




Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest

Cecilia M. Prada , Arturo Morris, Kelly M. Andersen, Benjamin L. Turner, Pedro Caballero & James W. Dalling

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Nomenclature

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Prada, C.M. (cprada@illinois.edu)^{1,2},

Morris, A. (inaurdin@hotmail.com)³,

Andersen, K.M.

(kelly.andersen.m@gmail.com)^{2,4},

Turner, B.L. (turnerbl@si.edu)²,

Caballero, P.

(pedrocaballeroruiz@gmail.com)³,

Dalling, J.W. (corresponding author,

dalling@illinois.edu)^{1,2}

¹Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA;

²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama;

³Universidad Autónoma de Chiriquí, Calle de la UNACHI, David, Panama;

⁴Department of Geography, University of Exeter, Exeter, EX4 4RJ, UK

Abstract

Questions: Premontane tropical forests harbour exceptionally high plant species diversity; understanding which factors influence their species composition is critical to conserving them, and to predicting how global environmental change will affect them. We asked: (1) how do α - and β -diversity vary at the landscape scale; (2) how important is environmental filtering in structuring these communities; and (3) which soil and climate variables account for the most compositional variation?

Location: Old-growth premontane forest, Fortuna Forest Reserve, western Panama.

Methods: All trees ≥ 5 -cm DBH were censused in 12 1-ha plots up to 13 km apart. For each plot, we measured soil properties (0–10 cm depth) at 13 locations, and estimated or measured monthly rainfall. To evaluate how the environmental and spatial variables are associated with community composition, we used ordination and Mantel tests.

Results: Diversity varied nearly three-fold among plots (68–184 species·ha⁻¹). β -Diversity was also high, with only one of 364 species present in all plots. Turnover reflected distinct forest community types that have developed on different parent materials: forests on rhyolite had an abundance of either ectomycorrhizal-associated trees or canopy palms, while forests on the other rock types (andesite, dacite and basalt) were dominated by trees that form arbuscular mycorrhizal associations. While NMDS ordination showed that species turnover was significantly correlated with rainfall seasonality, and also co-varied with geographic distance. Nonetheless, large compositional differences were apparent among sites < 2 km apart with similar rainfall but differing soils. Partial Mantel tests controlling for geographic distance highlighted the relationship between total phosphorus and species composition.

Conclusions: Soil nutrient availability and rainfall seasonality in premontane forests at Fortuna are associated with striking variation in the taxonomic and functional composition of nearby tree communities, and with plot differences in species richness comparable in magnitude to those reported over > 1000 m a.s.l. in previous studies. Accounting for how local edaphic conditions structure premontane and montane tropical forests will be critical to predicting how tree communities will respond to climate change.

Introduction

Montane forests are among the world's most diverse habitats (Kappelle & Brown 2001). Despite their limited area

and geographic extent, some support plant species diversity comparable to lowland tropical forests (Henderson et al. 1991), harbour unique assemblages of epiphytic and hemi-epiphytic plants, and contain many locally and

regionally endemic species (D'Arcy 1977; Gentry 1992). Despite this diversity we understand far less about the ecology and biogeography of montane forests than lowland forests. In particular, montane and premontane forests have few permanent forest plots with data on species richness and composition (Scatena et al. 2010).

Without adequate baseline data on species distribution patterns and on factors determining these patterns, such as soils and climate, we cannot predict how environmental change will affect montane forests. Montane forest communities may be especially at risk from regional changes in precipitation regime when lowland forests are replaced by fields, or when global climate change affects both temperature and rainfall (Ray et al. 2006; Barradas et al. 2010). While lowland and montane taxa are predicted to move to higher elevations, numerous biotic and abiotic barriers to plant migration cause uncertainty about future forest communities (Feeley & Silman 2010; Feeley et al. 2013).

Plant communities in montane forest often have narrow environmental ranges constrained by steep gradients of rainfall and mist interception (Young 1994; Vázquez 1995; Jump et al. 2009). Precipitation regime can vary dramatically over short distances, particularly at the lower elevational limits of cloud formation, and when passing from windward to leeward mountain slopes (Shreve 1914; Haber 2000). Aspect may also influence disturbance regime through exposure to prevailing winds or hurricanes (Bellingham 1991). Moreover, in common with lowland forests, soils of montane forests can vary greatly in fertility, reflecting heterogeneity in age, parent material and topography, in interaction with climate and forest composition (Silver et al. 1994; Benner et al. 2010).

To date most studies have emphasized the importance of elevation as a correlate of species diversity and structural variation in montane forests (Lieberman et al. 1996; Vázquez & Givnish 1998; Asner et al. 2014; Girardin et al. 2014). However, these transect-based studies may under-sample much of the compositional variability within elevational zones or ecotones that is attributable to topography, soils and microclimate (Aiba & Kitayama 1999; Homeier et al. 2010). In particular, premontane forests mark an elevational transition between lowland forests, where productivity and species composition is often considered determined by P availability (Vitousek 1984; Condit et al. 2013), and montane forests, where N availability is considered most limiting (Vitousek 1984; Tanner et al. 1998). Forests growing at this elevational transition may therefore be subject to N and P co-limitation, or may shift between N and P limitation over short spatial scales depending on parent material, disturbance history and plant–soil feedbacks, leading to high compositional turnover across the landscape.

Here we explored the α - and β -diversity of forests in 12 1-ha forest plots distributed across 13 km within a relatively narrow elevational band between lowland and montane forest (850–1330 m a.s.l.) in western Panama. Our previous work, at a subset of seven of these plots, has shown that the Fortuna forests occupy a geologically complex terrain that includes rhyolitic tuff, andesite, dacite and basalt (Andersen et al. 2010). These different parent materials are associated with contrasting soil physical and chemical properties, and form a mosaic of soil nutrient availability influencing understorey palm community composition (Andersen et al. 2010), functional trait composition (Andersen et al. 2012; Heineman et al. 2016) and seedling growth performance (Andersen et al. 2014). Here we explore broader compositional patterns within the tree community over a more intensively sampled rainfall and soil fertility gradient at Fortuna. If the understorey palm and the overstorey tree community composition are controlled by similar processes, then we predict high compositional dissimilarity across the plot network, and that climate and soil variables, particularly soil N and cation availability, will be important correlates of species distributions (Andersen et al. 2010). However, inclusion of additional sites, and a focus on the tree community, may also reveal an important role for P availability, a major driver of β -diversity in tree communities in lowland forest in Panama (Condit et al. 2013). In Central America and S.E. Asia, premontane forests often define the lower elevational limits of forests that are dominated by temperate plant lineages, primarily Fagales, that form associations with ectomycorrhizal fungi (Whitmore & Burnham 1975; Kappelle 2006). The occurrence of plant lineages associated with N-limited temperate forest ecosystems may therefore indicate sites with a predominance of N limitation. We therefore also describe how the broader functional group composition of tree communities (palms vs dicots; angiosperms vs gymnosperms; arbuscular vs ectomycorrhizal trees; N-fixing legumes vs non-legumes) are distributed along the same environmental gradients.

Methods

Study site

The study was carried out in the Fortuna Forest Reserve (19 500 ha) and the southern edge of the adjacent Palo Seco Forest Reserve (125 000 ha) in western Panama (8°45'N, 82°13'W; Fig. 1). The study area supports super-humid premontane forests (Holdridge 1947) between 700 and 1500 m a.s.l. Mean annual rainfall ranges between 4600 and 6300 mm (Appendix S1). Although there is seasonality in rainfall across all but the most northerly sites along the Caribbean slope of the continental divide, mean rainfall in the drier months (Jan–Apr) is rarely

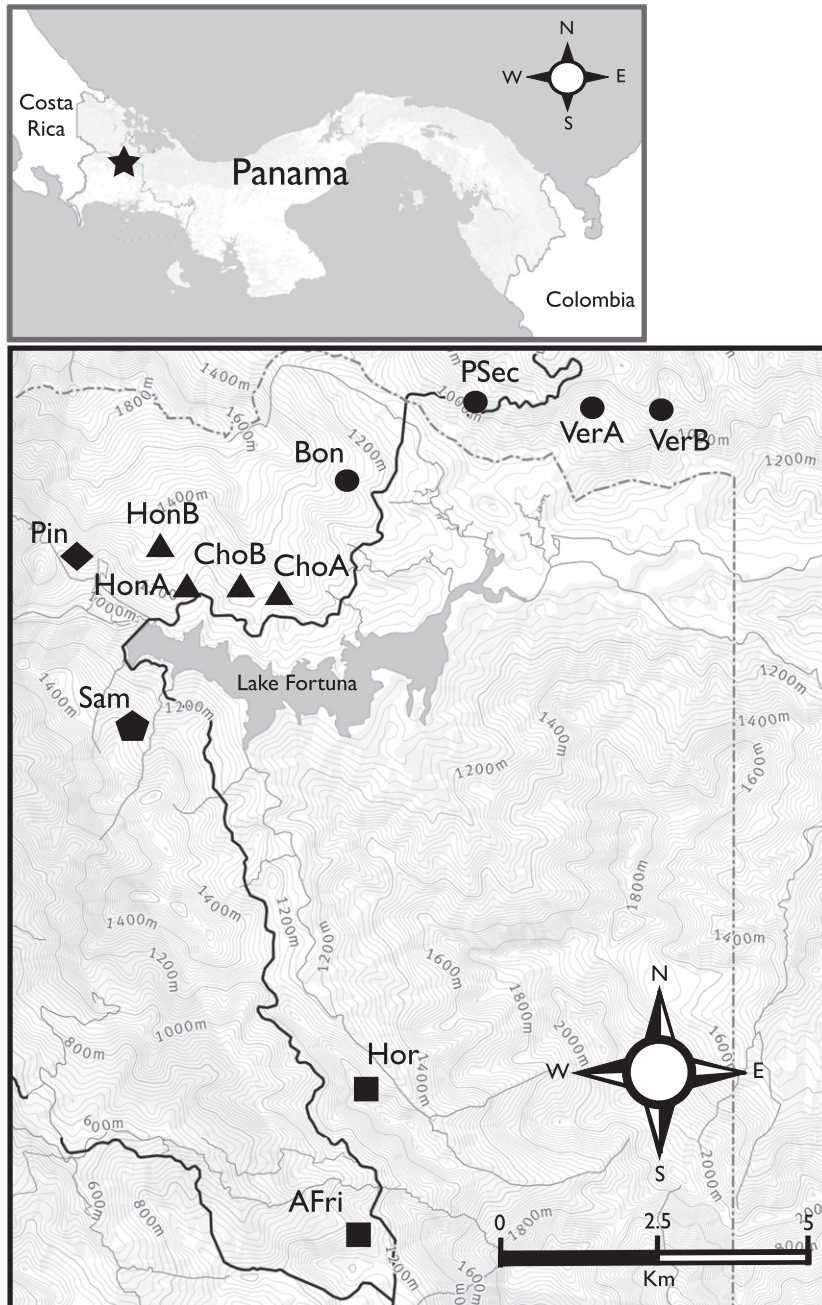


Fig. 1. Location of the 12 1-ha forest plots in the Fortuna and Palo Seco forest reserves. High fertility sites derived from porphyritic dacite are shown by square symbols, intermediate fertility andesite (circles) and basalt (diamond), low fertility rhyolite (triangles) and transition between andesite and rhyolite (pentagon).

<100 mm·mo⁻¹ except at the most southerly (leeward) side of Fortuna (Appendix S1).

Within the study region we established 12 permanent 1 ha (100 m × 100 m) forest inventory plots (Fig. 1; Appendix S1, Appendix S2). Plots were located on relatively gentle slopes, avoiding exposed ridge tops. Plot area was corrected for slope inclination. Six plots were

established in 2003, with an additional six plots added in 2008. Data from the 2013 re-census are reported, which included all trees ≥5 cm DBH. Analyses of α -diversity includes all confirmed tree species identifications (333 species), and an additional 106 morphospecies for which species epithets are provisional. Vouchers of fertile specimens have been deposited at the University of Panama (PMA)

herbarium. Analyses of β -diversity are restricted to the 364 species or morphospecies for which we have high confidence that identifications are consistent across plots. Species were classified as ectomycorrhizal (EM) if they occurred in families known to contain EM taxa (Smith & Read 2008), and if subsequent examination of fine roots revealed the presence of a hyphal mantle (15 species; A. Corrales, unpublished data). Remaining tree taxa are assumed to be arbuscular mycorrhizal, with the exception of non-mycorrhizal *Proteaceae* (two species at the study site). A list of 44 potentially N-fixing taxa (including 26 species of *Inga*) consisted of all species in the legume sub-families Mimosoideae and Papilionoideae.

Rainfall and soils data

Rainfall data were collected every 2 wk from 2007 to 2009 and 2011 to 2014 in a rain gauge 2–5 m above the ground in the centre of a large gap close to a subset of sites spanning the study area (Appendix S1, Appendix S3). For the sites of Pinola and Alto Frio, rainfall data were only available for 2013 and 2014. However, annual rainfall averaged across sites measured over the 5 yr from 2007 to 2012 (5772 ± 1039 mm; mean \pm 1 SD) was similar to that in 2013–2014 (5506 ± 809 mm). For four sites (Bonita, Chorro B, Verrugosa A and B) that lacked rainfall gauges, data were used from the closest sites (<3 km away) that had similar slope position (Appendix S1).

Soil variation reflects the complex geology at Fortuna, with two distinct mountain ranges – the Cordillera Central (parent material: rhyolitic tuff, basalt and andesite) and Cerro Hornito (dacite outcrops) – separated by a few kilometers. The 12 plot sites sample these contrasting parent materials. Soil from each 1-ha plot was analysed for pH, bulk density, total C, N and P, extractable inorganic N (NH_4 and NO_3), resin extractable P, extractable cations (Al, Ca, Fe, K, Mg, Zn), effective cation exchange capacity (ECEC), and total exchangeable bases (TEB). All samples were collected in the mid-wet season (Jul 2008 or Jul 2010). Soil samples were collected after removing un-decomposed litter from the surface 0–10 cm of soil, where most fine roots are located (Cavelier 1992), at 13 locations per plot, and from a subset of five locations per plot at 10–50 cm depth. Inorganic N extractions were completed within 6 h of sample collection, and other extractions within 24 h.

Bulk density (BD) was determined by drying a known volume of soil at 105 °C. Soil pH was measured in water with a glass electrode in a 1:2 dry soil:water solution ratio. N fractions (ammonium, nitrate) were determined by extraction in 0.5 M K_2SO_4 for 1 h, with detection by automated colorimetry on a Lachat Quikchem 8500 (Hach, Manchester, UK). Readily exchangeable phosphate (resin

P) was determined by extraction with anion-exchange membranes. Exchangeable cations were determined by extraction in 0.1 M BaCl_2 (2 h, 1:30 soil to solution ratio), with detection using inductively coupled plasma spectrometry on an Optima 7300 DV (Perkin-Elmer, Shelton, CT, US; Hendershot et al. 2008). Total exchangeable bases (TEB) was calculated as the sum of Ca, K, Mg and Na; ECEC was calculated as the sum of Al, Ca, Fe, K, Mg, Mn and Na; base saturation was calculated as $(\text{TEB} \div \text{ECEC}) \times 100$. Total P was determined by ignition (550 °C for 1 h) and acid extraction (1 M H_2SO_4 for 16 h), with phosphate detected using molybdate colorimetry (Walker & Adams 1958). Total C and N were determined by elemental analysis (Thermo Flash 1112 analyser, Bremen, DE).

Data analysis

Analyses of tree communities and environmental variables were implemented using the R statistical software package “vegan” (v 2.0-10; R Foundation for Statistical Computing, Vienna, AT).

Alpha-diversity and compositional variation

Species accumulation curves were compared among plots using 95% CI of species richness after rarefaction of 1000 stems per plot. Fisher's α was used to compare species diversity among plots. Variation in species composition was assessed using a Steinhaus dissimilarity matrix, calculated using the Bray–Curtis method, double-standardized by species maxima and plot totals of square root-transformed species abundance data for each plot. NMDS, an unconstrained ordination technique, was used to visualize compositional variation among sites. Analysis of similarity in R (ADONIS) was then used to examine plot differences and parent material effects (andesite, rhyolite, dacite and basalt) on species composition. To describe geographic distance-decay in similarity, a matrix of three-dimensional Euclidean geographic distances among plots was calculated from GPS coordinates for the SW corner of each plot; elevation was measured using a digital altimeter (Suunto USA, Ogden, UT, US).

Relationship between compositional variation, geographic distance and environmental variables

To explore how environmental variables varied among plots, the 21 soil variables and two rainfall variables (Appendix S1) were jointly subject to PCA. To assess the strength of correlation between tree community composition, environment variables and geographic distance we used Mantel tests. The environmental matrix was constructed based on Euclidean distance using the first three

axes of the PCA of soil and rainfall data combined. Mantel tests were used to correlate environmental matrices with geographic distance, and partial Mantel tests to correlate the tree community with environmental variables while controlling for geographic distance (a test of 'pure environmental' effects) and between the tree community and geographic distance controlling for environmental variables ('pure spatial'). Standardized Mantel statistics are based on Pearson's correlation coefficients, and significance was assessed using randomization tests with 1000 permutations (Legendre & Legendre 2012). We assessed the strength of association of individual environmental variables with the Steinhaus dissimilarity matrix of tree community composition by fitting environmental variables *a posteriori* to the NMDS, maximizing their correlation to the ordination configuration. Finally, we also used DCA to explore species responses to environmental gradients.

Results

Functional and compositional variation among plots

Plots varied considerably in stem number (range 1112–2435 stems ≥ 5 cm DBH) and basal area (range 30.3–50.3 $\text{m}^2 \cdot \text{ha}^{-1}$; Table 1). However, only basal area varied significantly with parent material ($F = 5.16$, $df = 2, 9$, $P = 0.032$), with lower values on andesite-derived soils (mean 34.2 $\text{m}^2 \cdot \text{ha}^{-1}$) than dacite-derived soils (mean 46.35 $\text{m}^2 \cdot \text{ha}^{-1}$; Tukey HSD, $P < 0.05$).

There were also striking differences in the ecological dominance of different plant functional groups (Table 1). Most notable were differences between adjacent pairs of plots at Chorro and Honda (all on rhyolite geology, but with different soil orders), and between Honda and the nearby plots with similarly aseasonal rainfall patterns: Pinola (on basalt), Bonita (on andesite) and Samudio (rhyolite-andesite transition). The two Chorro plots were dominated by three species of palm (*Colpothrinax aphenopetala*, *Wettinia quinaria* and *Euterpe precatoria*) that accounted for 25–41% of basal area. In contrast, palms accounted for <1% of basal area in the two Honda plots, which were instead dominated by the ectomycorrhizal (EM) tree *Oreomunnea mexicana* (Juglandaceae; 25–46% of basal area). *Oreomunnea* rarely occurred in other plots. A single species of conifer, *Podocarpus oleifolius* (Podocarpaceae, exclusively AM) also occurred on the two Chorro plots (6–8% of basal area); otherwise it only occurred at Honda B. Finally, plots showed substantial variation in the abundance of potentially N-fixing taxa (primarily *Inga* spp), with low representation in the Hornito and Chorro plots.

Alpha- and β -diversity

In total 18 856 trees ≥ 5 cm DBH were censused in the 12 1-ha plots, representing 439 species and 73 families. Species richness per plot ranged between 68 and 184 species $\cdot \text{ha}^{-1}$, and between 59 and 170 species 1000 stems $^{-1}$ (Table 1, Appendix S1). The three lowest

Table 1. Number of stems, species number (including morphospecies), rarified species number per 1000 stems and Fisher's α for individuals ≥ 5 and ≥ 10 cm DBH. Percentage of stems ≥ 5 cm DBH that are of species forming ectomycorrhizal associations (EM), palms, conifers, potential N-fixing taxa (all mimosid and papilionid legumes). Total basal area per plot ($\text{m}^2 \cdot \text{ha}^{-1}$), and percentage of basal area in each group.

	Rhyolite		Rhy/And Transition			Andesite		Basalt		Dacite		
	ChorroA	ChorroB	HondaA	Honda B	Samudio	Bonita	P. Seco	Verrug.A	Verrug.B	Pinola	Hornito	A. Frio
≥ 10 cm DBH												
Stems	1015	1143	787	935	754	649	617	562	696	784	647	964
No. Spp.	59	53	120	102	103	77	145	114	126	80	89	75
Fisher α	13.65	11.49	39.44	29.15	32.25	22.74	59.73	43.17	44.96	22.29	27.95	19.00
≥ 5 cm DBH												
Stems	1866	2435	1597	1578	1781	1314	1246	1233	1425	1424	1112	1845
No. Spp.	80	68	149	128	141	98	184	151	163	98	108	90
Spp./1000	67	59	132	113	126	93	170	143	148	91	106	84
Fisher α	16.9	12.9	40.2	32.9	35.9	24.5	59.6	45.2	47.5	23.9	29.5	19.8
Basal Area	35.1	40.4	46.3	47.4	35.6	32.6	32.5	30.3	30.3	43.6	50.3	42.4
% for Basal area												
% EM	8.7	21.8	24.9	46.1	1.8	–	3.9	2.4	1.8	0.02	3.8	7.4
% Palm	41.9	25.7	0.7	0.3	1.6	0.2	4.5	3.5	4.3	0.2	0.05	0.04
% Conifer	8.2	6.5	–	0.4	–	–	–	–	–	–	–	–
% N fixer	0.4	0.1	4.4	4.2	10.8	10.1	16.0	6.9	5.9	11.5	0.3	13.7
No. Stems												
Palm	686	697	48	15	86	25	196	190	81	25	9	7
Conifer	7	5	–	1	–	–	–	–	–	–	–	–

diversity sites (Alto Frio, Chorro A, Chorro B), each with <90 species-ha⁻¹, also had the highest stem density per hectare. Similar diversity patterns were observed for canopy trees (>30 cm DBH; Appendix S4).

Compositional similarity declined linearly with the logarithm of distance over the 13 km spanning the sites ($r^2 = 0.26$, $P < 0.001$; Fig. 2). Similarity values dropped to <0.2 for plots 10 km apart, however, similarity at the intermediate spatial scale (2–4 km) varied greatly, reflecting in part the effect of parent material on compositional similarity (ADONIS: $F = 2.09$, $P = 0.003$). Only one tree species, *Tapirira guianensis* (Anacardiaceae) was present in all plots, and 27.4% of species were only recorded in a single plot (Fig. 3).

Rainfall and soil variation among plots

Rainfall varied considerably across the 13 km separating plot locations (Appendix S1). However, only the two dacite plots, Hornito and Alto Frio, at the southern side of the Fortuna reserve, experienced dry season moisture deficits. Over a 7-yr period, Hornito had eight different months with <100 mm of rainfall (Appendix S3). In contrast, plots further north and east of Pinola received >5 m of rain annually and had <1 mo with <100 mm of rainfall over the same 7 yr.

Soil nutrient concentrations also varied greatly among plots, with pH ranging from 3.6–5.6, 20-fold variation in resin extractable P, eight-fold variation in NH₄, 13-fold variation in NO₃ and six-fold variation in cation exchange capacity (Appendix S1). Extractable nutrients are

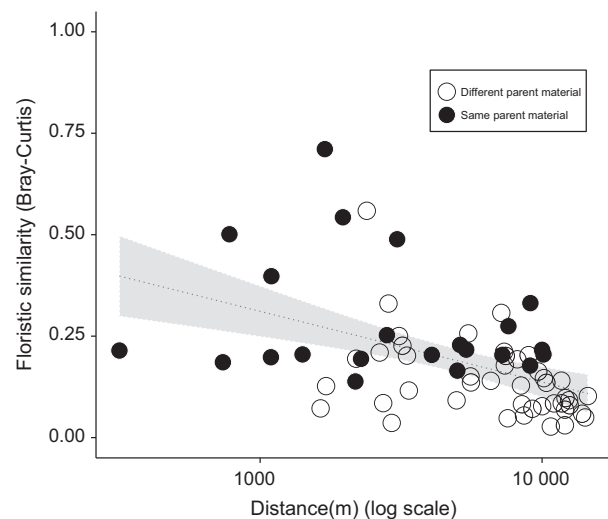


Fig. 2. Decay in Bray-Curtis floristic similarity based on species abundance between all pairs of 1-ha plots with geographic distance across the Fortuna and Palo Seco forest reserves. Linear regression fit and 95% CI are shown. Pairs of plots on different parent material are shown by open circles and pairs on the same parent material by filled circles.



Fig. 3. The number of plots occupied by each tree species with individuals >5 cm DBH.

expressed on a per volume basis because soil bulk density also varied five-fold across the plots, primarily reflecting differences in soil total C (Appendix S1).

The first two axes of the PCA of the rainfall and soil environmental variables measured at 0–10 cm depth (Fig. 4) explained 68.8% of the variance in the data set, and indicated that, with some exceptions, plots grouped according to parent material. The two dacite-derived plots grouped with Pinola, a basalt plot, and were characterized by relatively high plant available P, Ca, and extractable ammonium. The low pH andesite plots clustered in a group along PC1 characterized by high rainfall and low total exchangeable bases. The rhyolite plots of Chorro and Honda were characterized by low bulk density, pH, inorganic N and resin P. Much of the overall variation in soil nutrient availability (captured in the first PC axis) was

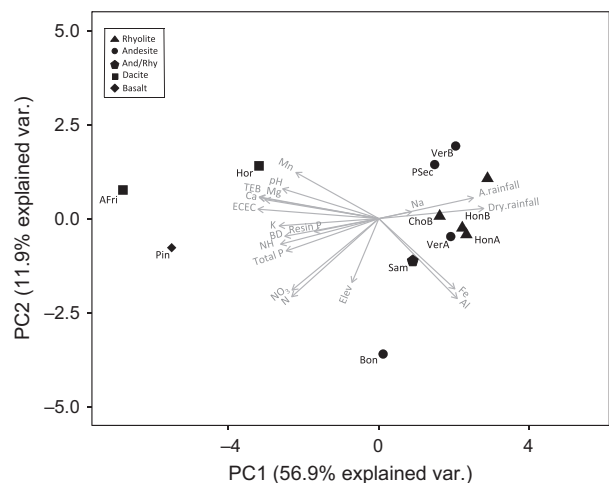


Fig. 4. PCA of variation in elevation, rainfall and soil variables for 12 1-ha plots.

encompassed in five plots (Pinola, Chorro A and B, Honda A and B) distributed over only 3 km. A similar PCA generated for less intensively sampled sub-surface mineral soils of 20–50 cm depth (Appendix S4) explained a similar proportion of variance in the data set (69.6%), and for the most part revealed similar grouping of plots and correlations with environmental variables.

Compositional variation in relation to rainfall and soil nutrients

The NMDS ordination of plant communities revealed that plots grouped according to underlying geology and geographic location (Fig. 5). The andesite plots on the Caribbean slope (Palo Seco, Verrugosa A and B) formed a cluster distinct from the andesite plots closer to the reservoir (Samudio and Bonita). The two rhyolite plots at Honda also grouped with the nearby rhyolite–andesite transition plot of Samudio, despite the abundance of the EM tree *Oreomunnea* at Honda. The two rhyolite sites at Chorro were also distinct (high values on MDS axis 1; Appendix S4), while Alto Frio was distinct in having by far the lowest value on the same axis. The basalt site, Pinola, geographically close to Samudio and Honda, was also distinct in the vegetation ordination.

Environmental vectors fitted to the ordination showed that dry season rainfall, annual rainfall, elevation, ECEC, pH and total P were all significantly correlated with compositional variation ($P < 0.05$). The two sites on the southern side of Fortuna, Hornito and Alto Frio, were characterized by high ECEC and drier and more seasonal

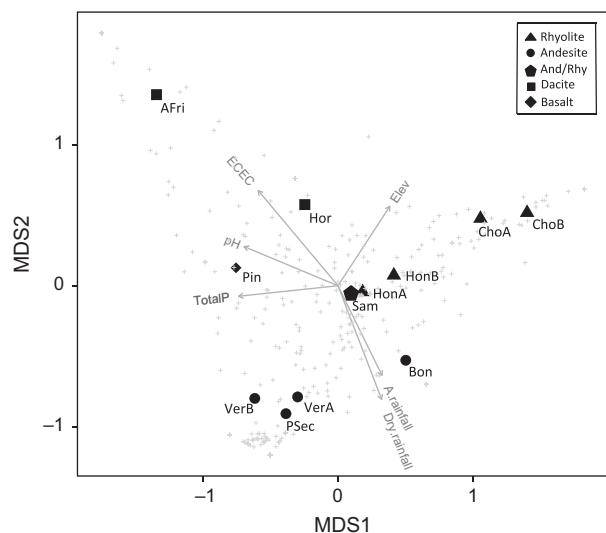


Fig. 5. NMDS ordination for 12 1-ha plots based on species abundance data. Environmental variables with $P \geq 0.05$ were fitted in the NMDS represented by arrows. Parent material is symbolized by the geometric figures and species are in grey.

rainfall, while the rhyolite sites and basalt site (Pinola) were distributed across the gradient of P availability. The Caribbean slope sites (Verrugosa A and B, Palo Seco) were not strongly associated with any of the significant environmental vectors except elevation (Fig. 5). Analysis of the sub-surface mineral soils resulted in correlations with environmental variables that were largely congruent with those of surface soils (Appendix S4), as was a DCA of the same data (Appendix S4).

Mantel test results did not differ for species abundance or presence/absence (Table 2). Floristic dissimilarity was significantly correlated with geographic distance, the PCA environmental matrix, dry rainfall season, pH, bulk density, total P, Ca, ECEC and TEB. After controlling for spatial variation, the ‘pure environmental’ partial Mantel test showed that only the PCA environmental matrix, bulk density and total P were correlated with floristic dissimilarity.

Discussion

We found striking variation in α and β -diversity, and in the functional group composition of tree communities in forest plots <13 km apart in premontane forest in western Panama. In part, compositional variation reflects dispersal limitation as floristic similarity between plots declined with distance, a result we found previously for understorey palm communities at Fortuna (Andersen et al. 2010). Differences in diversity and composition, however, are also attributable to a combination of soil fertility effects, the amount of rainfall and its seasonality. In common with lowland forests, differences in fertility reflect co-variation in pH, P variables, inorganic N and ECEC in soils that developed on diverse parent materials (Turner & Engelbrecht 2011), and to a lesser extent may reflect differential rates of leaching under different rainfall regimes.

Diversity of premontane forest tree communities

To date, the most extensive analysis of the composition of premontane and montane forest tree communities is based on 0.1-ha transect samples arrayed across Andean and Central American sites (Clinebell et al. 1995; Gentry 1995). These studies found remarkable consistency in patterns of species and familial diversity in both Andean and Central American montane forests. For Andean forests, elevation explained 71% of variation in species richness, with twice as many species on average in premontane forest at 1200 m a.s.l. than in montane forest at 2500 m a.s.l. (Fig. 2 in Gentry 1995). Similar patterns have been reported for 1-ha plots arrayed along elevational transects in Central America and Peru (Lieberman et al. 1996; Fierer et al. 2011; Girardin et al. 2014).

Table 2. Mantel and partial Mantel test results showing correlation between floristic composition, environmental and geographic distance matrices among 12 lower montane forest plots in Panama. The Env PCA matrix encompasses the first three axes of the PCA of all environmental variables. To assess the correlation of individual environmental variables we only included those that were significant ($P < 0.05$) in the MDS. Mantel tests were performed between compositional dissimilarity matrices based on Steinhaus index (for abundance and presence/absence) and each environmental matrix. Additionally, each environmental variable matrix was correlated to the geographic distance matrix (Geo. distance) to evaluate if environmental variables are correlated with the spatial component. The floristic composition matrix was also correlated with geographic distance. Partial Mantel tests were performed to evaluate the correlation of floristic dissimilarity with (1) 'Pure environmental' variables, after partialling out the influence of the geographic distance and (2) 'Pure spatial' variables, after partialling out the influence of environmental variables. Values in the table represent the Pearson correlation coefficient (r) and significance was based on 999 permutations (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

Environmental Variable	Mantel Test			Partial Mantel Test			
				Pure Environmental		Pure Spatial	
	Abundance	Pre/Abs	Geo. Distance	Abundance	Pre/Abs	Abundance	Pre/Abs
Env PCA	0.54***	0.48**	0.31	0.47**	0.38*	0.42**	0.51**
Rainfall	0.19	0.23	0.13	0.15	0.19	0.49**	0.57**
Dry Rain	0.40**	0.50**	0.64***	0.11	0.20	0.35*	0.39*
pH	0.25*	0.29*	0.26	0.14	0.17	0.46**	0.54**
Bulk Density	0.42**	0.53**	0.28	0.33*	0.47**	0.44**	0.52***
Total P	0.45**	0.37*	-0.08	0.57***	0.51**	0.61***	0.66***
Ca	0.46**	0.50**	0.54*	0.26	0.27	0.34*	0.42**
Fe	0.18	0.15	0.11	0.14	0.10	0.49**	0.57**
ECEC	0.45**	0.50*	0.56**	0.24	0.26	0.33*	0.41**
Total Exchangeable Bases	0.47**	0.51**	0.56*	0.26	0.28	0.33*	0.41**
Geographic Distance	0.50**	0.58**					

While these broad-scale studies highlight the importance of elevation in structuring communities, they have overlooked the variation in composition and richness that occurs within narrow elevational limits. For example, Clinebell et al. (1995) concluded in their study that "tropical forest species richness is surprisingly independent of soil quality." Here we found that forests distributed across a few kilometres, with similar elevation, and often with very similar climate, can vary three-fold in species richness – equivalent to the mean richness differences that occur over >1000 m a.s.l. (Gentry 1995). This variation appears to be attributable to differences in parent material, and therefore, soil nutrient availability.

Tree diversity is expected to peak at the lower elevational limits of montane forest. This could arise if less seasonal premontane forests support the inclusion of species otherwise excluded from lowland forests by dry season water deficits (Wright 1992). A mid-elevational peak in diversity has been reported for elevational transects in Peru and Bolivia (Girardin et al. 2014), Costa Rica (Lieberman et al. 1996) and almost certainly exists in Panama. At Fortuna, the highest species richness was recorded at Palo Seco (145 species ≥ 10 cm DBH), and is only exceeded by two lower elevation and relatively wet sites, both in central Panama: Santa Rita (400 m a.s.l.; 152 species; Pyke et al. 2001) and Nusagandi (350 m a.s.l.; 191 species; Paredes unpubl data, cited in Leigh 1999).

Structural and compositional variation at Fortuna

Differences in species richness at Fortuna are also accompanied by large variation in stem density and basal area, and in the representation of different functional and taxonomic groups (Table 1). Whereas tree communities on andesite, dacite and basalt are almost exclusively composed of species that form arbuscular mycorrhizal (AM) associations, forests on relatively infertile rhyolite-derived soils in the Honda watershed, and to a lesser extent at Chorro, have a substantial representation of ectomycorrhizal (EM) taxa from the predominantly temperate order Fagales.

At the Honda B plot, EM taxa account for nearly half of basal area, an effect that is largely attributable to a single EM tree species, *Oreomunnea mexicana* (Juglandaceae; Corrales et al. 2016a). EM associations may be particularly beneficial in high elevation forests because the ability of EM to acquire N from a variety of organic sources (Read & Perez-Moreno 2003; Treseder et al. 2008) may compensate for a decline in N mineralization with decreasing temperature and increasing soil moisture content (Marrs et al. 1988; Raich et al. 1997). Rhyolite plots, however, did not appear to be especially N-limited relative to other plots (Appendix S1). Furthermore, the EM tree *O. mexicana* also grows in soil relatively rich in mineral N close to the Alto Frio plot (Corrales et al. 2016a). Instead, EM-associated tree species may induce feedback effects on soil N

availability. In the Honda watershed resin-extractable nitrate and ammonium are lower beneath *Oreomunnea* trees than neighbouring AM tree species, an effect attributed to direct uptake of organic N by EM fungi and a suppression of microbial mineralization of organic matter by free-living saprobes (Corrales et al. 2016b).

Although *Oreomunnea* is locally dominant at Honda, it is absent from the two most infertile plots in the adjacent Chorro watershed <1 km away. Chorro is dominated by three species of canopy palms that collectively account for 29–37% of stems. The slow leaf production rate and tall stature (>25 m) achieved by these palms, particularly *Colpotherinax aphanopetalum* (Heineman et al. 2015), suggests that they may be particularly strong competitors under extremely infertile conditions, where long-lived leaves with low nutrient concentrations, as well as reduced investment in wood, results in higher nutrient use efficiency and potentially allows greater allocation to reproductive biomass than dicot trees (Heineman et al. 2015). Chorro also supports a population of the only conifer at Fortuna, *Podocarpus oleifolius*, a pattern consistent with the affinity for low fertility soils shown by other tropical and temperate *Podocarpaceae* (Coomes & Bellingham 2011; Punyasena et al. 2011). In contrast, N-fixing taxa, primarily *Inga* (*Fabaceae*), the largest genus in Neotropical lower montane forests (Gentry 1995), were far rarer at Chorro than all other sites except Hornito (Table 1). The rarity of N fixers at Chorro may reflect critical limitation of P or molybdenum (Vitousek & Field 1999; Wurzburger et al. 2012).

More generally, species turnover was high across sites, with low floristic similarity even for plots <1 km apart. Although there is a significant effect of geographic distance on compositional similarity when controlling for environmental variables, consistent with dispersal limitation, compositional similarity also reflects variation both in soil properties and in rainfall regime. While annual rainfall exceeds 4 m at all plots, occasional dry season moisture deficit may still act as an ecological filter for tree species occurring on the Pacific side of the reserve. A study at the Monteverde Reserve in Costa Rica also found low community similarity between nearby Pacific and Atlantic slope plots at similar elevation along a 2.5-km transect (Häger 2010). As seasonally drier sites also tend to be more fertile, with higher pH, cation exchange capacity, inorganic N and extractable P (Fig. 4), the effects of climate and soils cannot be completely distinguished. Overall, sites generally clustered in the NMDS ordination of forest composition data based on underlying soil properties and rainfall (Fig. 5). However, the composition of plots located at sites near the centre of the reserve (Pinola, Samudio, Honda and Chorro), with similar total dry season rainfall, differed markedly, reflecting a clear effect of soil properties.

Given the high degree of co-variation in soil variables across the Fortuna sites (Fig. 4) it remains unclear whether compositional variation reflects differential sensitivity among taxa to the same soil nutrient or a combination of soil nutrients. Our earlier analysis of understorey palms at Fortuna highlighted base cations and inorganic N as the soil variables most strongly correlated with compositional similarity (Andersen et al. 2010). In addition, N limitation to productivity appears to be important for the overstorey tree community in the rhyolite-derived soils at Honda, where N fertilization increases litterfall and stem growth (Adamek et al. 2009; Heineman et al. 2015). The absence of N as a significant correlate of compositional variation in the tree community ordination in this study however may also indicate that neither total N nor inorganic N effectively characterize plant available N pools when plants use both organic and inorganic sources of N (Lipson & Näsholm 2001; Andersen & Turner 2013).

In contrast to the weak influence of N, there was a strong effect of P availability on compositional variation across the landscape. This effect is consistent with observed patterns of species turnover across similar gradients of P availability at larger spatial scales in lowland forest in central Panama (Condit et al. 2013) and with structural and compositional change across the Amazon basin (ter Steege et al. 2006; Quesada et al. 2009). Productivity responses to N fertilization at Fortuna further suggests the potential for N co-limitation among species adapted to the prevailing conditions of P availability, consistent with evidence for co-limitation by N and P observed in other montane forests (Tanner et al. 1992; Homeier et al. 2012).

Implications of variation in species composition for understanding responses to climate change

Tropical montane forests are vulnerable to climate change because their biota is adapted to continually moist conditions involving high rainfall and frequent cloud immersion (Pounds et al. 1999). Rising temperatures could dramatically shift moisture regimes, particularly at transitional sites in premontane forests by increasing the basal altitude at which cloud cover forms (Foster 2001; Nair et al. 2010; but see van der Molen et al. 2010). Decreases in the frequency of cloud cover, as has been observed in lower montane forests in Costa Rica and Mexico (Pounds et al. 1999; Barradas et al. 2010), could therefore result in upward migration of species from the lowlands, or horizontal migration of species adapted to similar temperature regimes, from leeward mountainsides.

Variation in soil properties on mountains adds another dimension to potential global change effects. At Fortuna, where differences in soil and parent material play an

important role in shaping forest composition, migrations must contend with both a reduction in habitat area as migration pushes species off the top of mountains, and with the potential of encountering unfavourable edaphic conditions.

Conclusions

The premontane forest tree communities at Fortuna differ markedly in diversity and species composition, with almost complete species turnover across just 13 km. As noted in previous studies, compositional variation potentially reflects climate and dispersal limitation, but here we show that soil properties also matter. These effects are unlikely to be unique to Fortuna; mountain uplift often results in landscapes composed on heterogeneous parent material and substrate age (e.g. Aiba & Kitayama 1999). A recent compilation of forest diversity and structure data from elevational transects from Peru, Ecuador and Bolivia shows regional variation in richness at 1000 m a.s.l. (Fig. 5 in Girardin et al. 2014) that is similar to the local variation observed at Fortuna. Furthermore, and in accordance with plot networks in lowland tropical forests, soil P as well as rainfall patterns appear to drive variation in α - and β -diversity in this mid-elevation forest. Nonetheless, the importance of edaphic specialization, and the relative importance of N, P and base cation limitation has received little consideration when interpreting plant responses to environmental change along elevational transects. Additional exploration of ecosystem properties and plant response to fertility gradients may provide new insights into the biogeographic patterns of montane taxa and their future response to global change.

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Author contributions

J.D., K.A., P.C. and B.T. designed the study, C.P., J.D., B.T. and A.M. collected field data, C.P., J.D., B.T. and K.A. analysed the data and all authors discussed the results and wrote the manuscript.

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Supporting Information

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

Appendix S1. Environmental characteristics and species accumulation curves of 12 1-ha plots.

Appendix S2. Images of forest plots occurring on different parent material.

Appendix S3. Rainfall information of the plots in the Fortuna and Palo Seco forest reserves.

Appendix S4. Supporting information of α - and β -diversity.