

Local and regional dominance of woody plants along an elevational gradient in a tropical montane forest of northwestern Bolivia

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Abstract The aim of this study was to investigate the dominance patterns of woody plants in a tropical montane forest of northwestern Bolivia and to understand underlying processes at the local and regional scales. We inventoried three elevation ranges: lower (1,200–1,500 m), intermediate (2,000–2,300 m), and upper montane forests (2,800–3,100 m). At each elevation, we inventoried two sites that were ~100 km apart. Specifically, we asked the following questions: (1) are dominant taxa distributed locally, or are they also dominant at larger scales? And (2) is the local importance of shared taxa congruent among sites at the same elevation range? We inventoried 18,876 woody plant individuals with a diameter at breast height ≥ 2.5 cm belonging to 877 species, 286 genera, and 100 families in 54 0.1-ha plots. A strong floristic congruence was found at the family and genus levels within and across elevations, but not at the species level. The pattern of species dominance for the whole study regions was similar to that reported for similar scales in the Amazonia (10–15 % of species accounted for 50–75 % of individuals), although dominant species were not oligarchic across the whole elevational gradient due to the high environmental heterogeneity. Dominant taxa were shared to a larger degree between sites at the same elevational range

than non-dominant taxa, indicating that oligarchy does not mean uniformity. Finally, the shared taxa exhibited similar importance between sites at the lower elevation range but dissimilar importance at the higher elevation range, reflecting an increase in the relative importance of local processes versus regional processes with increasing elevation.

Keywords Altitudinal zonation · Dispersal limitation · Environmental filtering · Oligarchy hypothesis · Species turnover · Tropical Andes

Introduction

The knowledge of dominant taxa is essential for the understanding of any ecosystem because they account for the majority of individuals, biomass, and energy flows (Vázquez and Gaston 2004; Gaston 2010). If dominant species are affected by human or natural disturbances, such as overexploitation or climatic changes, pronounced cascades of reductions and losses of other species could result because dominant species shape their environments and are involved in large numbers of biotic interactions (Gaston 2010). Tropical montane forests suffer some of the highest rates of habitat conversion of any tropical ecosystem and extreme fragility with regard to climate change (Doumenge et al. 1995; Pounds et al. 1999; Foster 2001; Laurance et al. 2011; Larsen et al. 2012). Unfortunately, the challenging terrain of this

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ecosystem and limited accessibility, resources, and manpower have long hampered the study of its flora. To date, the understanding and conservation of this fragile ecosystem have relied on a few (quantitative) floristic inventories to shed light on ecological and biogeographical processes, including those of species dominance (e.g., La Torre-Cuadros et al. 2007; Bruijnzeel et al. 2010; Jones et al. 2011; Martin et al. 2011).

Most tropical forest inventories have indicated that the floristic composition of a given locality tends to be a combination of a limited set of dominant species together with a large number of rare species (Hubbell and Foster 1986; Warren et al. 2011; Gaston 2012). Beyond the local scale, it has also been widely reported that the same set of locally dominant species tends to prevail over large areas, conforming to what has been called an “oligarchic pattern” (Pitman et al. 2001, 2013; Macía and Svenning 2005). The oligarchy hypothesis originally proposed that such a pattern applies for Amazonian *terra firme* forests, but many recent works have found the same pattern in other tropical forests at the regional scale (Bridgewater et al. 2004; Eilu et al. 2004; Paoli et al. 2006; Norden et al. 2009; Williams et al. 2010; Keppel et al. 2011; Jabot and Chave 2011). However, whether this hypothesis applies to tropical Andean forests at different scales remains poorly studied.

The goal of this study was to investigate the dominance patterns of woody plants in tropical montane forests of northwestern Bolivia and to understand which processes (local or regional) influence the observed patterns the most. We focused on three elevational ranges; at each elevation, we inventoried two sites approximately 100 km apart to answer the following four research questions:

(1) Which are the dominant families, genera, and species in lower, intermediate, and upper montane forests?

(2) Is the dominance of a taxon limited to the local scale (i.e., to one site), or are such groups also dominant at larger scales (i.e., at the two sites of the same elevation ~100 km apart) or in different habitats (i.e., across different elevations)? The oligarchy hypothesis predicts that oligarchies are weak or may even be undetectable when the environmental heterogeneity in a given forest is too high (Pitman et al. 2013). Because montane forests are

characterized by strong elevational gradients and rapid shifts in edaphic and micro-environmental variables at any elevation (Gentry 1995; Vitousek 1998; Gerold 2008), we would expect weak oligarchies at the regional scale and within the whole elevational gradient under study.

(3) Is the overlap of dominant taxa among sites similar to the overlap of non-dominant taxa? Oligarchic taxa tend to homogenize the floristic composition within the same habitat where conditions are relatively homogeneous, but at the regional scale, the plant community often exhibits high species turnover (Pitman et al. 1999, 2001; Macía and Svenning 2005; Macía 2011). If locally dominant taxa are both important at the regional scale and compatible with high floristic heterogeneity, we would expect greater overlap for dominant taxa than for non-dominant taxa.

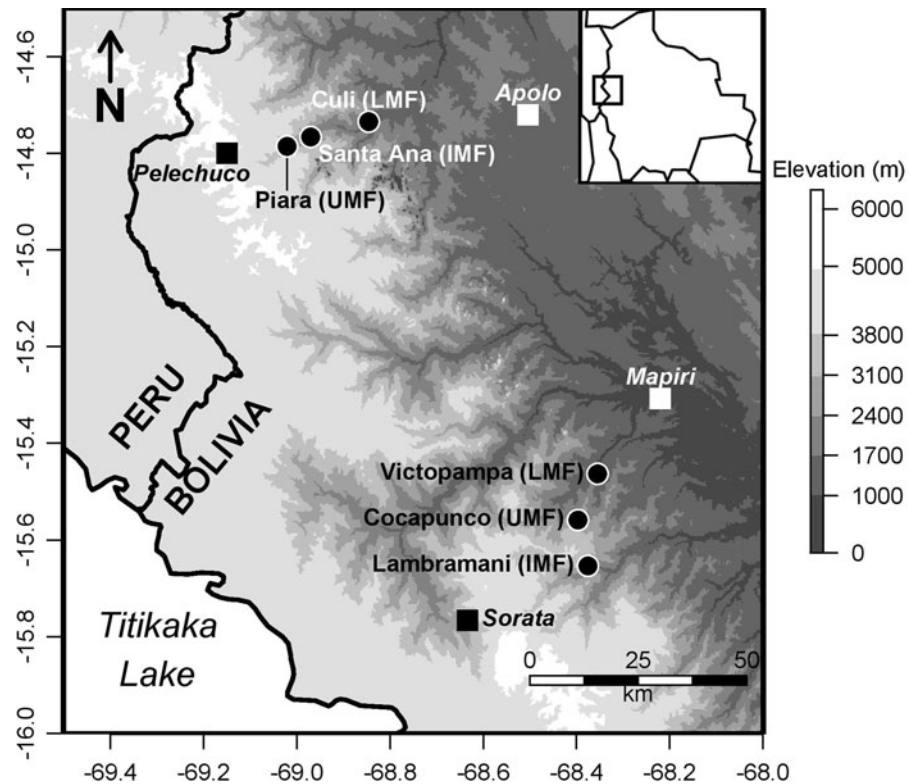
(4) Is the local importance of shared taxa congruent among sites at the same elevation? Two alternative predictions arise from this question. (A) If local environmental conditions determine the local importance of taxa, a taxon will have the same importance across the landscape as long as the conditions are the same. Therefore, we would expect that taxa have the same importance in different sites at the same elevation. (B) If high landscape connectivity at the regional scale homogenizes the local abundances of taxa between different sites regardless of specific local conditions, we would expect similar taxon importance across different sites at lower elevations, but dissimilar importance across sites at higher elevations because of the lower landscape connectivity at such elevations (Wiens 2004; Kozak and Wiens 2006; Graham and Fine 2008).

Methods

Sampling design and study area

Fieldwork was conducted in three elevational bands of northwestern montane forest in Bolivia (Fig. 1). The bands had elevation ranges of 300 m and were separated by 500 m of elevation, as follows: lower montane forest at 1,200–1,500 m (LMF), intermediate montane forest at 2,000–2,300 m (IMF), and upper montane forest at 2,800–3,100 m (UMF). At each band we inventoried two sites; one was in

Fig. 1 Location of the study area and the six inventoried sites (*circles*) in the Franz-Tamayo (three northern sites) and Larecaja Provinces, (three southern sites) in the Bolivian Andes. Each site contains nine plots at three different elevations: lower montane forest (LMF 1,200–1,500 m), intermediate montane forest (IMF 2,000–2,300 m), and upper montane forest (UMF 2,800–3,100 m)



Franz-Tamayo Province within the limits of Madidi National Park, and the other was ~ 100 km away in Larecaja Province, close to the Pilón-Lajas Biosphere Reserve. At LMF we conducted inventories in the sites of Culi (Franz-Tamayo Province) and Victopampa (Larecaja Province); at IMF we conducted inventories in the sites of Santa Ana (Franz-Tamayo Province) and Lambramani (Larecaja Province); and in UMF we conducted inventories in the sites of Piara (Franz-Tamayo Province) and Cocapunco (Larecaja Province). At each of the sites, we established nine 0.1-ha (20×50 m) plots with a minimum inter-plot distance of 250 m, for a total of 54 plots.

All studied sites were only accessible by foot and were from 1 to 4 days away from the nearest village. The vegetation at all sites was old-growth mature tropical rainforest with sporadic disturbances due to landslides, but there were no recent signs of human perturbation. Plots were installed to inventory internally homogeneous forests, but maximizing the within-site environmental variation. We avoided secondary forests, characterized by a high abundance of *Cecropia* trees, small bambusoids, or vines and/or a lack of large trees. All plots had $>2,000$ mm annual mean precipitation and

a 2- to 3-month dry period (Ribera 1992; Navarro et al. 2004). The annual mean temperatures varied from 22°C at the lowest elevation to 10°C at the highest elevation. At all elevations, soils were acidic ($\text{pH} < 5$) and rich in organic matter in the top layer.

In the present paper the usage of “site,” “local,” “habitat,” “region,” and “regional” is defined as follows: (1) site: a group of nine plots spanning <5 km in extent; (2) local: patterns and processes happening within a site; (3) habitat: each of the three elevational bands considered, characterized by relatively homogeneous conditions compared with the whole elevational gradient studied; (4) region: a pair of sites at the same elevation and ~ 100 km apart; and (5) regional: patterns and processes happening within a region. The “whole study area” or “whole elevational gradient” refers to the six sites inventoried at the three elevations considered.

Data collection

All woody plant individuals rooted within the plot with at least one stem of diameter at breast height (dbh, measured at 130 cm from the ground) equal to or

greater than 2.5 cm were measured. Multiple stems of the same individual were measured down to 1 cm dbh to more accurately measure the basal area of shrubs, a common life-form in montane forests. All individuals were identified or assigned to a morphospecies, all of which were collected at least once in a site. The full set of vouchers was deposited at LPB and a nearly complete set at MO (acronyms according to Thiers 2012). Less than 5 % of individuals were excluded from the analysis because they were sterile specimens that could not be assigned to reliable morphospecies names. All data are available for query in the TROPICOS database (www.tropicos.org/PlotSearch.aspx?projectid=20; see Table 1).

Data analysis

We measured taxa dominance at site level. To do so, we calculated the importance value index (IVI) at the species and genus levels (Curtis and McIntosh 1951) and the family importance value index (FIVI) (Mori et al. 1983). The sum of total IVI or FIVI values for species, genera, and families is 300 at each site. We ranked the species, genera, and families in decreasing order of importance at each site based on the importance value index (IVI or FIVI). We defined “important taxa” as those whose values summed to 150 of the total of 300 for the IVI or FIVI. In this way, the number of important taxa decreases with decreasing diversity but remains at a constant proportion of importance at each site. Therefore, this category is directly comparable between sites with different floristic compositions, diversity and dominance patterns. Finally, to compare our inventories with earlier studies, we calculated the percentage of individuals represented by the top 10 and 15 % of species.

For each pair of sites at the same elevation, we tested whether the important taxa were less than, more than, or equally floristically similar to the rest of the community. To do so, we compared all possible pairs of plots at different sites of the same elevation ($9 \times 9 = 81$ pairs of plots per elevational range). We did not compare plots within a site because the oligarchy hypothesis is intended to apply at larger scales. For each pair of plots, we calculated the proportion of shared important taxa between the two plots with the Jaccard similarity index (J_I). The same was repeated for the remaining taxa, obtaining the proportion of shared non-important taxa (J_{no-I}) for

each pair of plots. Finally, for each elevational range and taxonomic level, we compared J_I and J_{no-I} by performing Wilcoxon signed-rank tests.

To analyze regional-scale congruence in the importance of shared taxa in the community, we conducted Pearson correlations between the importance of shared taxa at one site and their importance at another site at the same elevation. Importance values were log-transformed prior to the analysis to make the analysis more robust against the extreme importance of some taxa at some sites. The significance level was established at 0.05. All calculations and analyses were performed with R (R Development Core Team 2012).

Results

Floristic composition

We found a total of 877 species, 286 genera, and 100 families in the inventory of 18,876 individuals. At each site, 4–8 families were important (Table 2). Overall, Melastomataceae was the most important family among sites and across elevations, being the only family that was important at all sites. Sites at LMF shared as important families Euphorbiaceae, Lauraceae, Melastomataceae, Moraceae, and Rubiaceae. The same families, with the exception of Moraceae, were shared as important between the sites at IMF. At UMF, the important shared families were Clusiaceae, Cunoniaceae, and Melastomataceae. The abovementioned seven families (7 % of the total number of identified families) accounted for 35 % of species and 50 % of individuals.

At the generic level, floristic differences were more pronounced between sites and across elevations. *Miconia* was the only genus that was important at all elevations (Table 3). *Alchornea*, *Hieronyma*, *Ocotea*, and *Piper* were important at LMF and IMF, whereas *Clusia*, *Hedyosmum*, and *Clethra* were important at IMF and UMF. These eight genera (2.8 % of the total) accounted for 18 % of the species and 34 % of the individuals. Another 38 genera were important in only one of the studied elevation ranges.

At the species level, we found a low overlap of important species between sites and across elevations (see Table 4). *Alchornea glandulosa* Poepp. was important at all LMF and IMF sites, and *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult. was important at all IMF and UMF sites. Five other species (*Hedyosmum*

Table 1 Codes, location and features of 54 plots of montane forest in the Madidi region, northwestern Bolivia

Plot name	Latitude (south)	Longitude (west)	Elevation (m)	<i>N</i>	<i>S</i>
PT_Culi_353	14°43'33"	68°49'51"	1,240	226	68
PT_Culi_354	14°43'44"	68°50'14"	1,277	295	82
PT_Culi_355	14°43'43"	68°50'40"	1,497	464	104
PT_Culi_356	14°43'53"	68°50'39"	1,329	306	76
PT_Culi_357	14°44'43"	68°51'16"	1,443	324	87
PT_Culi_358	14°44'35"	68°51'10"	1,438	378	98
PT_Culi_359	14°44'18"	68°51'03"	1,271	258	76
PT_Culi_360	14°43'57"	68°50'57"	1,457	428	94
PT_Culi_361	14°44'06"	68°50'51"	1,286	278	74
PT_Victop_372	15°28'06"	68°21'22"	1,490	470	85
PT_Victop_373	15°28'04"	68°21'19"	1,482	364	86
PT_Victop_374	15°27'42"	68°20'59"	1,537	442	103
PT_Victop_375	15°27'25"	68°21'20"	1,163	403	76
PT_Victop_376	15°27'36"	68°21'23"	1,246	336	83
PT_Victop_377	15°27'45"	68°21'15"	1,353	340	111
PT_Victop_378	15°27'37"	68°21'11"	1,423	431	93
PT_Victop_379	15°27'59"	68°21'23"	1,362	383	91
PT_Victop_380	15°27'53"	68°21'20"	1,283	411	107
PT_Santaa_344	14°46'18"	68°58'18"	2,216	228	38
PT_Santaa_345	14°46'22"	68°58'29"	2,264	385	28
PT_Santaa_346	14°45'30"	68°57'39"	2,296	281	41
PT_Santaa_347	14°46'07"	68°58'46"	2,180	402	36
PT_Santaa_348	14°46'05"	68°58'15"	2,114	395	50
PT_Santaa_349	14°45'33"	68°57'48"	2,235	262	42
PT_Santaa_350	14°45'41"	68°57'52"	2,329	229	40
PT_Santaa_351	14°45'45"	68°57'58"	2,235	282	29
PT_Santaa_352	14°46'18"	68°58'54"	2,352	243	50
PT_Lambra_434	15°39'20"	68°22'45"	2,282	181	41
PT_Lambra_435	15°39'25"	68°22'30"	2,021	284	75
PT_Lambra_436	15°38'57"	68°22'27"	2,213	198	37
PT_Lambra_437	15°38'56"	68°22'13"	2,214	279	56
PT_Lambra_438	15°39'05"	68°22'15"	2,033	224	58
PT_Lambra_439	15°39'07"	68°22'38"	2,284	175	49
PT_Lambra_440	15°39'20"	68°22'23"	2,031	197	64
PT_Lambra_441	15°39'35"	68°22'56"	2,208	311	69
PT_Lambra_442	15°39'15"	68°22'37"	2,196	328	69
PT_Piara_387	14°46'36"	69°00'54"	2,804	319	38
PT_Piara_388	14°46'45"	69°00'56"	2,746	414	41
PT_Piara_389	14°47'02"	69°00'54"	2,813	235	27
PT_Piara_390	14°46'58"	69°01'14"	2,799	310	28
PT_Piara_391	14°47'01"	69°01'17"	2,803	276	38
PT_Piara_392	14°47'13"	69°01'36"	3,069	382	37
PT_Piara_393	14°47'17"	69°01'10"	2,961	351	34
PT_Piara_394	14°47'46"	69°01'48"	2,975	307	41

Table 1 continued

Plot name	Latitude (south)	Longitude (west)	Elevation (m)	<i>N</i>	<i>S</i>
PT_Piara_395	14°47'34"	69°01'33"	2,946	304	28
PT_Cocapu_396	15°33'11"	68°23'36"	2,786	273	38
PT_Cocapu_397	15°33'20"	68°23'35"	2,832	493	38
PT_Cocapu_398	15°33'22"	68°23'43"	2,882	228	35
PT_Cocapu_399	15°33'30"	68°23'40"	2,984	765	50
PT_Cocapu_400	15°33'35"	68°24'00"	3,023	610	45
PT_Cocapu_401	15°33'45"	68°24'08"	3,137	395	41
PT_Cocapu_402	15°33'39"	68°23'59"	3,091	604	33
PT_Cocapu_403	15°33'46"	68°23'43"	3,119	591	45
PT_Cocapu_404	15°33'36"	68°23'50"	3,083	598	44

The Plot Name is employed by TROPICOS to index the inventory (www.tropicos.org/PlotSearch.aspx?projectId=20)

N number of individuals, *S* number of species

Table 2 Comparison of the important (bold) families of six study sites at three different elevations, as inventoried in 54 0.1-ha plots of tropical montane forest in the Franz-Tamayo and Larecaja Provinces, northwestern Bolivia

Family (number of species)	Lower montane forest		Intermediate montane forest		Upper montane forest		Average FIVI
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco	
Melastomataceae (94)	37.25	22.78	24.66	37.64	22.87	33.39	29.77
Rubiaceae (71)	31.92	35.71	42.75	24.93	8.00	5.09	24.73
Lauraceae (74)	34.22	24.50	21.69	31.30	8.01	12.06	21.96
Clusiaceae (17)	5.30	6.05	24.82	11.37	17.92	44.17	18.27
Cunoniaceae (18)	–	0.36	0.92	4.53	27.74	62.14	15.95
Chloranthaceae (6)	2.48	2.27	22.52	7.67	31.20	4.81	11.83
Asteraceae (50)	2.39	2.90	10.96	11.28	34.08	4.12	10.96
Moraceae (23)	25.68	19.38	7.60	10.08	1.74	–	10.75
Euphorbiaceae (13)	12.67	10.72	17.27	11.89	8.50	–	10.18
Cyatheaceae (13)	4.46	4.12	3.51	36.71	0.86	8.74	9.73
Primulaceae (12)	5.86	3.57	8.82	7.00	11.13	16.56	8.82
Ericaceae (16)	1.54	0.84	5.56	0.97	20.52	8.27	6.28
Myrtaceae (37)	8.19	11.58	5.99	5.57	3.30	–	5.77
Fabaceae (33)	8.66	20.21	1.29	0.82	1.83	–	5.47
Phyllanthaceae (8)	6.34	11.25	4.83	6.61	–	–	4.84
Meliaceae (9)	1.38	3.78	0.67	18.58	1.34	–	4.29
Monimiaceae (3)	9.69	0.97	2.27	2.35	–	–	2.55

Families are ranked by average FIVI

racemosum (Ruiz & Pav.) G. Don, *Dendropanax* sp. nov. = G. Arellano 1271, *Topobea multiflora* (D. Don) Triana, *Piper bolivianum* C. DC., and *Hieronyma* vel sp. nov. = G. Arellano 658) were important at 2–3 sites at LMF and IMF. The species *H. angustifolium* (Ruiz & Pav.) Solms was important at the IMF and UMF sites in

Franz-Tamayo Province. These eight species (0.9 % of the total) comprised 7.7 % of the individuals. The remaining important species (104; 11.9 % of the total) were restricted to one elevational range and accounted for 55.5 % of all individuals. Overall, the 10 % of species with the highest abundances accounted for 64 %

Table 3 Comparison of genera that were important (bold) in at least two of the six study sites at three different elevations, as inventoried in 54 0.1-ha plots of tropical montane forest in the Franz-Tamayo and Larecacha Provinces, northwestern Bolivia

Genus (number of species)	Lower montane forest		Intermediate montane forest		Upper montane forest		Average IVI
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco	
<i>Clusia</i> (11)	1.82	0.55	25.64	10.72	20.21	47.33	17.71
<i>Miconia</i> (70)	22.32	11.19	17.91	18.81	9.94	25.87	17.67
<i>Weinmannia</i> (18)	–	0.23	0.68	4.46	27.67	55.59	14.77
<i>Hedyosmum</i> (6)	3.12	3.16	23.35	9.03	31.84	5.16	12.61
<i>Psychotria</i> (17)	3.68	3.49	35.30	6.62	7.68	4.88	10.27
<i>Ocotea</i> (32)	12.91	7.35	10.48	17.03	2.73	5.31	9.30
<i>Myrsine</i> (7)	3.61	1.66	8.37	6.02	12.63	16.81	8.18
<i>Clethra</i> (9)	0.23	0.20	14.82	2.27	13.70	14.33	7.59
<i>Alchornea</i> (5)	5.16	3.13	16.14	10.63	9.00	–	7.34
<i>Piper</i> (21)	7.63	8.71	4.08	9.01	3.44	–	5.48
<i>Hieronyma</i> (5)	6.02	8.30	6.72	7.10	–	–	4.69
<i>Tapirira</i> (1)	6.10	11.56	–	–	–	–	2.94
<i>Perebea</i> (2)	8.24	8.65	–	–	–	–	2.82
<i>Guatteria</i> (5)	6.21	6.51	0.42	2.11	–	–	2.54
<i>Pseudolmedia</i> (3)	7.05	5.49	–	0.86	0.47	–	2.31
<i>Inga</i> (17)	4.62	6.96	0.83	1.22	–	–	2.27
<i>Pourouma</i> (5)	7.22	6.25	–	–	–	–	2.25
<i>Schizocalyx</i> (1)	7.40	5.73	–	–	–	–	2.19
<i>Aparisthium</i> (1)	5.81	7.04	–	–	–	–	2.14
<i>Protium</i> (2)	7.85	3.97	–	–	–	–	1.97
<i>Virola</i> (6)	4.34	5.38	–	–	–	–	1.62

Genera are ranked by average IVI

of all individuals, and the top 15 % most abundant species accounted for 74 % of all individuals.

Overlap of important taxa versus non-important taxa

When pairs of plots at different sites within the same elevational range were compared, we found that the overlap between important taxa was greater than the overlap for non-important taxa (Fig. 2). In all cases, the results were highly statistically significant ($p < 0.001$).

Correlations for the importance of taxa between sites

The correlation between the importance of shared taxa at one site and their importance at another site at the same elevation indicated that the strength of the correlation diminished at higher elevations and at lower taxonomic

levels (Fig. 3). The correlation was positive and statistically significant in most cases, with the exception of genera and species between the two sites at UMF.

Discussion

Floristic patterns

We found a strong floristic congruence between sites and across elevations at the family and genus levels. The paradigmatic dominant montane families in the Andes (Melastomataceae, Rubiaceae, and Lauraceae) previously reported to be among the most important taxa (e.g., Gentry 1995; Fuentes 2005; La Torre-Cuadros et al. 2007; Macía and Fuertes 2008) were strongly represented in our study region. As expected, below 1,500 m, we found a floristic composition with a high importance of Amazonian-originated taxa whose importance tends to diminish at intermediate

Table 4 Comparison of species that were important (*) in at least one of the six study sites at three different elevations, as inventoried in 54 0.1-ha plots of tropical montane forest in the Franz-Tamayo and Larecaja Provinces, northwestern Bolivia

Family	Species	1,200–1,500 m		2,000–2,300 m		2,800–3,100 m	
		Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	5.74*	11.21*	–	–	–	–
Annonaceae	<i>Guatteria boliviana</i> H.J.P.Winkl.	1.22	3.26*	–	0.25	–	–
	<i>Guatteria glauca</i> Ruiz & Pav.	4.76*	1.55	0.35	–	–	–
	<i>Guatteria oblongifolia</i> Rusby	–	2.22*	–	1.52	–	–
Araliaceae	<i>Dendropanax</i> sp. nov. = G. Arellano 1271	2.27*	–	–	3.56*	–	–
	<i>Schefflera</i> = Gabriel Arellano 1589	–	3.07*	–	–	–	–
Arecaceae	<i>Dictyocaryum lamarckianum</i> (Mart.) H.Wendl.	0.88	3.55*	–	–	–	–
	<i>Euterpe precatoria</i> Mart.	2.47*	2.94*	–	–	–	–
Asteraceae	<i>Baccharis</i> = Gabriel Arellano 2500	–	–	0.41	–	11.39*	–
Burseraceae	<i>Protium</i> aff. <i>montanum</i> Swart = Gabriel Arellano 938	7.26*	3.61*	–	–	–	–
Calophyllaceae	<i>Calophyllum brasiliense</i> Cambess.	1.30	3.85*	–	0.24	–	–
Chloranthaceae	<i>Hedyosmum angustifolium</i> (Ruiz & Pav.) Solms	–	–	5.24*	–	17.51*	–
	<i>Hedyosmum cuatrecazanum</i> Occhioni	–	–	7.31*	4.39*	–	–
	<i>Hedyosmum dombeyanum</i> Solms	–	–	–	4.72*	3.28	3.89
	<i>Hedyosmum racemosum</i> (Ruiz & Pav.) G.Don	2.82*	2.81*	9.63*	–	–	–
	<i>Hedyosmum</i> vel sp. nov. = Gabriel Arellano 2377	–	–	1.37	–	11.90*	–
Clethraceae	<i>Clethra cuneata</i> Rusby	–	–	5.23	–	8.37*	–
	<i>Clethra revoluta</i> (Ruiz & Pav.) Spreng.	–	–	5.73*	1.22	2.56	0.57
	<i>Clethra scabra</i> Pers.	0.17	–	–	0.55	0.73	8.40*
Clusiaceae	<i>Clusia sphaerocarpa</i> Planch. & Triana	–	–	–	–	14.93*	45.64*
	<i>Clusia trochiformis</i> Vesqne	1.11	0.45	8.04*	7.78*	–	–
	<i>Clusia</i> = Gabriel Arellano 174	–	–	9.19*	–	–	–
	<i>Symphonia globulifera</i> L.f.	3.24*	2.05*	–	–	–	–
	<i>Tovomita</i> = Gabriel Arellano 1568	–	2.79*	–	0.50	–	–
Cunoniaceae	<i>Weinmannia crassifolia</i> Ruiz & Pav.	–	–	–	–	13.41*	0.64
	<i>Weinmannia davidsonii</i> A.Fuentes & Z.S.Rogers	–	–	–	–	1.70	13.87*
	<i>Weinmannia microphylla</i> Kunth	–	–	–	–	–	16.96*
	<i>Weinmannia pinnata</i> L.	–	–	0.61	–	13.29*	–
	<i>Weinmannia yungasensis</i>	–	–	–	–	–	15.70*
Cyatheaceae	<i>Alsophila erinacea</i> (H. Karst.) D.S. Conant	–	–	–	13.89*	–	–
	<i>Cyathea caracasana</i> (Klotzsch) Domin	0.21	1.06	2.44	8.89*	–	1.65
	<i>Cyathea herzogii</i> H. Karst.	–	–	–	12.92*	–	2.96
Dicksoniaceae	<i>Dicksonia sellowiana</i> Hook.	–	–	–	2.94*	–	–

Table 4 continued

Family	Species	1,200–1,500 m		2,000–2,300 m		2,800–3,100 m	
		Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Ericaceae	<i>Cavendishia bracteata</i> (Ruiz & Pav. ex J.St.Hil.) Hoerold	–	–	–	1.12	15.5*	0.30
Euphorbiaceae	<i>Alchornea brittonii</i> Secco	–	–	1.05	–	8.67*	–
	<i>Alchornea glandulosa</i> Poepp.	4.10*	2.34*	8.55*	3.43*	–	–
	<i>Alchornea grandiflora</i> Müll.Arg.	–	–	6.81*	6.76*	–	–
	<i>Aparisthium cordatum</i> (A.Juss.) Baill.	5.51*	6.73*	–	–	–	–
	<i>Chaetocarpus myrsinites</i> Baill.	3.04*	2.76*	–	–	–	–
Fabaceae	<i>Ormosia</i> = Gabriel Arellano 2043	–	4.83*	–	–	–	–
Lauraceae	<i>Beilschmiedia tovarensis</i> (Klotzsch & H.Karst. ex Meisn.) Sachiko Nishida	2.28*	2.69*	0.87	1.73	–	–
	<i>Nectandra laurel</i> Klotzsch ex Nees	–	–	5.47*	0.50	–	–
	<i>Nectandra</i> vel sp. nov. = Gabriel Arellano 1351	3.48*	–	–	–	–	–
	<i>Ocotea comata</i> van der Werff	–	–	–	9.85*	–	–
	<i>Ocotea aciphylla</i> (Nees & Mart.) Mez	9.42*	2.08*	–	–	–	–
	<i>Ocotea albida</i> Mez & Rusby	–	–	7.85*	0.29	–	–
	<i>Ocotea cuprea</i> (Meisn.) Mez	2.51*	1.06	–	–	–	–
	<i>Ocotea</i> aff. <i>andina</i> = Gabriel Arellano 2970	–	–	–	5.46*	–	–
	<i>Persea subcordata</i> (Ruiz & Pav.) Nees	0.91	0.23	–	4.16*	0.48	–
	<i>Pleurothyrium</i> vel sp. nov. = Gabriel Arellano 1407	0.41	3.84*	–	–	–	–
	Linaceae	<i>Rouchea laxiflora</i> H.J.P.Winkl.	–	2.46*	–	–	–
Melastomataceae	<i>Miconia brittonii</i> (Cogn.) Kuntze	0.17	–	6.04*	3.23*	–	–
	<i>Miconia calvescens</i> DC.	2.66*	0.33	0.82	–	–	–
	<i>Miconia cordata</i> (Triana) Kuntze	–	–	0.39	2.98*	–	–
	<i>Miconia cyanocarpa</i> Naudin	0.58	1.11	8.12*	1.04	–	–
	<i>Miconia micropetala</i> Cogn.	–	–	–	0.49	2.02	12.34*
	<i>Miconia minutiflora</i> (Bonpl.) DC.	2.70*	2.38*	–	–	–	–
	<i>Miconia punctata</i> (Desr.) D. Don ex DC.	3.81*	2.65*	–	–	–	–
	<i>Miconia</i> = Gabriel Arellano 746	5.42*	–	–	–	–	–
	<i>Miconia</i> = Gabriel Arellano 3209	–	–	–	4.16*	–	–
<i>Topobea multiflora</i> (D. Don) Triana	0.79	2.49*	1.28	3.94*	–	–	
Meliaceae	<i>Cedrela fissilis</i> Vell.	–	–	–	7.15*	–	–
	<i>Cedrela odorata</i> L.	–	2.26*	–	–	–	–
	<i>Guarea kunthiana</i> A.Juss.	0.18	–	–	7.75*	–	–
Monimiaceae	<i>Mollinedia lanceolata</i> Ruiz & Pav.	2.49*	–	0.33	0.24	–	–
	<i>Mollinedia ovata</i> Ruiz & Pav.	5.74*	–	–	0.78	–	–
	<i>Mollinedia repanda</i> Ruiz & Pav.	3.13*	1.39	2.18	1.76	–	–
Moraceae	<i>Ficus cuatrecasana</i>	0.44	–	2.56	3.17*	–	–
	<i>Ficus obtusifolia</i> Kunth	3.96*	–	–	–	–	–
	<i>Helicostylis tomentosa</i> (Poepp. & Endl.) J.F.Macbr.	2.81*	4.10*	–	1.08	–	–
	<i>Perebea guianensis</i> Aubl.	7.76*	8.24*	–	–	–	–

Table 4 continued

Family	Species	1,200–1,500 m		2,000–2,300 m		2,800–3,100 m	
		Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
	<i>Pseudolmedia laevigata</i> Trécul	–	4.69*	–	0.78	0.36	–
	<i>Pseudolmedia rigida</i> (Klotzsch & H.Karst.) Cuatrec.	6.18*	–	–	–	–	–
Myristicaceae	<i>Virola elongata</i> (Benth.) Warb.	3.40*	0.84	–	–	–	–
	<i>Virola sebifera</i> Aubl.	–	3.01*	–	–	–	–
Myrtaceae	<i>Myrcia</i> = Gabriel Arellano 1514	0.18	2.43*	–	1.38	–	–
Nyctaginaceae	<i>Neea ovalifolia</i> Spruce ex J.A.Schmidt	2.33*	0.20	–	–	–	–
Pentaphragaceae	<i>Ternstroemia</i> aff. <i>subserrata</i> (Rusby) Melch. = Gabriel Arellano 2371	–	–	–	–	9.70*	–
Phyllanthaceae	<i>Hieronyma moritziana</i> Briq.	–	3.73*	–	2.12	–	–
	<i>Hieronyma oblonga</i> (Tul.) Müll.Arg.	1.65	4.00*	–	0.26	–	–
	<i>Hieronyma</i> vel sp. nov. = Gabriel Arellano 137	0.22	–	6.22*	–	–	–
	<i>Hieronyma</i> vel sp. nov. = Gabriel Arellano 658	2.42*	0.50	–	4.27*	–	–
	<i>Richeria grandis</i> Vahl	–	2.76*	–	–	–	–
Piperaceae	<i>Piper bolivianum</i> Vell.	3.40*	–	1.16	4.76*	–	–
	<i>Piper percostatum</i> Yunck.	3.91*	5.43*	–	–	–	–
	<i>Piper rusbyi</i> C. DC.	–	–	–	2.82*	–	–
Podocarpaceae	<i>Podocarpus ingensis</i> D. Don	–	–	–	2.61*	3.07	–
	<i>Podocarpus oleifolius</i> D. Don	–	–	–	–	8.54*	–
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. ex Roem. & Schult.	–	–	7.88*	3.92*	11.52*	7.86*
	<i>Myrsine pellucida</i> (Ruiz & Pav.) Spreng.	0.44	–	–	0.25	0.38	7.72*
Rosaceae	<i>Prunus amplifolia</i> Pilg.	2.51*	–	–	–	–	–
Rubiaceae	<i>Amaioua guianensis</i> Aubl.	4.70*	3.19*	–	–	–	–
	<i>Elaeagia mariae</i> Wedd.	2.77*	6.87*	0.52	2.31	–	–
	<i>Faramea candelabrum</i> Standl.	2.54*	4.16*	0.69	2.01	–	–
	<i>Ladenbergia oblongifolia</i> (Humb. ex Mutis) L.Andersson	1.10	4.68*	–	–	–	–
	<i>Psychotria carthagenensis</i> Jacq.	0.49	0.21	26.25*	0.35	–	0.30
	<i>Psychotria conephoroides</i> (Rusby) C.M.Taylor	1.03	2.66*	–	–	–	–
	<i>Psychotria</i> = Gabriel Arellano 411	–	–	6.08*	1.05	–	–
	<i>Psychotria</i> = Gabriel Arellano 2318	–	–	–	–	6.92*	–
	<i>Psychotria</i> = Gabriel Arellano 2945	–	–	–	4.38*	–	–
	<i>Elaeagia</i> vel sp. nov. = Gabriel Arellano 2955	–	–	–	4.04*	–	–
	<i>Schizocalyx obovatus</i> (K. Schum. ex Standl.) Kainul. & B. Bremer	6.93*	5.42*	–	–	–	–
Symplocaceae	<i>Symplocos fuliginosa</i> B. Ståhl	–	–	–	2.85*	–	–
	<i>Symplocos polyphylla</i> B. Ståhl	–	–	–	–	–	10.73*
Urticaceae	<i>Cecropia tacuna</i> C.C. Berg & P. Franco	–	–	11.5*	–	–	–
	<i>Pourouma guianensis</i> Aubl.	1.24	2.67*	–	–	–	–

Table 4 continued

Family	Species	1,200–1,500 m		2,000–2,300 m		2,800–3,100 m	
		Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Vochysiaceae	<i>Pourouma minor</i> Benoist	3.87*	1.54	–	–	–	–
	<i>Erisma</i> vel sp. nov. = Gabriel Arellano 602	3.54*	–	–	–	–	–
	<i>Vochysia boliviana</i> Rusby	1.10	3.18*	–	–	–	–

Values in the table are importance value indexes (Curtis and McIntosh 1951)

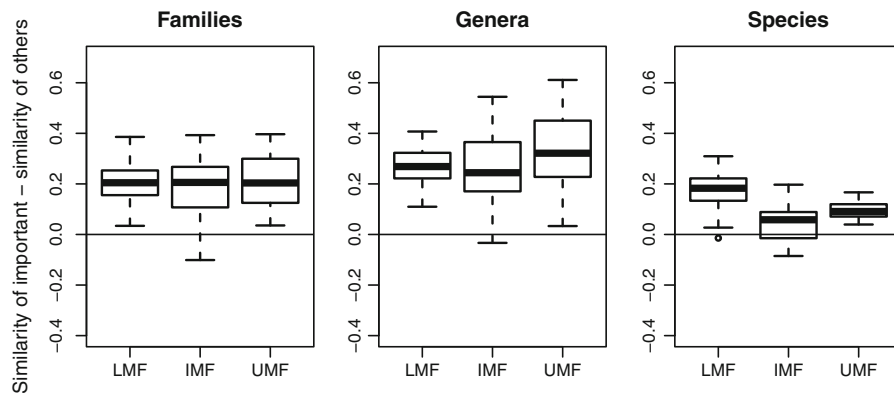


Fig. 2 Differences between the overlap of important taxa and the overlap of non-important taxa, calculated between pairs of plots of different sites within the same elevation range in 54 0.1-ha plots of tropical montane forests in northwestern Bolivia: lower montane forest (LMF 1,200–1,500 m); intermediate

elevations, such as Moraceae and a significant set of genera that are shared as important by the two sites at LMF but are important nowhere else (e.g., *Guatteria*, *Inga*, *Pourouma*, *Pseudolmedia*). This elevational filter of Amazonian-originated taxa continues above 2,500 m, where only the most widespread Amazonian-originated families, such as Melastomataceae or Rubiaceae, co-occur with distinctive Andean taxa such as *Clusia*, *Weinmannia*, or *Hedyosmum* (Beck et al. 1993; Gentry 1995; Webster 1995). This pattern is again in accordance with previous floristic studies in the Andes (Araújo-Murakami et al. 2005a, b; Fuentes 2005; Silman et al. 2005; La Torre-Cuadros et al. 2007; Feeley et al. 2011), whose results also indicate that the importance of a given family in Andean forests is due generally to one or a few genera, especially above 2,000 m, where Melastomataceae owes its importance to *Miconia*, Rubiaceae to *Psychotria*, Lauraceae to *Ocotea*, Clusiaceae to *Clusia*, and Cunoniaceae to *Weinmannia*.

montane forest (IMF 2,000–2,300 m); and upper montane forest (UMF 2,800–3,100 m). The horizontal line at $y = 0$ represents the null hypothesis that important taxa and non-important taxa are equally shared between sites

We found relatively few species that were important at more than one site, especially at the IMF and UMF sites, together with a very large pool of site-restricted species. Additionally, some of the most important species are endemic to Bolivia (*P. bolivianum*) or to the Madidi region (*Dendropanax* sp. nov. and *Hieronyma* vel sp. nov.). As tropical montane forests are full of uniqueness, we could not find strong floristic similarities at the species level to other floristic inventories in the Andes (e.g., Smith and Killeen 1995; La Torre-Cuadros et al. 2007; Macía and Fuentes 2008; Ledo et al. 2012) or even to other inventories in the Madidi area (Araújo-Murakami et al. 2005c; Bascope and Jørgensen 2005; Cabrera-Condarcó 2005; Loza et al. 2010). Such high species heterogeneity is a common characteristic of many organisms in the Andes and is assumed to be a result of the relatively recent diversification during the Andean uplift caused by strong population isolation (Fjeldsa and Lovett 1997; Jetz et al. 2004; Parra-Olea et al.

2012). Unfortunately, this heterogeneity prevents understanding the main floristic patterns of the area using data at species-level, and therefore, the utilization of higher-taxon surrogates has been demonstrated to be a more useful tool, as previously indicated for Andean forests (Kessler and Bach 1999; La Torre-Cuadros et al. 2007).

Dominance across elevations

The most abundant 10 and 15 % of the species accounted for 64 and 74 % of the individuals respectively, values almost equal to the numbers reported for oligarchic species in the lowlands of northwestern Amazonia. For example, in Yasuní, 48–63 % of individuals belong to 10–11 % of the recorded species (Macía 2011; Pitman et al. 2013); in Manu, 73 % of the individuals belong to 15 % of the species (Pitman et al. 2013); and in the Madidi lowlands, 62 % of individuals belong to 11 % of the species (Macía 2008). In that sense, the overall pattern in montane forests appears to be similar to that of lowland forests. However, if we look more carefully at the top 10–15 % most abundant species, they cannot be qualified as “true” oligarchic species because they are not clearly distributed among different environmental conditions (Ruokolainen and Vormisto 2000; Pitman et al. 2001; Bridgewater et al. 2004; Macía and Svenning 2005; Paoli et al. 2006). For instance, only *M. coriacea*, *A. glandulosa*, and six other species (<1 % of all species) exhibit importance in two adjacent elevational ranges (500 m apart, with a maximum range of 1,100 m), and these species only account for ~8 % of all individuals. Moreover, most individuals belong to important species that are restricted to a single elevational range, and no species qualifies as oligarchic along the whole elevational gradient.

Regarding the oligarchy hypothesis, this finding confirms the prediction that large-scale oligarchy is limited within very heterogeneous conditions (Tuomisto et al. 2003a, b; Vormisto et al. 2004; Macía and Svenning 2005; Réjou-Méchain et al. 2008; Toledo et al. 2011, 2012), although the data are compatible with the existence of strong oligarchies at smaller scales (Guevara Andino 2006; Honorio Coronado et al. 2009; Toledo et al. 2011, 2012). Overall, it holds our expectation that montane forests, in contrast with lowland forests, harbor weak oligarchies at the regional scale, very likely to the strong elevational

gradients, and the great changes from place to place regarding edaphic, micro-environmental and topographic conditions at any elevation (Gentry 1995; Vitousek 1998; Gerold 2008). All these aspects are central to the understanding of forest heterogeneity, and suggest that spatial heterogeneity and abiotic constraints play a prominent role in the distributions of species and habitats in the Andes, whereas biotic interactions are of secondary importance, at least when compared with Amazonian forests (e.g., Young 1995; Young 2012).

Dominance within elevational ranges

The greater overlap of important taxa between different sites within the same elevation range compared with non-important taxa indicates that oligarchy does not lead to uniformity and that the dominant taxa at each site are not a random subset of the local pool of taxa, as predicted (Pitman et al. 2001, 2013). This also applies to the non-important taxa in the community: the local importance of any taxon at a given site is not random, as shown by the generally positive correlation between the importance of a given taxon at one site and its importance at the other sites in the same elevation range. However, the overlap of important species diminishes with elevation, becoming very weak or absent in the UMF. Although the UMF sites are only ~100 km apart and are environmentally and floristically alike, there is no clear relationship between the local importance of shared species, whereas such a relationship does exist in lowland species at greater scales (see Fig. 3 in Pitman et al. (2001) involving a 1,400 km extent and Fig. 3 in Macía and Svenning (2005) involving a 1,900 km extent). This is congruent with the prediction based on the decrease in landscape connectivity at higher elevations (Wiens 2004; Kozak and Wiens 2006; Graham and Fine 2008). It is long known that species distributions in mountains chains tend to be restricted to narrow and linear belts (Graves 1988), which implies that the movement of individuals, pollen, and seeds along the Andes are erratic (Young 1995). The biogeographical barriers imposed by the landscape configuration, a major driver of Andean endemism, very likely explain why even some of the most abundant species are endemics to our study area. Additionally, we find support for long distance dispersal as a major driver of dominance patterns that

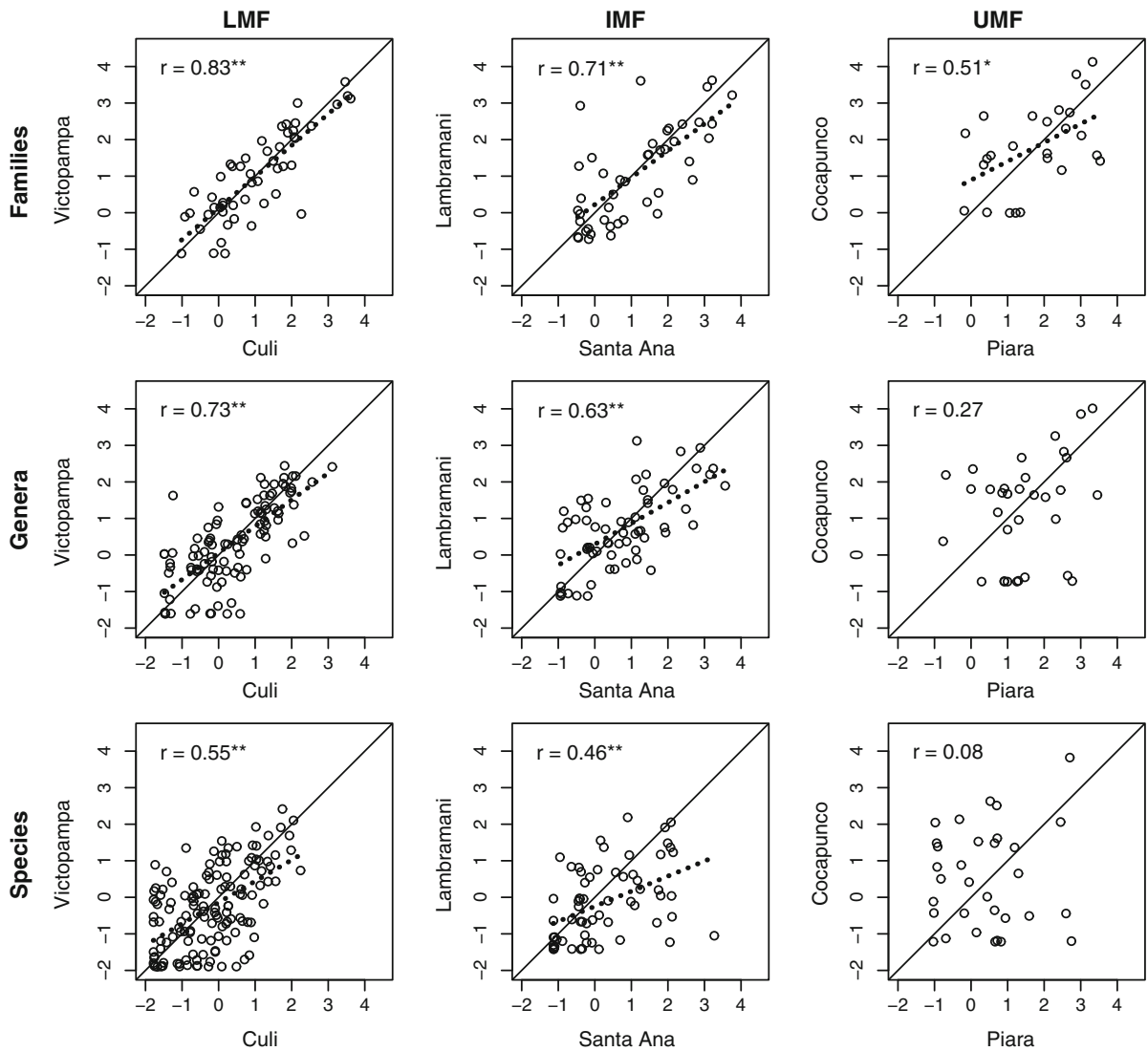


Fig. 3 Results of Pearson correlations between the importance of taxa at one site and at another site at the same elevation, for three elevational ranges characterized by 54 0.1-ha plots of tropical montane forest in northwestern Bolivia: lower montane forest (LMF 1,200–1,500 m); intermediate montane forest (IMF 2,000–2,300 m); and upper montane forest (UMF 2,800–

3,100 m). Axes represent IVI or FIVI indexes on a logarithmic scale. The *solid line (diagonal)* represents the hypothesis that the importance of taxa are identical at the two sites, and the *dotted line* represents the observed relationship between importance at the two sites. Statistical significance: ** $p < 0.001$; * $p < 0.01$

is at least as important as local environmental determinism in shaping the patterns of importance of taxa at regional scales (Ruokolainen and Vormisto 2000; Kristiansen et al. 2009, 2011).

In conclusion, we find that the dominance patterns at local and regional scales in tropical montane forests are strongly driven by the environmental heterogeneity and mosaicist character of these forests, together with a great importance of dispersal limitations

imposed by the lower landscape connectivity at higher elevations. The combination of both species environmental tolerance and dispersal abilities are very likely to determine which species are dominant in these forest and how communities will face future climatic changes and landscape transformation. Moreover, these processes are the same shaping endemism and speciation throughout the Andes, suggesting important mechanistic links between (1) ecological local and

regional dominance, and (2) evolution of taxa in tropical forests along the elevational gradient and across different points of the landscape. Whereas, some of the ecological and biogeographical paradigms proposed for the lowland Amazonian forests have been found to apply also to the Andean forests, the idiosyncratic complexity of tropical montane forests should be taken into account for an adequate understanding and biodiversity conservation strategies in these fragile ecosystems.

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