

Environmental drivers of tree community turnover in western Amazonian forests

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A more comprehensive understanding of the factors governing tropical tree community turnover at different spatial scales is needed to support land-management and biodiversity conservation. We used new forest inventory data from 263 permanent plots in the Carnegie Biodiversity-Biomass Forest Plot Network spanning the eastern Andes to the western Amazonian lowlands of Peru to examine environmental factors driving genus-level canopy tree compositional variation at regional and landscape scales. Across the full plot network, constrained ordination analysis indicated that all environmental variables together explained 23.8% of the variation in community composition, while soil, topographic, and climatic variables each explained 15.2, 10.9, and 17.0%, respectively. A satellite-derived metric of cloudiness was the single strongest predictor of community turnover, and constrained ordination revealed a primary gradient of environmentally-driven community turnover spanning from cloudy, high elevation sites to warm, wet, lowland sites. For three focal landscapes within the region, local environmental variation explained 13.4–30.8% of compositional variation. Community turnover at the landscape scale was strongly driven by topo-edaphic factors in the two lowland landscapes examined and strongly driven by potential insolation and topography in the montane landscape. At the regional scale, we found that the portion of compositional variation that was uniquely explained by spatial variation was relatively small (2.7%), and was effectively zero within the three focal landscapes. Overall, our results show strong canopy tree compositional turnover in response to environmental gradients at both regional and landscape scales, though the most important environmental drivers differed between scales and among landscapes. Our results also highlight the usefulness of key satellite-derived environmental covariates that should be considered when conducting biodiversity analyses in tropical forests.

Determining the factors governing changes in plant community composition at different spatial scales is a major challenge in tropical forest ecology. Documenting changes in plant community composition and understanding the main factors underpinning those changes is needed to support biodiversity conservation in the face of forest loss and forest degradation, and to predict species and community responses to changing environmental conditions (Guisan and Zimmermann 2000, Margules and Pressey 2000, Araújo and Guisan 2006, Ferrier et al. 2007). However, while many studies examining plant compositional turnover in tropical forests have focused on the relative contribution of niche (environmental filtering) and neutral (distance-based) processes in shaping community composition (Clark et al. 1999, Condit et al. 2002, Duivenvoorden et al. 2002, Potts et al. 2002, Phillips et al. 2003), less is known about the relative importance of different environmental factors that may affect plant species composition, and how the relative importance of these factors changes across different spatial scales.

In lowland tropical forests, edaphic and climatic gradients have been found to strongly correlate with plant community turnover (Baillie et al. 1987, Balslev et al. 1987,

Duivenvoorden 1996, Swaine 1996, Potts et al. 2002, Tuomisto et al. 2002, Phillips et al. 2003, ter Steege et al. 2006, Bohlman et al. 2008). In the western Amazon basin, forests extend from the vast stretches of lowland Amazonia into the montane forests of the eastern slopes of the Andes mountains up to 2500 m a.s.l. This broad-scale variation in elevation is expected to contribute greatly to the overall biodiversity of western Amazonia; however, the contribution of this steep elevational gradient to forest community turnover within this region has not yet been evaluated. Additionally, community responses to elevational gradients within sub-montane and montane areas have been rarely examined, as the majority of studies examining tropical plant community turnover with respect to environmental variation have been focused on lowland forests. Digital elevation models derived from airborne or satellite remote sensing have proven useful in modeling community composition and ecosystem structure in a variety of ecosystems (Mascaro et al. 2011, Higgins et al. 2012, Dahlin et al. 2013, Baldeck et al. 2014), but this information has been underutilized in analyses of community compositional variation in tropical forests.

Lowland forests of western Amazonia contain some of the most species-rich forests in the world, where over 300

tree species ≥ 10 cm dbh (diameter at breast height) may occur in a single hectare (Valencia et al. 1994). These forests also exhibit high compositional turnover (beta diversity) at relatively small spatial scales (< 10 km) associated with changes in soils and microtopography (Tuomisto et al. 1995, Valencia et al. 2004, Normand et al. 2006, Fine et al. 2010). However, it has also been argued that lowland forest communities show relatively little compositional turnover at larger, regional spatial scales, which has been attributed to relatively homogenous environmental conditions over vast areas in this region (Pitman et al. 2001, 2002, Condit et al. 2002, Normand et al. 2006). On the other hand, significant turnover in tree composition at species to family levels has been demonstrated in response to climatological and edaphic gradients over the full expanse of the Amazon basin (Terborgh and Andresen 1998, ter Steege et al. 2006, Honorio Coronado et al. 2009). The spatial scale of analysis is therefore a critical factor underpinning the relative importance of environmental filtering in shaping compositional turnover within these forests.

We present an analysis of tree community turnover in relation to changes in soils, topography, and climate, using new forest inventory data for trees ≥ 10 cm dbh collected from the eastern Andes to the lowland Amazonian forests of Peru. We sought to determine the degree to which changes in forest composition were explained by environmental factors and compared these relationships at regional and landscape scales using constrained ordination techniques. Our analysis included an exploration of a number of continuously

mapped, satellite-derived climatological and hydrological metrics that have shown promise in explaining above-ground biomass (Mascaro et al. 2011, Asner et al. 2012) and biodiversity patterns (Higgins et al. 2012, Dahlin et al. 2013, Baldeck et al. 2014) but have seldom been applied for the examination of ecological gradients in tropical forests. Spatial correlation in community composition can arise as a consequence of species' responses to a patchy environment, or as a consequence of biotic processes such as dispersal limitation or historical influences. Therefore, we also sought to quantify the degree to which compositional gradients were explained by purely spatial variation relative to environmental variables. Our main objectives were 1) to determine the primary drivers of tree compositional turnover among our western Amazonian forest plots and evaluate their relative importance, and 2) to evaluate how the relative importance of these drivers differed between the regional and the landscape scale.

Methods

Forest community data and predictor variables

A network of permanent field plots was established across Peru, extending from the Madre de Dios Region in the south to the Loreto Region in the North, from the Amazonian lowlands to the Andean montane forest (Fig. 1). This new Biodiversity-Biomass Forest Plot Network was established

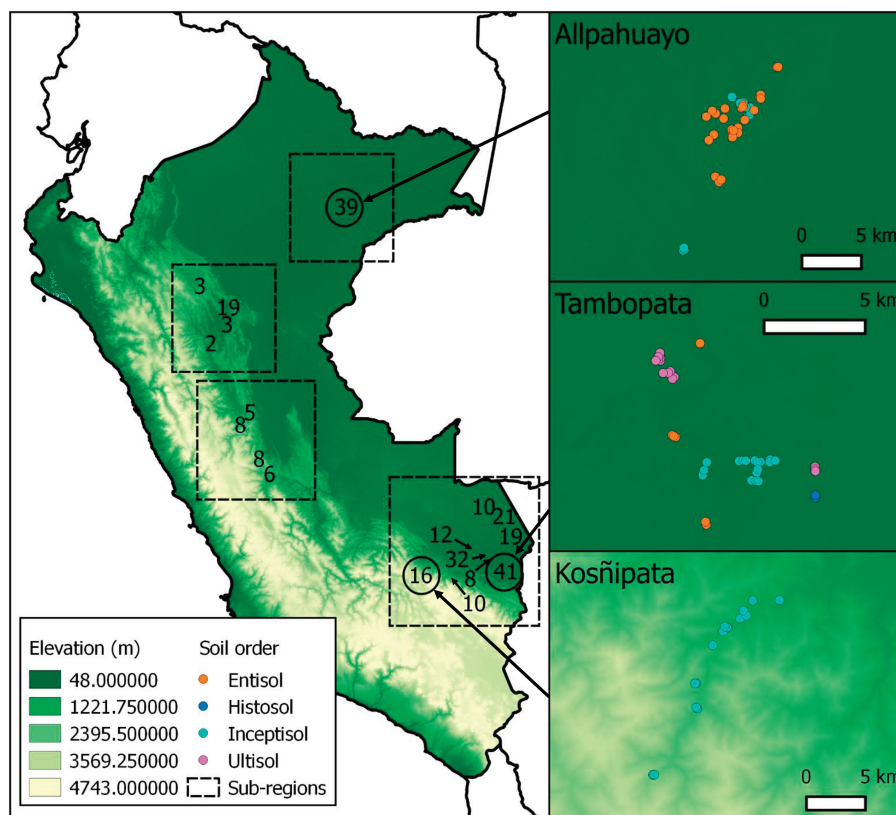


Figure 1. Map of the study area and the forest inventory plots. Numbers on the map indicate the number of forest plots in that area. Zoomed-in maps show the three focal landscapes. The plots were divided roughly into four sub-regions for use in the determining which genera were common and widespread (see Methods section).

and is maintained by the Carnegie Inst. for Science, Dept of Global Ecology. This study utilizes a portion of the network containing 263 circular 0.14-ha field plots that were censused between July 2010 and November 2013, in which each tree and liana individual with dbh (diameter at breast height) ≥ 10 cm was marked and identified. For each censused individual, a voucher was collected and matched to type vouchers in three different herbariums (duplicate vouchers are permanently housed at the National Agrarian Univ. La Molina Herbarium in Peru and the Carnegie Spectranomics Library at Stanford Univ.).

All family and genus names were checked against the Tropicos (tropicos.org) and iPlant taxonomic name resolution service (ver. 3.2; <tnrs.iplantcollaborative.org>) databases, with 97.8% of individuals matched to a recognized genus. Most individuals were identified to species or morphospecies with the exception of those from plots established early in the study in the Madre de Dios region, where 48% of the individuals were not identified to species. Therefore, we used the genus-level determinations to perform our analysis of compositional turnover to allow analysis across the entire region and to compare results at the regional and local spatial scales. Lianas were included in our analysis, though these made up a very small portion (approximately 0.3%) of the stems. We analyzed data from only those plots with at least 30 stems identified to genus, leaving 263 plots that contained 19 132 stems from 110 families and 455 genera. Basic statistics (including the number of stems, number of genera, families, and number of stems identified to species) for the field plots are provided in Supplementary material Appendix 1, Table A1.

The underlying geology of each site was extracted from a map documenting the spatial extent of the major geological formations throughout Peru created by the Peruvian national geological agency (INGEMMET 2000). The plots spanned 11 geological categories that describe the geological age of the substrate: Late Jurassic Continental (JC), Late Cretaceous Marine (CM), Neogene Continental (NC), Neogene-Quaternary Continental (NQC), Paleocene Continental (PcC), Paleozoic Metasediments (PzM), Paleogene Continental (PgC), Late Permian Continental (PC), Quaternary-Holocene Continental (QHC), Quaternary-Pleistocene Continental (QPIC), and Late Triassic-Early Jurassic Marine (TJM). The soil order and soil type of each plot was characterized in the field. Soil orders found among the plots included Histosol, Inceptisol, Entisol, and Ultisol (defined according to the USDA soil classification system; Soil Survey Staff 1999). The soil type within each plot was characterized based on texture, and was classified into one of the following six categories: clay, clay-lithic, clay-sand, sand, sand-lithic, or wet sand.

A series of geomorphological and hydrological terrain variables was created from a digital elevation model (DEM) of Peru obtained from Shuttle Radar Topography Mission (SRTM) data at 90 m resolution. The DEM was used to generate a number of topographic indices in SAGA GIS (ver. 2.1, <saga-gis.org>) using the morphometry and hydrology modules, including slope, plan curvature, profile curvature, topographic wetness, and potential insolation. Three potential insolation variables were calculated using the March equinox and the June and December solstices for the sun

position. These estimates of potential insolation were used in place of the commonly used northness (cosine of aspect) and eastness (sine of aspect) because solar insolation was expected to be more biologically meaningful and preliminary analyses confirmed that these insolation variables had greater explanatory power. Relative elevation above stream was also created using the elevation DEM in conjunction with a flow direction raster obtained from the hydroSHEDS database (<hydrosheds.cr.usgs.gov>). This resulted in a total of nine topographic variables used for analysis: elevation, slope, plan curvature (Plan curv), profile curvature (Prof curv), topographic wetness index (TWI), March potential insolation (Mar insol), June potential insolation (Jun insol), December potential insolation (Dec insol), and relative elevation above stream (REM). The strongest pairwise correlation among topographic variables was between slope and TWI (Pearson's $r = -0.891$; Supplementary material Appendix 1, Table A2).

Climate variables were derived from several different sources. Variables representing temperature and its variability were taken from the BioClim database (<worldclim.org>; Hijmans et al. 2005) at 30 arc-second (approximately 1 km) spatial resolution, including mean annual temperature (MAT), mean diurnal range (MDR), temperature seasonality (TS), and temperature annual range (TAR). Variables representing precipitation were derived from Tropical Rainfall Measuring Mission (TRMM) data, at 0.04-degree spatial resolution (<trmm.gsfc.nasa.gov>). We chose to derive precipitation variables from TRMM rather than use BioClim precipitation variables because TRMM provides a measurement of precipitation which was less correlated with topography for the study region. Precipitation variables were derived from long-term (1998–2012) mean monthly precipitation values, and the derived variables included mean annual precipitation (MAP), maximum monthly precipitation (Pmax), minimum monthly precipitation (Pmin), precipitation seasonality (PS), dry season length (DSL), and maximum climatological water deficit (MCWD). PS was calculated as the coefficient of variation of the mean monthly precipitation values, DSL was calculated as the number of months receiving less than 100 mm of precipitation, and MCWD was calculated as the most negative value obtained by the cumulative sum of monthly precipitation (in mm) minus estimated monthly evapotranspiration, approximated as 100 mm per month (Aragão et al. 2007). Additionally, we calculated a measure of long-term (2000–2010) average cloudiness derived from 1-km Moderate Resolution Imaging Spectroradiometer (MODIS) data (<modis.gsfc.nasa.gov>). Cloudiness was based on the number of times a pixel was identified as being affected by clouds in the MODIS QA flags of the 8-d reflectance product (including 'pixel adjacent to cloud', 'internal cloud algorithm', 'cirrus detected', 'cloud shadow' and 'MOD35 cloud'; NASA LPDAAC 2011). The cloud flags for each pixel were aggregated to yield a percent cloudiness per pixel. The 11 climatological variables used in this analysis were chosen for their expected biological importance while a number of other bioclimatic variables were omitted because they were highly correlated with those already included in the set. The strongest pairwise correlation among climate variables used here was between PS and MCWD (Pearson's $r = -0.855$; Supplementary material Appendix 1, Table A3).

Throughout this study, we refer to the soil, topographic, and climatic variables collectively as environmental variables. In addition to these, we derived a set of spatial variables to represent the spatial relationships among plots using principal coordinates of neighbor matrices (PCNM; Borcard and Legendre 2002). For this, a geographic distance matrix was produced from the plot locations. This matrix was then truncated using a threshold distance equal to the maximum distance from the minimum spanning tree created from the inter-site distances, and all distances greater than this threshold were replaced with a value of four times the threshold distance. A principal coordinates analysis was performed on the truncated geographic distance matrix, and all eigenfunctions with positive eigenvalues were retained. As the plots were irregularly spaced with some very large distances between plots (yielding a large maximum distance in the minimum spanning tree), we followed the suggestion of Borcard et al. (2011) and added nine additional dummy points to the plot locations to create greater connectivity among plots prior to creating the PCNM eigenfunctions. We further filtered the PCNM eigenfunctions to retain only those representing positive spatial correlation (with a Moran's *I* value greater than the expected value of Moran's *I*), as the processes of dispersal limitation, the responses of taxa to environmental variation, and historical influences were expected to result in positive spatial correlation in community composition. These PCNM eigenfunctions are able to model positive spatial correlation in the data at any scale that can be captured by the study design (plot locations plus dummy points; Borcard and Legendre 2002, Borcard et al. 2004, 2011, Dray et al. 2006).

Regional-scale analysis

We measured the compositional dissimilarity among plots as the Bray–Curtis distance based on the presence or absence of genera. To test the explanatory power of the environmental and spatial variables, we performed distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999). Distance-based RDA works similarly to traditional RDA (Rao 1964); however, whereas a traditional RDA of a community matrix preserves the Euclidian distances among samples, dbRDA allows the use of any distance measurement. In dbRDA, a principal coordinates analysis is performed on the matrix of the pairwise compositional dissimilarities among plots, and all eigenfunctions with positive eigenvalues are retained. These eigenfunctions are then used as the response matrix in a traditional RDA.

To increase model flexibility and allow non-linear relationships among environmental and compositional gradients, two orthogonal polynomials (first and second degree) were generated for each of the topographic and climatic variables. Each of the three qualitative soil factors (geology, soil type, and soil order) was transformed into a set of binary dummy variables representing each class, omitting the last class to produce the correct number of degrees of freedom. This resulted in a total of 18 soil, 18 topographic, and 22 climatic variables. Forward selection was performed separately on each expanded environmental variable set (soil, topography, and climate), the set of all expanded environmental variables

combined, and the set of spatial variables. Forward selection was performed using a double stopping criteria in which new variables added to the model had to achieve a 0.05 α -level and the cumulative adjusted R^2 of the model could not exceed the adjusted R^2 of the model created from all variables (Blanchet et al. 2008). This reduced each set of variables to a more parsimonious set that retained nearly all of the original explanatory power (Blanchet et al. 2008, Borcard et al. 2011).

We then examined the relative importance of each of the reduced environmental and spatial variable sets through variation partitioning. This procedure divides the total variation contained in the response variable set into the fractions explained uniquely by each explanatory variable set, as well as the overlaps in explained variation that can be attributed to more than one explanatory variable set. The proportion of variation explained is given as the adjusted R^2 of the explanatory variable set in the dbRDA, which is an unbiased estimator that corrects for the number of explanatory variables (Peres-Neto et al. 2006). Variation partitioning between environmental and spatial variation can provide insight into the relative contribution of environmental filtering versus other spatially-structured ecological processes in shaping community structure. The presence of variation in the community matrix that is explained by spatial variables (i.e. variation that is spatially structured) but unexplained by the environmental variables can indicate the influence of ecological processes that are unaccounted for by the measured environmental factors. These may include purely spatially-structured ecological processes, such as limited dispersal or historical constraints on the distributions of taxa, or the response of taxa to unmeasured environmental variables (Anderson et al. 2011, Dray et al. 2012).

For the variation partitioning analysis, we first assessed the relative contribution of each environmental component by partitioning the total compositional variation explained by the environment among soil, topography, and climate using their reduced variable sets. We acknowledge that the assignment of the environmental variables to the categories of soil, topography, and climate is somewhat arbitrary; however, these designations provide a rough grouping of the different types of ecological effects captured by these variables and provide some separation by data source (field observation, satellite type, meteorological stations). Second, we performed variation partitioning between the environmental and spatial factors. This was performed four times using each of the reduced variable sets for soil, topography, climate, and all environmental variables combined. The results of the forward selection procedures were also examined to gain a better understanding of the most important individual variables for predicting community compositional turnover.

Lastly, we examined the inter-relationships among variables and genera by plotting the results of dbRDA using all environmental variables in a joint display of the environmental variables and genera in the constrained ordination space. For readability, we plotted only the first order polynomials of the quantitative environmental variables and only the most common and widespread genera. We defined a genus as being 'common and widespread' if it was represented by at least 100 individuals in at least 20 plots, and was present in more than one of the four sub-regions covered by the plot

network (sub-regions were determined by a rough spatial clustering of plots, depicted in Fig. 1). All analyses were performed in R (R Core Team); creation of PCNM variables, dbRDA, and variation partitioning were performed with the ‘vegan’ package (Oksanen et al. 2013), and forward selection was performed with the ‘packfor’ package (Dray et al. 2013).

Landscape-scale analysis

We repeated the dbRDA analysis for three distinct western Amazonian landscapes to examine the degree to which community compositional turnover was shaped by environmental gradients at this scale. The three landscapes were Allpahuayo, located in northeastern Peru, Tambopata, located in the Departments of Cusco, and Kosñipata Valley, located in the Dept of Madre de Dios (Fig. 1). The Allpahuayo landscape is composed entirely of lowland Amazon forest, and this area has been found to be among the highest in the world in vascular plant species richness (Gentry 1988). The Allpahuayo plots were arrayed across a matrix of terrace and varrillal forest types, with corresponding differences in soil clay and sand content, and with soil orders classified as either Inceptisol (corresponding to terrace) or Entisol (corresponding to varrillal). The Tambopata landscape is also located in the Amazon lowlands, and the plots were arrayed similarly to Allpahuayo on the floodplain and hillslopes surrounding the Tambopata River. The Tambopata region has somewhat lower species diversity than Allpahuayo, and the flooding regime of the river creates the classic division of floodplain and terrace forest, which roughly corresponds to the two geological types found among the plots: Pleistocene terraces (QPIC) and Holocene sediments (QHC). The plots of Kosñipata Valley were located in the submontane and montane forests of the southern Peruvian Andes. The soils in all of the Kosñipata plots were classified as Inceptisols with a clay-lithic soil type. These plots were arrayed along a broad elevational gradient, spanning ~1200 to 2600 m a.s.l. Maps of the three landscapes are shown in Fig. 1, with summary information provided in Table 1.

Topography and soil were found to vary among plots within the Allpahuayo and Tambopata landscapes, but climatic variables did not. In contrast, measured soil variables did not differ among plots in the Kosñipata landscape, though plots were arrayed across vast topographic and climatic gradients. Thus, when examining the contribution of the environment in explaining compositional variation within these landscapes, we used the combination of soil and topographic variables to represent the environment in Allpahuayo and Tambopata, while the combination of

topography and climate variables were used in Kosñipata. Spatial variables were created for each landscape via the PCNM method described above, without the use of dummy point locations. Forward selection was performed on each of the sets of environmental and spatial variables, followed by variation partitioning between the environmental and spatial variables within each landscape.

To investigate the possible influence of performing our analyses on genus-level community turnover, we compare our genus-level results with those obtained from species-level analysis for the Allpahuayo and Kosñipata landscapes, which had 95.1 and 91.9% of stems identified to the species level, respectively. For these landscapes, we repeated the analysis described above at the species level using all stems that had been identified to species or morphospecies.

Results

Regional-scale effects

Over the entire set of 263 plots, all environmental variables combined explained a total of 23.8% of the variation. Soil, topography, and climate each explained 15.2, 10.9, and 17.0%, respectively. There was a large degree of overlap between the soil, topography, and climate components, though this was greatest for topography (Fig. 2). Both soil and climate explained a substantial portion of variation after accounting for the other variable sets (5.2 and 5.7%, respectively), but topography explained much less after accounting for soil and climate (0.8%).

When variation partitioning was performed between each of the environmental variable sets and the set of spatial variables, the largest portion of the explained variation was accounted for jointly by the environmental component and the spatial variables (Fig. 3), often termed ‘spatially structured environmental variation’. Each environmental variable set also made a unique contribution to the overall variation explained after accounting for spatial variation (2.9–11.1%). Variation explained uniquely by space was greatest when spatial variables were paired with soil or topography (6.8–7.1%) and was smaller when paired with climate (with climate considered alone or as part of the total set; 2.7–3.9%). For the soil and climate analyses, the proportion of variation explained uniquely by the environmental variables was greater than the variation explained uniquely by space, and when all environmental variables were combined, the proportion of variation explained uniquely by the environmental variables (11.1%) was much greater than the variation explained uniquely by space (2.7%).

Table 1. Summary of the forest inventory data and landscape characteristics for the three landscapes analyzed.

Landscape	Plots	Stems	Genera	Families	Min/max distance (km)	Elevation range (m a.s.l.)	Soil orders
Allpahuayo	39	2939	255	66	0.1/17.4	116–150	Entisol, Inceptisol
Tambopata	41	2968	207	62	0.1/10.7	189–232	Entisol, Histosol, Inceptisol, Ultisol
Kosñipata	16	1442	141	67	0.1/18.6	1166–2578	Inceptisol

‘Min/max distance’ gives the minimum and maximum of the pairwise geographic distances among plots. ‘Elevation range’ and ‘soil orders’ are the range of elevation and the soil orders spanned by the plots, respectively. Mean B–C dissimilarity is the average of the pairwise dissimilarity values among plots.

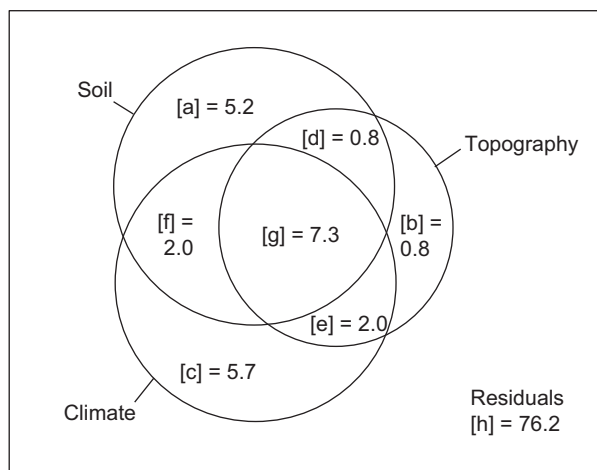


Figure 2. Venn diagram depicting the variation partitioning between soil, topographic, and climatic variables. Each circle represents the contribution of a variable set in explaining the compositional turnover among all plots, and overlapping areas indicate variation that is co-explained by two or more variable sets.

The forward selection procedure indicated which individual variables from each larger set of environmental variables were the most important in explaining compositional turnover among plots (the top ten selected variables from each set are shown in Table 2). From the expanded set of 18 soil variables, 16 were selected as significant ($p < 0.05$). Variable selection indicated that the most important soil variable was the soil type category of 'clay', which explained 2.6% of community compositional variation, followed by the soil order category of Inceptisol, which explained an additional 2.6%. Soil variables representing categories from geology, soil type, and soil order all appear in the top selected

variables, indicating that each of these original soil factors is relevant in explaining compositional variation. From the 18 topographic variables, ten significant variables were selected. Elevation was the most important, explaining 4.5% of variation, and the second most important variable, relative elevation above stream (REM), explained an additional 1.8% of variation. Beyond these first two variables (including their first and second order polynomials), topographic wetness (TWI) and five potential insolation variables complete the list of selected variables. It is interesting to note that no variables derived from slope, plan curvature, or profile curvature were selected (though these were correlated with some of those that were selected). Of the 22 climate variables, the forward selection process selected a total of 21 climate variables (all but one was selected by the procedure). Of these, the most important was cloudiness, explaining 4.5% of variation. This was followed by mean annual temperature (MAT), which explained an additional 2.8%. Lastly, when all 58 environmental variables were examined together, a total of 36 were selected by the forward selection procedure. Of these, cloudiness followed by MAT remained the top-two selected variables. Nearly all of the other top-ten selected environmental variables were soil and topographic variables.

The ordination diagram shows the associations among the environmental variables and the genera included in the study (Fig. 4). This diagram shows a main environmentally-driven compositional gradient representing increasing cloudiness and elevation and decreasing mean annual temperature (MAT) and topographic wetness (TWI). This gradient also roughly coincided with the occurrence of clay soils at the higher MAT and TWI end of the gradient and sandy soils at the higher elevation and cloudiness end of the gradient. The genera associated with higher cloudiness and elevation include *Miconia*, *Alchornea*, *Cyathea*, and *Hieronyma*, and genera associated with lowland elevation sites with higher MAT and TWI include *Trichilia*, *Euterpe*, *Acacia*, *Cordia*, and *Pseudolmedia*. There was also a secondary gradient representing increasing temperature annual range (TAR) and decreasing March insolation and relative elevation above stream (REM). The genus *Sapium* was associated with high TAR and the genera associated with high March insolation included *Virola* and *Aspidosperma*.

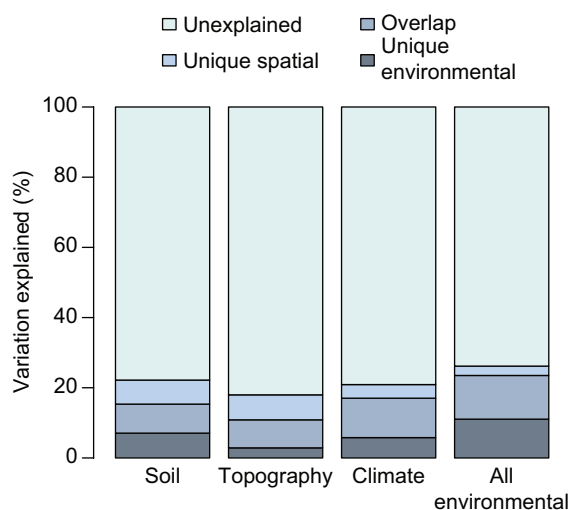


Figure 3. Partitioning of compositional variation between each environmental variable set (soil, topography, climate, or all environmental variables) and the spatial variables. The contribution of the environmental variables is equal to the sum of 'unique environment' and 'overlap', and the contribution of the spatial variables is equal to the sum of 'unique spatial' and 'overlap'. 'Overlap' is the spatially structured environmental fraction.

Landscape-scale effects

Environmental gradients had a large influence on tree community composition evaluated at the genus level in all of the three landscapes examined. A total of 19.4, 13.4, and 30.8% of compositional variation was explained by the set of forward-selected environmental variables at Allpahuayo, Tambopata, and Kosñipata, respectively (Table 3). Within all three of the landscapes, none of the compositional variation was explained uniquely by space, though the proportion of variation explained jointly by space and the environment was substantial, especially in Tambopata (Fig. 5). The environmental variables found to exert the strongest influence on compositional turnover differed substantially among sites, though many of these differences were inevitable due to the differences in the environmental variables that we were able to examine in the different landscapes.

Table 2. Results of the forward selection procedure for each of the soil, topography, and climate variable sets.

Order	Soil		Topography		Climate		All environmental	
	Variable	$R^2_{adj} \times 100$	Variable	$R^2_{adj} \times 100$	Variable	$R^2_{adj} \times 100$	Variable	$R^2_{adj} \times 100$
1	Clay	2.6	Elevation	4.5	Cloudiness	4.5	Cloudiness	4.5
2	Inceptisol	5.2	REM	6.3	MAT	7.4	MAT	7.4
3	PC	6.6	Elevation sq	7.5	TAR sq	8.5	Inceptisol	8.8
4	PzM	8.0	Dec insol	8.6	MAT sq	9.5	REM	10.0
5	JC	9.2	TWI	9.3	DSL	10.5	Sand	11.4
6	Clay-sand	10.1	Mar insol	9.9	TS	11.2	Elevation sq	12.5
7	QHC	10.9	Jun insol sq	10.2	Pmax	11.8	TAR sq	13.3
8	Entisol	11.8	REM sq	10.4	Pmin	12.4	Dec insol	14.1
9	Histosol	12.6	Jun insol	10.6	Cloudiness sq	13.0	Histosol	14.7
10	QPIC	13.3	Mar insol sq	10.9	TAR	13.5	Elevation	15.3

Only the top ten selected variables for each set are shown. A 'sq' following the variable name indicates that it is the second order polynomial. Variables are listed in order according to the size of their additional contribution to the overall amount of variation explained (R^2_{adj}). $R^2_{adj} \times 100$ is the cumulative percent of variation explained by the model that includes that variable and all previous variables.

Allpahuayo – only four of the combined soil and topographic variables were considered significant by the forward selection procedure at Allpahuayo. For this landscape, three dummy variables representing the categories 'sand', 'clay', and 'clay-sand' fully represent the original soil type factor. These were found to be the three most important variables in this landscape, explaining a cumulative 16.8% of the variation. This categorization based on soil type also captured the dichotomy at this site between Entisol (which coincided with the soil type categories 'clay-sand', 'sand', and 'wet sand') and Inceptisol (which coincided with the soil type category 'clay'). After soil type had been accounted for, plan curvature explained an additional 2.6% of variation.

Tambopata – the Tambopata plots did not cleave as cleanly as the Allpahuayo plots based on soil type, but instead the explained variation was more evenly spread among topographic and soil variables. Only three variables were selected, the most important of which was relative elevation above stream (REM) explaining 6.7% of variation. This was followed by the soil order category Inceptisol, explaining an additional

4.7% of variation. Geological formation at Tambopata was represented by a single binary variable, 'QHC', distinguishing the only two formations present, Pleistocene terraces and Holocene sediments. This was the last variable selected, explaining an additional 2.0% of variation.

Kosñipata – while both topography and climate varied among the Kosñipata plots, only topographic variables were selected as significant by the variable selection procedure. Of the five topographic variables selected, each appeared to make a large contribution to explaining compositional variation within this landscape. The most important variable was December potential insolation, explaining 8.0% of variation, and two of the other selected variables also represented insolation. Aside from these three insolation variables, the other two variables selected were slope and topographic wetness index. Together, these five topographic variables explained the greatest amount of variation of all of the landscapes (30.8%).

When the analysis was repeated at the species-level for the Allpahuayo and Kosñipata landscapes, less variation was

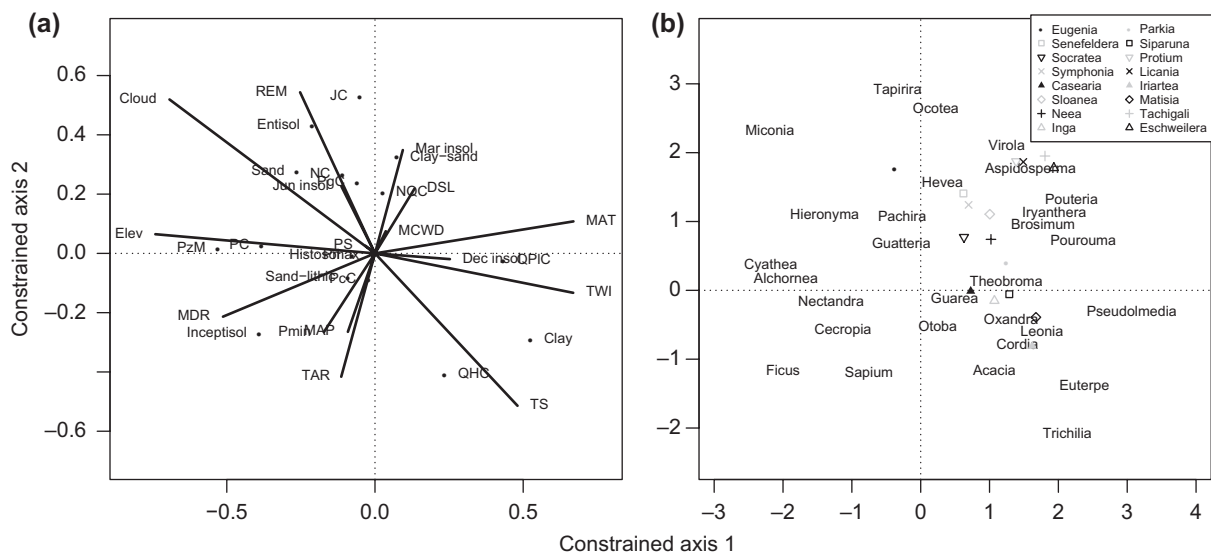


Figure 4. Results of the first two axes of the dbRDA: (a) coefficients of environmental variables, and (b) species scores. The first constrained axis accounts for 20% of the total variation explained by the environmental variables, and the second accounts for 11% of the explained variation. For readability, in (a) only the first order topographic and climatic variables are shown as lines; centroids of all soil variable factor levels are shown with points. In (b), only the 46 most 'common and widespread' genera are displayed.

Table 3. Results of the forward selection procedure for each of the three focal landscapes.

Order	Allpahuayo		Tambopata		Kosñipata	
	Variable	$R^2_{adj} \times 100$	Variable	$R^2_{adj} \times 100$	Variable	$R^2_{adj} \times 100$
1	Sand	8.9	REM	6.7	Dec insol	8.0
2	Clay	11.7	Inceptisol	11.4	Slope	14.2
3	Clay-sand	16.8	QHC	13.4	Jun insol sq	21.1
4	Plan curv sq	19.4			TWI sq	25.6
5					Dec insol sq	30.8

A 'sq' following the variable name indicates that it is the second order polynomial. Variables are ranked in order according to the size of their additional contribution to the overall amount of variation explained (R^2_{adj}). $R^2_{adj} \times 100$ is the cumulative percent of variation explained by the model that includes that variable and all previous variables.

explained by the environmental variables and by the environmental and spatial variables combined (Supplementary material Appendix 1, Table A4; Fig. A1). However, results of the variable selection procedure were qualitatively similar to those obtained at the genus-level. In the species-level analysis, four forward-selected environmental variables explained 13.4% of the compositional variation at Allpahuayo (versus 19.4% of the variation at the genus-level). The selected variables were the same as those selected in the genus-level analysis, except that slope was selected as significant and plan curvature was not. In the species-level analysis, slightly less variation was explained by the spatial variables (3.9 versus 5.6%) and a small amount of variation (1.3%) was explained uniquely by space. In the Kosñipata landscape, four selected environmental variables explained at total of 19.1% of the variation in the species-level analysis (versus five selected variables explaining 30.8% at the genus-level). Three of these selected variables were topographic variables and one of these (mean annual temperature) was a climatic variable. Slightly more variation was explained by the spatial variables (6.8 versus 4.8%) and some variation (2.6%) was explained uniquely by spatial variables.

Discussion

Community turnover in western Amazonian forests was strongly influenced by environmental gradients in both

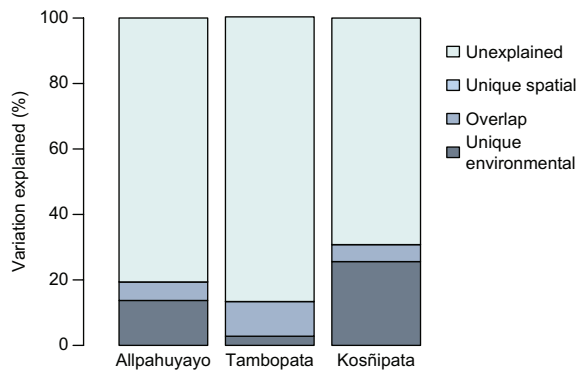


Figure 5. Partitioning of compositional variation between environmental and spatial variables in the three focal landscapes. The contribution of the environmental variables is equal to the sum of 'unique environment' and 'overlap', and the contribution of the spatial variables is equal to the sum of 'unique spatial' and 'overlap'. 'Overlap' is the spatially structured environmental fraction.

the regional- and landscape-scale analyses. At the regional scale (over all plots), all three environmental components – soil, topography, and climate – contributed substantially to explaining compositional turnover. Soil, topography, and climate had largely overlapping influences on the community turnover, which is expected as variables from each of these categories can be highly inter-correlated and causally-linked. Our constrained ordination also revealed the closely related effects of climate and topography, as the primary environmentally-driven compositional gradient was associated with key climatic and topographic variables. In contrast, while climate was slightly more influential than topo-edaphic factors at the regional scale, the primary drivers of community turnover within individual landscapes were soil and topography, though this was largely due to the lack of observed variation in climatic variables within two of the landscapes.

There were also critical differences among landscapes in the specific factors that accounted for community turnover in our analysis. Allpahuayo and Tambopata, where the same set of environmental factors were examined, differed in the composition of the environmental factors that most strongly drove community turnover, with the former being strongly determined by the clay content of the soil and the latter showing smaller responses to a greater variety of factors. The Kosñipata landscape provided an informative contrast to the lowland western Amazonian landscapes examined in this study and others (Tuomisto et al. 2003, Vormisto et al. 2004, Normand et al. 2006). This landscape showed the strongest association between environmental factors and community turnover. Though the plots in this landscape did not show contrasting soil types according to the broad soil categorizations used here, more variation might have been explained if more detailed soil information were available for these plots. As revealed also by the constrained ordination of all plots (Fig. 4), the gradient from cloudy, high elevation to lowland areas with high temperatures and topographic wetness was the main environmental gradient driving community turnover across the region. However, despite spanning an elevational gradient of over 1200 m, Kosñipata did not display a smaller-scale version of this pattern; instead, variable selection indicated that local differences in potential insolation, slope, and topographic wetness drove community turnover within this montane landscape. This is consistent with the work of Jones et al. (2011) who found plant species composition on mountain slopes to be strongly influenced by potential insolation. Insolation modifies local temperature and humidity, which are likely to be important drivers of plant community turnover on mountain slopes.

Corresponding changes in community composition could confound elevational turnover patterns, which may explain why elevation was not selected as a significant explanatory variable in the Kosñipata landscape.

In our regional-scale analysis, the cloudiness metric derived from MODIS data was more closely related to compositional turnover among plots than any other single predictor. This measurement is new to biodiversity analysis and may work as an integrated metric of precipitation, light availability, and humidity. It is well known that precipitation is critically important in shaping compositional gradients in the tropics (Gentry 1988, Swaine 1996, ter Steege et al. 2006, Engelbrecht et al. 2007, Silman 2011). Less is known about the importance of light availability at the regional scale, though the frequent appearance of topographically-derived potential insolation variables among those selected by our models suggests that insolation is also highly relevant. Potential insolation may also act as a master variable that influences not only light availability, but temperature and humidity as well (Jones et al. 2011).

Geomorphological variables derived from a land surface DEM, particularly topographic wetness and relative elevation above stream, were also important predictors of community composition. In tropical ecosystems, the importance of topographic wetness and ground elevation in relation to streams is consistent with the known importance of morphological and hydrological landscape factors, especially the flooding regime, which often creates distinct forest types (Gentry 1988, Terborgh and Andresen 1998, Fine et al. 2010). However, dividing a landscape into different classes based on flooding patterns is a highly localized process, and different regions may or may not divide cleanly into distinct classes with respect to this hydrological variation (for example, while the forests in the Allpahuayo landscape divide cleanly into flooded and non-flooded forests, this same classification does not apply to the forests of Tambopata). Producing quantitative, continuous hydrological metrics from a land surface DEM can facilitate comparisons within and among different landscapes.

Many previous studies of compositional turnover of plant communities in western Amazonia have focused on determining the relative importance of environmental filtering (representing niche processes) and purely spatial variation (representing dispersal, or neutral processes) in explaining compositional gradients (Condit et al. 2002, Vormisto et al. 2004, Normand et al. 2006, Bohlman et al. 2008). To parse the contributions of these different processes, the relative ability of geographic distance and environmental distance to predict compositional dissimilarity (using a distance matrix approach), or the relative ability of environmental variables and spatial eigenvectors to predict covariance in the occurrences of different taxa (using a constrained ordination approach), may be evaluated. At the regional scale, we found that the portion of compositional variation that was uniquely explained by spatial variation was relatively small (2.7%), and was effectively zero within the three focal landscapes. Thus, the environmental variables accounted for nearly all of the explained variation in community composition. This result is consistent with Tuomisto et al. (2003), who found that environmental dissimilarity explained more variation in compositional dissimilarity than geographic distance in

lowland western Amazonia. In contrast, many other studies found a large portion of variation in the community matrix or community dissimilarity matrix that is explained by spatial variation but not environmental variation (Condit et al. 2002, Vormisto et al. 2004, Normand et al. 2006, Bohlman et al. 2008, Honorio Coronado et al. 2009). However, caution should be used when comparing the results of distance-based and raw-data approaches, as these differ in their treatment of the data and underlying assumptions (Legendre et al. 2005). Additionally, our finding that nearly all of the explained variation in community composition was traceable to the measured environmental variables does not mean that purely spatial neutral processes – such as limited dispersal or historical constraints – are not acting in these communities or across these scales, but rather that their presence cannot be detected above what was accounted for by the environment.

It is important to note that our results pertain to genus-level turnover, and results may differ if based on species-level data. Indeed, we found that a smaller proportion of variation was explained by the environment for the two focal landscapes where our analysis was repeated at the species level. However, the proportion of variation explained by space was slightly greater for one landscape and slightly less for the other. It is difficult to draw conclusions about the relative importance of environmental dependence versus purely spatial processes if community turnover were assessed at the species level. The influence of purely spatial processes may be expected to play a more important role in structuring community compositional variation at the species level, as species may be more likely than genera to show effects of limited dispersal or to be historically restricted. On the other hand, environmental constraints may be expected to continue to dominate, with purely spatial processes having limited influence on species distributions over regional scales. A species-level analysis of compositional dissimilarity would be needed to assess the relative merits of these alternate hypotheses.

Conclusions

We combined new data on large tree community composition at the genus level with constrained ordination techniques and a wide variety of environmental variables to examine the relative importance of different environmental factors on compositional turnover in western Amazonian forests. At the regional scale, we found that environmental factors representing climate explained slightly more community compositional variation than those representing soil and topography. Furthermore, we found that the large majority of the spatially structured variation was accounted for by the environmental variables that were measured. The primary environmental drivers of community turnover differed at the landscape scale, where changes in soils and topography were more important, though the specific topographic factors found to be relevant differed among landscapes. Our results also indicate the usefulness of a suite of satellite-derived environmental metrics – namely cloudiness, topographic wetness, and relative elevation above stream – for modeling ecological and biodiversity gradients in tropical forests. These results provide greater clarity on some of

the long-standing questions regarding the relative importance of environmental variation versus geographic distance in explaining compositional turnover in Amazonian forests and the specific environmental variables driving this variation at different spatial scales.

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Supplementary material (Appendix ECOG-01575 at <www.ecography.org/appendix/ecog-01575>). Appendix 1.