




Modern pollen rain predicts shifts in plant trait composition but not plant diversity along the Andes–Amazon elevational gradient

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Abstract

Aims: Terrestrial ecosystems are changing in biodiversity, species composition and functional trait composition. To understand the underlying causes of these changes and predict the long-term resilience of the ecosystem to withstand future disturbances, we can evaluate changes in diversity and composition from fossil pollen records. Although diversity can be well estimated from pollen in temperate ecosystems, this is less clear for the hyperdiverse tropics. Moreover, it remains unknown whether functional composition of plant assemblages can be accurately predicted from pollen assemblage composition. Here, we evaluate how community-weighted mean (CWM) traits and diversity indices change along elevation.

Location: Amazon–Andes elevation gradient in Peru.

Methods: We used 82 modern pollen samples and 59 vegetation plots along the elevation gradient, and calculated CWM traits and diversity indices for each pollen sample and vegetation plot. We also quantified the degree to which taxa are over- or under-represented by their pollen, by dividing the relative pollen abundance by the relative basal area abundance in the nearby vegetation survey plots (i.e. the R-rel values).

Results: We found that CWM wood density increased, and CWM adult height and leaf area decreased with elevation. This change was well predicted by pollen assemblages, indicating that CWM trait–environment relationships based on pollen abundance data provide meaningful results. Diversity (richness, Shannon and Simpson) decreased with elevation for vegetation plots, but these trends could not be observed from pollen assemblages.

Conclusions: Our results demonstrate that more research is needed to develop methods that lead to accurate diversity estimates from pollen data in these tropical ecosystems, but that CWM traits can be calculated from pollen data to assess spatial shifts in functional composition. This opens opportunities to calculate CWM traits from fossil

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pollen data sets in the tropics, with broad implications for improving our understanding and predictions of forest dynamics, functioning and resilience through time.

KEYWORDS

diversity, elevation, functional traits, pollen, richness, R-rel values, taphonomy, tropical Andes, tropical forest

1 | INTRODUCTION

Many ecosystems are shifting in plant diversity and composition, likely due to human disturbance and climate change (e.g. Harrison *et al.*, 2015; van der Sande *et al.*, 2016; Muelbert *et al.*, 2018). Reductions in diversity may strongly impact the productivity and stability of ecosystems (e.g. Hector *et al.*, 2010; Morin *et al.*, 2014; Poorter *et al.*, 2017). Moreover, changes in species composition – especially the functional trait composition (i.e. the community-average trait value) – may affect ecosystem processes (e.g. Wu *et al.*, 2016; Poorter *et al.*, 2017). Evaluating long-term historical changes in diversity and functional composition may improve our understanding of the sensitivity of ecosystems to external forces.

The high diversity of tropical forest systems is manifested both in species number and traits, but little is known of how long-term changes in climate influence the balance of those traits within the system. Fossil pollen from dated sediment cores have been used to infer changes in taxon diversity (e.g. Jaramillo *et al.*, 2006; Peros and Gajewski, 2008) and functional composition over time (Brussel *et al.*, 2018; van der Sande *et al.*, 2019), but we yet have a poor understanding of how well such pollen data represent changes in vegetation diversity and composition. Modern pollen data sets are routinely used to calibrate fossil pollen data, in terms of temperature, precipitation and seasonality (e.g. Huntley, 1990; Markgraf *et al.*, 2002; Cárdenes-Sandí *et al.*, 2019), but to date there has been no such calibration for plant functional trait composition. Here we assess to what extent patterns of vegetation diversity and functional composition along a tropical elevation gradient can be replicated from modern pollen data.

Taxa differ in the amount of pollen they produce (Davis, 1963; Bush, 1995; Gosling *et al.*, 2009) and in their pollen dispersal distances (Bush and Rivera, 1998), and therefore taxa that are present and abundant in the pollen rain are not necessarily present and abundant in the vegetation, and vice versa (Huntley, 1990; Whitmore *et al.*, 2005; Davis *et al.*, 2013). Such differences may be determined by pollination syndrome, with especially high overrepresentation of wind-pollinated taxa that produce large amounts of pollen that can be dispersed far (Tauber, 1977; Bush and Rivera, 2001). Unfortunately, our understanding of the degree to which taxa are over- or underrepresented by pollen data remains poor, especially for species in tropical ecosystems. Such information may be necessary to correct for the bias in pollen data and accurately predict taxon composition and diversity.

Despite the differences among taxa in pollen production, a previous study on Andean forests (Jantz *et al.*, 2014), as well as most studies in temperate and arctic systems, find a positive relationship

between vegetation and pollen richness (Birks *et al.*, 2016). However, a local-scale study in lowland tropical forests and savannas (Gosling *et al.*, 2018) found that pollen richness and diversity could not predict vegetation richness and diversity at the plot scale. Species richness estimates based on pollen are sensitive to the size of the source area, missing taxa, and pollen count sizes (Cassino *et al.*, 2015), which are all likely to be a greater problem in highly diverse ecosystems than in comparatively simple ones. Abundance-weighted species diversity indices may also be difficult to predict from pollen data because abundance is often poorly represented by pollen data (Birks and Line, 1992; Odgaard, 1999). This observation implies that variation in diversity would only be captured after correcting for differences in pollen production among taxa.

Changes in species composition, and hence functional composition, may be easier to predict from pollen than changes in diversity because they are less sensitive to the size of the source area and missing taxa (Pakeman and Quedsted, 2007). Changes in modern pollen data appear to capture variability along elevation gradients in the Andes (Weng, Bush, and Silman, 2004; Niemann *et al.*, 2010; Urrego *et al.*, 2011; Hagemans *et al.*, 2019). That is, even though the total amount of pollen per taxon may not reflect their absolute abundance, relative changes within taxa along elevation gradients reflect relative changes in the observed vegetation. However, no studies have tested how well functional composition (i.e. the community-average trait value) of plant assemblages can be predicted from pollen assemblage composition.

Here, we combine data from moss polsters, a vegetation plot network, and functional plant traits from an elevation gradient in Peru. Elevation gradients present an important framework to test the response of ecosystems to changing climate (Malhi *et al.*, 2010) because they capture variability across space that is projected to occur through time in the future (Bush *et al.*, 2004). From low to high elevation, water availability, temperature, atmospheric pressure and insolation generally decrease (though not monotonically), structuring species and trait composition (Swenson and Enquist, 2007). Based on these environmental gradients, as elevation increases the abundance of species with conservative trait values such as high wood density (which is associated with growth–survival trade-off and drought resistance) might be expected to rise, while the abundance of species with acquisitive trait values such as large adult height and large leaves should fall (Chave *et al.*, 2006; Asner *et al.*, 2017; Enquist *et al.*, 2017). Furthermore, the increasing environmental harshness with elevation would decrease the number of species that are able to establish and survive, resulting in a lower diversity at high elevation (Rahbek, 1995; Lomolino, 2001). Hence, with increasing elevation we would expect to see a shift in trait

composition towards more conservative traits (i.e. that enhance tissue lifespan and tolerance to harsh environmental conditions) and towards lower species diversity.

We address three questions. Firstly, how do taxa differ in their over- or underrepresentation by pollen? We expect that taxa that are wind-pollinated would be overrepresented relative to other taxa. Secondly, how do community-average trait values and species diversity change with elevation? We expect that with increasing elevation, the abundance of taxa with more conservative trait values would increase and the abundance of taxa with acquisitive trait values (i.e. that enhance resource use and fast growth) would decrease, leading to increasing community-weighted mean (CWM) values of conservative traits. For example, we expect that CWM wood density will increase with elevation (Slik *et al.*, 2010, but see Chave *et al.*, 2006), while specific leaf area and maximum tree height will decrease. We also expect a decrease in species diversity with increasing elevation. Thirdly, can pollen data predict the shifts in plant functional traits and diversity along the gradient? We expect that a similar trend along the elevation gradient is shown for indices based on modern pollen and vegetation data. However, for community-mean traits, the intercept and steepness of the slope of the regression line would be different between vegetation-based and pollen-based estimates because of differences in pollen production and pollen dispersal distances among species (Bush and Rivera, 1998). Changes in diversity would be poorly predicted by pollen because of unknown differences in the pollen source area, missing taxa and low taxonomic resolution.

2 | METHODS

2.1 | Vegetation data

We used vegetation data from the ABERG plot network (Andes Biodiversity Ecosystems Research Group; ABERG; <http://www.andesconservation.org>). This data set consists of 59 inventory forest plots along three elevational transects: Kosñipata with 18 1-ha plots and 22 0.1-ha plots between 867 and 3,627 m a.s.l., Callanga with 2 1-ha plots and 14 0.1-ha plots between 1,241 and 3,528 m a.s.l., and Palotoa with 3 1-ha plots between 425 and 843 m a.s.l. (Table 1). We used plot data from the census year closest to 2004 (when most of the modern pollen samples were taken, see next paragraph), ranging between 2002 and 2006, except for three of the plots that were only established after 2011. Within each plot, all trees with diameter at breast height (DBH) ≥ 10 cm were tagged, measured and identified to species level.

2.2 | Modern pollen data

To link the vegetation composition data with taxon composition data from the modern pollen, we used 125 modern pollen samples that were collected along the same transects as the vegetation plots (Urrego *et al.*, 2011). All samples were collected between 2001 and

2004. For the Kosñipata and Callanga transects, modern pollen samples were collected along the same elevation transect within or between the vegetation plots. In total, we had 125 modern pollen samples: 58 for Kosñipata ranging from 470 to 3,530 m a.s.l., 58 for Callanga ranging from 430 to 3,570 m a.s.l., and nine for Palotoa ranging from 480 to 1,420 m a.s.l. (Table 1). Modern pollen samples were collected from moss tissues. Moss tissue can accumulate 2–3 years of pollen input from vegetation in wet settings (Pardoe *et al.*, 2010) and serve as an effective pollen trap (Carroll, 1943; Hansen, 1949; Weng, Bush, and Silman, 2004). Each moss sample was composed of 10–20 small subsamples of moss within an area of c. 100 m² to ensure a representative sample. Samples were prepared using standard methodologies (Moore *et al.*, 1991). At least 300 pollen from each moss sample were counted and identified to genus or family level using published pollen atlases and databases (Colinvaux *et al.*, 1999; Bush and Weng, 2007). For more details on pollen preparation and analysis, see Urrego *et al.* (2011). In total, 534 different morphologically distinct pollen types (i.e. morpho-taxa) were counted, of which 428 (80%) were identified to genus level.

2.3 | Pollen representation

To assess the degree to which taxa are over- or underrepresented by pollen data, we calculated R-rel values per taxon across all samples and plots per elevation band: <1,000, 1,000–1,500, 1,500–2,000, 2,000–2,500, 2,500–3,000 and >3,000 m a. s. l. We calculated R-rel values per elevation band because pollen samples were often taken adjacent to but not within the plots (to avoid disturbance), which limits our ability to directly link plot and pollen data. We used only the 38 vegetation plots (16 1-ha and 22 0.1-ha plots) and 47 pollen samples that overlapped along the Kosñipata transect, because these samples were taken to sample the very same vegetation and can therefore be compared for the purpose to construct local R-rel values. Hence, vegetation and pollen samples from Callanga and Palotoa were not used to calculate R-rel values, but were included in all other analyses. The 0.1-ha and 1-ha plots of the Kosñipata transect were established along the whole elevational range. We

TABLE 1 Three elevation transects (Kosñipata, Callanga, and Palotoa) with their elevation range and sample size of vegetation plots and pollen samples

Site name	Vegetation/ pollen	Elevation range (m a.s.l.)	Sample size
Kosñipata	Vegetation	867–3,627	18 (1-ha) & 22 (0.1-ha)
	Pollen	470–3,530	15
Callanga	Vegetation	1,241–3,528	2 (1-ha) & 14 (0.1-ha)
	Pollen	430–3,570	58
Palotoa	Vegetation	425–843	3 (1-ha)
	Pollen	430–1,420	9

grouped the pollen samples and plots into elevation bands and performed the calculations per elevation band. R-rel values were calculated at genus and family level as percentage mean abundance in pollen rain divided by the percentage basal area of all stems ≥ 10 cm DBH in the vegetation plots.

2.4 | Trait data

We focused on three traits that describe different aspects of plant functioning: (a) wood density (*WD*), which is associated with the growth–survival trade-off and drought resistance; (b) adult height (*H*), which enhances light exposure and potential growth rates but reduces resistance to drought because of long hydraulic pathways and increases risk of wind breakage (Jackson *et al.*, 2019); and (c) leaf area (*LA*), which is a measure of light capture and associated with fast growth rates (Poorter and Bongers, 2006). These traits were derived from multiple sources to increase the number of taxa in the pollen and vegetation data sets with trait data.

For *WD*, we used locally collected wood core samples from 892 tree individuals (Farfan-Rios *et al.*, unpublished data) and the global wood density database (Zanne *et al.*, 2009). For *H*, we used the trait “maximum whole plant height” from the Botanical Information and Ecology Network (BIEN) database (<http://bien.nceas.ucsb.edu/bien/>) using the BIEN package in R (Maitner *et al.*, 2018). For *LA*, we used data from the CHAMBASA (CHallenging Attempt to Measure Biotic Attributes along the Slopes of the Andes; Malhi *et al.*, 2017) project and from BIEN. In all cases, we used data from the Neotropics only. We calculated trait averages at the species, genus and family level. Genus- and family-level averages were calculated if we had trait data for at least three species within that genus or family, to assure accurate estimates of the trait values. From the 395 genera present in the plots, we had data on *WD* for 342, on *H* for 238, and on *LA* for 248 genera. From the 383 genera present in the pollen traps, we had data on *WD* for 254, on *H* for 374, and on *LA* for 376 genera.

2.5 | Community-level average traits

We calculated CWM values for each trait per modern pollen sample and per vegetation plot. CWM trait values for modern pollen locations were weighted by the pollen count per taxon in two ways: (1) by using the original pollen abundance data per taxon, and (2) by correcting the pollen counts by dividing by the R-rel values calculated per taxon per elevation range (see section 2.3 *Pollen representation*). We applied the R-rel values for the taxa that we considered to be strongly overrepresented per elevation range. This included taxa that had R-rel ≥ 5 , and taxa that had no presence in the plots but more than 3% of total pollen count. For the latter group (which had missing R-rel values) we used R-rel values of 500, which practically excludes these taxa from the CWM trait calculations. The CWM trait values for the vegetation plots were weighted by the

relative basal area of individuals ≥ 10 cm DBH for each species in each plot. Morpho-species were included in the CWM calculations, and were given the same trait values. Data for leaf area and adult height were ln-transformed before calculating CWM values to reduce the influence of high values. To evaluate the effect of taxonomic resolution on the CWM estimates, we calculated the CWM trait values for the vegetation plots based on species-level, genus-average and family-average traits, and the CWM trait values for the modern pollen locations based on genus-average and family-average traits.

2.6 | Species diversity

We calculated the species richness, Shannon index, and Simpson index using Hill numbers (Hill, 1973). Because these indices represent the effective number of species, values of Shannon and Simpson diversity are generally higher than those calculated using other approaches. Hill numbers ($q = 0$ for richness, $q = 1$ for Shannon, and $q = 2$ for Simpson) were calculated using the iNEXT package in R (Hsieh *et al.*, 2016). This approach allows for rarefaction and extrapolation of species diversity, and hence for comparison of samples that differ in e.g. the number of individuals (or pollen) and the completeness of the sample (i.e. the number of species as compared to the total expected number of species) (Chao *et al.*, 2014). We estimated the diversity in each vegetation and pollen sample using the asymptote, i.e. the maximum predicted diversity in the sample (Appendix S1). In other words, diversity indices were calculated based on an increasing number of randomly drawn pollen or individuals, which then provided information on the increase in functional diversity with increasing sample size (i.e. pollen count or tree number). According to Chao *et al.* (2014), such asymptotic diversity estimates are reliable for any extrapolated sample sizes for Shannon ($q = 1$) and Simpson ($q = 2$), but are only reliable up to double the original sample size for richness ($q = 0$). However, we found strong correlation between rarefied richness and asymptotic richness ($r = 0.84$, $p < 0.001$, Appendix S2), and therefore also used asymptotic richness indices. For both modern pollen and vegetation plot data, we treated all morpho-species as separate “species,” as has been done before (e.g. Jaramillo *et al.*, 2006). For example, pollen that were identified as different types but could not be identified to genus level were included as a separate morpho-species. Note, however, that most pollen were identified to genus and family level and, hence, absolute plant diversity measures will likely be underestimated. Nevertheless, here we evaluate relative changes of diversity with elevation, and the similarity in this pattern between pollen- and vegetation-derived diversity indices. Diversity estimates were calculated based on the original pollen counts and on the R-rel corrected pollen counts (Appendix S3). For both approaches, we calculated diversity indices based on the whole pollen sample, and on all except wind-pollinated species because these can be strongly overrepresented in pollen records (Bush and Rivera, 2001). To test for the effect of sample size of the

modern pollen samples, we additionally calculated asymptotic diversity indices after pairing the samples by elevation per site, summing pollen in the two samples, and recalculating diversity indices (Appendix S4). Results were similar to the original analyses and are therefore not further discussed.

2.7 | Analyses

To test how CWM traits change with elevation, we used a linear mixed effects model for each trait, including elevation (and elevation squared if needed) as predictor variable and transect as random effect. Per trait, we ran this model for vegetation plots at the genus level and family level, and for pollen samples at the genus level and family level. Plots or samples were only included if trait data were available for taxa that together covered at least 50% of the plot basal area or pollen abundance. Species-level analyses for the vegetation data are shown in Appendix S5.

To test how diversity changes along elevation, we also used a linear mixed-effects model per diversity index for vegetation and pollen with elevation as predictor variable and transect as random effect. Because diversity is scale-dependent, we included an interaction between elevation and plot size for the vegetation-derived indices. All analyses were performed in R version 3.5.1 (R Core Team, R Foundation for Statistical Computing, Vienna, AT').

3 | RESULTS

Taxa differed strongly in their representation by pollen data, with some taxa being strongly overrepresented especially at high elevation (Appendix S6a), and others being strongly underrepresented especially at low elevation (Appendix S6b). Changes in CWM traits along elevation showed a similar direction of change for vegetation-derived vs pollen-derived estimates (Figure 1, Table 2): CWM wood density increased with elevation and CWM adult height and leaf

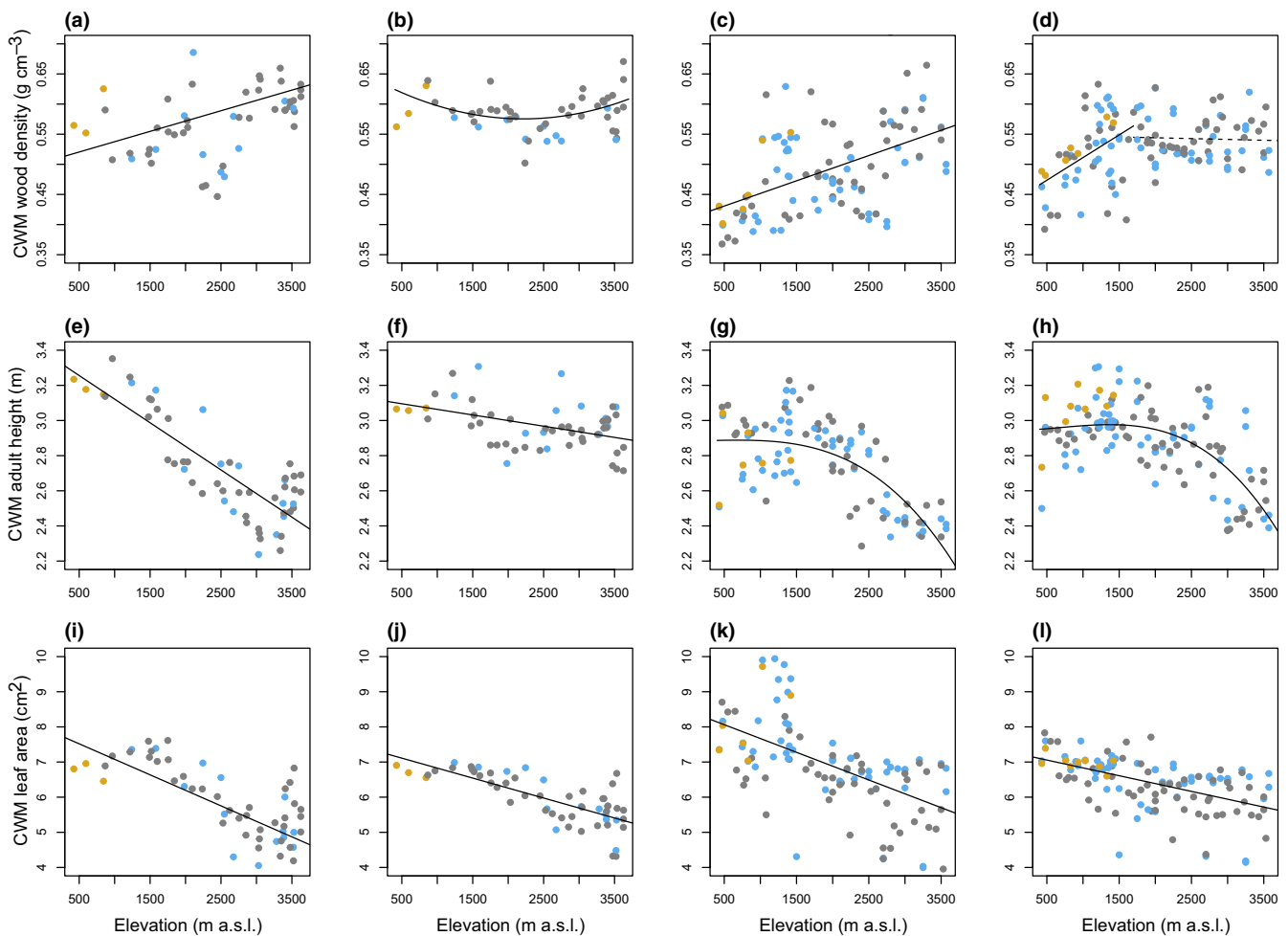


FIGURE 1 Relationships between elevation and community-weighted mean (CWM) traits: wood density (a–d), adult height (e–h), and leaf area (i–l). CWM traits were calculated from vegetation plot data (left two columns) and from pollen data (right two columns), both at genus level (first and third column) and family level (second and fourth column). Grey dots correspond to plots or pollen samples from the Kosnipata transect, blue dots to plots or pollen samples from the Callanga transect, and orange dots to plots and pollen samples from the Palotoa transect (Table 1). Continuous lines represent significant relationships. The estimated lines are based on predicted results from linear mixed models. Dots are only shown if the trait coverage was at least 50% of plot basal area or total pollen count. Leaf area and adult height data were ln-transformed prior to calculating CWM traits

area decreased with elevation (Figure 1). However, the form of the relationship differed between vegetation- and pollen-derived indices for CWM wood density and CWM adult height. Both genus- and family-level estimates from pollen samples showed similar results (i.e. similar direction and significance).

Species richness, Shannon diversity and Simpson diversity decreased with elevation in the vegetation plots (Figure 2, Table 3). The pollen samples, however, did not show this pattern. As upslope transport of pollen could be an important factor (Reese *et al.*, 2005), the data were re-analyzed excluding wind-pollinated taxa, but pollen diversity did still not show a relationship to elevation. When using original pollen count data (i.e. without corrections of R-rel values), diversity indices even increased along elevation (Appendix S3). This finding indicates that correcting pollen counts using R-rel values slightly improves diversity estimates, but not enough to detect diversity changes. In the vegetation plots, within-community variation [calculated as the coefficient of variation (CV)] in wood density and adult height had an optimum at mid-elevation, whereas variation in leaf area increased with elevation (Figure 3). In the pollen samples, these patterns could not be found. In vegetation plots, diversity estimates strongly depend on plot size (0.1 vs 1 ha), with the 1-ha plots showing a steeper decline of diversity along elevation (Figure 2a–c).

4 | DISCUSSION

We assessed how the relative abundance of plant taxa are over- or underrepresented in the modern pollen rain that they produce, and how changes in vegetation-derived and pollen-derived CWM traits and diversity indices change along an elevational gradient. We found

that taxa and elevation ranges differ strongly in their representation in modern pollen. Moreover, shifts in CWM traits were well predicted from modern pollen, while shifts in diversity indices were poorly predicted from modern pollen.

4.1 | Representation of pollen abundance data

Taxa differ strongly in their representation in the modern pollen samples (Appendix S6). On average, taxa are most strongly overrepresented at higher elevations (e.g. 2,500–3,000 m a.s.l.), and most strongly underrepresented at lower elevations (Appendices S6, S7). Forests at low elevation are more diverse, and therefore, the pollen of a higher number of taxa can potentially be transported upslope to higher elevations. This may be especially the case for wind-pollinated taxa (Bush and Rivera, 1998; Weng, Bush, and Chepstow-Lusty, 2004; Williams *et al.*, 2011). Moreover, high-elevation forests have greater canopy openness (Asner *et al.*, 2014), which increases the likelihood of pollen from other source areas to reach the lower canopy layers where pollen samples are taken (e.g. Gosling *et al.*, 2018; Hagemans *et al.*, 2019). At lower elevations, a larger number of “silent” taxa may lead to a strong underestimation of diversity (Appendix S6b). Moreover, lower pollen production at high elevation may lead to low influx of pollen to lower elevations. Such strong differences in pollen representation across taxa and elevation ranges indicates that it is important to use local data on pollen representation to quantify spatial or temporal changes in diversity or CWM traits. In the following sections, we discuss how well diversity and CWM traits can be predicted from pollen data.

TABLE 2 Results from linear regression models to test how community-weighted mean wood density, adult height, and leaf area change along elevation (in km), for vegetation- and pollen-derived indices at different taxonomic resolutions (genus and family)

Response variable	Vegetation/ pollen	Taxonomic resolution	Predictor variable	Coefficient (/ km)	SE	DF	t-value	p-value
Wood density	Vegetation	Genus	Elevation	0.034	0.008	55	4.49	<0.001
		Family	Elevation	-0.066	0.025	54	-2.62	0.011
		Family	Elevation ²	1.49E-05	5.33E-06	54	2.79	0.007
	Pollen	Genus	Elevation	0.042	0.007	101	5.94	<0.001
		Family	Elevation	0.017	0.005	119	3.41	0.001
		Family	Elevation ²	0.017	0.005	119	3.41	0.001
Adult height	Vegetation	Genus	Elevation	-0.269	0.024	50	-11.03	<0.001
		Family	Elevation	-0.064	0.018	52	-3.50	0.001
	Pollen	Genus	Elevation ²	0.278	0.090	95	3.08	0.003
		Genus	Elevation ³	-1.15E-04	2.24E-05	95	-5.11	<0.001
		Family	Elevation ²	0.361	0.085	119	4.24	<0.001
		Family	Elevation ³	-1.21E-04	2.06E-05	119	-5.89	<0.001
		Family	Elevation ³	-1.21E-04	2.06E-05	119	-5.89	<0.001
Leaf area	Vegetation	Genus	Elevation	0.101	0.010	50	9.70	<0.001
		Family	Elevation	-0.568	0.068	51	-8.32	<0.001
	Pollen	Genus	Elevation	-0.787	0.110	101	-7.18	<0.001
		Family	Elevation	-0.446	0.064	121	-6.99	<0.001

Unstandardized coefficient, standard error (SE), degrees of freedom (DF), t-value and p-value are given. Statistics correspond to Figure 1.

4.2 | Changes in functional composition along an elevational gradient

As we had expected, we found that the CWM wood density increased, and the CWM adult height and leaf area decreased with elevation, for vegetation plots and pollen samples. The slightly higher CWM wood density in the lowest elevation plots (i.e. orange dots in Figure 1a, b) was probably caused by spatial differences in species composition, as this vegetation transect (Palotoa) was farther

from the other transects. With increasing elevation, temperature decreases and cloudiness increases, leading to declining insolation, and precipitation reaches a maximum at mid-elevation (Malhi *et al.*, 2017). Such a decline in available resources may favor conservative species (i.e. with dense wood, small leaves and short adult stature) that are able to survive and cope well with such conditions. Dense wood is associated with tolerance to drought- and freezing-induced embolism (Hacke *et al.*, 2001) and shade (Markestijn *et al.*, 2011; Eller *et al.*, 2018), and should be an advantage at the lower

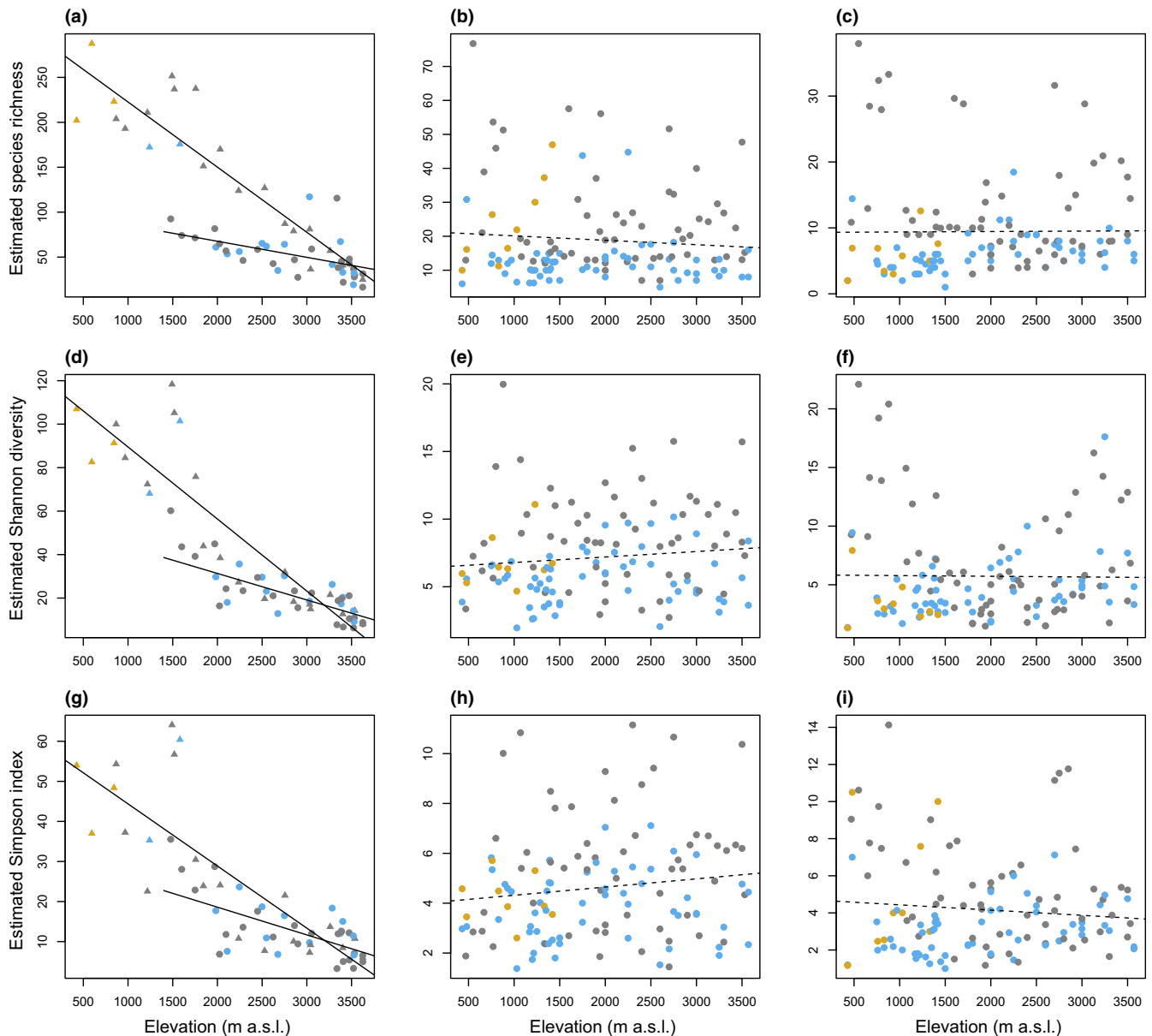


FIGURE 2 Relationships between elevation and the estimated maximum species richness (a–c), Shannon index (d–f) and Simpson index (g–i) from vegetation plots (left column), pollen samples (middle column), and pollen samples excluding wind-pollinated taxa (right column). Maximum (morpho-)species richness is based on the estimated asymptote of the species accumulation curves (Appendix S1). Grey dots correspond to plots or pollen samples from the Kosñipata transect, blue dots to plots or pollen samples from the Callanga transect, and orange dots to plots and pollen samples from the Palotoa transect (Table 1). Continuous lines represent significant relationships, and dashed lines represent non-significant relationships. Elevation effects on diversity from vegetation (left column) are estimated for 0.1-ha plots (circles) and 1-ha plots (triangles), and the two regression lines refer to the different plot sizes. The figures for pollen data are based on the R-rel-corrected pollen abundances



TABLE 3 Results from linear regression models to test how diversity indices (species richness, Shannon index and Simpson index) change along elevation, for vegetation- and pollen-derived indices

Diversity response variable	Vegetation vs pollen	Predictor variable	Value	SE	DF	t-value	p-value
Species richness	Vegetation	Elevation	-0.02	0.01	53	-2.67	0.010
		Plot size	191.71	23.09	53	8.30	<0.001
		Elevation * plot size	-0.05	0.01	53	-6.31	<0.001
	Pollen	Elevation	<0.01	<0.01	123	-0.98	0.331
		Pollen excl. wind	Elevation	<0.01	<0.01	123	0.09
Shannon index	Vegetation	Elevation	-0.01	<0.01	53	-3.40	0.001
		Plot size	66.93	12.34	53	5.42	<0.001
		Elevation * plot size	-0.02	<0.01	53	-4.52	<0.001
	Pollen	Elevation	<0.01	<0.01	123	1.23	0.221
		Elevation	0.00	<0.01	<0.01	-0.14	0.892
Simpson index	Vegetation	Elevation	-0.01	<0.01	53	-2.79	0.007
		Plot size	27.47	8.52	53	3.22	0.002
		Elevation * plot size	-0.01	<0.01	53	-2.69	0.010
	Pollen	Elevation	<0.01	<0.01	123	1.52	0.132
		Pollen excl. wind	Elevation	<0.01	<0.01	123	-1.07

Unstandardized coefficient, standard error (SE), degrees of freedom (DF), t-value and p-value are given. Statistics correspond to Figure 2.

rainfall, temperature and insolation at high elevation. Species with short adult stature face less hydraulic limitation, less risk of cavitation (Olson *et al.*, 2018) and less mechanical stress due to wind, and hence should have a relative advantage over large-stature species at high elevation. Large leaves allow high light interception and growth rates, but their higher production costs make them a disadvantage at low resource availability (Wright *et al.*, 2017). Results were similarly strong when using species-level (Appendix S5), genus-level or family-level abundance and trait data, probably because these traits have a strong phylogenetic signal (Coelho de Souza *et al.*, 2016; van der Sande *et al.*, 2019).

4.3 | Vegetation changes in functional composition are well represented by pollen rain

After correcting for the overrepresentation of some taxa, we found that CWM traits calculated using abundance data from pollen showed similar direction of change along elevation as those calculated from vegetation data (Figure 1). This indicates that when the community composition shifts towards, for example, a higher abundance of taxa with dense wood, also the pollen composition shifts towards a relatively higher abundance of such taxa. These results are in line with previous studies that demonstrated good representations of relative changes in species composition from pollen data along elevation gradients (Weng, Bush, and Silman, 2004; Niemann *et al.*, 2010; Urrego *et al.*, 2011; Hagemans *et al.*, 2019), and with a study showing strong correlation of CWM traits between pollen

and vegetation in Estonia and Latvia (Reitalu *et al.*, 2015). Without correcting for overrepresentation of certain taxa, pollen-derived CWM changes with elevation show a similar direction to those of vegetation-derived estimates (Appendix S8). However, the slopes of the regression lines are flatter compared to results corrected for overrepresentation, indicating that CWM changes along elevation can more clearly be picked after correcting for overrepresentation. If R-rel values are not available to correct for variation in pollen production and dispersal among taxa, then a sufficiently high sample size and strong environmental gradient are needed to detect significant changes in CWM traits along the gradient using pollen data, and emphasis should be on understanding relative changes in CWM trait values rather than on the reconstruction of absolute CWM trait values. We found that genus- and family-level CWM traits from pollen records show similar changes with elevation (Figure 1), indicating that this approach is also applicable to fossil pollen records with a relatively low taxonomic resolution. Hence, our results demonstrate that relating CWM traits from pollen assemblages to environmental gradients provide meaningful results. This opens doors to track long-term changes in functional trait composition and underlying drivers (e.g. van der Sande *et al.*, 2019).

4.4 | Decreasing diversity with elevation is not captured by pollen rain

Species richness, the Shannon index and the Simpson index all decrease with elevation in vegetation plots (Figure 2a,d,g), in agreement

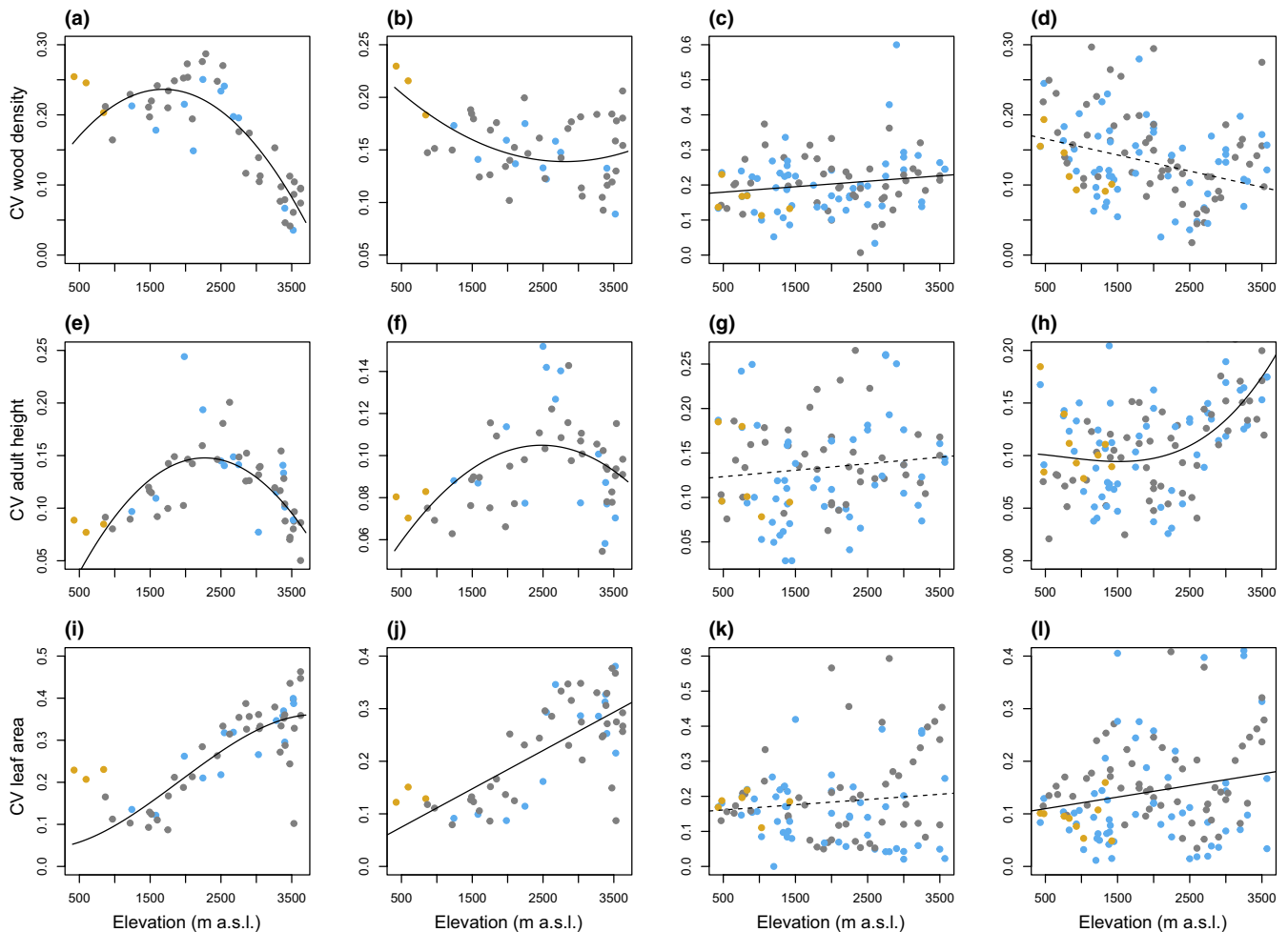


FIGURE 3 Relationships between elevation and functional diversity (coefficient of variation; CV) of wood density (a–d), adult height (e–h), and leaf area (i–j). CV values were calculated from vegetation plot data (left two columns) and from pollen data (right two columns), both at genus level (first and third column) and family level (second and fourth column). Grey dots correspond to plots or pollen samples from the Kosñipata transect, blue dots to plots or pollen samples from the Callanga transect, and orange dots to plots and pollen samples from the Palotoa transect (Table 1). Continuous lines represent significant relationships. The estimated lines are based on predicted results from linear mixed models. Dots are only shown if the trait coverage was at least 50% of plot basal area or total pollen count. Leaf area and adult height data were ln-transformed prior to calculating CV values

with earlier studies (e.g. Rahbek, 1995; Lomolino, 2001). Variation in functional traits, however, shows optima at mid-elevation for variation in wood density and height, and an increase along elevation for leaf area (Figure 3). However, these clear changes in diversity with elevation cannot be seen from pollen-derived diversity indices (Figures 2b,e,h and 3b,e,h). This discrepancy is found for richness as well as the abundance-weighted diversity indices (Shannon, Simpson and the trait variation). Multiple reasons may explain why diversity cannot be estimated from pollen. First, wind-pollinated taxa could distort the signal, because their pollen can disperse far and increase the pollen source area and, hence, the spatial scale (Bush and Rivera, 1998; Meltsov *et al.*, 2011). Since diversity indices are strongly dependent on the size of the sampled area, pollen input from a larger area can distort diversity estimates. However, even after excluding wind-pollinated taxa, diversity did not decrease with increased elevation (Figure 2c,f,i). Note, however, that the results excluding wind-pollinating taxa are also based on a reduced data set, which further

increases uncertainty. Second, the over- or underrepresentation of taxa may strongly influence diversity estimates. For example, many species may be underrepresented by pollen at low elevation, causing an underestimation of diversity (Reitalu *et al.*, 2019). This suggestion is supported by our diversity estimates based on the original pollen count data (Appendix S4, which show increases instead of decreases with elevation. Hence, our correction using R-rel values partly removed the relative overestimation of diversity at high elevation, but not enough to detect the diversity decrease with elevation. Third, low taxonomic resolution leads to an underestimation of diversity, especially when multispecies genera are common. Fourth, taphonomic processes (i.e. that affect pollen as they become fossilized) may result in a greater diversity of pollen being accumulated in pollsters at high elevation. For example, it could be that higher wind speeds transport more pollen upslope, longer-lasting mosses accumulate a higher diversity of pollen, and canopy openness increases the influx of pollen at high elevation. Such and other processes may

determine local-scale differences in pollen accumulation. This is supported by our results, which show no diversity changes along elevation across the three transects, but significant decreases in diversity indices when assessing only *Kosñipata*, and significant increases in diversity indices when assessing only *Callanga* (Appendix S9). Finally, although the rarefaction curves (Appendix S1) showed that a mismatch in diversity estimates is found at different pollen counts, higher pollen count numbers may result in more accurate diversity estimates.

Our results are in agreement with some studies (Gosling *et al.*, 2018) but in disagreement with a review that compares diversity from pollen and vegetation (Birks *et al.*, 2016). Studies that find an agreement between both measures of diversity are often measured in flat (Jantz *et al.*, 2014) or temperate ecosystems (Felde *et al.*, 2016), at coarser scales (Matthias *et al.*, 2015; Reitalu *et al.*, 2019), do not use actual diversity measured from the vegetation (Weng *et al.*, 2007), or are based on very large pollen sums (Meltsov *et al.*, 2011). This indicates that pollen can provide information on differences in diversity among forest types and at landscape or global scales (Flenley, 2005), but are not accurate enough to provide information on smaller-scale environmental changes, especially in hyperdiverse ecosystems such as tropical forests. Further studies are needed to assess pollen production and dispersal for different taxa, to develop a more robust way of determining local diversity from pollen samples, and to assess if and how diversity can be estimated at long temporal scales using fossil pollen data.

5 | CONCLUSIONS

We show that changes in functional composition (i.e. CWM traits) along elevation can be predicted based on modern pollen rain data. Both vegetation plot data and pollen rain data show that the CWM wood density increases, and the CWM adult height, CWM leaf area and diversity indices decrease with increased elevation. Changes in diversity along environmental gradients, however, cannot yet be reliably predicted from pollen along these tropical elevation gradients in Peru, and probably reflect the dominance of taphonomic rather than diversity-related processes. Nevertheless, the ability to predict shifts in CWM traits opens opportunities to evaluate temporal shifts in functional composition over long temporal scales using fossil pollen records. Such an approach could strongly enhance our functional understanding of Andean and Amazonian forest responses and resilience in response to climate change and human disturbances.

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AUTHOR CONTRIBUTIONS

MvdS, MBB and WG conceived the idea of the study. DHU and CHM contributed the pollen data; MS, WFR and KGC contributed vegetation plot data; AS, WFR and YM contributed functional trait data. MvdS analyzed the data and wrote the manuscript. All authors discussed the results and contributed substantially to the manuscript and revisions.

DATA AVAILABILITY STATEMENT

The data used for the analyses are published in the open access data repository DANS. <https://doi.org/10.17026/dans-xs8-raum>. A full list of R-rel values can be found in Appendices S10 and S11.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species richness, Shannon index and Simpson index at different levels of randomly sampled trees, different levels of randomly sampled pollen counts, and at different levels of randomly sampled animal-dispersed pollen counts.

Appendix S2. Correlation between the asymptotic richness estimates of the pollen samples versus the rarefied pollen richness based on 180 pollen counts per sample.

Appendix S3. Relationship between elevation and the estimated maximum species richness, Shannon index and Simpson index from pollen samples and pollen samples excluding wind-pollinated taxa

Appendix S4. Relationship between elevation and asymptotic estimates of species richness, Shannon diversity and Simpson diversity, based on the pollen samples that were pooled in pairs (closest in elevation) to increase the sample size

Appendix S5. Relationship of species-level community-weighted mean (CWM) wood density and leaf area with elevation, based on vegetation plot data

Appendix S6. Genera that are overrepresented or underrepresented by pollen data per elevation range class (<1,000, 1000–1500, 1500–2000, 2500–3000 and > 3,000 m a.s.l.)

Appendix S7. Number of genera present in the plots, and the number of these genera that are also present in the modern pollen samples

Appendix S8. Relationships between elevation and community-weighted mean (CWM) traits: wood density, adult height, and leaf area. CWM traits were calculated from pollen data at genus level and family level, based on pollen abundance data uncorrected for overrepresentation of taxa

Appendix S9. Changes in diversity indices (species richness, Shannon and Simpson) along elevation based on pollen-derived indices, separately tested for the elevation transect Kosñipata and Callanga

Appendix S10. R-rel values of all genera

Appendix S11. R-rel values of all families

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