every 10 species can inhabit floodplains, albeit many of them at low densities. Importantly, a substantial fraction of Amazonian tree diversity may be strongly dependent on floodplain habitat, as our estimates indicate that nearly one in every six tree species in Amazonia is a floodplain specialist. Floodplains are a prominent feature of fine-scale habitat

heterogeneity in Amazonia, which has long been a leading hypothesis for the maintenance of the region's exceptional tree richness[3,7,8,10]. Yet, regional examinations of tree diversity have typically not taken into account the type of fine-scale habitat heterogeneity that floodplains generate[22,30], limiting our understanding of how biodiversity is organized on landscapes. Our results perhaps illustrate more clearly than ever the substantial complement of the Amazon's regional tree diversity that floodplains accommodate.

For most floodplain specialists identified here, detailed ecological data are still lacking. Strong habitat preference presumably reflects a high degree of adaptation that confers advantages for a particular species in a particular habitat but disadvantages in other habitats, so it is often linked to increased vulnerability to environmental change and unique ecological function. Our results indicate that together these specialists typically account for at least 20% of tree species richness or tree abundance in most floodplains, meaning that this select group of specialized species is likely to have a disproportionate influence on patterns of primary production, resource availability and forest structure that directly sustain adjacent terrestrial and aquatic biodiversity. Such findings raise questions about the safeguarding of ecological function of a critical group of several hundred floodplain specialists.

While ideas about integrating floodplains into entire watershed-based strategies have existed as general recommendations for some time, area-based conservation strategies in Amazonia have over-whelmingly focused on purely terrestrial, non-flooded habitats[14–16]. Because our maps of species turnover reflect the spatial arrangement of tree diversity on local landscapes, they offer an interesting tool that may enable us to move beyond general recommendations and towards more geographically explicit frameworks better able to place the opportunity costs of competing land-use strategies into sharper focus. For example, putting greater emphasis on capturing areas of high species turnover may better permit watershed-based conservation frameworks to identify and locate high benefit/cost opportunities for landscape-level biodiversity while optimizing benefits to future floodplain systems. According to our findings, these benefits will typically be highest along the large, lowland rivers with strong flood seasonality, where landscape-level beta diversity is high. Regrettably, on current landscapes these river attributes tend to combine high human accessibility with low protection status[31].

Identifying sensitive floodplains

Despite mounting evidence that basin-wide precipitation patterns and proliferating hydro-electric dams are increasingly changing key ecological aspects of river hydrology[12,13,32], our knowledge regarding the responses of tree communities has come from a small number of sites already undergoing hydrological degradation[33] and is thus largely retrospective and highly fragmentary. Our results may offer a viable path towards understanding the geography of floodplain sensitivity to hydrological alteration within a more anticipatory framework. For example, high species turnover implies not only high concentrations of specialized species with potentially unique ecological functioning but also narrow circumscription of species populations to floodplain habitat, putting both species and function at greater risk of local extinction, should floodplain conditions change. In areas of high species turnover, therefore, hydrological alteration will arguably be more ecologically disruptive than in other areas. We found that the spatial configuration of these vulnerable floodplains is very much concentrated in central Amazonia, a position placing them at the heart of the fluvial network. The vulnerability of these floodplains to accumulating downstream and upstream hydrological impacts that propagate from elsewhere in the basin is a concern. With up to 300 flood days annually and flood amplitudes of 9–12 m, the floristically unique forests occupying this central Amazonian region are contingent on some of the most exceptional hydrologic conditions worldwide[1]. It is doubtful that any restoration technology could

reverse damaging hydrological impacts on their tree communities, the species interactions they support or the ecological services they underpin. It therefore seems clearer than ever that conserving the Amazon's tree diversity and its ecological functioning will require both landscape-level planning that incorporates floodplain habitat into protected areas and regional strategies for water management to safeguard whole-catchment hydrological integrity.

Limitations

We have produced a spatially explicit look at the geography of species turnover and the habitat specificity of floodplain forests that covers wide environmental and floristic variation in the Amazon basin. However, it is important to acknowledge that we have done so only at the coarsest of spatial scales. Large spatial gaps in forest inventories still exist, which we have currently resolved by interpolating species abundance information over considerable distances. Moreover, our measure of flood wave position remains a simplified estimate of more complex geographic variation in local flood regimes. Complementary approaches at smaller, basin-level spatial scales will undoubtedly reveal important local nuance not captured at our scale of analysis[18]. Our results also suggest that species turnover may be maintained in floodplains by one or more (unmeasured) factors that interact with flooding. For example, river meandering (and the resulting primary succession that follows) undoubtedly shapes the species composition of floodplain forests in important ways, but its unique contribution to maintaining species turnover with terra firme remains unknown. Similarly, the amount and fertility of sediment transported by rivers, and the allochthonous alluvial soil that develops from it, often differ considerably from those of uplands in ways that impact water and nutrient availability and therefore species composition. Ongoing hydrological degradation will considerably alter these and other unknown factors, yet their individual effects on the maintenance of species turnover remain unexplored. These limitations notwithstanding, our findings provide the most comprehensive view yet of the remarkable contribution that floodplains make to Amazonian tree diversity, offer a valuable window into the sensitivity of floodplain forests and have practical implications for floodplain conservation.

Methods
Environmental data
Data were obtained from publicly available gridded datasets or constructed from georeferenced data. To capture regional variability in annual flooding, we used TWS from NASA's GRC-Tellus satellite[34]. GRC-Tellus measures spatiotemporal changes in the Earth's gravity field, which are largely the result of alterations in water thickness near the Earth's surface. In the Amazon region, most annual TWS variability is governed by changes in the mass of surface flood waters and thus captures the hydrological signal resulting from seasonal flooding[35]. TWS is measured in centimetres of equivalent land water thickness and is available as monthly, 1°-gridded data expressed as anomalies relative to a baseline average from January 2004 to December 2009. The data are previously corrected using an independent component analysis approach to remove north–south stripes and are post-processed with a 300-km-wide Gaussian filter (a spatial grain analogous to our community grids based on 3° interpolations) to produce smoothed solutions[26,34]. As a measure of the magnitude of seasonal flooding for each pixel, we calculated the average yearly range for TWS over a 15-year period (2002–2017).

To capture regional variation in annual rainfall, we obtained gridded data from WorldClim Bioclimatic variables (bio 12)[36].

For analysis, environmental grids for flooding and rainfall were sampled to the same 1° grids used for the composition data, using a bilinear interpolation. For visualization in Fig. 1b, the flooding grid was resampled to higher (0.1°) resolution using a bilinear interpolation.

Composition data

We produced three analogous compositional grids of 567 1° cells covering the Amazon region for terra firme, várzea and igapó, using tree inventory data from the ATDN[22]. ATDN inventories falling outside of the grid were excluded. The final data subset comprises 1,705 mostly 1 ha tree inventory plots with relatively complete information on species composition and abundances (Extended Data Fig. 1 and Supplementary Table 1). Only species-level identifications were retained, accounting for 85% of species and 89% of stems. Plots were classified as terra firme ($n = 1,250$, 73%), várzea ($n = 271$, 16%) or igapó ($n = 184$, 11%), following the original habitat designations of the contributors, and species stem densities in plots were standardized to stems per ha to account for variable plot areas. We used habitat-specific plot data to populate compositional grids for each habitat separately, in two alternative manners. In the first approach, species cell abundances were interpolated from abundance information in plot inventories located within a 3° search radius, using inverse distance weighting set to a power of 2 (Extended Data Fig. 2). The search radius ensures that a species is predicted to be absent in cells where it has no nearby records of occurrence, and its maximum distance set at 3° is an optimization previously determined[37] by the match between inverse-distance-weighting maps of all species and a Fisher's alpha-diversity map of Amazonian forests[28]. In the second approach, species cell abundances were generated by pooling plots contained inside individual grid cells, without any spatial interpolation. Whereas the approach based on spatial interpolation constructs plausible cell metacommunities using all sampling localities within ~300 km, the approach of pooling samples within individual grid cells makes considerably less use of the available data but removes spatial dependencies in the response variable.

Species turnover

We assessed species turnover at analogous 1° cells of várzea–terra firme and igapó–terra firme grid pairs, using both interpolated and pooled versions of compositional data in parallel analyses. Species turnover is a function of the number of species shared between floodplain and terra firme samples (a) and the numbers of species unique to either sample (b and c). We used Simpson dissimilarity, $\beta_{cell} = 1 - a/(a + \min(b,c))$, where $\min(b,c)$ refers to the smallest number of unique species[38]. This species turnover metric is not influenced by differences in richness that are expected between terra firme and floodplain samples and is thus more suited to our questions regarding species replacement. Species turnover at a given cell location was assessed by repeatedly subsampling analogous terra firme and floodplain cells, each time drawing 500 stems from each habitat with replacement, setting the probability of species selection proportional to cell density of each species. Although species selection is based on predicted abundance information, our presence/absence measure of species turnover is robust to highly abundant species that alternative abundance-based indices may be overly sensitive to. Each sampled assembly is therefore of similar size to a standard hectare plot and reflects average, habitat-specific tree composition on the basis of information from the nearby plot inventories. For each cell, we report the mean Simpson's dissimilarity of 1,000 subsamples. As an additional precaution to avoid calculating species turnover at severely undersampled cells, we required cell richness for each habitat grid to be >100 species. Species tend to accumulate rapidly in tropical forests, so an accumulation of fewer than 100 species is a strong indication that sampling was either too limited or skewed towards environmentally extreme or disturbed environments. For similar reasons, for analysis based on compositional grids derived from pooling inventories, we additionally required that cells contain at least two floodplain and two terra firme inventories. In both the interpolated and pooled approaches, the total number of cells where species turnover was calculated depended on the spatial configuration of terra firme and floodplain inventories and how these overlapped geographically. Bivariate relationships of species

turnover with flooding were examined using least absolute deviation (quantile regression) models. Quantile regression was preferred over least squares because initial inspection revealed flooding to be a better predictor of minimum levels of species turnover rather than mean levels. Quantile regression models of the lower bounds of species turnover ($\tau = 0.1$) therefore provide more appropriate estimates of the relationship between flooding and minimum levels of species turnover, and residual levels of species turnover can be interpreted as the summed effect of unmeasured or unknown factors that interact with flooding to maintain species turnover[27,28]. To test whether annual rainfall interacted with flooding to maintain species turnover, we used least squares models, comparing competing least squares models with and without a rainfall interaction using F tests. Prior to running least squares regression, we checked for multi-collinearity among environmental factors by assessing variance inflation factors. Moran's I was used to check for residual spatial autocorrelation. All analyses were performed in R v.4.1.2 (ref. [39]) using custom code and the packages vegan[40], quantreg[41], raster[42], rgdal[43], gstat[44,45] and ape[46].

For visualization of the geographic patterns of species turnover, as well as residual levels of species turnover remaining from quantile regression models, we projected the original 1° grids onto higher-resolution (0.05°) floodplain maps using a bilinear interpolation method. To do this for várzea and igapó individually, we first delineated floodplains on the basis of ref. [47] and assigned floodplains to either igapó or várzea using the habitat classifications from georeferenced sampling localities in ATDN.

Habitat association

The ecological association of species to floodplain or terra firme habitat was computed as the Pearson correlation between the vector of a species' abundance among inventories and the binary vector of inventory habitat membership (that is, terra firme, igapó and várzea)[29]. In contrast to the alternative approach using indicator values, Pearson correlation additionally takes into account absences outside the target habitat and is arguably preferable for determining the ecological preference of a given species among a set of alternative habitats[29,48]. Because some species may associate with more than one floodplain habitat, we allowed for floodplain combinations (for example, igapó + várzea). A permutation test was used to evaluate statistical significance for the habitat or combination for which the correlation was highest, implemented with the multipatt function of the R package indicspecies, using the r.g option[29,48]. Differences in sampling effort among habitats, which can influence estimated coefficients, were accounted for using a group-based stratified resampling procedure[48]. Most species have smaller ranges than the extent of the study area, so species permutations were performed on the subset of plot inventories contained within cells predicting >0 abundance, on the basis of 3° inverse-distance-weighted interpolations of plot abundance information. Only species occurring in over 20 inventories were assessed to ensure sufficient sampling. We used a $P < 0.05$ threshold to identify habitat specialists; all others were considered as habitat generalists.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Metadata for all plots used in this study are available in Supplementary Table 1. Habitat correlation scores for 1,666 species are available in Supplementary Table 3. GRC-Tellus data on monthly land water thickness are publicly available from https://grace.jpl.nasa.gov/data/get-data/monthly-mass-grids-land/. WorldClim Bioclimatic data are available from https://www.worldclim.org/data/bioclim.html. All tree inventory data can also be made available upon reasonable request to H.t.S.

Code availability

The R scripts used in the analysis are available upon reasonable request to J. E. Householder.

References

1. Junk, W. J., Piedade, M. T. F., Wittmann, F., Schöngart, J. & Parolin, P. *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management* (Springer, 2010).
2. Salo, J. et al. River dynamics and the diversity of the Amazon lowland forest. *Nature* **322**, 245–258 (1986).
3. Gentry, A. Changes in plant community diversity and floristic composition on environmental and geographic gradients. *Ann. Mo. Bot. Gard.* **75**, 1–34 (1988).
4. Wittmann, F. et al. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *J. Biogeogr.* **33**, 1334–1347 (2006).
5. Meave, J., Kellman, M., MacDougall, A. & Rosales, J. Riparian habitats as tropical forest refugia. *Glob. Ecol. Biogeogr. Lett.* **1**, 69–76 (1991).
6. Ferreira, C. S., Piedade, M. T. F., Junk, W. J. & Parolin, P. Floodplain and upland populations of Amazonian *Himatanthus sucuuba*: effects of flooding on germination, seedling growth and mortality. *Environ. Exp. Bot.* **60**, 477–483 (2007).
7. Wittmann, F. et al. Habitat specificity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. *Ecography* **36**, 690–707 (2013).
8. Kubitzki, K. The ecogeographical differentiation of Amazonian inundation forests. *Plant Syst. Evol.* **163**, 285–304 (1989).
9. Terborgh, J. & Andresen, E. The composition of Amazonian forests: patterns at local and regional scales. *J. Trop. Ecol.* **14**, 645–664 (1998).
10. Fine, P. V. A., Zapata, F. & Daly, D. C. Investigating processes of Neotropical rain forest tree diversification by examining the evolution and historical biogeography of the Protieae (Burseraceae). *Evolution* **68**, 1988–2004 (2014).
11. Latrubesse, E. M. et al. Damming the rivers of the Amazon basin. *Nature* **546**, 363–369 (2017).
12. Marengo, J. A. & Espinoza, J. C. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. *Int. J. Climatol.* **36**, 1033–1050 (2016).
13. Barichivich, J. et al. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Sci. Adv.* **4**, eaat8785 (2018).
14. Junk, W. J. & Piedade, M. T. F. Status of knowledge, ongoing research, and research needs in Amazonian wetlands. *Wetl. Ecol. Manage.* **12**, 597–609 (2004).
15. Killeen, T. J. & Solórzando, L. A. Conservation strategies to mitigate impacts from climate change in Amazonia. *Proc. Natl Acad. Sci. USA* **363**, 1881–1888 (2008).
16. Castello, L. et al. The vulnerability of Amazon freshwater ecosystems. *Conserv. Lett.* **6**, 217–229 (2013).
17. Correa, S. B. et al. Biotic indicators for ecological state change in Amazonian floodplains. *Bioscience* **72**, 753–768 (2022).
18. Householder, J. E. et al. Modeling the ecological responses of tree species to the flood pulse of the Amazon Negro River floodplains. *Front. Ecol. Evol.* **9**, 628606 (2021).
19. Luize, B. G. et al. The tree species pool of Amazonian wetlands forests: which species can assemble in periodically waterlogged habitats? *PLoS ONE* **13**, e0198130 (2018).
20. McKinney, M. L. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495–516 (1997).
21. Socolar, J. B., Gilroy, J. J., Kunin, W. E. & Edwards, D. P. How should beta diversity inform biodiversity conservation? *Trends Ecol. Evol.* **31**, 67–80 (2016).
22. Ter Steege, H. et al. Hyper-dominance in the Amazonian tree flora. *Science* **342**, 325–334 (2013).
23. Pitman, N. C. A., Terborgh, J., Silman, M. R. & Nunez, P. Tree species distributions in an upper Amazonian forest. *Ecology* **80**, 2651–2661 (1999).
24. Junk, W. J., Bayley, P. B. & Sparks, R. E. The flood-pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**, 110–127 (1989).
25. Junk, W. J. et al. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* **31**, 623–640 (2011).
26. Frappart, F., Seoane, L. & Ramillien, G. Validation of GRACE-derived water mass storage using a regional approach over South America. *Remote Sens. Environ.* **137**, 69–83 (2013).
27. Cade, B. S., Terrel, J. W. & Schrowder, R. L. Estimating effects of limiting factors with regression quantiles. *Ecology* **80**, 311–323 (1999).
28. Ter Steege, H. et al. A spatial model of tree alpha diversity and tree density for the Amazon. *Biodivers. Conserv.* **12**, 2255–2277 (2003).
29. De Cáceres, M. & Legendre, P. Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**, 3566–3574 (2009).
30. Silva de Miranda, P. L. et al. Dissecting the difference in tree species richness between Africa and South America. *Proc. Natl Acad. Sci. USA* **119**, e2112336119 (2022).
31. Peres, C. A. & Terborgh, J. Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. *Conserv. Biol.* **9**, 34–46 (1995).
32. Timple, K. & Kaplan, D. The changing hydrology of a dammed Amazon. *Sci. Adv.* **3**, e1700611 (2017).
33. Schöngart, J. et al. The shadow of the Balbina dam: a synthesis of over 35 years of downstream impacts on floodplain forests in Central Amazonia. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **31**, 1117–1135 (2021).
34. Wahr, J., Molenaar, M. & Bryan, F. Time variability of the Earth's gravity field: hydrological and oceanic effects and their possible detection using GRACE. *J. Geophys. Res.* **103**, 30205–30229 (1998).
35. de Paiva, R. C. D. et al. Large-scale hydrologic and hydrodynamic modeling of the Amazon River basin. *Water Resour. Res.* **49**, 1226–1243 (2013).
36. Fick, S. E. & Hijmans, R. J. WorldClim2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
37. Gomes, V. H. F. et al. Species distribution modelling: contrasting presence–absence only models with plot abundance data. *Sci. Rep.* **8**, 1003 (2018).
38. Simpson, G. G. Notes on the measurement of faunal resemblance. *Am. J. Sci.* **258**, 300–311 (1960).
39. R Core Team. R: A Language and Environment for Statistical Computing v.4.1.2 (R Foundation for Statistical Computing, 2021).
40. Oksanen, J. et al. vegan: Community ecology package. R package version 2.5-7 (2020).
41. Koenker, R. quantreg: Quantile regression. R package version 5.88 (2022).
42. Hijmans, R. J. raster: Geographic data analysis and modeling. Version 3.6-26. R package (2021).
43. Bivand, R., Keitt, T. & Rowlingson, B. rgdal: Bindings for the 'Geospatial' data abstraction library. Version 1.5-8. R package (2021).
44. Pebesma, E. J. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* **30**, 683–691 (2004).
45. Gräler, B., Pebesma, E. & Heuvelink, G. Spatio-temporal interpolation using gstat. *R J.* **8**, 204–218 (2016).
46. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2019).

47. Melack, J. M. & Hess, L. L. in *Amazonian Floodplain Forests: Ecological Studies (Analysis and Synthesis)* (eds Junk, W. et al.) 43–59 (Springer, 2010).
48. Dufrêne, M. & Legendre, P. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**, 345–366 (1997).

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○ Terra firme   ○ Várzea   ○ Igapó
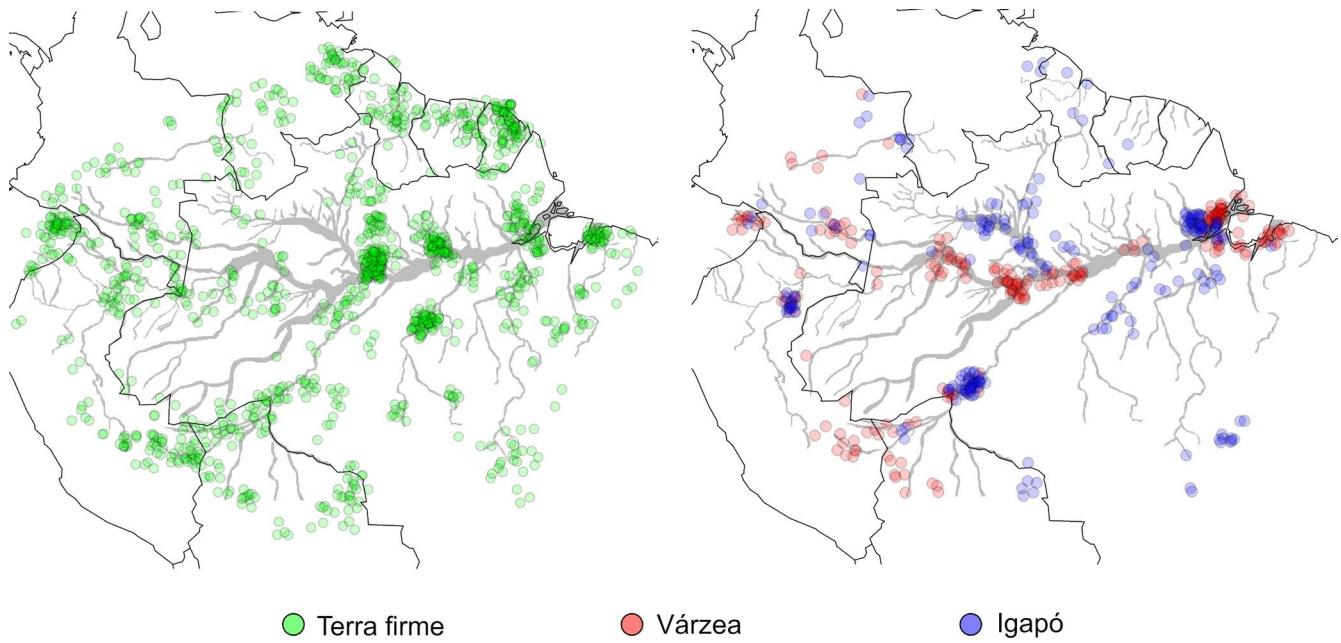
Extended Data Fig. 1 | Distribution of inventory data used to create habitat-specific compositional grids. Sampled sites include 1,705 mostly 1-ha tree inventory plots with full information on species composition and abundances. Plots were classified as terra firme (n = 1,250, 73%), *várzea* (n = 271, 16%), or *igapó* (n = 184, 11%), following habitat designations of ATDN contributors.
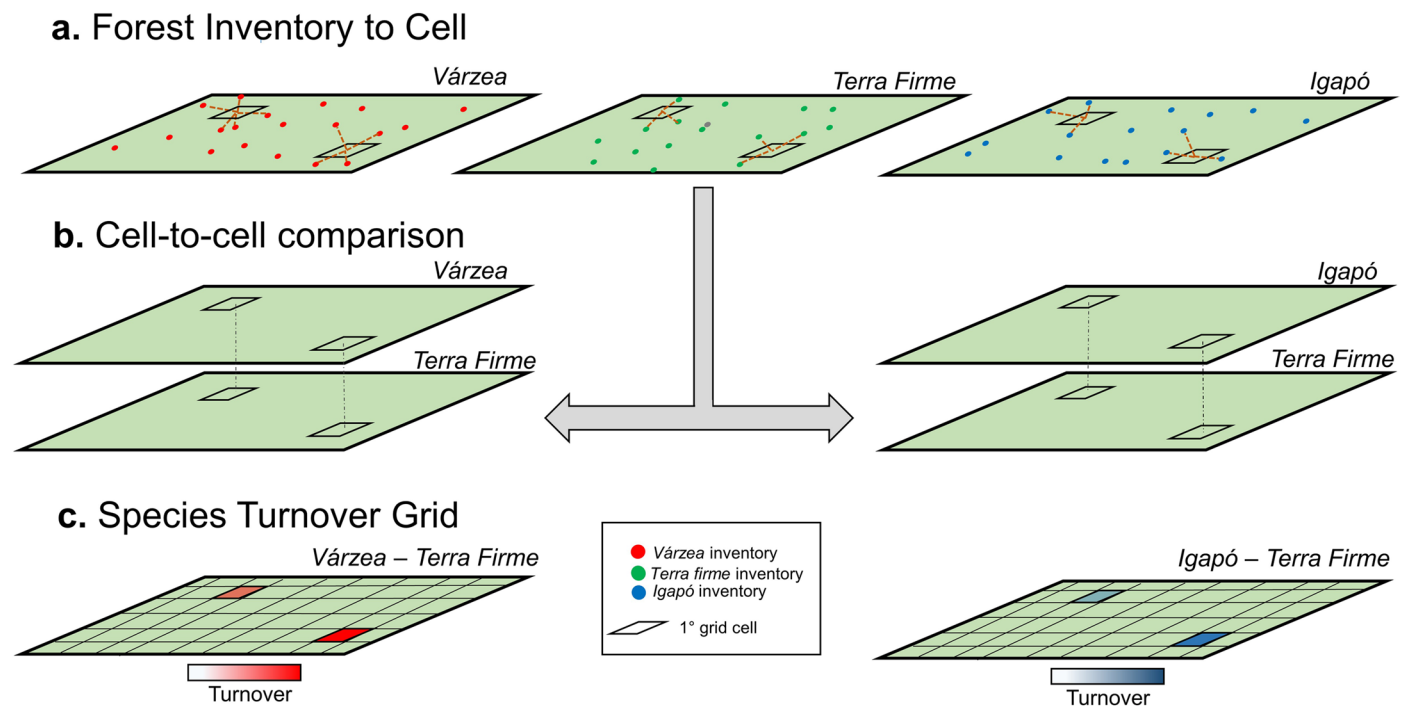
Extended Data Fig. 2 | Schematic of the methods used to compare floodplain and terra firme tree compositions, illustrated for two grid cells. (a) Forest plot inventories (colored dots) were separated into *várzea*, *igapó* and terra firme categories, and species abundance information for separate *várzea*, *igapó* and terra firme grids was calculated at each 1-degree cell (only two shown), using distance-weighted interpolations of inventory plot data from an approximately 300 km circular window (red lines). (**b**) Floodplain and terra firme grids were overlaid and species turnover computed at analogous (vertically overlapping) cells. (**c**) Spatially-continuous grids of species turnover for *várzea*-terra firme and *igapó*-terra firme comparisons. The number of cells where species turnover is calculated depends on the spatial distribution of floodplain inventories and how it overlaps with terra firme inventories. This included 301 cells and 347 cells for *várzea*-terra firme and *igapó*-terra firme comparisons, respectively. In an alternative procedure of calculating species turnover, the interpolation step was excluded and cell compositional data was pooled only from plots located inside cells. For this second approach, the resulting number of cells where species turnover was calculated was 25 and 22 for *várzea*-terra firme and *igapó*-terra firme comparisons, respectively.
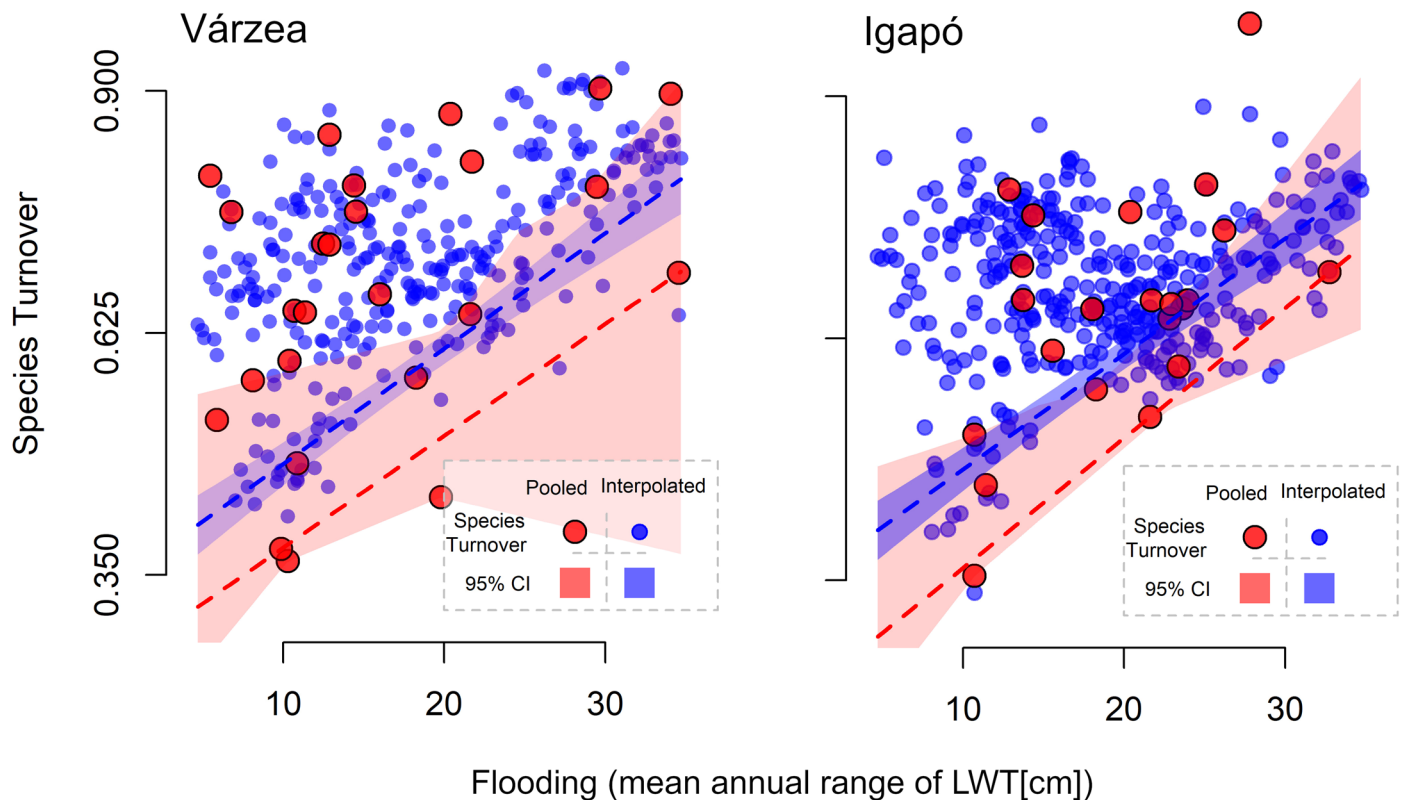
Extended Data Fig. 3 | Comparison of flooding relationships with species turnover using two alternative procedures for populating cell compositional data. While interpolating species abundances maximizes the number of cells where species turnover can be calculated, it introduces spatial autocorrelation. On the other hand, pooling inventories within grid cells reduces the number of cells where species turnover can be calculated, but it maintains spatial independence among cells. We compared both methods to assess the robustness of our results to spatial dependencies. For the approach based on pooling, species cell abundance information was pooled only from inventories located inside individual grid cells, rather than interpolated from inventories from a larger 300 km circular window, in order to avoid residual spatial autocorrelation.

Quantile regression slopes (at tau = 0.1) and their 95% confidences intervals are shown for *várzea*- and *igapó*-terra firme. The lower bounds of *várzea*-terra firme species turnover with flooding are statistically equivalent between pooled compositional data (slope ± 95% CI = $1.29 \times 10^{-2} \pm 1.21 \times 10^{-2}$, t = 2.20, n = 25, p = 0.038) and interpolated data (slope ± 95% CI = $1.21 \times 10^{-2} \pm 2.48 \times 10^{-3}$, t = 9.57, n = 301, p < 0.001). The lower bounds for *igapó*-terra firme are likewise similar between pooled (slope ± 95% CI = $1.54 \times 10^{-2} \pm 1.19 \times 10^{-2}$, t = 2.66, n = 22, p = 0.015) and interpolated methods (slope ± 95% CI = $1.05 \times 10^{-2} \pm 2.60 \times 10^{-3}$, t = 7.86, n = 347, p < 0.001). Slopes from all comparisons were significant (p < 0.05) and had overlapping 95% confidence intervals.

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No specific software was used to collect the data. Vegetation data was collected in the field. Environmental data was collected from publically available sources.
Data analysis	All analyese were perfomed in R -- R Core Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2021). All standard statisical tests (ordinary least squares regressions, F-tests) were done using base R tools. We also used a number of standard R packages for data manipulation, analysis, visualization, and statistical analysis -- For basic datatable wrangling of plot inventory data -- vegan package -- Oksanen, J. et al. vegan: Community ecology package. R package version 2.5-7. (2020). For quantile regression -- quantreg package -- Koenker, R. quantreg: Quantile regression. R package version 5.88 (2022). For mapping visualization and geospatial data manipulation -- raster package -- Hijmans, R.J. raster: Geographic data analysis and modeling (2021). rgdal package -- Bivand, R., Keitt, T. & Rowlingson, B. rgdal: Bindings for the 'Geospatial' data abstraction library. (2021). For spatial interpolation of species abundances -- gstat package -- Pebesma, E.J. Multivariable geostatistics in S: the gstat package. Computers and Geosciences 30, 683-691 (2004).

For basic tools required by other packages --
ape package -- Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526-528 (2019).

For the indicator species analysis (package indicspecies)
indicspecies package -- De Cáceres, M. & Legendre, P. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566-3574 (2009).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The tree inventory data and code are available upon reasonable request.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	There are no human participants.
Population characteristics	There are no human participants.
Recruitment	There are no human participants.
Ethics oversight	There are no human participants.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We examine the geographic patterns and environmental drivers of beta diversity between seasonal floodplain forests and adjacent terra firme forests in the Amazon region.
Research sample	We used tree inventory data from the Amazon Tree Diversity Network (ATDN), which collates tree inventories from hundreds of collaborators. The research is based on 1,715 mostly 1-ha inventories in both floodplain and terra firme habitats. Inventory information includes species names and abundances. This underlying data was sampled in a variety of ways (see below).
Sampling strategy	We had three sampling stategies 1) Inventory data on species abundances of floodplain and terra firme habitats were projected (using inverse distance weighting) onto separate 1-degree grids spanning the Amazon, so that each floodplain or terra frime grid cell contains information on species composition and abundance of species, based on nearby inventories. Resulting floodplain and terra firme grids were overlaid and beta diversity calculated at each cell, producing a gridded betadiversity map. Grid cells of this beta diversity product were the basic sampling unit, and sampling size was determined by the geographic distirbution of floodplains, terra firme, and their overlap. 2) Same as 1, but no initital projection of species abundance information was performed. This second sampling strategy was performed to limit potential issues with spatially autocorrelation of model residuals. Species abundance information cell for floodplains and terra firme was pooled inside each grid cell, and beta diversity calculated at each grid cell that included both floodplain and terra firme information of species abundance. Grid cells of this beta diversity product were the basic sampling unit, and sampling size was determined by the geographic distirbution of floodplains, terra firme, and their overlap.

	3) Species indicator analyses were performed for each species separately. This is a plot-based approach, where all inventories within a species range were utilized. Sample units are therefore inventories, a pvalues determined by randomization of habitat designations.
Data collection	Vegetation data was collected in the field, over a number of years, and by hundreds of collaborators (co-authors).
Timing and spatial scale	Only inventories in the Amazon region were included.
Data exclusions	Inventories outsize the Amazon region were excluded, as inventories outside this region have very different environmental conditions and could bias the results. This exclusion criteria was pre-established. Individuals without species-level identifications were also excluded, representing about 10% of individuals. We cannot calculate betadiversity without species names. This exclusion rate is typical for Amazonia.
Reproducibility	In the manuscript we employ analytical strategies with important differences in methodological choices, so the question of reproducibility is reported in the manuscript. We report in the manuscript that our main findings are robust to important methodological choices, and we detail where some minor results are not.
Randomization	Inventories are allocated into habitat clasess (floodplains or terra firme) based on the determination of the field collector. For species indicator analyses habitat classes were iteratively randomized to obtain a null distribution of species-habitat association strengths. But there was no experimental randomization approach.
Blinding	Not relevant. We did not use an experimental approach.

Did the study involve field work? ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	The Amazon is not an easy place to work. It is hot, humid, rainy, and field conditions are most often rustic.
Location	The Amazon region, northern South America.
Access & import/export	All collaborators have individually obtained the necessary permits for working and transportation of botanical vouchers.
Disturbance	Tree inventories have minimal impact for brief periods of time.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒ ☐	Antibodies
☒ ☐	Eukaryotic cell lines
☒ ☐	Palaeontology and archaeology
☒ ☐	Animals and other organisms
☒ ☐	Clinical data
☒ ☐	Dual use research of concern

Methods

n/a	Involved in the study
☒ ☐	ChIP-seq
☒ ☐	Flow cytometry
☒ ☐	MRI-based neuroimaging