

Strong congruence in tree and fern community turnover in response to soils and climate in central Panama

Mirkka M. Jones^{1*}, Simon Ferrier², Richard Condit³, Glenn Manion⁴, Salomon Aguilar³ and Rolando Pérez³

¹Department of Bioscience, Ecoinformatics and Biodiversity Group, Aarhus University, 8000, Aarhus C., Denmark;

²CSIRO Ecosystem Sciences, Black Mountain Laboratories, Clunies Ross Street, Canberra, ACT 2601, Australia;

³Smithsonian Tropical Research Institute, Panama City, Panama; and ⁴Landscape Modelling and Decision Support Unit, Scientific Services Division, Office of Environment and Heritage, Department of Premier and Cabinet, Armidale NSW 2350, Australia

Summary

1. Plant species turnover in central Panamanian forests has been principally attributed to the effects of dispersal limitation and a strong Caribbean to Pacific gradient in rainfall seasonality. Despite marked geological heterogeneity, the role of soil variation has not been rigorously examined.

2. We modelled the compositional turnover of trees and ferns in the Panama Canal watershed as a function of soil chemistry, climate and geographical separation, using generalized dissimilarity models (GDMs).

3. Predictability in both plant groups was strong, with 74% of turnover explained in trees and 49% in ferns. Major trends in the two plant groups were strikingly similar. The independent effects of soils, and of climate for trees, were sizeable, but those of geographical distance were minor. In both plant groups, distance and climatic effects on species turnover covaried strongly.

4. Including floristic dissimilarity of the other taxon as a predictor increased explained deviance to 81% in trees and 59% in ferns. Controlling for differences in plant density among plots reduced deviance explained by climate and distance, while soil effects remained strong. Limiting the analyses to soils of volcanic origin increased deviance explained by climate, soils and distance, but their effects covaried strongly. Independent soil effects on tree turnover were reduced, but their effects on fern turnover remained pronounced.

5. Dry season length was the most important climatic predictor for both taxa, and P and pH were the most important soil predictors. Particularly, rapid species turnover was associated with the driest end of the seasonality gradient, linked to declining individual densities and species richness, and with the low end of the phosphorus gradient.

6. *Synthesis.* While changes in rainfall and seasonality undoubtedly limit plant distributions in this region, soil effects are at least as important, and interactions between the two are sizeable. This is likely to hold elsewhere in the Caribbean region, where mosaics of marine and volcanic soils combined with pronounced rainfall gradients are common. Strong congruence between our focal taxa suggests that our results can be extrapolated to other plant groups, particularly as trees and ferns are distantly related and represent different life-forms.

Key-words: biotic interactions, determinants of plant community diversity and structure, edaphic variation, environmental control, matrix regression, precipitation, Pteridophyta, seed and spore dispersal, tropical forests, turnover rates

Introduction

A major challenge in plant community ecology lies in understanding the factors generating changes in species com-

position in space and time. In tropical forests, this is a question of practical as well as theoretical relevance, in light of swiftly advancing deforestation and predicted climatic change (IPCC 2007; FAO 2010). Plant distributions are dependent on their fecundities and dispersal capacities, their environmental tolerances and their inter- and intraspecific interactions

*Correspondence author. E-mail: mjones@biology.au.dk

(Gurevitch, Scheiner & Fox 2002). However, ecological theories differ in the importance they attribute to these factors.

The relative roles of deterministic species responses to environmental variation and dispersal limitation in generating floristic turnover in tropical forests have been debated for decades (Ashton 1969; Hubbell & Foster 1986). Niche and neutral theories of community assembly represent two extremes on this spectrum (Hubbell 2001), and the reality will lie somewhere between these. Put simply, under the former one would expect species turnover to be governed by changing biotic and abiotic environmental conditions and under the latter solely by random fluctuations in recruitment, dispersal and mortality. A common approach to estimating the relative contributions of dispersal limitation and environmental filtering to species turnover is to partition variation in floristic similarity among sites into fractions explained by their spatial separation and environmental differences (e.g. Tuomisto, Ruokolainen & Yli-Halla 2003b).

To complicate matters, however, interspecific niche differences are not necessarily a prerequisite of species turnover along environmental gradients. Turnover could also arise from changes in the carrying capacity of the environment, with equal effects on all species. On a gradient in rainfall, for example, drier sites might support progressively fewer individuals than wetter sites, and also have fewer species, simply by chance. This would result in a directional trend in the proportion of species shared by sites along the gradient without any deterministic replacement of species. To test for this effect, analyses of species turnover along environmental gradients can be run before and after controlling for variation in individual densities among sites.

Comparisons across taxa are essential for identifying generalities in the factors structuring tropical forest plant communities. An effective strategy may be to compare trees with understorey herbs that are distinct in their life-form and biology. If there is congruence in their community patterns, these are likely to hold for other groups as well. Similar turnover patterns across taxa will arise if they respond to common external factors, such as environmental conditions, but may also arise due to their direct biotic interactions (Wolters, Bengtsson & Zaitsev 2006). For example, tree canopy cover modifies the environment experienced by understorey herbs in numerous ways (Denslow, Ellison & Sanford 1998; Geiger, Aron & Todhunter 2003). A practical implication of congruence is that patterns in one plant group can be used as surrogates of those in other taxa in biodiversity mapping (Pearson 1994; Rodrigues & Brooks 2007).

Here, we study floristic turnover both in large trees and in understorey pteridophytes (ferns and lycophytes) in tropical forests within the Panama Canal watershed. Numerous studies have proposed using ferns as floristic and environmental indicators in tropical forests (e.g. Tuomisto *et al.* 2003a; Tuomisto, Ruokolainen & Yli-Halla 2003b; Salovaara, Cárdenas & Tuomisto 2004), but relatively few of these have included trees (Ruokolainen, Linna & Tuomisto 1997; Duque *et al.* 2005; Ruokolainen *et al.* 2007). Trees and ferns might be expected to differ in the strength of their responses to

environmental variation, due, for example, to differences in their size, drought tolerance or dispersal ability (Webb *et al.* 1967; Wolf, Schneider & Ranker 2001; Duque *et al.* 2002; Chust *et al.* 2006; Qian 2009; Brodribb & McAdam 2011; McAdam & Brodribb 2012). Moreover, it is conceivable that species turnover patterns in trees will approximate neutral expectations more closely than those in sparser understorey plant groups, like ferns, because ecological equivalence of species is proposed to arise as a consequence of variable biotic neighbourhoods in diverse and dense plant communities (Hubbell 2001).

Earlier studies on tree species turnover in this region have emphasized the importance of dispersal limitation and a strong Caribbean to Pacific gradient in rainfall and dry season length (Condit *et al.* 2002; Chust *et al.* 2006; Engelbrecht *et al.* 2007). Patterns in herbaceous plants have not been compared with those in trees. Furthermore, although the region is geologically complex (Coates & Obando 1996), the effects of soil chemistry on species turnover have not been evaluated, except at a local scale (< 50-ha, John *et al.* 2007). We model floristic turnover in each plant group as a function of inter-site soil and climatic differences and geographical distances. We then include floristic dissimilarity in each plant group as an added predictor of turnover in the other plant group to test for cross-taxon congruence beyond that, which is explained by common responses to our measured environmental variables. We also run individual-based rarefactions to test whether individual density differences are a major driver of species turnover. Finally, we examine the relative importance of climate and soils for floristic turnover after restricting the analyses to sites of volcanic origin, as volcanic soils predominate elsewhere in Panama.

Materials and methods

STUDY AREA

Field sites were located in forests within a c. 3000 km² area in and around the watershed of the Panama Canal (Fig. 1). Most were located within or close to national parks or other protected areas. Elevation in the region ranges up to more than 800 m a.s.l., but all except two sample sites were located at below 300 m. Average annual rainfall near the Caribbean Coast is around 3000 mm and declines to slightly below 2000 mm near the Pacific coast. Dry season length is also more pronounced towards the Pacific. The region contains a complex mix of volcanic and marine geological formations (Coates & Obando 1996; ACP 1998). The former include intrusive and extrusive igneous and metamorphic formations, and the latter limestone, sandstone and mixed sedimentary formations.

FLORISTIC DATA

Data on tree species occurrences, including palms, within forty-one 1 ha sample plots (100 m × 100 m) in the study region were extracted from data bases managed by the Center for Tropical Forest Science (CTFS, www.ctfs.si.edu). The plots represent a subset of those analysed by Engelbrecht *et al.* (2007). All trees > 10 cm d.b.h. were inventoried in these plots between 1996 and 2004. Additionally, we

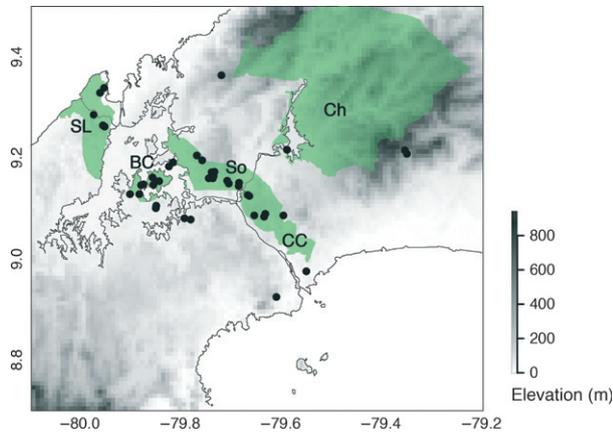


Fig. 1. Locations of the 43 study sites in relation to the Soberanía (So), Chagres (Ch) and Camino de Cruces (CC) national parks, the Barro Colorado National Monument (BC) and the San Lorenzo (SL) protected area. Plots and protected areas are superimposed on an elevation map of the study region [elevation in m a.s.l. interpolated from CGIAR-SRTM data using the raster package in R (R Development Core Team 2011)]. Latitude and longitude are given in decimal degree

extracted corresponding tree data from two hectares (each 200 m × 50 m) located within the 50-ha tree inventory plot on Barro Colorado Island (BCI) (Condit 1998; Hubbell *et al.* 1999; Hubbell, Condit & Foster 2005). These plots, henceforth referred to as BCI1 and BCI2, were located based on two criteria: first, to overlap with a 1000 m × 5 m pteridophyte inventory transect run through the BCI 50-ha plot by Hanna Tuomisto in 2004, and second, they were placed as far apart as possible (centres 760 m apart) on this transect to minimize autocorrelation in their floristic composition. The tree data base was checked for synonymy prior to analysis, and 85% of the original morphospecies names were retained. In addition, those tree individuals whose morphospecies identifications were taxonomically uncertain were excluded prior to analysis ($n = 350$ individuals, 1.8% of the total).

Pteridophytes (ferns and lycophytes) were inventoried within the same forty-one 1-ha tree plots between January and November 2008. For simplicity, we subsequently refer to all species as ferns. Within each plot, two parallel transects were sampled, each 100 m long and 5 m wide, giving a total sample area of 0.1 ha. All individuals (or ramets, in clonal species) with green fronds ≥ 10 cm in length and growing within 2 m of the ground were recorded, including low-trunk epiphytes and climbers. Transects ran either parallel to the north–south or east–west axis of each tree inventory plot. The axis with the strongest elevational difference was selected. They were furthermore placed avoiding large treefall gaps or dense regeneration. The separation of the two transects in each plot was usually 35 m (min. 20 m, max. 45 m). Within the BCI 50-ha plot, two fern transect sections from the 2004 census described above, with their long axes identical to those of the BCI1 and BCI2 subplots for trees, were selected for inclusion in this study. These sections were each 200 m × 5 m long; hence, the total area sampled for ferns within both BCI1 and BCI2 was the same as in the other plots (0.1 ha). All plants were identified to species or morphospecies level, and specimens for each species inventoried in BCI1 and BCI2 were cross-referenced for taxonomic consistency with those from the other plots. Specimens are deposited at the herbaria of the Universidad de Panamá (PMA) and Smithsonian Tropical Research Institute (STRI) herbaria in Panama, and at the University of Turku (TUR) in Finland. Unicates are at PMA.

ENVIRONMENTAL DATA

Soil data

At all sites except for BCI1 and BCI2, soil samples were taken during the fern inventory. Cores were taken at 40 locations, of which 20 were in the highest part of each tree inventory plot and 20 in the lowest part. Samples were taken to 10 cm depth after removing the leaf litter layer to expose the soil surface. Spacing between samples was at least 5 m and usually > 10 m. The 20 cores from the highest areas were pooled, as were the 20 cores from the lowest areas, giving two pooled soil samples per plot. The pooled samples were put through a 2-mm sieve to remove roots and stones, air-dried for 24 h in an air-conditioned laboratory, then oven-dried for a further 72 h at a low temperature ($c. 45$ °C). The dry samples were stored in sealed, airtight containers for subsequent nutrient analysis at the STRI soil laboratory. The soil chemical variables analysed were pH (in 1 M KCl), Mehlich-III extracted Al, Ca, K, Mg, Mn, P (mg kg^{-1} dry soil), and total C and N (%), from which the C:N ratio was calculated. Values for the two soil samples per plot were averaged before statistical analysis.

Estimates of the same soil chemical variables for BCI1 and BCI2 were partly generated from existing soil maps for the BCI 50-ha plot. Predictions of Mehlich-III extracted Al, Ca, K, Mg, Mn and P are available for the entire 50-ha plot at a 20 m × 20 m resolution (www.ctfs.arnarb.harvard.edu/webatlas/datasets/bci/soilmaps/BCI-soil.html). Values for those 20 m × 20 m subunits that overlapped with BCI1 and BCI2 were extracted and averaged to give estimated values for these six variables for our analyses. Values for C were not available for the 50-ha plot, and those for N and pH were derived using different laboratory methods to ours. We hence ran linear regression models to derive predictions of soil C, N and pH as a function of Al, Ca, K, Mg, Mn and P for these two plots, using data from a total of 55 plots in which we had measured all nine soil variables to parameterize the model. Adjusted R^2 values were 0.52, 0.58 and 0.82, respectively, for the C, N and pH models. The soil data used to parameterize the model included all 41 1-ha plots analysed in this study, and a further 14 sites within the same region that were sampled identically for soils during the same census period. Estimates for all nine soil variables are less certain for BCI1 and BCI2 than for the other sites. Nonetheless, generating these estimates was deemed preferable to excluding the two sites because the Barro Colorado 50-ha plot has been a major target of research on tropical plant community assembly for decades.

Climatic data

Average annual rainfall over the years 2001–2007 was estimated for each plot based on a third-order polynomial regression of the centred site X and Y coordinates and elevation. The model was parameterized using rainfall, coordinate and elevational data from 33 meteorological stations operated by the Panama Canal Authority (ACP) within the study region. All stations with continuous rainfall data for this 8-year period were included. Average annual rainfall at these stations was 2594 mm (SD = 663 mm, range = 1738–4679 mm). The adjusted R^2 value for the regression was 0.89 and prediction errors for the meteorological stations averaged 141 mm (max = 407 mm, SD = 107 mm). Predicted dry season length (the number of days between November and March when evaporation is predicted to exceed rainfall) was taken from Engelbrecht *et al.* (2007). Dry season moisture deficit (predicted cumulative rainfall – predicted potential evapotranspiration during the dry season, mm) was similarly generated by kernel regression parameterized using ACP meteorological data, daily

evaporation data recorded on BCI between 1994 and 2007, and site coordinates and elevations. Plot elevation (m a.s.l.) was recorded in the field using a Garmin GPSmap 60CSx and was analysed together with the climatic variables.

STATISTICAL ANALYSES

To visualize the main environmental gradients over the study area, we plotted the site scores on the first axes of principal component analyses (PCA) of (i) the climatic variables and elevation combined, and (ii) the soil chemical variables combined. Variables were standardized to give them equal weight before ordination. We similarly visualized the main gradients in tree and fern species turnover across the study area by running a principal coordinates analysis (PCoA) of floristic dissimilarity, and plotting scores on the first PCoA axis. Floristic dissimilarity was calculated as 1-Sørensen similarity, which quantifies the similarity in species composition of each pair of sample sites based on species presence-absence data (Legendre & Legendre 1998).

Generalized Dissimilarity Modelling (GDM, Ferrier *et al.* 2002, 2007) and variation partitioning (Borcard, Legendre & Drapeau 1992) were then run to test which climatic and soil variables were the best predictors of floristic turnover in each plant group, and how much floristic turnover was explained by these relative to inter-site geographical distances. The dependent variable in these analyses was a Sørensen dissimilarity matrix of either trees or ferns.

Generalized dissimilarity modelling offers two major advantages over classical linear matrix regression. First, GDM transforms each of the observed environmental variables by iterative maximum-likelihood fitting to provide a best fit of interplot environmental differences to floristic differences (Ferrier *et al.* 2002, 2007). Secondly, the linear predictor is transformed via a link function to accommodate the curvilinear relationship between floristic dissimilarity, which is constrained to the range 0–1, and environmental dissimilarity. Transformations of environmental variables are flexible in shape, to allow for variable rates of species turnover at different points along the environmental gradient. No assumptions are made regarding either the shape of underlying species distributions, or expected turnover rates along environmental gradients, except that the relationship between floristic and environmental dissimilarity is constrained to be monotonically increasing. However, the flexibility of the fit is constrained by the number of I-spline basis functions used in model fitting. Here, the default of three I-splines was used. Geographical distances between plots are similarly transformed.

First GDMs were run including each of the environmental variables separately. The only variables retained for further analysis were those that had significantly higher explained deviance ($P < 0.05$) than that observed after 999 random permutations of the environmental variable in question. Best sets of soil and climatic explanatory variables for explaining tree and fern dissimilarity were then selected from among these by permutation-based backward elimination. Selection of soil and climatic variables was run separately. Plot elevation was analysed together with the three climatic variables. At each step of the backward elimination procedure, each environmental variable included in the model was permuted in turn and the change in explained deviance relative to the unpermuted model was calculated. Permutations were run 999 times, and the variable with the least significant contribution to explained deviance was excluded. This procedure was repeated until all variables retained in the model made significant unique contributions to explained deviance ($P < 0.05$). Subsequently, variation partitioning (Borcard, Legendre & Drapeau 1992) was run to calculate the unique and shared statistical contribu-

tions to explained deviance of the selected soil variables, climatic variables and geographical distance. We tested whether these results were changed by excluding the BCI1 and BCI2 plots, whose soil data differed from that in the other plots. We also tested how much additional deviance was explained by including the fern dissimilarity matrix as a predictor of tree dissimilarity, and vice versa. The fraction of deviance explained uniquely by dissimilarity in the other plant taxon may reflect either common responses to unmeasured environmental variables, or biotic interactions between the two taxa.

We repeated the GDM modelling procedure after running individual-based rarefaction to test whether observed species turnover patterns are driven by changing tree and fern individual densities among plots. The original species abundance values per plot were rarefied to the minimum tree and fern densities observed in any plot (150 and 65 individuals, respectively). Rarefaction was repeated 10 times to test whether the best set of explanatory variables and explained deviance differed depending on which species and individuals were retained. The mean and range of values for the fractions of deviance explained by soils, climate and geographical distance are reported.

The inclusion of soils of very different geological origins in analyses is likely to result in a strong apparent influence of soil chemistry on plant species turnover, but this may not hold within soil formations. Hence, we also ran analyses of species turnover (without rarefaction) on a subset of 23 plots retained after curtailing the soil nutrient gradient by including those plots with positive values on soil PCA axis 1 only (filled circles in Fig. 2). Comparison with geological maps (ACP 1998) indicated that the plots retained were mainly limited to volcanic geology, excluding sites on limestone, sandstone and other marine formations. We split the data according to measured soil chemistry rather than the geological map of the region because many of the mapped categories are coarse and their boundaries are spatially imprecise. Volcanic soils were selected as the focus of these analyses because they are prevalent outside the canal zone in Panama, and hence analyses of this subset of data may be more broadly representative.

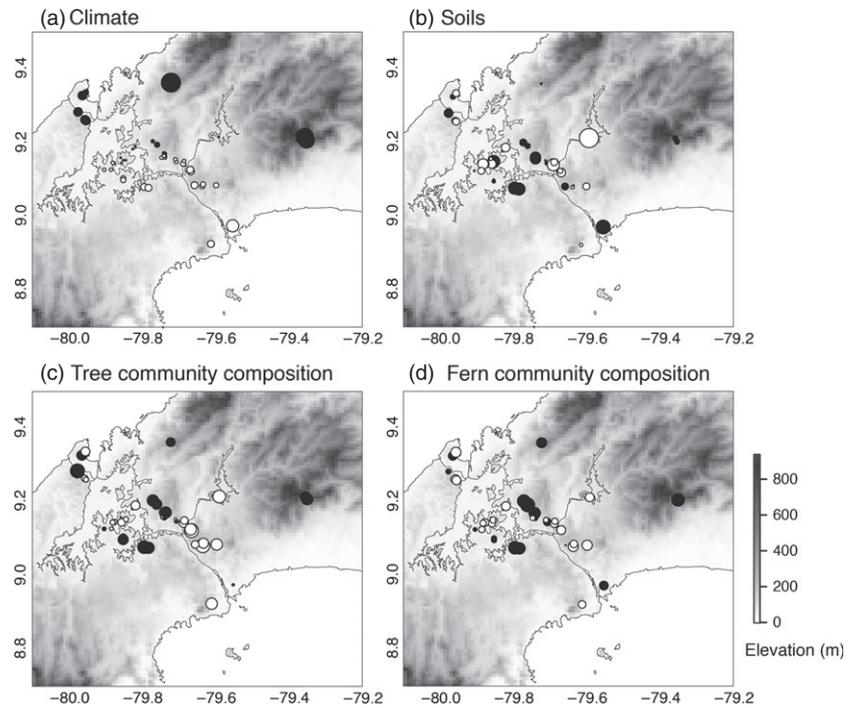
To support the interpretation of the species turnover results, we also ran generalized additive models (GAMs) of tree and fern individual densities and species richness as a function of dry season length and soil Ca content for the 43-plot data set, and dry season length alone for the 23-plot data set. Dry season length and soil Ca were selected for this analysis, because they were the individual variables with the strongest weights on the first axes of the climatic and soil PCAs, respectively. GAMs were generated using penalized regression splines (Wood & Augustin 2002) with a Poisson error structure and a basis dimension of four to constrain the flexibility of the models and thereby avoid over-fitting. All analyses were run in the R language v. 2.13.2 (R Development Core Team 2011) using the packages *vegan* and *mgcv*, and a modified version of the *gdm* package.

Results

PLOT ENVIRONMENTAL CONDITIONS

There was a pronounced trend from the Caribbean towards the Pacific in all three climatic variables, captured well by PCA axis 1 of the climatic variables and elevation (Fig. 2a). This axis summarized 73% of variance in these four variables and was most strongly a function of dry season length, dry season moisture deficit and total annual rainfall. The two highest elevation plots near Cerro Azul (at 526 and 655 m)

Fig. 2. Main trends in (a) climate, (b) soils and (c) tree and (d) fern community composition across the 43 study sites as summarized by the first axis of a principal component analyses of the climatic or soil variables, respectively, or the first axis of a principal coordinates analysis of floristic similarity as quantified by the Sørensen index for trees or ferns, respectively. Black circles indicate positive values on the ordination axis in question, and white circles indicate negative values. The larger the circle, the larger the absolute value, thus sites represented by the largest white-and-black circles in each panel are either environmentally or floristically most distinct. The values are superimposed on an elevation map of the study region (details in Fig. 1 legend). Latitude and longitude are in decimal degrees.



are outliers in the overall Caribbean to Pacific trend, having high rainfall and relatively low seasonality, despite their closer proximity to the Pacific. All other plots were located at below 300 m elevation.

The major gradient in soil chemistry among plots, described by PCA axis 1 of the soil variables, reflects underlying geology far more strongly than climate (Fig. 2b, ACP 1998). Plots with positive values on PCA axis 1 (black circles in Fig. 2b) are largely volcanic or metamorphic in origin, whereas those with negative values (white circles) are largely marine sedimentary. Soil PCA axis 1 summarized 50% of variance in soil chemistry and was most strongly a function of Ca and pH.

Curtailing the soil nutrient gradient to include volcanic-origin soils only (those 23 plots with positive values on soil PCA axis 1) did not much alter the range of climatic conditions or of soil Mn, C or N sampled (Table 1). However, soil Ca, P, Mg and K gradients were considerably curtailed relative to the 43-plot data set. The strengths of correlations between the soil variables differed considerably between the two data sets (Table S1 in Supporting Information). For example, in the 43-plot data set, soil P, Ca and pH were moderately to strongly correlated ($R = 0.60\text{--}0.83$, $P < 0.001$ in all cases), whereas in the curtailed 23-plot data set only the relationship between Ca and pH was statistically significant ($R = 0.85$, $P < 0.001$). In the full data set, correlations between Ca and P, and P and pH, were hence driven by the major geological division between marine and volcanic geologies. There were no significant correlations between any pair of soil and climatic variables in the full data set, and correlations were also generally weak in the 23-plot data set (Table S1). In the latter, the strongest correlation was between dry season length and soil P ($R = 0.66$, $P < 0.001$).

Table 1. Mean and range of each of 14 environmental variables across the 43-plot and 23-plot data sets. The three climatic variables are regression model predictions based on meteorological station data, whereas elevation and the soil variables are based on field sampling

	Mean 43 plots	Range 43 plots	Mean 23 plots	Range 23 plots
Elevation (m a.s.l.)	133	13–655	159	39–655
Dry season length (days)	130	104–148	128	104–148
Dry season moisture deficit (mm)	–852	–916 to –685	–844	–917 to –685
Annual rainfall (mm)	2421	1727–3376	2458	1763–3376
Al (mg kg ^{–1})	639	338–1361	755	384–1361
Ca (mg kg ^{–1})	3094	42–9327	1260	42–2756
K (mg kg ^{–1})	183	58–517	107	58–256
Mg (mg kg ^{–1})	712	28–2382	366	28–772
Mn (mg kg ^{–1})	203	4–555	230	4–555
P (mg kg ^{–1})	4.8	1.4–23.3	2.6	1.4–5.2
pH (1 M KCl)	4.7	3.4–5.9	4.4	3.4–5.1
C (%)	4.6	2.8–8.1	4.2	2.8–5.4
N (%)	0.4	0.2–0.7	0.3	0.2–0.4
C/N	12.2	10.0–16.4	12.6	10.7–16.4

GENERAL CHARACTERISTICS OF THE TREE AND FERN FLORA

Four hundred and eighty-six tree species represented by 19 584 individuals were retained for analysis. Species richness per plot (1 ha) then ranged from 22 to 123, averaging 79, and individual densities ranged from 150 to 672, averaging 455. The most diverse tree genera were *Inga* (22 species), *Ficus* and *Pouteria* (14), *Miconia* (11), *Eugenia* (9),

Ocotea and *Trichilia* (8), *Protium* (7), *Casearia*, *Nectandra* and *Virola* (6).

A total of 92 pteridophyte morphospecies represented by 17 097 individuals (or ramets, in the case of clonal species such as those in the genus *Selaginella*) were encountered in the same plots. Of these, 87 were true ferns and five were lycophytes in the genus *Selaginella*. Two congeneric species, *Bolbitis portoricensis* (Spreng.) Hennisman and *B. aliena* (Sw.) Alston, were confused in the field, and so are lumped in the analyses, which hence include 91 morphospecies. Species richness per plot (0.1 ha) ranged from 3 to 26, averaging 11, and densities per plot ranged from 67 to 1171, averaging 398. The most diverse genera were *Adiantum* (18 morphospecies), *Tectaria* and *Thelypteris* (8) and *Asplenium* and *Selaginella* (5).

Visually, patterns of floristic turnover in trees and ferns across the study region were strikingly similar and clearly reflect responses to both soil and climatic variation (Fig. 2a–d). The correlation between plot scores on tree and fern PCoA axes 1 was 0.91, and that between their overall floristic dissimilarities was 0.75.

GDMS OF FLORISTIC TURNOVER

All species and plots

Total deviance in tree species turnover explained by selected soil and climatic variables and geographical distances was

74% and the corresponding value in ferns was 49% (Fig. 3a,e and Table S2). Dry season length was the best climatic predictor for both plant groups, and dry season moisture deficit and total annual rainfall were selected as added predictors of tree turnover (Fig. 4a–c). Steady species turnover in both plant groups was apparent with increasing dry season length and turnover rates were very high once a threshold dry season length of c. 135 days was exceeded. Similarly, rapid turnover was predicted in trees at high dry season moisture deficits, whereas relatively steady turnover was predicted with increasing total annual rainfall. Climate alone explained 47% of deviance in trees and 21% of deviance in ferns.

Among soil variables, the best predictors of species turnover in both plant groups, in order of statistical significance, were soil P, pH and Ca and these explained 46% of tree turnover and 43% of fern turnover. Very high rates of species turnover in trees, and especially in ferns, were predicted at low levels of exchangeable soil P (below c. 0.3 mg kg⁻¹ dry soil), but little turnover in response to P increases above this threshold (Fig. 4d). In contrast, steady turnover in species composition in response to soil Ca and pH was apparent in both plant groups, although the response to pH was steeper in ferns (Fig. 4e–f).

Geographical distances alone explained 33% of tree turnover and 14% of fern turnover. The predicted response of tree turnover to geographical distance was strongest at distances below 15 km, when soil and climatic differences were taken into account, whereas ferns were predicted to show gradual

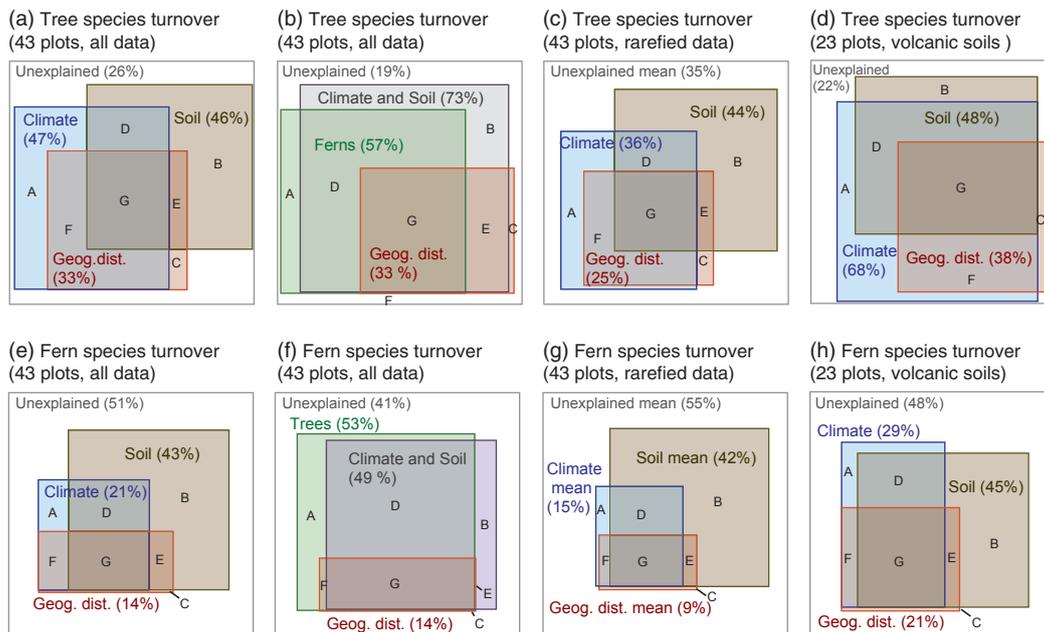


Fig. 3. Generalized dissimilarity model deviance in tree species turnover (a–d) and fern species turnover (e–h) explained by distance matrices of selected climatic and soil variables and geographical distance, as well as by floristic dissimilarity in the other taxon (ferns or trees) in panels (b) and (f). The bounding box in each figure represents total deviance in species turnover, and the shaded boxes represent the fractions explained by each of these explanatory data sets. The exact sizes of fractions A–G, representing their unique vs. shared contributions to explained deviance, are given in Supporting Information Tables S2 and S4. The results are illustrated for all 43 sites and all plant data [(a), (b), (e), (f)], all 43 sites and those plant species retained after rarefying individual densities in each site to the value observed in the least dense plot (mean values over 10 rarefactions) [(c), (g)] and all plant data in sites on volcanic-origin soils (those 23 sites with positive values on soil principal component analyses axis 1) [(d), (h)].

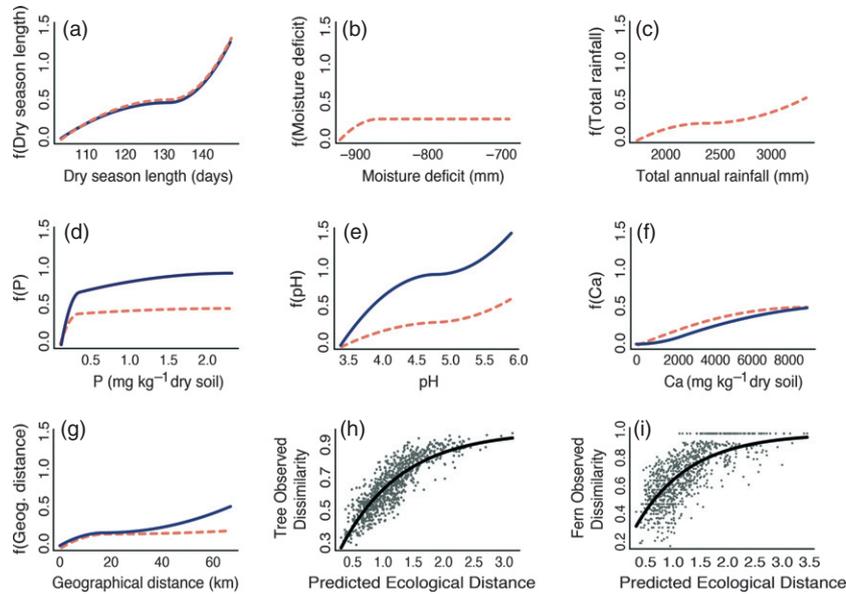


Fig. 4. Generalized dissimilarity model-fitted transformations (partial regression fits) of selected climatic (a–c) and soil (d–f) variables and geographical distance (g) as predictors of tree (dashed lines in orange) and fern (solid lines in dark blue) species turnover across the 43 study plots, without rarefaction. The steeper the slope of the transformed relationship, the greater the predicted species turnover on that section of the gradient. Dry season moisture deficit and total annual rainfall were selected as predictors of tree species turnover only. All other variables were selected as significant predictors of turnover in both plant groups. The final two panels illustrate the relationships between observed tree (h) and fern (i) compositional dissimilarity for each site pair and the linear predictor of the regression equation, that is, the predicted ecological distance between those sites.

turnover across all distances encompassed by the study (Fig. 4g). In general, the shapes of the partial regression fits were similar to those obtained when the same variables were modelled individually, except steeper (Fig. S1 in Supporting Information), because they explained a greater fraction of total deviance in species turnover when tested alone than when covariance with other variables was taken into account.

There was substantial covariance between deviance in species turnover explained by climate, soils and distance in both plant groups (Fig. 3a,e). In particular, deviance explained by geographical distance covaried almost entirely with that explained by climate. Nonetheless, the unique fractions of deviance explained by climate and soils were considerable in trees (12% and 23%, respectively). In ferns, the fraction of deviance explained uniquely by soils was large (26%), but little deviance was explained by climate alone (3%).

Exclusion of the BCI1 and BCI2 plots, whose soil data differed from that of the other plots, resulted in minor increases in overall explained deviance (77% for trees and 56% for ferns, as compared with 74% and 49% for all plots). For both trees and ferns, soil effects were slightly stronger than in the model including all plots. BCI1 and BCI2 are included in all subsequent analyses.

Including fern dissimilarity as an added predictor of tree species turnover increased total explained deviance to 80.5% (Fig. 3b, Table S3), representing an increase of 6.5% relative to the model including environmental variables and geographical distance alone. Including tree dissimilarity as an added predictor of fern species turnover increased total explained deviance by 10%, to 59% (Fig. 3f, Table S3).

Rarefied species, all plots

After rarefaction of tree individual densities, on average, 397 (range over 10 rarefactions 390–405) of the original 486 tree species were retained, and mean species richness per plot fell, on average, by 38% to 49.2 species (range 48.6–49.7). As for the full tree data set, dry season length and moisture deficit were consistently included in the climatic model. However, unlike in the original tree model, annual rainfall was never included, but site elevation was included in five of 10 models. The soil variables included were always the same as before rarefaction (P, pH and Ca), and deviance explained by soils was little altered (deviance explained before rarefaction 46%, mean after rarefaction 44.2%, Fig. 3c and Table S2). In contrast, deviance explained by climate (mean after rarefaction 36%) and geographical distances (mean 25%) fell after rarefaction.

After rarefaction of fern individual densities, on average, 73 (range 69–76) of the original 91 fern species were retained, and species richness per plot fell, on average, by 31% to 7.6 (range 7.3–7.9). The soil and climatic models were in all 10 cases identical to those obtained before rarefaction (soil P, pH and Ca were always selected, as was dry season length among climatic variables). Deviance explained by the selected soil variables was almost identical to that observed before rarefaction (mean after rarefaction 42% relative to 43% before rarefaction, Fig. 3g, Table S2). However, paralleling the results for trees, deviance explained by dry season length (mean after rarefaction 15%) and by interplot geographical distances (mean 9%) fell after rarefaction.

All species, volcanic soil plots only

Limiting soil variation by including only those 23 plots of volcanic origin (those with positive values on soil PCA axis 1) retained 430 of the original 486 tree species and 78 of the original 91 fern species. Deviance in tree floristic dissimilarity explained by selected soil variables (P, Ca and Al, 48.4%) was marginally higher than for the full 43-plot data set (Fig. 3d, Table S2), and deviance explained by climatic differences (dry season length and moisture deficit) and geographical distance increased significantly. However, covariance between the effects of climate, soils and distance was substantial. Consequently, total explained deviance was similar to that in the full data set (78%). In ferns deviance explained by climatic differences (dry season length alone) and geographical distances, as well as their overlap, also increased substantially relative to the full 43-plot data set (Fig. 3h and Table S2), whereas deviance explained by the selected soil variables, P and pH (45%), remained almost identical to that in the full 43-plot data set, as did total explained deviance (52%). The independent effects of soils on tree species turnover were reduced relative to the full data set, whereas their effects on fern turnover remained pronounced.

GAMS OF SPECIES RICHNESS AND INDIVIDUAL DENSITIES

Species richness, and to a lesser extent individual densities, of trees and ferns showed predictable relationships with dry season length and soil Ca content. Tree and fern species richness were moderately correlated ($R = 0.52$, $P < 0.001$), but their individual densities were uncorrelated ($R = -0.10$, $P = 0.52$). For the 43-plot data set, GAMs including both dry season length and Ca explained 67% of deviance in tree species richness and 36% of deviance in tree individual densities, and the corresponding values for ferns were 51% and 30% (Fig. 5). For the 23-plot data set, dry season length alone predicted

82% of deviance in tree species richness, and 49% of deviance in tree individual densities. The corresponding values for ferns were 59% and 25%. In all cases, the shapes of the fits to dry season length were similar to those for species turnover, that is, predicted strong declines in species richness and individual densities above a threshold dry season length of c. 130 days.

Discussion

Our results indicate strong effects of both soil chemistry and climate on tree and fern species turnover in the Panama canal watershed. The major patterns of turnover were strikingly similar in both plant groups, which suggest these will be reflected in the flora more generally.

Previously, turnover in tree species composition across the region has mainly been discussed in terms of the effects of dispersal limitation, species responses to rainfall and, to a lesser extent, major geological transitions (Pyke *et al.* 2001; Condit *et al.* 2002; Chust *et al.* 2006; Engelbrecht *et al.* 2007). The inclusion of soil chemistry changes this picture considerably. The effects of soil differences were much stronger than those captured by the inclusion of broad geological categories in earlier studies. Distance and climatic effects were particularly pronounced in trees, and covaried strongly, but the independent effects of geographical distance were minimal.

The effects of geographical distance on species turnover in both plant groups were statistically almost inseparable from those of the strong Caribbean to Pacific rainfall gradient. Nonetheless, the fact that dry forests towards the Pacific tended to have fewer species and individuals than forests on the wet Caribbean, after controlling for soil differences, suggests that species responses to water availability are a major driver of spatial distance decay in floristic similarity across this region. In support of this, after controlling for variation in individual densities among plots by rarefaction, the explanatory power of both climatic differences and geographical

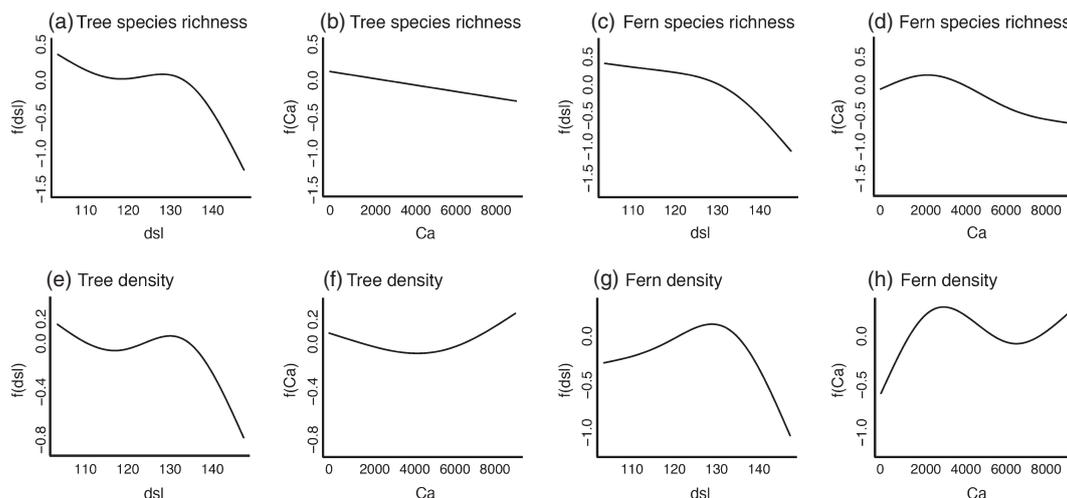


Fig. 5. Generalized additive model-fitted transformations (partial regression fits) of dry season length (dsl, days) and soil Ca (mg kg^{-1}) as predictors of tree species richness (a, b), and fern species richness (c, d), tree densities (e, f) and fern densities (g, h) across the 43 study plots.

distances was somewhat reduced, while the importance of soil differences in explaining species turnover was unchanged. Species turnover along the dry season length and rainfall gradients is, hence, partly a function of changing individual densities and species richness. Nonetheless, species composition in the drier forests clearly does not represent a random subset of individuals (and species) represented in wetter forests. Rather, species are gained and lost in a deterministic fashion along both climatic and soil gradients.

Overall, climatic differences and geographical distances explained a clearly greater proportion of species turnover in trees than in ferns. Ferns may be less dispersal limited, on average, than trees, due to their prolific spore production (Wolf, Schneider & Ranker 2001; Qian 2009), and this could explain a part of this pattern. However, although the independent effects of geographical distance were very small for both plant groups, the independent effects of climate relative to soils were much greater for trees than for ferns, which suggests that trees respond more strongly to our measured climate variables. This is somewhat surprising because one would expect ferns to be more drought-sensitive than angiosperms (Brodribb & McAdam 2011; McAdam & Brodribb 2012), and in particular woody angiosperms, such as trees, and strong responses of tropical fern community composition to microclimatic variation have been found at a local scale (Jones, Szyska & Kessler 2011). It is possible that our climatic parameters better reflected water availability for large trees than for understorey fern species, of which just over a quarter were epiphytes and the remainder were shallow-rooting terrestrials. Furthermore, trees themselves significantly modify the understorey microclimate (Geiger, Aron & Todhunter 2003). Including tree floristic dissimilarity as a predictor of fern species turnover increased explained deviance by 10% relative to the model including environmental variables and geographical distance alone, and for trees the effect of adding fern floristic dissimilarity increased explained deviance by 6.5%. These increases may reflect common responses of the two plant groups to unmeasured environmental conditions. However, direct biotic interactions between the two plant groups may also be involved. Most plausibly, fern species composition in the understorey might respond to consistent changes in microclimate and light conditions with changing tree species composition.

Although soil nutrient status and rainfall covary to some extent in this region, the patterns are weaker and more spatially complex than has previously been implied (e.g. Brenes-Arguedas *et al.* 2008). Lower rainfall sites are not necessarily more fertile than sites with higher rainfall. Furthermore, the strengths of correlations between soil variables are quite different within major geological classes than across them. For example, although soil Ca and P contents were strongly correlated across all 43 plots, particularly because both have high contents on limestone soils, they were entirely uncorrelated within those plots on soils of mainly volcanic origin. Species turnover is likely to be driven by different factors at different positions on environmental gradients, depending on which of these are most strongly limiting. In our study, soil P was

predicted to have a stronger effect on species turnover than Ca, and particularly high turnover rates were predicted with increasing P at the low end of the phosphorus gradient. Similarly, our results suggest that changes in dry season length are a stronger driver of turnover in drier than in wetter forests.

It is somewhat tempting, viewing the inflexion points in the predicted responses of both species richness and species turnover of trees and ferns to dry season length, to invoke the hypothesis that there might be a relatively abrupt transition in water availability beyond, which only a relatively small number of sufficiently drought-tolerant species can persist. While the partial regression fits to our predictors should not be interpreted over-simplistically, our field observations, as well as experimental studies (Engelbrecht *et al.* 2007; Brenes-Arguedas *et al.* 2008, 2011; Brenes-Arguedas, Coley & Kursar 2009), support the idea that increasing dry season length towards the Pacific contributes strongly to plant species turnover by filtering out species without adaptations to drought. This implies that floristic responses to climate change may be sudden if critical thresholds in water availability are altered. However, the fact that sample size in our study is relatively limited, and that the inflexion points were so similar in both plant groups, suggests their precise values were determined by our sampling scheme. The same is probably true of the inflexion in the predicted response of floristic turnover to soil phosphorus, although phosphorus availability is expected to limit plant growth, especially on nutrient-poor, weathered tropical soils (Wright *et al.* 2011).

Curtailling soil variation to sites on volcanic soils unsurprisingly increased the fraction of tree and fern species turnover explained by climate and geographical distance. In trees, turnover explained by soils independently of climate was simultaneously reduced relative to the full data set. There was, however, strong covariance between soil and climatic effects on tree species turnover in volcanic soils. In contrast, the independent effects of soil variation on fern turnover remained strong. This suggests that while tree and fern communities on soils of marine geological origin in this region are very distinct from those on volcanic-origin sites, within the latter, the effects of soil chemistry on tree species turnover may be largely mediated by changes in nutrient, and particularly soil phosphorus, availability along the rainfall gradient. Fern communities, however, appear to remain strongly differentiated by soils, independently of climate, even when volcanic sites alone are examined.

Overall, our results indicate strong environmental determinism of tree and fern community turnover in this region, which by far outweighs the effects of dispersal limitation. In combination with results demonstrating non-random tree species distributions on topographic and soil gradients at local scales (Harms *et al.* 2001; John *et al.* 2007), and significant links between species' local topographic distributions, their regional distributions in relation to rainfall, and experimentally assessed drought tolerances (Engelbrecht *et al.* 2007), this implies that plant community structure in these forests deviates significantly from neutral expectations. Earlier work on the tree flora across this region has focused strongly on the effects of rainfall and its

seasonality. Our results suggest that while these undoubtedly limit the distributions of many plant species in this region, soil effects are at least as important, and it is likely that interactions between the two are sizeable. This probably holds true for many regions around the Caribbean, where both marine and volcanic-origin soils, in combination with strong changes in rainfall over relatively short distances, are common. The observed congruence between tree and fern communities in this area suggests that our results can be extrapolated to the flora more generally, particularly as trees and ferns are distantly related plant groups, with different reproductive biologies and representing different life-forms.

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References

- ACP (1998) *Geología de la Cuenca del Canal de Panamá*. Proyecto de Monitoreo de la Cuenca del Canal (PMCC), Autoridad del Canal de Panamá.
- Ashton, P.S. (1969) Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society*, **1**, 155–196.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- Brenes-Arguedas, T., Coley, P.D. & Kursar, T.A. (2009) Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*, **90**, 1751–1761.
- Brenes-Arguedas, T., Ríos, M., Rivas-Torres, G., Blundo, C., Coley, P.D. & Kursar, T. (2008) The effect of soil on the growth performance of tropical species with contrasting distributions. *Oikos*, **117**, 1453–1460.
- Brenes-Arguedas, T., Roddy, A., Coley, P.D. & Kursar, T.A. (2011) Do differences in understorey light contribute to species distributions along a tropical rainfall gradient? *Oecologia*, **166**, 443–456.
- Brodribb, T.J. & McAdam, S.A.M. (2011) Passive origins of stomatal control in vascular plants. *Science*, **331**, 582–585.
- Chust, G., Chave, J., Condit, R., Aguilar, S., Lao, S. & Pérez, R. (2006) Determinants and spatial modeling of tree β -diversity in a tropical forest landscape in Panama. *Journal of Vegetation Science*, **17**, 83–92.
- Coates, A.G. & Obando, J.A. (1996) Geological evolution of the Central American Isthmus. *Evolution and Environment in Tropical America* (eds J.B.C. Jackson, A.F. Budd & A.G. Coates), pp. 21–56. University of Chicago Press, Chicago, IL, USA.
- Condit, R. (1998) *Tropical Forest Census Plots*. Springer-Verlag and R. G. Landes Company, Berlin, Germany, and Georgetown, Texas.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R. *et al.* (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.
- Denslow, J., Ellison, A.M. & Sanford, R.E. (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, **86**, 597–609.
- Duque, A., Sánchez, M., Cavallier, J. & Duivenvoorden, J.F. (2002) Different floristic patterns of woody understorey and canopy plants in Colombian Amazonia. *Journal of Tropical Ecology*, **18**, 499–525.
- Duque, A.J., Duivenvoorden, J.F., Cavelier, C., Sánchez, M., Polanóa, C. & León, A. (2005) Ferns and Melastomataceae as indicators of vascular plant composition in rain forests of Colombian Amazonia. *Plant Ecology*, **178**, 1–13.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–83.
- FAO (2010) *Global Forest Resources Assessment 2010*. Main report. FAO forestry paper 163. Food and Agriculture Organization of the United Nations, Rome.
- Ferrier, S., Drielsma, M., Manion, G. & Watson, G. (2002) Extended statistical approaches to modeling spatial pattern in biodiversity in north-east New South Wales: II. Community-level modeling. *Biodiversity and Conservation*, **11**, 2309–2338.
- Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modeling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13**, 252–264.
- Geiger, R., Aron, R.H. & Todhunter, P. (2003) *The Climate Near the Ground*, 6th edn. Rowman & Littlefield, New York.
- Gurevitch, J., Scheiner, S.M. & Fox, G.A. (2002) *The Ecology of Plants*. Sinauer Associates, Sunderland, MA, USA.
- Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, **89**, 947–959.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.
- Hubbell, S.P., Condit, R. & Foster, R.B. (2005) Barro Colorado Forest Census Plot Data. URL <https://ctfs.arnarb.harvard.edu/webatlas/datasets/bci>.
- Hubbell, S.P. & Foster, R.B. (1986) Biology, chance, and history and the structure of tropical rain forest tree communities. *Community Ecology*. (eds J. Diamond & T.J. Case), pp. 314–329. Harper and Row, New York.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Lao de Lao, S. (1999) Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R.B. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, **104**, 864–869.
- Jones, M.M., Szyska, B. & Kessler, M. (2011) Microhabitat partitioning promotes plant diversity in a tropical montane forest. *Global Ecology and Biogeography*, **20**, 558–569.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier Science BV, Amsterdam.
- McAdam, S.A.M. & Brodribb, T. (2012) Stomatal innovation and the rise of seed plants. *Ecology Letters*, **15**, 1–8.
- Pearson, D.L. (1994) Selecting indicator taxa for the quantitative assessment of biological diversity. *Philosophical Transactions of the Royal Society of London B*, **345**, 75–79.
- Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.
- Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, **18**, 327–332.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution and Systematics*, **38**, 713–737.
- Ruokolainen, K., Linna, A. & Tuomisto, H. (1997) Use of Melastomataceae and pteridophytes for revealing phylogeographical patterns in Amazonian rain forests. *Journal of Tropical Ecology*, **13**, 243–256.
- Ruokolainen, K., Tuomisto, H., Macía, M.J., Higgins, M.A. & Yli-Halla, M. (2007) Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? *Journal of Tropical Ecology*, **23**, 13–25.
- Salovaara, K.J., Cárdenas, G. & Tuomisto, H. (2004) Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. *Ecography*, **27**, 689–700.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003b) Dispersal, environment, and floristic variation of Western Amazonian forests. *Science*, **299**, 241–244.

- Tuomisto, H., Ruokolainen, K., Aguilar, M. & Sarmiento, A. (2003a) Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology*, **91**, 743–756.
- Webb, L.J., Tracey, J.G., Williams, W.T. & Lance, G.N. (1967) Studies in the numerical analysis of complex rain-forest communities. II. The problem of species sampling. *Journal of Ecology*, **55**, 525–538.
- Wolf, P.G., Schneider, H. & Ranker, T. (2001) Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *Journal of Biogeography*, **28**, 263–270.
- Wolters, V., Bengtsson, J. & Zaitsev, A.S. (2006) Relationship among the species richness of different taxa. *Ecology*, **87**, 1886–1895.
- Wood, S.N. & Augustin, N.H. (2002) GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. *Ecological Modelling*, **157**, 157–177.
- Wright, J.S., Yavitt, J.B., Wurzbarger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N. & Corre, M.D. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, **92**, 1616–1625.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Pearson correlations between environmental variables in the 43-plot and 23-plot data sets.

Table S2. GDM deviance in tree or fern species turnover between sample sites explained by distance matrices of selected climatic variables, soil variables and geographical distances.

Table S3. GDM deviance in tree or fern species turnover explained by floristic dissimilarity in the other taxon, that is, ferns or trees, respectively, selected climatic and soil variables combined and geographical distances.

Figure S1. GDM-fitted transformations (individual and partial regression fits) of selected soil and climatic variables and geographical distance as predictors of tree and fern species turnover across the 43 study plots.