

MSc Biological Sciences
Ecology & Evolution
Research Project

Environment or Taxonomy?

*Identifying the major drivers of leaf wax trait diversity
in the Peruvian rainforest and cloud forest*

by

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August 2015
42 ECTS

10 January 2015 - 10 August 2015

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Summary

- This study analyzes leaf wax biochemical traits from tropical trees within a plot-based, multi-trait survey spanning a 200 to 3600 m.a.s.l elevation transect in the Peruvian tropical rainforest (TR) and tropical montane cloud forest (TMCF). We report an unprecedented leaf wax *n*-alkane dataset comprising 639 individuals, 158 species, 105 genera and 55 families.
- Leaf wax *n*-alkane molecular abundance distributions were quantified for each individual via gas chromatography flame ionization detection (GC-FID). Controlling factors were identified using statistical partitioning of variances.
- We find taxonomic controls dominate leaf wax *n*-alkane chain length distributions (>50% of variance). Towards lower elevations and higher temperatures, mean distributions shift towards slightly longer carbon chain lengths and a reduced preference for the synthesis of odd over even chain length preference *n*-alkanes. *n*-Alkane abundance on a leaf area basis (KMA) shows a step shift to more waxy leaves between 1494 and 1713 m.a.s.l., a key division in many forest traits.
- The pattern of waxier leaves in the Andean sites matches increases in leaf mass per area (LMA) and leaf lifespan (LL), suggesting a concerted trait response in foliar investment across the elevation gradient. We introduce a new concept of wax net primary production (NPP), and show that waxier leaves counteract suppressed foliar NPP in the TMCF, thus forest wax production increases with elevation (from 500 to 3000 g C ha⁻¹ yr⁻¹) in this Amazon-Andes transect.

Introduction

The western Amazon contains some of the highest plant species diversity in the world (Ter Steege, 2010). The uplift of the Andes in the Miocene (Luebert & Muller, 2015) dramatically altered landscape and climate, and is considered to have been an agent in Amazonian species diversification (Hoorn *et al.*, 2010). Today a fully forested elevation transect across the eastern flank of the Andes, has been sampled by a series of forest plots that allow the study of species diversity (Silman, 2011), forest productivity (Girardin *et al.*, 2014a; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014), and the effects of temperature, precipitation and other environmental variables on plant traits (Malhi *et al.*, 2010; Asner *et al.*, 2014a,b; Girardin *et al.*, 2014b). Additional studies of these forest plots for plant ‘traits’, i.e. leaf venation, foliar chemistry, leaf waxes, and soil interactions, are a major collaborative research endeavor, the results of which are reported in the chapters of this special issue. Some plant traits can only be measured in living plants or rare macrofossils (e.g. leaf anatomy, Salinas *et al.*, pers. comm.; Aizen & Eczurra, 2008), but some plant biochemicals (e.g., waxes, lignin) have exceptional preservation potential and are exported from plants into soils, rivers and ultimately may be preserved in the geological record (Hedges & Oades, 1997). In particular, the waxy molecules on the surface of plant leaves are notably resilient tracers of past plant production, surviving fluvial export in the rivers draining the Andes (Ponton *et al.*, 2014). These waxes are derived from the waxy layer on the surface of

plant leaves and their molecular abundance distribution and isotopic composition can be diagnostic or informative about environmental conditions and ecological communities (Eglinton & Hamilton, 1967). Very little direct data on plant leaf waxes exist from the forests of western Amazonia and adjacent Andean regions, although these plant biomarkers have been studied in lakes and rivers (Polissar & Freeman, 2010; Ponton *et al.*, 2014; Fornace *et al.*, 2014). The overarching research question here is to what extent do the high biodiversity in the western Amazon and the strong environmental gradients across the elevation changes in the Andes, manifest in leaf wax traits? This is of interest as these leaf wax traits can be measured for both current ecosystems and in the sedimentary molecular fossil record of past ecosystems.

Leaf waxes have been studied since the late 19th Century as a component of the leaf cuticular anatomy (De Bary, 1871). Study of their chemistry began in the early 20th Century (Chibnall *et al.*, 1934) and advanced with the availability of gas chromatography (Eglinton and Hamilton, 1967). The epicuticular and intracuticular waxes on plant leaves serve to protect the plant from desiccation, from pathogen and fungal attack, as well as altering leaf wettability and runoff (Jenks & Ashworth, 1999; Koch *et al.*, 2009). This protective role extends to other functions, including protection from UV radiation (Shepherd & Griffiths, 2006). Many of these functions of leaf waxes would be expected to vary across elevation gradients, including the temperature, precipitation, insolation and biotic stresses that vary across the 4km profile of the Andes; but this has, as yet, been entirely undocumented.

Leaf waxes are comprised of mixtures of long-chain hydrocarbons, such as *n*-alkanes, *n*-alkanols, aldehydes, fatty acids, and wax esters (Eglinton & Hamilton, 1967). Waxes are thought to be synthesized early in leaf ontogeny (Jetter & Schäffer, 2001) and likely not to be regenerated during the lifespan of the leaf (Tipple *et al.*, 2013; Kahmen *et al.*, 2013). However if removed mechanically, leaf waxes can be regenerated, and thus some wax may be abraded in the natural world through wind, water or insects, and then might be replaced during a leaf's lifespan (Jetter & Schäffer, 2001). Leaf waxes, thus abraded, or carried on leaves into leaf litter and soils, after which they may be stored, or eroded and transported further to lake and ocean sediments. Some fraction of the leaf waxes are remineralized by microbial activity, but in general the leaf waxes are the more recalcitrant of plant biochemicals and thus their proportion of plant-derived organic matter increases as other more labile compounds such as carbohydrates and cellulose degrade (Hedges and Oades, 1997). Of the leaf waxes, *n*-alkanes are especially well preserved (Cranwell, 1981), and this has led to their extensive use in palaeoenvironmental studies often based upon their carbon isotopic composition, which allows for the separation of C₃ and C₄ photosynthetic pathways (e.g., Freeman & Colarusso, 2001; Garcin *et al.*, 2014), or based upon their hydrogen isotopic composition that records changes in the hydrological cycle (e.g., Feakins & Sessions, 2010; Sachse *et al.*, 2012; Niedermeyer *et al.*, 2014).

The abundance and molecular abundance distribution of *n*-alkanes may also be an important part of the plant's physiological and biochemical response to its environment, whether derived earlier in plant evolution or recently materializing as a plastic response to the present environment. *n*-Alkanes in terrestrial plants are long-chain hydrocarbons (C_nH_{2n+2}) where n typically is 21 to 35, of which one or two are usually dominant and have a strong odd-over-even

preference (Eglinton & Hamilton, 1963, 1967). Some studies have suggested that the chain length distributions of *n*-alkanes vary between species and thus can discern shifts in vegetation communities such as forest-grassland transitions (e.g. Jansen *et al.*, 2010; Carr *et al.*, 2014). But variations in molecular abundance distributions have also been suggested to be plastic responses to temperature or aridity at the time of leaf production in *Juniperus virginiana* (Tipple & Pagani, 2013). Studies using atmospheric dust (e.g. Kawamura *et al.*, 2003) or sedimentary records (e.g. Castañeda *et al.*, 2009) provide supporting evidence for this suggested relationship between chain length and temperature or aridity. However, globally, there appears to be little confidence that there are diagnostic chain length fingerprints with environment climatic conditions, because both species and environmental effects confound the search for globally consistent patterns (Bush & McInerney, 2013). Even if wax composition is not uniquely identifying in a way that would make it useful as a universal geological biomarker, there may still be plant types and regions where molecular abundance distributions may be diagnostic. For example, *Sphagnum* in peat bogs dominantly make C₂₃ (Bingham *et al.*, 2010), whereas *J. virginiana* dominantly makes C₃₅ (Tipple & Pagani, 2013). But very little work has been done to date in the tropics. The high biodiversity of the western Amazon and elevation gradients of the Andes provides a diverse context in which to analyze taxonomic patterns and environmental controls on plant wax traits in the tropics.

Leaf ‘waxiness’ is not commonly reported except in a recent study of forest-grassland transition in Cameroon where the varying proportions of wax production in different chain lengths was shown to impact the overall isotopic signature (Garcin *et al.*, 2014). However, the impact of foliar biomass (Maass *et al.*, 1995; Luo *et al.*, 2004), or leaf ‘waxiness’ (Ashton & Berlyn, 1992; Liu *et al.*, 2005), on the production of leaf waxes by plant communities and varied community inputs into the soil is a question that has not yet been addressed. There is a lack of available information on leaf wax traits in the context of leaf net primary production (NPP) and taxonomic diversity, and this is a void that this study seeks to comprehensively address by nesting leaf wax trait analysis within a comprehensive study of the region’s ecology as part of the CHAMBASA project (CHallenging Attempt to Measure Biotic Attributes along the Slopes of the Andes) as well as prior studies in the region (e.g., Silman, 2011; Girardin *et al.*, 2014b; Asner *et al.*, 2014b).

This study of plant wax traits may reveal useful insights into the taxonomy and ecology of wax production, and the degree of plasticity of wax trait responses across environmental gradients. It is well known that plants invest in foliar biomass production (Wright *et al.*, 2004) and biochemistry (Asner *et al.*, 2014b) with varying strategies depending on environmental constraints, the so-called leaf economics spectrum (Wright *et al.*, 2004). In this region, leaf mass per unit area (LMA; Asner *et al.*, 2014a,b) and leaf lifespan (LL; Girardin *et al.*, 2014a; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014) increase with elevation. Higher LMA leaves represent a costly investment for plants, especially when the montane forests are nitrogen (N) limited (Fisher *et al.*, 2013). The high cost is also reflected in the longer LL, which suggests that the duration of complete investment return is longer than in lowland forests. We likewise predict differences in leaf wax investments, although waxes comprised of C and H may be comparatively

metabolically ‘cheap’ for the plant. Differences in the wax composition and ‘waxiness’ of leaves may be driven by a need to protect their investments from abiotic (e.g. UV-B radiation) and biotic (e.g. fungi, pathogens) stress. However, no information about the involvement of wax biochemistry with LMA and LL at montane cloud forests is available yet.

The Peruvian lowland rainforests and montane cloud forests offer a steep elevation transect with changes in several key (a)biotic factors, including temperature, precipitation, net primary production, and carbon allocation (Malhi *et al.*, 2013; Girardin *et al.*, 2014; Huaraca Huasco *et al.*, 2014). This diverse environment allows for the exploration of correlations between *n*-alkane characteristics and potential controlling factors. Previous studies have related changes in chain length distributions to both environment, or climate, and the taxonomy (e.g. Brincat *et al.*, 2000; Schwark *et al.*, 2002). This study aims to determine whether *n*-alkane chain length and abundance is primarily determined by a plant’s environment or its taxonomy. We collect an unprecedented leaf wax dataset comprising results from leaf samples from 639 individual trees of which 158 species from nine sites. We report leaf ‘waxiness’ or *n*-alkane loading, which is an entirely novel data contribution from anywhere in the world. We also vastly expand the catalogue of information on the variations in molecular abundance distribution in this unprecedented tropical tree leaf wax dataset. This study yields new insights into the patterns of *n*-alkane abundance and molecular composition to reveal taxonomic, environmental controls and with the potential of further developing leaf wax traits as tools to study contemporary and ancient ecosystems.

Specific questions addressed by this manuscript include

- Are there systematic changes in leaf wax *n*-alkane traits across the transect?
- Does the average chain length of *n*-alkanes increase with temperature (decrease with elevation)?
- How does leaf wax *n*-alkane loading, or ‘waxiness’, and composition vary across a three-kilometer elevation transect?
- How do variations in leaf wax composition or abundance compare to known patterns in LMA and LL?
- What are the main drivers of diversity in leaf wax traits?

Materials and Methods

Study site

This study included 9 plots (Table 1) that belong to a group of permanent 1-ha plots in the Kosñipata Valley in the province of Paucartambo, department of Cusco (Malhi *et al.*, 2010) All plots are operated by the Andes Biodiversity Ecosystems Research Group (ABERG, <http://www.andesconservation.org>) and are part of the ForestPlots (<https://www.forestplots.net/>) and Global Ecosystems Monitoring Network (GEM; <http://gem.tropicalforests.ox.ac.uk/projects/aberg>) networks. Plots are located in areas that have relatively homogeneous soil substrates and stand structure, and which have minimal evidence of

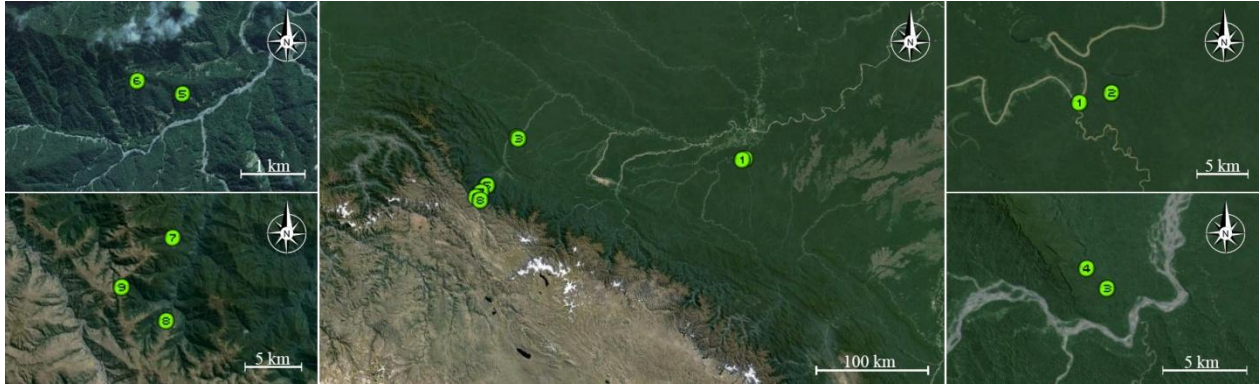


Figure 1 Study location map. Sites Tambopata VI, Tambopata V, Pantiacolla II, Pantiacolla III, San Pedro II, San Pedro I, Trocha Union IV, Esperanza, and Acjanaco are numbered 1-9, respectively.

human disturbance (Girardin *et al.* 2014a). Plots were established between 2003 and 2013, with all stems ≥ 10 cm diameter at breast height tagged and identified to species-level, and plots have been annually measured for carbon allocation and cycling following standard the GEM Network protocol (Marthews *et al.*, 2012). As such, net primary productivity estimates (Girardin *et al.* 2010) and comprehensive descriptions of the carbon cycle exist for many of these plots (Girardin *et al.* 2014b; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014; Malhi *et al.*, 2015). From February 2013 to January 2014, mean annual air temperature varied from 9°C to 24.4°C and precipitation ranged from 1560 mm y^{-1} to 5302 mm y^{-1} across all sites along the gradient (Table 1).

Field sampling

From April – November 2013, plant traits were measured as part of the CHAMBASA project. Based on the most recently available census and diameter data, a sampling protocol was adopted wherein species were sampled that maximally contributed to plot basal area (a proxy for plot biomass or crown area). The aim was to sample the minimum number of species that contributed to 80% of basal area, although in the diverse lowland forest plots only sampled species comprising 60-70% of plot basal area were sampled. Within each species, 3-5 individual trees were chosen for sampling (5 trees in upland sites and 3 trees in lowland sites). If 3 trees were not available in the chosen plot, additional individuals of the same species from an area immediately surrounding the plot were sampled. Using advanced tree climbing techniques, samples from one fully, sunlit canopy branch and, where it existed, a fully shaded branch, each at least 1 cm diameter, were taken from each tree. Across all plots, about 40% of trees had shade branches sampled in addition to sun branches. From each branch, measurements were taken of 5 leaves from simple-leaved species, or 5 individual leaflets from compound-leaved species (both referred to as ‘leaf’ below) for trait measurements. In the case of compound leaves, the entire compound leaf was also collected for whole-leaf area calculations. Leaves were chosen with minimal damage (i.e. herbivory). Leaves were placed in coolers from the field plot to the field lab for drying, at low temperatures (ca. 50 °C), and thereafter stored in paper envelopes prior to lipid analysis.

Table 1 Environmental and ecological characteristics of 1 hectare study plots along a 3300 m tropical montane elevation gradient (Malhi *et al.*, in prep.)

CHAMBASA plot code	Tambopata VI	Tambopata V	Pantiacolla II	Pantiacolla III	San Pedro II	San Pedro I	Trocha Union IV	Esperanza	Acjanaco
RAINFOR site code	TAM-06	TAM-05	PAN-02	PAN-03	SPD-02	SPD-01	TRU-04	ESP-01	ACJ-01
Latitude	-12.8385	-12.8309	-12.6495	-12.6383	-13.0491	-13.0475	-13.1055	-13.1751	-13.14689
Longitude	-69.296	-69.2705	-71.2626	-71.2744	-71.5365	-71.5423	-71.5893	-71.5948	-71.6323
Elevation* (m)	215	223	595	859	1494	1713	2719	2868	3537
Slope* (deg)	2.2	4.5	11.5	13.7	27.1	30.5	21.2	27.3	36.3
Aspect* (deg)	169	186	138	160.5	125	117	118	302	104
Solar radiation (GJ m ⁻² yr ⁻¹)	4.8	4.8			4.08	4.36	3.49		
Mean annual air temperature** (°C)	24.4	24.4	23.5**	21.9**	18.8	17.4	13.5	13.1	9
Precipitation (mm yr ⁻¹)	1900	1900	2366**	2835**	5302	5302	2318	1560	3487
Soil moisture (%)	35.5	21.8			37.3	37.6	37.3	24.3	
Vegetation height*	28.2	27.5	24.4	18.7	22.8	14	15.7	16.9	12.5
Soil type	Alisol	Cambisol	Plintico	Alisol	Cambisol	Cambisol	Umbrisol	Umbrisol	Cambisol
P _{total} (mg kg ⁻¹)	528.8	256.3			1630.7		746.8	980.8	
Soil total N (%)	0.17	0.16			0.9	1.2	1.99	1.48	
Soil total C (%)	1.2	1.51			13.6	22.7	28.33	28.59	
Soil C stock (Mg C ha ⁻¹ from 0-30 cm)	37.4	43.7			93.5	75.6	289	133.9	
Soil organic layer depth (cm)	37	13			30	32	20	50	

* Derived from high-resolution airborne Light Detection and Ranging (LiDAR) data (see Asner *et al.* (2013) for methodology)

** Derived from observations between 6 February 2013 and 7 January 2014

To biomass-weight plot-level means, diameter data from the year with the most recent census data was used. While this year ranges between 2009 to 2014, it is not expected that variation in census year introduces bias into analyses since plots have not experienced major disturbance (e.g. landslide, fire, deforestation) during that time.

Lipid extraction

Lipid extraction and chemical analysis was performed in Sarah Feakins' lab. The dried leaves were cut using solvent-cleaned scissors and leaf waxes were subsequently extracted by washing the leaf three times with dichloromethane (DCM)/MeOH (9:1) using a Pasteur pipette. The use of cut leaves was deemed preferable over that of pulverized leaf material to minimise contamination with intracellular lipids, which otherwise complicates preparation and analysis (Romero & Feakins, 2011).

The obtained total lipid extract was separated into two fractions using column chromatography (5 cm x 4 mm Pasteur pipette, 5% water-deactivated silica gel, 100-200 mesh), eluting first with hexane, followed by DCM, and finally MeOH. This resulted in an alkane fraction (hexane) and a 'rest' fraction (DCM and MeOH), of which only the alkane fraction was used for further analysis here.

n-Alkane identification and quantification

The alkane fraction was analyzed by an Agilent Technologies[®] gas chromatograph connected to a mass spectrometer and flame ionization detector (GC-FID/MS) to both identify (by MS) and quantify (by FID) *n*-alkanes. Peak areas by FID were manually integrated to quantify odd and even chain length *n*-alkanes in the range of C₂₁ to C₃₅ carbon chain length, relative to an in-house mixture of *n*-alkanes of known abundance. Leaf wax *n*-alkane abundances for these individual *n*-alkanes as well as summed to report Σn -alkanes were calculated as:

$$\sum n\text{-alkanes} = \sum ([C_{21}] + [C_{22}] + [C_{23}] + [C_{24}] + [C_{25}] + [C_{26}] + [C_{27}] + [C_{28}] + [C_{29}] + [C_{30}] + [C_{31}] + [C_{32}] + [C_{33}] + [C_{34}] + [C_{35}])$$

The "waxiness" of the leaf (i.e. here meaning Σn -alkanes) can be considered relative to per unit dry leaf mass (Specific alKane load; SK) reported in units of $\mu\text{g g}^{-1}$ or per unit leaf lamina area (alKane Mass per unit Area; KMA) reported in units of $\mu\text{g cm}^{-2}$. SK can also be converted from units of $\mu\text{g g}^{-1}$ of leaf biomass into $\mu\text{g g C}^{-1}$ by normalizing for the C content of biomass (Asner *et al.*, pers. comm.). Each of these ways of presenting the alkane loading are useful for various calculations and comparisons that we will consider here. We further calculate ratios of *n*-alkanes including the carbon preference index (CPI), i.e. the preference for the odd over even chain length, and the average chain length (ACL), computed as:

$$CPI = \frac{\sum C_{n,odd}}{\sum C_{n,even}} \quad (\text{Eqn. 1}) \quad \quad ACL = \frac{\sum (C_n \cdot n)}{\sum C_n} \quad (\text{Eqn.2})$$

The sample set for *n*-alkane quantification includes 639 individual samples with the following distribution across the forest plots: $n_{\text{tam-06}} = 75$, $n_{\text{tam-05}} = 93$, $n_{\text{pan-02}} = 39$, $n_{\text{pan-03}} = 37$, $n_{\text{spd-02}} = 103$,

$n_{\text{spd-01}} = 92$, $n_{\text{tru-04}} = 81$, $n_{\text{esp-01}} = 71$, $n_{\text{acj-01}} = 48$. These samples include 158 species from 105 genera and 55 families.

Statistical analysis

The statistical analysis was performed within R v3.1.3 (R Core Team, 2015), using the ‘lme4’ (Bates *et al.*, 2014), ‘plyr’ (Wickham, 2011), ‘Hmisc’ (Harrell *et al.*, 2015), ‘devtools’ (Wickham & Chang, 2015), and ‘gemtraits’ packages (Shenkin, in development).

Differences in the ACL and KMA were investigated by performing one-way ANOVAs and Tukey’s Honest Significant Difference tests for multiple comparisons. Individual ACL values were weighted by individual KMA and after calculating species averages the community-weighted mean was calculated on the basis of tree species basal area within the forest plot, using the ‘plyr’ package and custom scripts. Displayed error bars were plotted using functions from the ‘Hmisc’ package. The weighted mean and the weighted standard deviation were calculated using:

$$\bar{x}_w = \frac{\sum_{i=1}^N w_i \cdot x_i}{\sum_{i=1}^N w_i} \quad \sigma_w = \sqrt{\frac{\frac{\sum_{i=1}^N w_i \cdot (x_i - \bar{x}_w)^2}{(N' - 1) \cdot \sum_{i=1}^N w_i}}{N'}}$$

, where w_i is the weight for the i^{th} observation, N' is the number of non-zero weights, and \bar{x}_w is the weighted mean of the observations.

Partitioning of variances was performed using the ‘lme4’ package to separate phylogenetic from environmental control factors over either ACL or KMA. A nested linear mixed-effects model was developed using family, genus, species, and site as random factors:

$$y = F_i + G_{ij} + S_{ijk} + T_l + R_{ijkl}$$

where F_i is family i , G_{ij} is genus ij within family i , S_{ijk} is species ijk within genus ij , T_l is the site effect, and R_{ijkl} is the residual error of the measurement and non-site effects. The contribution of each factor to the variable of interest is reported as a percentage, assuming that the total variance σ_{total}^2 consists of the sum of the variances of the model factors:

$$\sigma_{total}^2 = \sigma_F^2 + \sigma_G^2 + \sigma_S^2 + \sigma_T^2 + \sigma_R^2$$

These obtained variances show whether the major impact on the variable of interest is taxonomy, site effects, or unknown factors (the residual).

Results

Molecular abundance distribution of n-alkanes

We found sampled trees to have n -alkanes with carbon chain lengths in the range of C_{21} to C_{35} . C_{29} and C_{31} were found to be the dominant homologues across all sites with abundances ranging from 20 to 430 $\mu\text{g g}^{-1}$ (n -alkane homologue abundance per unit mass of dry leaf). C_{27} alkanes are present at low abundances at the lowland sites, but are increasingly abundant at higher elevations. Most other chain length n -alkane homologues are of relatively low abundance throughout $< 30 \mu\text{g g}^{-1}$. The abundance of C_{21} - C_{35} n -alkane homologues was determined for each individual tree and the mean abundance is reported for each species, revealing considerable variability between species (Table S1). The mean molecular abundance distribution for each site (Fig. 2) displays

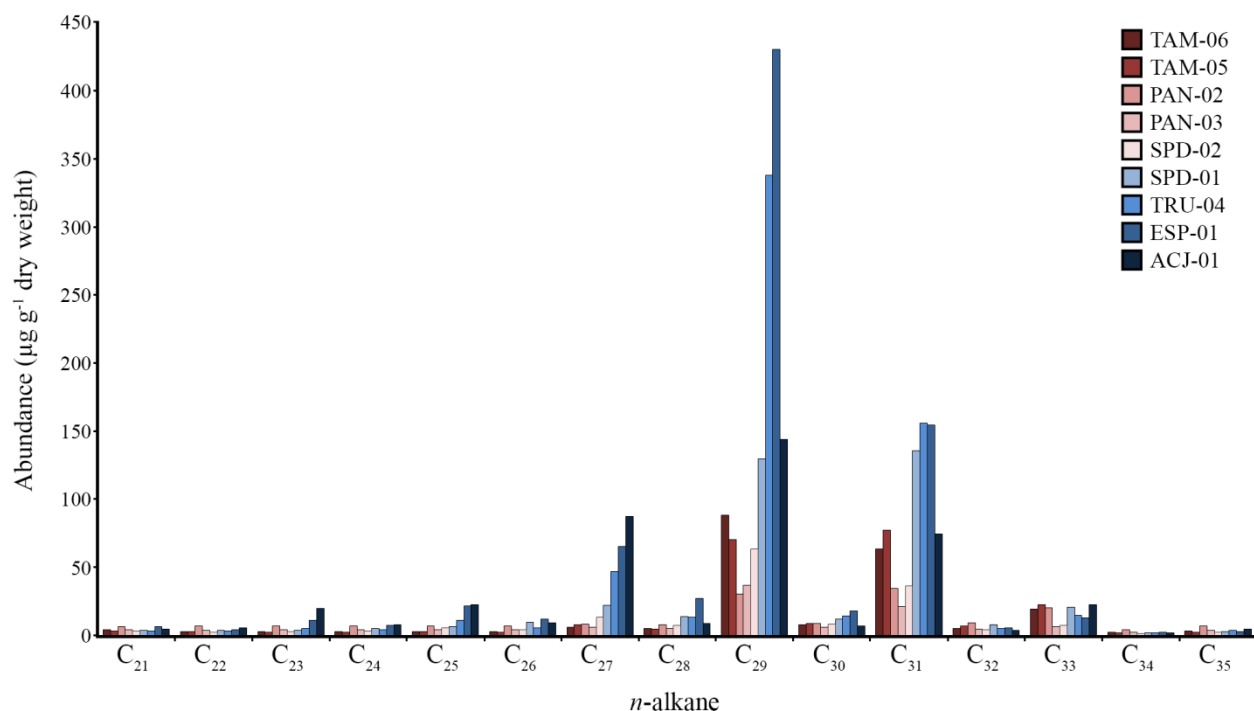


Figure 2 Mean *n*-alkane molecular abundance distribution by site. Variability not shown, see Table S1.

some tendency to shift with elevation (increasing abundance of C₂₇ with elevation already mentioned): C₃₅ is only present in detectable amounts in species present at the lowland sites.

The varied ‘fingerprints’ of chain length distribution can be summarized by a single number, the average chain length (ACL; Eqn. 2). The ACL of species is highly variable ranging from 24.1 to 32.6 overall. Only ACJ-01 (9 °C) is statistically different from all other sites by Tukey’s Honest Significant Difference test (Table S3), with a shorter mean ACL of 27.9. However despite the individual variability, the site mean ACL tends to increase with towards lower elevations (likely responding to temperature). Linear regression analysis reports a relationship between temperature and ACL of $ACL = 0.07 \text{ MAT} + 28.31$ with $R^2 = 0.87$ for ACL_{21-35} and 0.91 for ACL_{27-33} (Fig. 3).

Plants display a strong preference for synthesizing odd rather than even carbon chain length *n*-alkanes (Fig. 2). This tendency is summarized in a single number by the CPI_{21-35} (Eqn. 1), which averages 11.3 ± 0.3 (1 S.E.) but ranges from 0.5 to 43.5 across the entire sample set (Fig. 4). To reduce errors in detection of small peaks, and thus in determination of the true carbon preference index (CPI) we also calculated the CPI_{27-33} for a restricted range of dominant homologues, the C₂₇-C₃₃ chain lengths (Fig. 4b). The differences between sites mean values are not significant with the exception of TRU-04 and ACJ-01 ($p < 0.05$), which are different from all other sites except each other. These high elevation sites have higher CPI than the other sites; they also have no species with $CPI < 1$. This large sample set notably indicates that some species do not display the expected odd over even preference ($CPI < 1$) for example *Helicostylis towarensis* at SP-01 and SP-02 and *Huberodendron switenioides* at TAM-05. Both CPI_{21-35} and CPI_{27-33}

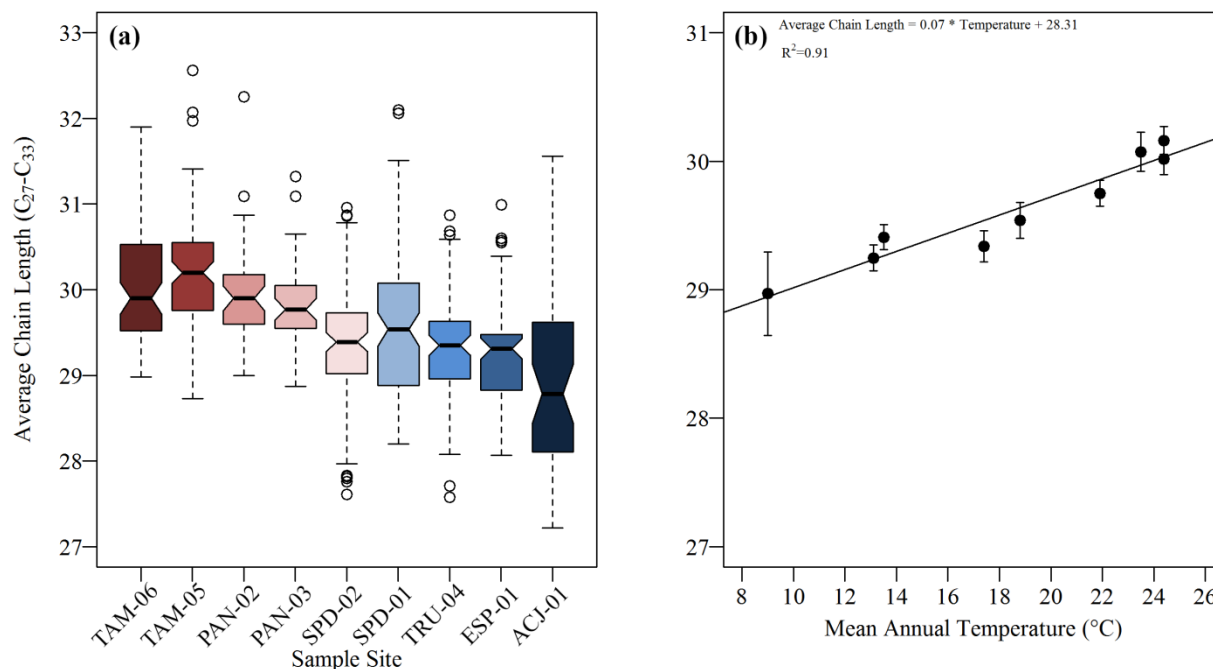


Figure 3 a) Box and whisker plots showing the ACL showing median (thick line), 95% CI around the median (notches), interquartile range (box), range (whiskers), and outliers (open circles). b) ACL by temperature (a function of elevation), showing community means after weighting for species wax loading and basal areas, and 1 S.E. (error bars).

show a positive trend of increasing CPI values with higher elevations ($R^2 = 0.78$ and 0.72 , respectively).

Total n-Alkane loading or “waxiness”

The total *n*-alkane load was calculated as the sum of the C₂₁₋₃₅ *n*-alkanes and reported as alkane load per unit dry leaf mass ($\mu\text{g g}^{-1}$; Fig. 5a,c), per unit mass carbon ($\mu\text{g g}^{-1}$ C; not shown) and per unit leaf area (KMA, $\mu\text{g cm}^{-2}$; Fig. 5b,d). Alkane load varies from 2.69 to 4722 $\mu\text{g g}^{-1}$ or 5.26 to 8827 $\mu\text{g g}^{-1}$ C and KMA varies from 0.02 to 74.7 $\mu\text{g cm}^{-2}$. Species with notably high KMA include *Clethra cuneata* and notably low KMA include *Guatteria glauca*. Tropical rainforest (TR) sites comprising TAM-05, TAM-06, PAN-02, PAN-03, and SPD-02, and tropical montane cloud forest (TMCF) sites comprising SPD-01, TRU-04, ESP-01, and ACJ-01 are significantly different by Tukey’s Honest Significant Difference test (Table 4). After community-weighting the KMA results from the individual species to generate site mean values, we find that KMA increases towards higher elevations (with a linear regression yielding $R^2 = 0.80$), although a clear transition occurs between TR and TMCF sites between 1494 and 1713 masl.

Partitioning of variances

Nested ANOVA statistical methods were used to attribute variance in *n*-alkane loading and molecular abundance distributions. Nested ANOVAs were performed on the ACL, CPI, and *n*-alkanes abundances ($\mu\text{g g}^{-1}$ and $\mu\text{g cm}^{-2}$; Fig. 6). Each of these analyses partitioned the observed variance into five different factors: family, genus, species, site, and residual. Taxonomy accounts

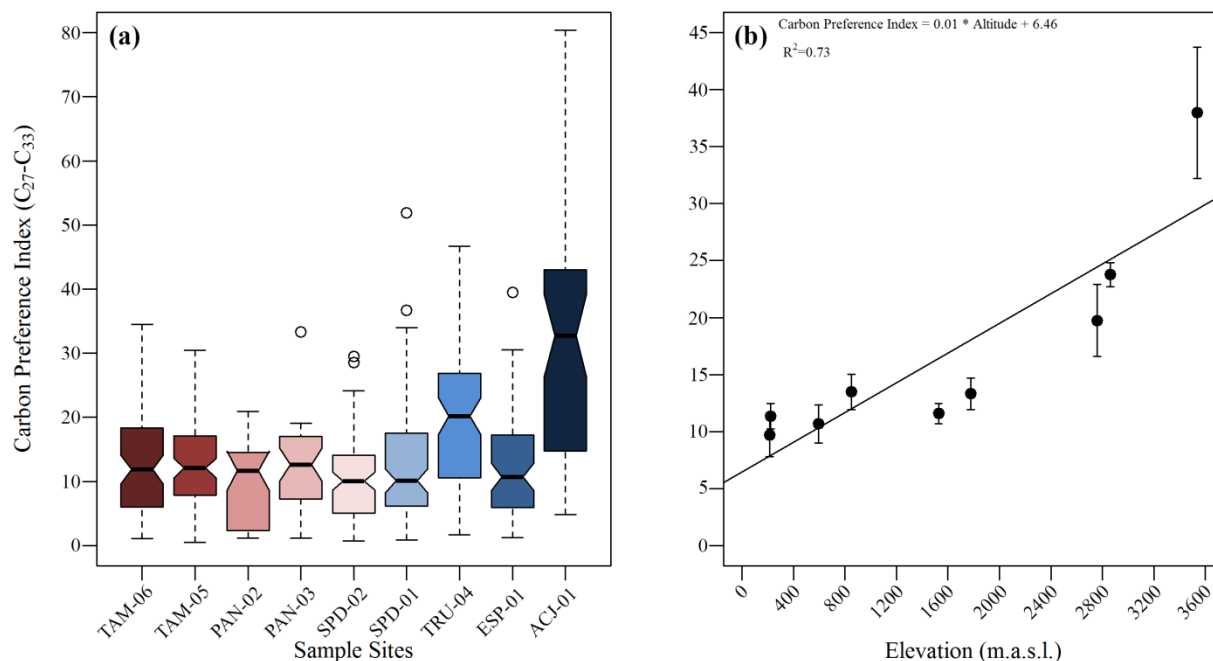


Figure 4 a) Box and whisker plots showing the CPI showing median (thick line), and 95% CI around the median (notches), interquartile range (box), range (whiskers), outliers (open circles). b) Carbon preference index (CPI) by showing the community mean value for each site, after weighting for species wax loading and basal area, along with 1S.E. (error bars).

for 64.4% of the total variance in ACL (Fig 6a; 20.7% family, 20.2% genus and 23.5% species), site for 19.1% and only 16.5% residual. For CPI (Fig. 6b), taxonomy accounts for 61% of variance (22.1% family, 0% genus, and 38.9% species), site accounts for 9.6% and residual for 29.4%. 36.3% of variance in alkane loading per unit weight (SK; Fig. 6c) is accounted for by taxonomy (20% family, 0% genus, 16.3% species), and site accounts for 4.6%, with a large residual (59.1%). When normalized by leaf area (KMA; Fig. 6d) taxonomy accounts for a larger share, 53.2% of the total variance (40.9%, 0% genus and 12.2% species), site accounts for 4.2% and residual for 42.6%. Thus a greater proportion of variance is accounted for when considering alkane loading per unit leaf area. Overall, plant taxonomy is the dominant factor in driving “waxiness” of the leaf (as Σ alkane) and chain length distribution (as ACL) of the *n*-alkanes.

Discussion

Molecular abundance distribution of n-alkanes

The molecular abundance distribution analysis (Fig. 2) shows two dominant carbon chains, C₂₉ and C₃₁, similar to that reported elsewhere (Eglinton & Hamilton, 1967). That these are common homologues in plant leaf wax *n*-alkane composition is not therefore new, but what is new here is the exceptional size of the dataset and that these are tropical tree species, previously understudied in the literature, thus representing an important addition to our global vision of plant leaf wax compositions. These are therefore cosmopolitan molecules that serve well as biomarkers for the majority of terrestrial tropical trees. However this survey also shows that despite the overall dominance of the C₂₉ and C₃₁ homologues, other homologues in the range C₂₁ to C₃₅ may be the

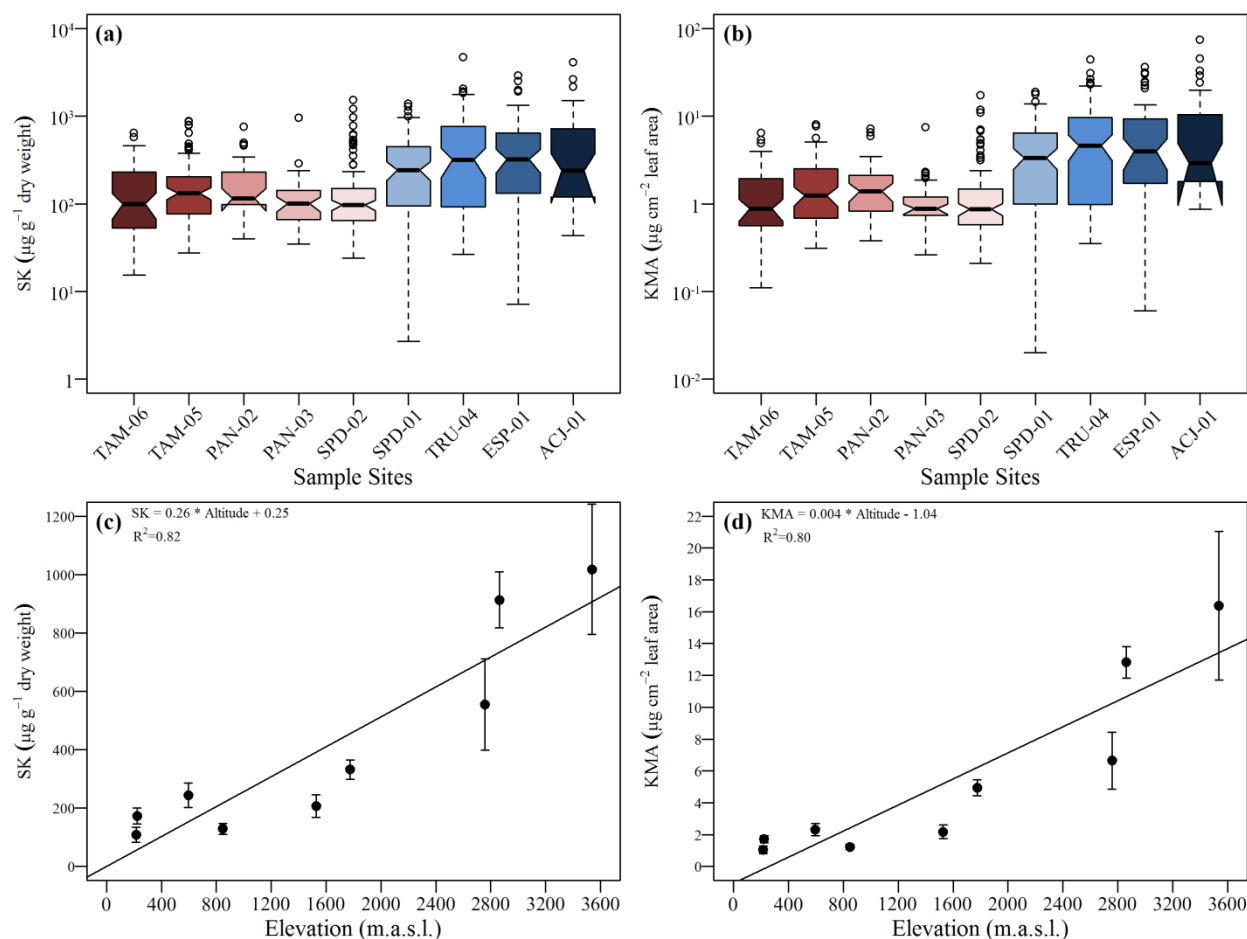


Figure 5 Leaf *n*-alkane loading with box and whisker plots (a and b) showing the *n*-alkane loading by a) leaf dry weight (SK) and b) lamina area (KMA), showing median (thick line), 95% CI around the median (notches), interquartile range (box), range (whiskers), and outliers (open circles). Also showing scatter plots with linear regression for c) SK and d) KMA, showing site community mean values weighted for species basal area with 1S.E. (error bars).

dominant *n*-alkane in any one species and that there are patterns in chain length distribution that vary with taxonomy and environment. The implications of this analysis in this large sample set, are that not all chain lengths can be followed across an environmental gradient; some chain lengths are more cosmopolitan than others; and no *n*-alkane is a unique ‘marker’ for a species (Table S1). Pragmatically then, C_{29} and C_{31} *n*-alkanes are useful as target molecules in isotopic analyses, whereas rarer compounds such as C_{35} would have more limited sources that may be preferentially sampling warmer environments or a smaller number of species, e.g. *Cavendishia bracteata* at ACJ-01.

The carbon preference index (CPI) shows a strong odd-over-even preference (Fig. 4) as is expected of terrestrial plant material (Eglinton & Hamilton, 1967). The preference for plants to make the odd over even chain lengths is based upon the synthesis of alkanes by decarboxylation from the *n*-alkanoic acid, which are dominantly even chain lengths. Long chain fatty acids are synthesized with the addition of a 2 carbon acetate unit from an even chain length precursor, however if plants begin with an odd chain length precursor an even chain length *n*-alkane will

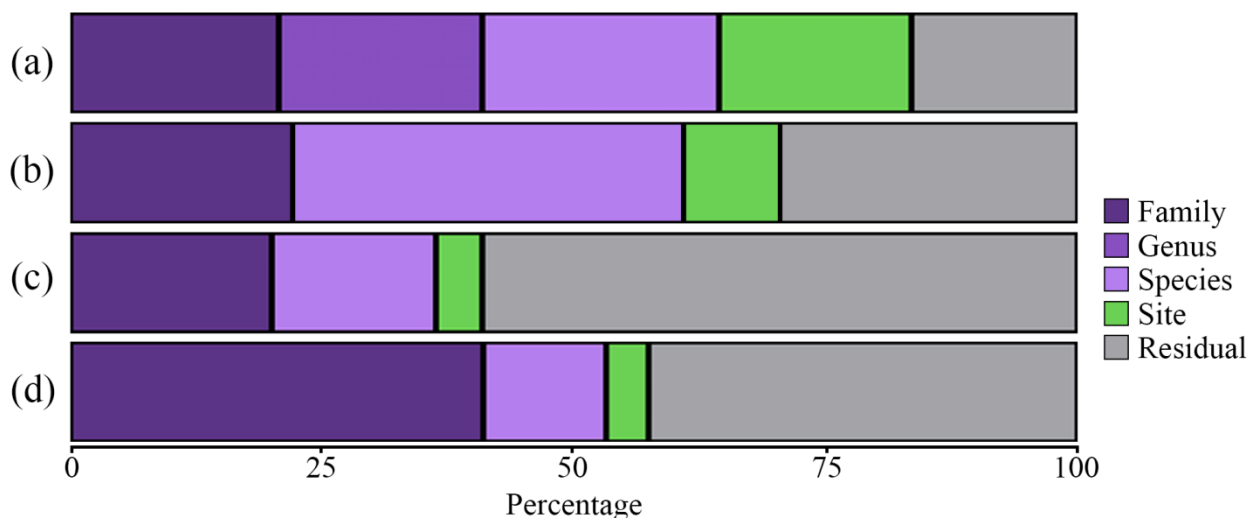


Figure 6 Partitioning of variance by nested ANOVA for a) ACL_{21-35} , b) CPI_{21-35} , c) n -alkane load by leaf dry weight (SK), d) n -alkane load standardized by lamina area (KMA).

result (Zhou *et al.*, 2010), and this can be viewed as a biochemical ‘mistake’ as it is not the dominant pathway. The extent to which plants make these ‘mistakes’ in biosynthesis has never before been so comprehensively sampled in a large dataset reporting CPI, and that this is done in a biodiverse tropical ecosystem provides for novel observations about the flexibility of this biosynthetic pathway. In order to study the propensity of plants to make biosynthetic mistakes, we focus on two species with low CPI: *Helicostylis towarensis* (Moraceae) and *Huberodendron swietenoides* (Malvaceae). Over 60% of individuals from these two species display CPI below one, which occur in the tropical rainforest (TR; *H. swietenoides*) and at the interface of TR and the tropical montane cloud forest (TMCF; *H. towarensis*). Low CPI values have been observed in gymnosperms, but are uncharacteristic for angiosperms sampled to date (Bush & McInerney, 2013). Past studies have not found low CPI in other species of Moraceae (Sonibare *et al.*, 2005; Guo *et al.*, 2014), and no comparison data are available for the Malvaceae. Overall we note that there is a tendency to lower CPI at lower elevation (Fig. 4a,b). Although we have no mechanistic proof, we hypothesize that at higher temperatures that there is greater possibility for biochemical ‘mistakes’ at faster reaction rates. Alternatively the greater biodiversity at lower elevations may present more variations in plant biochemistry in which such biochemical pathways, resulting in low CPI, can be found. This dataset provides information on individual species and patterns across the environmental gradient and the outliers and patterns could be used to empirically test the plasticity of these biosynthesis pathways further.

The average chain length (ACL) of n -alkanes tends to increase with higher temperatures (Fig. 3a,b). Based on first principles we infer that this relationship may be that longer carbon chains offer better thermal stability. However, the 15.4 °C temperature increase across the entire profile results in a mere one carbon increase in site mean ACL. We emphasize that this correlation is not sensitive enough to warrant its use as a palaeothermometer, particularly in the context of the large variability between individuals (Fig. 3a). Much of the variance in ACL has been linked to taxonomy (Fig. 6a) suggesting that the chain length distribution of plants may in

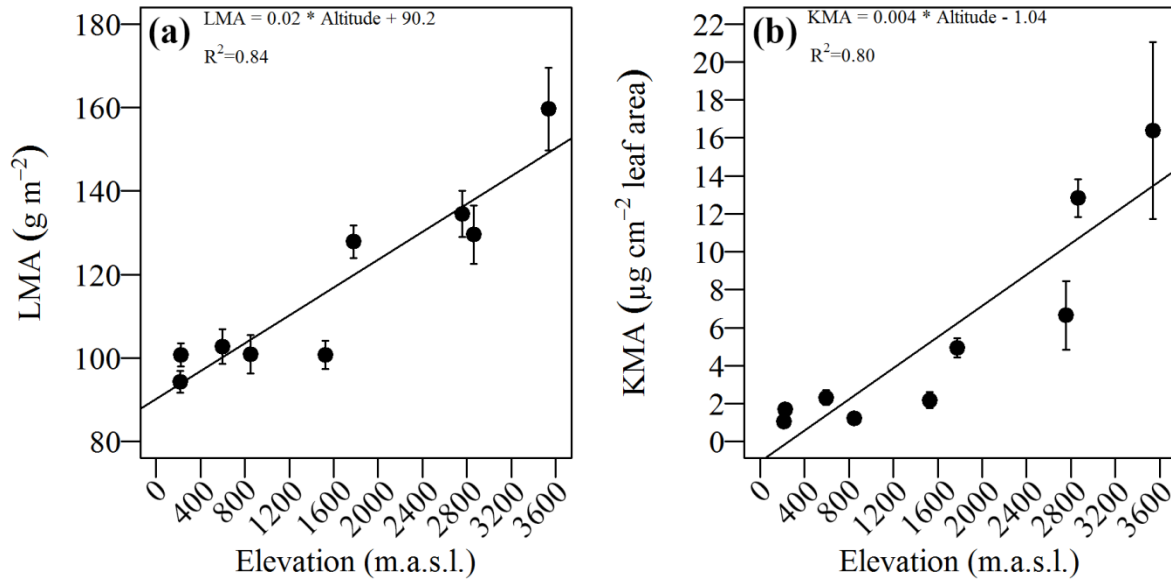


Figure 7 a) Scatter plot with linear regression of leaf mass per area (LMA; Malhi *et al.*, pers. comm.) across the elevation transect, showing 1 S.E. (error bars). b) Scatter plot with linear regression for KMA, showing site community mean values weighted for species basal area with 1 S.E. (error bars).

part relate to the plants' evolutionary past (perhaps as an adaptation to temperature). However the low temperature sensitivity across the profile and high interspecies variability (Fig. 3a) leads us to discount ACL as a proxy for temperature, at least in the TR and TMCF ecosystems studied here, and thus our findings are consistent with those of the prior 'global' survey of ACL data by Bush & McInerney (2015).

Greater n-Alkane loading or "waxiness" in the Andes

The quantification of *n*-alkane loadings show a trend of increases in wax loading with increasing elevations ($R^2 = 0.8$, Fig. 5c,d). Observing the distributions of *n*-alkane loadings (Fig. 5a,b) allows for the identification of a step shift in 'waxiness' between SPD-02 and SPD-01, occurring at 1494 and 1713 m a.s.l. respectively. This shift shows higher wax loading on a leaf area basis (KMA) at the Andean forest sites. Further analysis of the step shift shows that the Andean TMCF sites at and above 1713 m a.s.l. are significantly different from the lower TR sites (Table S2). This shift corresponds to the same elevation where forest canopy height is reduced (Table 1) and leaf mass per area (LMA) increases substantially (Fig. 8a; Asner *et al.*, pers. comm.). The step shift in KMA occurs along with strong physiological and biochemical responses across multiple plant traits at the same elevation. Environmentally, the step shift coincides with the cloud base (Halladay *et al.*, 2012a,b), and we hypothesize that increased KMA and LMA (Fig. 7a,b) have shared roots in 'economic' investment strategies in leaf construction (Wright *et al.*, 2004), as higher investments in the Andean sites being associated with longer leaf lifespan (LL; Girardin *et al.*, 2014a,b; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014). Leaf wax lipids are a costly investment (Villar & Merino, 2001), even considering the carbon (C) and hydrogen (H) are not limiting nutrients here (Fisher *et al.*, 2013). Plants in the TMCF produce more wax despite this

cost, diverting essential carbohydrates from other processes, and thus wax synthesis must fulfill an important function in these plants. This could be to protect the plant from the greater fungal pressure associated with the moist conditions within the TMCF, or even increases in harmful UV-B radiation (Steinmüller & Tevini, 1985; Kakani *et al.*, 2003; Liu *et al.*, 2005) at the highest sites (e.g. ACJ-01) due to reductions in protective cloud cover (Estupiñán *et al.*, 1996; Schafer *et al.*, 1996).

The only caveat is that the leaf wax quantification in this study captures only the *n*-alkane component of the waxes, and we do not have similar quantification for other ‘wax’ components. We note that *n*-alkanes are among the most abundant compounds found in leaf waxes, although their proportional abundance varies between different species (e.g. Bakker *et al.*, 1998; Jetter & Schäffer, 2001; Conte *et al.*, 2003) or with different leaf ages (e.g. Tulloch, 1973; Chachalis *et al.*, 2001). There remains more work to be done to quantify total ‘waxiness’ and wax composition, including the components of wax that have greater pathogen resistance, for example. However, the insights from leaf wax *n*-alkane loading and molecular abundance distributions here provide a geologically useful start – as these are the components best represented in the molecular fossil record.

Leaf wax trait diversity in the context of species diversity

In the western Amazon and adjacent Andean forests, species diversity and wax trait diversity are linked: taxonomy is the dominant factor identified in nested ANOVA analyses of KMA (53.2%), ACL (64.4%), and CPI (61.0%; Fig. 6a,b,d). Taxonomy encompasses the categories of family, genus and species shown individually in Fig. 6. A large portion of taxonomic control is at the family level, especially for KMA, which suggests deep phylogenetic controls on the variation of KMA, ACL, and CPI within plants – and presumably the molecular abundance distribution ‘fingerprints’ as well (which could not be analyzed in this way). Taxonomy is the main driver of variance, which resolves the origins of the considerable variability in leaf wax traits (i.e. KMA, ACL, and CPI) seen within the sites (Fig. 3, 4, 5; Table S1).

The partitioning of variance finds that a relatively small proportion of the variance in leaf wax traits is driven by site-to-site variations (ca. 5%, 10% or 20%; Fig. 6). This is perhaps surprising given the topographic range (>3000 m), temperature range (>15 °C) and precipitation

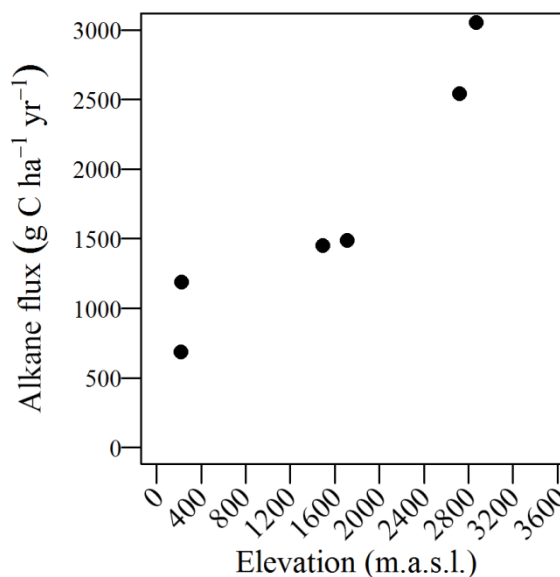


Figure 8 The wax production, or alkane flux, of leaf wax *n*-alkanes, showing site mean leaf wax *n*-alkane production, based on species’ *n*-alkane loadings (this study), species basal area proportions (Malhi *et al.*, this issue) and NPP for each site (Girardin *et al.*, 2014a; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014).

(>3000 mm yr⁻¹) across the transect, as well as other variables that shift markedly along the elevation profile. Given the high beta diversity, i.e. species turnover between sites, it is possible that the taxonomic factor encompasses current environmental factors. However, the large portion of variance at the family level suggests instead that long-term evolutionary responses dominate the shifting traits across the environmental gradient, rather than recent plastic responses to environment. It is likely then, that the origins of plant leaf wax traits are set much earlier in evolutionary history, and that these leaf wax traits are relatively insensitive to the current environmental changes. Ideally, additional experiments would be conducted to test whether some of the taxonomic effect here is environmental, e.g. through plant translocation experiments, or controlled greenhouse experiments. These experiments could directly test whether these leaf wax traits can adjust to the rapid environmental change, or if they are truly fixed by taxonomic controls with slower evolutionary responses. While these two options cannot be fully answered at this time, this study offers additional insights. Only a few species are identified at more than one site. For example, *Clusia elliptica* is found at sites SPD-01 and ESP-01, and the leaf wax KMA increases, ACL decreases, and CPI increases with higher elevations. These properties seem to suggest a plastic response of *C. elliptica* to changing environmental conditions, however, not all species respond in a similar way. Out of 23 species, 11 show decreasing ACL values and 6 show increases in KMA, and only 2 species (i.e. *Caryocar pallidum*, *Clusia elliptica*) show both. Previous research does not offer a unanimous solution to the separation of taxonomic and environmental signals. In a latitudinal transect along the eastern USA, Tipple & Pagani (2013) report correlations between temperature and ACL, as do Sachse *et al.* (2006) who show correlations between growing temperature and chain length distributions in plants. Acacia and Eucalyptus species in Australia have been reported to display opposite trends in ACL, while *n*-alkane concentrations rose under dry conditions for both (Hoffman *et al.*, 2013). Furthermore, there is weak correlation between leaf wax traits and climatic parameters in arid and semi-arid biomes in South Africa, likely due to inter-site differences in plant functional groups (Carr *et al.*, 2014). A majority of the consulted literature seems to support environmental control of leaf wax traits, a relationship this study cannot support, at least not for the presented elevation gradient. The divergence may lie in the large sample size in this study compared to the other studies that sampled a much smaller number of species across a larger geographic range, and point to strong taxonomic controls in the tropics.

Ecological scaling of leaf waxes

The leaf wax traits presented in this study (Fig. 3, 4, 5) were community-weighted based upon the proportions of those species sampled on within the forest plots and the wax production by those species. For example, the presented values of ACL take into account both the *n*-alkane abundance, or ‘waxiness’, and the species basal area. This allows for the study of chain length distributions without the confounding effects of plant species that are dominant in the environment, or have high wax production. This ecological scaling approach is unprecedented for leaf wax studies as far as we are aware and may represent a model for generating community

representative ‘calibrations’ for other leaf wax proxies including carbon (Wu *et al.*, pers. comm.) and hydrogen isotopes (Feakins *et al.*, pers. comm.).

Carbon flux along the elevation gradient

We found the waxiness of plant leaves tends to increase along the elevation gradient, and after generating forest plot weighted mean wax production, this can be connected with prior Net Primary Productivity (NPP) estimates for each forest plot where this data is available (Girardin *et al.*, 2014a; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014) to generate estimates of the Net Primary Productivity of leaf wax *n*-alkanes (NPP_{wax}) a term newly coined here. The wax production, or alkane flux, was calculated as follows:

$$NPP_{wax} = \left(\frac{C_{alkane} \cdot SK_{site}}{C_{biomass}} \right) \cdot NPP_{leaf}$$

, where C_{alkane} and $C_{biomass}$ represent the carbon fractions of *n*-alkanes and dry weight biomass, respectively, SK_{site} is mean *n*-alkane abundance per site, and NPP_{leaf} is the leaf net primary production (NPP_{leaf}).

We found that the NPP_{wax} increases towards higher elevations (Fig. 8). Wax production increases even as NPP_{leaf} decreases at higher elevations (Girardin *et al.*, 2014a; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014), likely because the increase in leaf waxiness counteracts the reduction in NPP_{leaf} . This has implications for both contemporary and palaeoecological research involving the extraction of leaf wax biomarkers from riverine systems or marine system receiving input from these rivers. Higher NPP_{wax} production in montane ecosystems would lead to over-representation of these systems further downstream on a per area basis and thus may lead to the over-representation of mountain ecosystems in downstream sedimentary records if inputs are well-preserved. However remineralization in transit could lead to the loss of this mountain input even given the higher NPP_{wax} . In terms of ecosystem productivity, the higher NPP_{wax} and lower NPP_{leaf} in the Andes implies a higher fraction of productivity is being diverted to wax production, and this higher proportional investment in a defense compound necessarily diverts resources from growth and illustrates the trait and production responses to changing adaptive pressures across the elevation profile.

Conclusions

This study has presented an unprecedented dataset of plant leaf wax traits in the megadiverse western Amazon tropical rainforest (TR) and adjacent Andean tropical montane cloud forests (TMCF) within Peru. It has quantified the molecular abundance distribution and amount of leaf wax *n*-alkanes on leaves and analyzed their association with taxonomic and environmental controls.

We find an expected response of increasing *n*-alkane chain length at lower elevations, as characterized by the average chain length (ACL). However, this response is very weak, with only an incremental increase of one carbon chain length in the community mean across the entire profile (Fig. 3b). Given the large range of variability associated with taxonomy (Fig. 6a), we find it unlikely that ACL could be used as a proxy for environmental conditions, at least within the

context of the TR and TMCF studied here. It remains possible that other unique environments may be diagnostic, such as the puna grasslands of the high Andes that are beyond the scope of this forest leaf wax survey.

Furthermore, this study identified a step shift in *n*-alkane loading between TR and TMCF ecosystems. This shift shows considerable physiological and biochemical responses across multiple plant traits, including reduced forest canopy height (Table 1) and a substantial increase in leaf mass per area (LMA; Asner *et al.*, pers. comm.). Environmentally, this shift coincides with the cloud base (Halladay *et al.*, 2014), and we thus hypothesize that the increases in KMA and LMA are related to leaf economics (Wright *et al.*, 2004), with higher investments occurring in the Andean sites along with longer leaf lifespan (LL; Girardin *et al.*, 2014a,b; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014). Wax synthesis is expensive (Villar & Merino, 2001) and it requires the diversion of carbohydrates away from growth and organ construction. Therefore, the increase in wax synthesis could be related to greater fungal pressure within the TMCF, or increases in UV-B radiation at the highest elevations.

We find that taxonomy is the dominant factor affecting variance in leaf wax traits, and that a portion of that variance has deep phylogenetic roots at a family level. This suggests that the observed changes in leaf wax traits across the environmental gradient are associated with long-term evolutionary responses and high species turnover.

This study has identified a primary taxonomic control on leaf wax traits, and finds that the protective wax layer on the leaf increases along with LMA in the Andes. This has provided a new insight into the leaf wax trait response to taxonomic change and environmental forcings, providing new insights into the functioning of tropical lowland and montane forest ecosystems.

Acknowledgments

This work is a product of the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk), the Andes Biodiversity and Ecosystems Research Group (ABERG; andesresearch.org), and the Amazon Forest Inventory Network (RAINFOR; rainfor.org) research consortia. The field campaign was funded by grants to Yadvinder Malhi from the UK Natural Environment Research Council (Grants NE/D01025X/1, NE/D014174/1), with additional support from European Research Council advanced investigator grants GEM-TRAITS (321131) and T-FORCES (291585) as well as the Jackson Foundation to Yadvinder Malhi. Gregory Asner was supported by the endowment of the Carnegie Institution for Science and a grant from the National Science Foundation (DEB-1146206). Laboratory work at the University of Southern California (USC) was in part supported by the US National Science Foundation (EAR-1227192) and the ACS Petroleum Research Fund (53747-ND2) to Sarah Feakins. We thank the Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP) and personnel of Manu and Tambopata National parks for logistical assistance and permission to work in the protected areas. We also thank the Explorers' Inn and the Pontifical Catholic University of Peru, as well as ACCA for use of the Tambopata and Wayqecha Research Stations, respectively. Many researchers were involved in the field, in particular we would like to thank Prof. Eric Cosio, Walter Huaraca-Huasca and Judit Huaman for advising on field logistics;

tree climbers: Cristian Costas Pacheco, Dino Chacón, Hugo Ninatay Rivera; field project supervision: Tatiana Erika Boza Espinoza, Mireya Natividad Raurau Quisiyupanqui; species identification and basal area: William Farfan, Felipe Sinca; leaf areas: Rosa Mercedes Castro Ccoscco, Gloria Rayme Paucar, Arturo Robles Cáceres, Yovana Yllanes Choque and Yolvi Valdez. The Carnegie Institute contributed the taxonomy. We thank USC undergraduate lab assistants: Lindsay Arvin, Alexandra Figueroa, Clara Hua, Krista McPherson, Evan Rosca, and Jeremy Sunwoo. Finally, I would like to thank Christine Wu for allowing me to integrate her data into this study, Sarah Feakins for fulfilling the role of supervisor, and Boris Jansen and William Gosling for being examiner and co-assessor, respectively, on this project.

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Table S1 Results of leaf wax n-alkane analysis by species and site.

Species	Abundance of alkanes in leaf wax ($\mu\text{g g}^{-1}$ dry weight)																C ₂₁ -C ₃₅				C ₂₇ -C ₃₃						
	C ₂₁	C ₂₂	C ₂₃	C ₂₄	C ₂₅	C ₂₆	C ₂₇	C ₂₈	C ₂₉	C ₃₀	C ₃₁	C ₃₂	C ₃₃	C ₃₄	C ₃₅	Total	C _{max}	ACL	σ	CPI	σ	ACL	σ	CPI	σ		
Tambopata VI																											
<i>Astrocaryum gratum</i>	2.3	2.3	2.4	2.3	2.6	2.5	3.1	2.5	2.9	3.3	3.6	2.6	2.7	1.6	2.4	39.1	31	29.2	0.3	2.8	0.6	30.0	0.1	3.6	1.0		
<i>Brosimum alicastrum</i>	3.6	3.6	3.7	3.7	3.8	3.8	3.9	3.9	6.1	4.4	10.1	4.8	7.1	3.7	3.7	69.9	31	30.8	0.1	4.8	0.4	31.1	0.2	5.7	0.6		
<i>Celtis schippii</i>	0.0	0.3	0.1	0.2	0.1	0.2	0.5	1.0	6.1	2.6	10.5	1.7	2.2	0.0	0.0	25.6	31	30.4	0.1	3.6	0.9	30.5	0.0	4.1	1.2		
<i>Chimarrhis hookeri</i>	3.6	3.6	3.6	3.7	3.7	3.7	5.2	4.0	37.2	6.5	100.2	8.2	41.1	3.9	4.6	232.8	31	31.0	0.0	18.6	3.3	31.0	0.0	19.7	3.5		
<i>Clarisia racemosa</i>	3.7	3.7	3.8	3.8	3.8	3.8	4.4	4.8	74.1	7.9	95.5	6.1	16.5	2.4	3.8	238.4	31	30.1	0.3	20.2	3.3	30.1	0.3	21.2	3.2		
<i>Endlicheria formosa</i>	2.3	2.3	2.3	2.4	2.5	2.4	3.7	3.2	39.8	7.1	34.0	2.5	2.4	1.0	2.3	110.1	29	29.7	0.2	10.6	2.9	29.8	0.2	11.1	2.7		
<i>Endlicheria sp. 28842</i>	2.3	2.3	2.3	2.2	2.5	2.7	8.5	6.9	200.2	16.1	72.4	2.5	2.4	2.2	2.3	327.7	29	29.5	na	14.2	na	29.5	na	14.6	na		
<i>Iriarteia deltoidea</i>	2.1	2.1	2.1	2.1	2.3	2.3	2.5	2.5	3.5	2.8	4.0	2.3	2.3	2.1	2.1	37.1	31	29.4	0.2	3.3	1.1	29.9	0.1	4.2	1.7		
<i>Lonchocarpus guillemineanus</i>	1.8	1.9	1.9	1.8	2.0	2.0	2.2	2.1	3.0	2.3	2.8	2.0	2.2	0.0	1.9	29.8	29	29.4	na	2.6	na	29.9	na	2.9	na		
<i>Mabea nitida</i>	0.0	0.4	0.2	0.4	0.6	0.7	8.4	8.0	220.0	14.1	66.3	4.1	12.9	0.7	1.3	338.0	29	29.6	0.2	11.4	1.2	29.5	0.1	12.2	1.3		
<i>Myroxylon balsamum</i>	3.2	3.2	3.3	3.4	3.9	3.5	5.4	4.8	41.4	5.9	27.1	4.2	4.3	3.2	3.2	119.9	29	29.6	0.0	11.5	2.2	29.8	0.1	13.2	2.6		
<i>Ocotea bofo</i>	0.0	0.3	0.2	0.4	0.6	1.3	7.0	2.7	51.6	3.9	26.5	0.2	0.2	0.0	0.0	94.9	29	29.4	0.1	10.3	1.2	29.4	0.1	12.8	1.3		
<i>Otoba parvifolia</i>	5.5	5.6	5.7	5.9	6.2	7.1	8.4	9.9	23.9	8.0	18.8	5.8	6.0	2.1	5.6	124.5	29	28.9	0.4	5.5	4.3	29.3	0.2	6.7	5.3		
<i>Pourouma cecropiifolia</i>	3.2	3.2	3.3	3.3	3.4	3.3	3.4	3.7	4.0	4.5	4.5	3.9	3.8	2.1	3.2	53.0	31	29.6	0.2	1.2	0.1	30.3	0.1	1.2	0.1		
<i>Pouteria torta</i>	2.9	3.0	3.0	3.1	3.1	3.0	3.7	2.5	77.7	5.4	58.6	3.8	4.4	1.1	2.3	177.6	29	29.8	0.1	26.7	4.3	29.8	0.1	32.2	1.7		
<i>Pterocarpus rohrii</i>	3.3	3.4	3.4	3.4	3.6	3.5	5.5	5.4	77.0	9.6	118.7	7.9	21.6	3.6	3.4	273.3	31	30.5	0.1	13.4	3.5	30.5	0.1	14.1	3.2		
<i>Rinorea viridifolia</i>	0.0	1.7	0.2	1.0	0.3	0.6	1.3	1.3	25.3	3.2	123.5	9.3	103.2	3.5	8.0	282.3	31	31.4	0.2	13.1	1.4	31.4	0.2	17.3	2.0		
<i>Scheelea cephalotes</i>	3.4	3.4	3.5	3.4	3.6	3.5	3.7	3.6	4.4	3.5	4.3	3.5	3.6	2.0	3.5	53.0	29	29.3	0.3	4.1	1.5	29.8	0.4	6.0	2.7		
<i>Socratea exorrhiza</i>	2.6	4.3	4.3	4.3	4.4	4.3	4.4	4.3	4.6	3.0	4.6	3.0	3.1	0.0	4.4	55.5	31	28.6	0.5	3.8	0.9	29.8	0.4	8.0	2.1		
<i>Swartzia arborescens</i>	2.7	2.7	2.7	2.8	3.0	2.9	6.6	5.6	237.8	11.6	201.3	7.6	35.8	2.8	2.8	528.7	29	30.1	0.2	27.4	1.2	30.1	0.2	28.3	1.3		
<i>Symphonia globulifera</i>	0.0	1.2	0.1	0.7	0.1	0.4	3.3	2.3	88.5	3.8	52.2	1.0	1.4	0.1	0.2	155.4	29	29.6	0.1	17.5	3.1	29.6	0.1	20.4	3.5		
<i>Zanthoxylum riedelianum</i>	2.0	2.1	2.1	2.1	2.1	2.1	8.2	4.4	153.1	5.7	17.3	2.3	2.4	2.1	2.1	210.1	29	29.1	0.0	25.7	1.7	29.1	0.0	26.6	1.5		
Mean	1.8	2.2	2.0	2.2	2.2	2.3	4.5	3.8	64.0	5.8	49.4	4.0	15.6	1.7	2.7	164.3		29.8		11.6		30.0		13.3			
σ	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.3	9.3	0.5	7.2	0.4	4.5	0.2	0.4	17.6		0.1		1.0		0.1		1.1			
Tambopata V																											
<i>Anthodiscus peruanus</i>	1.4	2.5	1.5	2.7	1.7	1.6	3.6	2.1	36.0	4.8	56.8	5.6	14.7	1.7	2.4	139.0	31	30.5	0.0	13.2	0.2	30.6	0.1	16.2	1.5		
<i>Bertholletia excelsa</i>	1.4	2.3	2.3	2.2	2.5	2.3	3.4	2.3	21.4	5.4	44.8	6.9	16.8	1.4	1.4	116.9	31	30.6	0.1	7.6	1.2	30.8	0.1	8.4	1.4		
<i>Bixa excelsa</i>	0.0	0.4	0.0	0.2	0.1	0.3	0.4	1.2	20.6	4.0	50.1	4.3	24.1	0.5	3.4	109.6	31	31.1	0.2	10.0	1.8	31.0	0.2	10.8	2.0		
<i>Brosimum lactescens</i>	2.0	2.3	2.1	2.3	2.2	2.2	2.5	3.0	88.5	7.3	38.7	3.0	3.7	0.0	1.5	161.2	29	29.6	0.1	15.3	2.4	29.7	0.1	17.5	2.1		
<i>Brosimum rubescens</i>	0.0	4.9	0.0	0.0	0.0	0.0	5.1	0.0	27.2	6.1	27.3	5.3	7.7	0.0	0.0	83.6	31	30.1	na	13.5	na	30.2	na	18.0	na		
<i>Calophyllum brasiliense</i>	0.0	0.7	0.1	0.4	0.1	0.4	0.5	1.8	10.9	4.1	37.5	1.1	1.9	0.1	0.1	59.8	31	30.6	0.1	6.4	0.4	30.6	0.1	7.2	0.4		
<i>Cedrelinga cateniformis</i>	2.4	3.1	2.5	2.4	2.5	1.2	3.2	4.4	62.5	8.8	68.7	6.7	11.6	1.3	1.3	182.6	31	30.2	0.0	11.8	0.8	30.2	0.0	12.1	0.7		
<i>Clarisia racemosa</i>	2.4	3.5	2.5	3.6	2.5	2.5	4.8	3.9	132.5	10.1	124.0	6.0	18.8	2.6	5.4	325.0	29	29.9	0.2	17.8	3.0	30.0	0.1	22.8	1.6		
<i>Diploptropis purpurea</i>	2.6	2.6	2.7	2.7	3.7	3.0	13.4	7.0	74.4	16.7	335.2	29.1	148.0	3.4	2.9	647.4	31	31.1	0.1	12.0	1.2	31.1	0.1	12.4	1.2		

<i>Eschweilera coriacea</i>	2.9	2.9	3.0	3.1	3.2	3.2	3.5	3.7	4.1	4.2	52.0	18.6	121.0	6.8	4.8	237.1	31	32.2	0.2	8.0	1.7	32.2	0.2	10.0	2.4
<i>Hebepetalum humiriifolium</i>	5.9	5.9	6.0	6.0	6.0	3.5	6.5	8.3	183.2	24.4	216.0	16.3	39.2	6.7	7.8	541.6	31	30.4	0.0	12.7	1.5	30.3	0.0	13.1	1.6
<i>Huberodendron swietenoides</i>	1.5	3.9	4.0	4.0	4.1	4.2	4.5	5.4	5.7	6.5	6.0	3.5	2.2	1.6	1.6	58.8	30	29.2	0.7	1.6	1.0	29.9	0.3	6.7	6.1
<i>Iriartea deltoidea</i>	1.9	1.9	1.9	1.9	1.9	1.9	2.1	2.1	2.7	2.3	3.8	2.1	2.1	0.0	1.2	29.7	31	29.6	0.4	3.0	0.2	30.3	0.0	3.6	0.2
<i>Jacaranda copaia</i>	2.3	2.3	2.3	2.4	2.7	3.0	4.9	8.6	95.8	9.1	24.4	3.0	3.7	0.6	2.4	167.4	29	29.3	0.1	7.8	0.4	29.4	0.1	8.4	0.5
<i>Leonia glycyarpa</i>	0.0	0.5	0.1	0.3	0.3	0.3	1.4	1.0	46.5	5.4	86.2	5.8	14.8	0.3	0.3	163.2	31	30.6	0.1	11.2	0.8	30.6	0.1	12.0	0.9
<i>Licania heteromorpha</i>	0.0	0.6	0.1	0.4	0.3	0.4	3.7	1.4	63.6	5.1	54.9	1.5	2.9	0.1	0.2	135.3	29	29.8	0.2	14.1	0.1	29.8	0.2	15.7	0.1
<i>Licania sp. 28729</i>	0.0	0.4	0.1	0.3	0.1	0.2	0.9	0.7	49.7	3.7	49.0	1.3	2.2	0.0	0.0	108.8	29	30.1	0.1	15.9	1.3	30.1	0.1	17.7	0.1
<i>Ocotea bofo</i>	0.0	0.3	0.1	0.3	0.4	1.0	34.1	6.5	101.1	8.2	63.9	1.2	1.4	0.0	0.0	218.6	29	29.1	0.2	11.3	1.8	29.1	0.2	12.1	1.7
<i>Ouratea iquitosensis</i>	3.8	3.8	3.8	3.8	3.9	2.0	4.1	4.0	98.1	8.8	95.3	5.3	9.4	1.0	1.0	248.1	29	30.1	0.0	27.1	1.4	30.1	0.0	27.6	1.5
<i>Pourouma bicolor</i>	3.4	3.5	3.5	3.6	3.7	3.7	5.0	4.7	14.1	6.1	11.2	5.1	6.2	2.4	2.5	78.6	29	29.8	0.2	2.9	1.4	30.1	0.2	3.0	1.5
<i>Pourouma minor</i>	2.8	4.2	4.3	4.4	4.5	4.5	5.1	5.1	6.4	7.0	7.7	5.4	5.3	0.0	0.0	66.7	31	29.6	0.2	1.5	0.0	30.2	0.1	1.6	0.1
<i>Pouteria torta</i>	3.9	4.0	4.1	4.2	7.9	5.0	75.1	11.4	258.0	14.6	188.2	7.9	32.8	4.1	5.6	626.7	29	29.9	0.7	23.4	1.6	29.9	0.7	25.2	1.9
<i>Pseudolmedia laevigata</i>	1.7	2.7	1.8	2.0	1.8	2.0	3.3	3.8	69.6	7.1	36.3	3.5	7.9	1.9	2.0	147.3	29	29.9	0.2	11.4	2.0	30.0	0.2	12.3	1.9
<i>Pseudolmedia laevis</i>	4.4	4.5	4.6	4.7	4.8	4.7	4.9	5.2	28.8	6.9	13.9	4.9	5.2	4.4	4.5	106.4	29	29.5	0.2	7.5	0.2	29.6	0.1	8.8	0.9
<i>Roucheria columbiana</i>	2.2	3.5	2.3	2.3	2.5	2.3	6.4	3.4	165.4	13.0	88.3	5.5	9.5	2.4	2.5	311.5	29	29.7	0.1	17.4	1.7	29.7	0.0	18.7	1.6
<i>Tachigali chrysaloides</i>	2.0	2.9	2.9	2.8	3.0	3.0	8.4	5.5	69.1	5.8	23.5	4.1	5.8	2.1	2.1	143.0	29	29.5	0.1	13.1	0.6	29.5	0.1	14.2	1.0
<i>Tachigali paniculata var. alba</i>	2.6	3.6	2.7	3.6	2.8	2.7	3.1	3.2	29.3	3.9	26.4	4.0	11.5	2.7	2.7	104.8	29	30.3	0.3	11.2	2.5	30.4	0.3	12.9	2.8
<i>Ticorea tubiflora</i>	5.0	5.0	5.0	5.0	5.1	5.0	5.8	5.2	54.9	8.1	78.2	6.7	9.4	5.0	5.1	208.3	31	30.3	na	24.0	na	30.3	na	25.2	na
Mean	1.8	2.4	2.0	2.2	2.3	2.1	7.3	3.9	63.1	7.5	65.5	5.7	18.2	1.6	2.1	187.7		30.1		11.2		30.2		12.6	
σ	0.2	0.2	0.2	0.2	0.2	0.2	1.8	0.3	7.6	0.6	8.2	0.7	3.9	0.2	0.3	18.7		0.1		0.7		0.1		0.7	
Pantiacolla II																									
<i>Bellucia aequioba</i>	7.1	7.1	7.2	7.4	7.3	7.4	7.6	8.5	8.4	7.4	8.5	7.1	7.6	0.0	7.0	105.5	28	28.5	na	1.6	na	29.6	na	2.0	na
<i>Bellucia grossularioides</i>	6.9	7.1	7.2	7.3	7.2	7.3	7.6	10.7	11.6	8.6	15.0	7.4	10.4	6.8	6.9	127.9	31	29.8	0.2	2.7	0.4	30.3	0.1	3.0	0.4
<i>Eschweilera coriacea</i>	6.2	6.2	6.3	6.2	6.3	6.3	6.5	6.5	11.2	8.6	112.7	31.6	224.8	10.8	9.1	459.0	33	32.3	na	10.0	na	32.3	na	11.7	na
<i>Hevea guianensis</i>	14.6	14.7	14.8	14.8	14.9	14.7	15.2	14.7	23.6	15.3	28.8	15.2	20.6	14.7	15.7	252.4	31	30.2	0.4	9.8	2.2	30.5	0.2	15.7	0.8
<i>Inga alba</i>	4.9	4.9	4.9	4.9	5.0	4.9	5.6	5.1	11.6	5.1	5.7	4.9	4.9	0.0	5.3	77.6	29	29.1	0.1	13.4	1.3	29.1	0.0	17.0	1.1
<i>Jacaranda copaia</i>	4.5	4.5	4.5	4.5	4.6	4.6	5.9	5.2	18.8	5.2	6.9	4.5	4.6	1.7	4.5	84.6	29	29.0	0.1	9.3	0.6	29.1	0.0	10.9	0.5
<i>Ocotea bofo</i>	11.6	11.6	11.8	11.7	11.8	11.7	14.3	12.2	28.3	13.0	27.7	11.9	12.1	3.0	11.7	204.2	29	29.6	0.1	12.5	1.1	29.7	0.1	14.4	0.8
<i>Ocotea insularis</i>	13.6	13.7	13.7	13.7	13.6	13.6	21.6	15.3	69.9	18.3	67.5	14.6	15.0	0.0	13.6	317.7	29	29.8	0.2	15.4	2.7	29.8	0.2	16.1	2.8
<i>Pourouma bicolor</i>	7.1	7.1	7.1	7.2	7.3	7.4	7.7	7.9	9.0	8.6	8.6	7.7	7.6	4.8	7.1	112.2	29	29.4	0.1	1.5	0.2	29.9	0.2	1.5	0.2
<i>Pourouma minor</i>	9.8	9.8	9.9	9.9	10.2	10.1	11.3	11.0	12.1	12.2	12.0	10.5	10.3	7.1	9.8	156.1	30	29.1	0.1	1.5	0.2	29.6	0.0	1.6	0.2
<i>Pourouma mollis</i>	3.0	3.1	3.1	3.1	3.4	3.5	4.0	4.3	4.9	5.2	5.2	3.6	3.4	1.0	3.1	53.8	30	29.2	0.1	1.3	0.0	29.7	0.1	1.3	0.1
<i>Pseudolmedia laevigata</i>	3.8	7.1	7.1	7.2	7.2	7.2	7.4	7.5	18.3	8.3	15.0	7.8	8.4	5.2	7.2	124.6	29	29.9	0.2	8.6	0.6	29.9	0.2	9.7	1.0
<i>Senefeldera inclinata</i>	7.8	7.8	7.8	7.8	7.9	7.8	8.2	8.4	35.7	10.7	29.3	9.1	9.8	5.6	7.9	171.6	29	30.0	0.1	10.6	1.1	30.0	0.1	10.9	1.2
<i>Tapirira guianensis</i>	6.2	6.3	6.3	6.3	6.4	6.4	11.4	9.3	151.0	15.0	142.4	15.9	42.8	6.6	6.4	438.9	29	30.2	0.3	13.2	1.2	30.3	0.3	14.0	0.9
<i>Vochysia majuscula</i>	7.7	7.7	7.9	7.8	8.0	7.8	8.1	8.0	25.6	10.2	90.1	11.1	28.1	5.6	7.8	241.6	31	30.3	0.5	12.7	4.1	30.6	0.3	14.4	3.3
Mean	7.6	7.9	8.0	8.0	8.1	8.1	9.5	8.9	30.8	10.2	35.9	10.0	19.0	4.9	8.1	184.8		29.7		8.5		29.9		9.9	

	σ	0.7	0.6	0.7	0.7	0.7	0.6	0.9	0.7	8.8	0.9	9.2	1.0	6.0	0.8	0.7	24.6		0.1	0.9	0.1	1.0				
Pantiacolla III																										
<i>Caryocar amygdaliforme</i>		5.4	5.6	6.2	5.9	7.4	6.3	10.5	10.0	174.0	13.5	97.5	12.3	23.2	6.1	6.4	390.3	29	30.0	0.3	7.9	3.6	30.3	0.2	10.1	4.0
<i>Faramea torquata</i>		4.5	4.5	4.6	4.6	4.8	4.6	5.6	5.2	22.4	5.7	11.2	4.7	5.0	0.0	3.4	91.1	29	29.4	0.1	10.7	1.2	29.5	0.0	12.6	1.0
<i>Hevea guianensis</i>		5.1	5.2	5.6	5.4	5.7	5.5	7.6	5.9	25.4	6.0	19.3	5.5	8.5	5.1	5.5	121.5	29	29.6	0.1	11.8	1.9	29.9	0.0	16.9	1.9
<i>Licaria cannella</i>		3.2	3.3	3.4	3.4	3.4	3.3	5.9	3.7	18.3	4.6	36.7	4.5	7.8	0.0	3.3	104.7	31	30.4	na	16.0	na	30.4	na	17.8	na
<i>Micropholis guyanensis</i>		3.6	3.7	3.8	3.8	3.9	3.9	5.1	5.6	53.0	7.7	28.2	4.7	5.3	3.6	3.7	139.6	29	29.6	0.1	9.4	1.1	29.7	0.1	10.3	1.2
<i>Ocotea oblonga</i>		4.9	4.9	5.0	4.9	5.1	5.1	8.9	5.5	21.9	5.7	15.3	5.0	5.1	0.0	4.9	102.1	29	29.3	0.0	15.8	0.4	29.4	0.0	19.0	0.0
<i>Plukenetia sp. 28917</i>		7.9	7.9	8.0	8.2	8.3	8.3	8.6	8.4	17.3	9.0	21.9	8.0	8.0	0.0	0.0	129.8	31	29.8	na	9.3	na	30.1	na	13.2	na
<i>Pourouma bicolor</i>		3.1	3.2	3.3	3.4	3.5	3.5	3.7	3.9	5.1	4.5	4.4	3.5	3.4	1.9	3.1	53.4	29	28.7	0.2	1.4	0.0	29.6	0.2	1.5	0.0
<i>Pourouma mollis</i>		3.5	3.6	3.7	3.6	3.8	4.1	5.4	5.3	5.0	6.4	6.5	4.9	4.1	0.0	3.4	63.2	31	29.2	na	1.1	na	29.8	na	1.2	na
<i>Qualea paraensis</i>		2.5	2.5	2.6	2.5	2.8	3.2	4.7	5.3	22.9	3.5	5.1	2.5	2.5	0.8	2.0	65.5	29	28.8	0.2	5.1	0.6	28.9	0.1	6.2	0.5
<i>Schizocalyx obovatus</i>		3.7	3.8	3.9	4.0	3.9	3.9	4.0	3.9	4.5	3.9	4.9	3.9	4.2	2.1	2.2	56.7	31	28.9	0.6	3.2	0.4	30.2	0.2	5.7	0.2
<i>Senefeldera inclinata</i>		4.6	4.7	4.8	4.8	5.0	4.8	5.9	5.5	47.9	7.8	43.9	6.1	7.9	1.2	4.0	158.8	29	29.7	0.2	12.0	1.2	29.9	0.1	15.0	1.8
<i>Sloanea guianensis</i>		4.0	2.9	4.1	4.1	4.2	4.2	4.7	4.6	37.0	5.7	16.8	4.5	7.0	2.7	4.4	110.9	29	29.7	0.2	12.3	1.9	29.8	0.1	14.6	2.1
<i>Sloanea meianthera</i>		5.3	5.3	5.4	5.3	5.4	5.3	5.9	5.5	11.4	5.6	10.1	5.5	8.1	3.6	5.3	93.0	29	30.3	0.6	12.9	1.2	30.6	0.6	16.1	1.5
<i>Tachigali setifera</i>		4.7	5.1	5.7	5.6	5.5	5.0	8.0	5.2	51.5	6.4	43.7	5.6	9.3	4.6	4.8	170.7	29	29.7	0.0	13.5	3.9	29.9	0.1	22.6	10.8
<i>Tetragastris panamensis</i>		3.9	4.0	4.1	4.3	4.3	4.2	6.4	5.5	88.5	11.5	36.8	5.2	6.6	0.0	4.0	189.1	29	29.6	na	10.5	na	29.6	na	11.4	na
	Mean	4.3	4.3	4.6	4.6	4.8	4.7	6.2	5.6	40.0	6.6	25.4	5.4	7.5	2.4	4.0	130.3		29.5		9.6		29.9		12.2	
	σ	0.2	0.3	0.3	0.3	0.3	0.2	0.5	0.4	13.4	0.7	7.1	0.6	1.3	0.4	0.4	24.5		0.1		0.8		0.1		1.1	
San Pedro II																										
<i>Alchornea latifolia</i>		1.5	3.0	3.9	4.1	17.1	10.9	51.9	34.8	265.4	34.3	124.0	9.8	17.2	1.2	2.1	581.1	29	29.4	0.2	12.5	3.0	29.6	0.1	13.5	3.3
<i>Brunellia stenoptera</i>		3.7	3.8	4.1	4.9	10.1	6.7	36.3	6.0	14.8	4.2	6.6	1.7	4.3	1.7	3.8	112.6	29	27.4	0.2	7.4	0.1	27.9	0.2	16.0	2.7
<i>Caryocar pallidum</i>		3.1	3.1	3.3	3.5	4.3	4.0	5.6	4.4	20.9	7.7	53.5	9.4	16.1	3.5	3.7	146.1	31	30.6	0.1	6.2	0.9	30.8	0.1	7.7	1.7
<i>Cecropia angustifolia</i>		2.9	2.9	3.1	3.2	3.7	3.4	6.7	4.7	46.2	6.2	51.4	4.5	9.4	1.9	3.1	153.2	31	30.0	0.1	13.9	1.3	30.1	0.1	15.6	1.3
<i>Cinchona micrantha</i>		2.5	2.5	2.7	3.0	10.6	3.4	3.7	3.3	12.2	3.2	9.3	2.6	2.9	0.0	2.5	64.3	29	28.5	1.2	9.3	1.8	29.6	0.2	10.2	2.9
<i>Coussapoa villosa</i>		1.5	1.8	3.3	2.6	4.6	2.9	4.3	3.0	4.4	3.0	3.3	2.3	1.9	1.6	1.5	42.1	25	27.3	0.2	2.1	0.4	29.2	0.0	2.2	0.3
<i>Cyathea sp. 28406</i>		6.8	6.9	7.1	7.4	8.5	8.2	12.6	7.9	9.6	7.3	7.8	5.2	4.3	6.4	6.4	112.6	27	27.5	0.2	4.3	2.6	28.6	0.2	7.2	4.5
<i>Endlicheria macrophylla</i>		3.4	3.5	4.0	4.7	6.1	5.8	14.0	5.2	7.7	3.9	3.9	1.7	1.7	1.7	2.5	69.7	27	27.2	0.3	4.7	2.2	27.9	0.1	8.2	3.0
<i>Ficus tonduzii</i>		2.5	2.5	3.0	3.2	4.4	4.9	7.3	9.1	14.5	16.6	24.0	8.5	6.7	2.5	2.5	112.1	31	29.7	na	1.5	na	30.1	na	1.6	na
<i>Guarea kunthiana</i>		3.9	3.9	4.0	4.1	4.3	4.2	4.7	4.2	8.8	4.4	12.6	4.3	4.5	0.0	4.0	71.8	31	29.4	0.7	8.1	2.6	29.9	0.3	11.0	1.7
<i>Gutteria glauca</i>		4.2	4.2	4.5	4.5	4.8	4.4	4.8	4.4	5.0	4.3	4.5	0.0	2.9	0.0	4.3	56.9	29	27.2	0.3	3.4	0.3	28.8	0.2	7.2	0.7
<i>Helicostylis tovarensis</i>		0.0	0.5	0.3	0.7	0.9	2.0	4.3	10.7	18.7	16.8	13.4	3.6	2.0	0.1	0.1	74.1	29	29.5	0.1	2.5	1.6	29.7	0.0	2.7	1.7
<i>Heliocarpus americanus</i>		4.8	4.9	5.1	5.1	5.5	5.3	6.7	5.8	14.4	5.1	6.4	5.1	4.9	5.6	4.9	89.6	29	28.7	0.1	4.6	0.6	29.0	0.0	8.8	0.9
<i>Hieronyma macrocarpa</i>		0.0	0.2	0.1	0.2	0.7	0.6	1.9	3.6	39.0	5.1	13.9	1.0	0.9	0.3	0.3	67.8	29	29.5	0.1	4.7	0.8	29.6	0.1	5.2	0.8
<i>Mollinedia lanceolata</i>		0.0	2.1	1.5	2.9	3.0	3.4	12.3	6.6	96.5	4.7	14.4	0.3	0.4	0.0	0.0	148.0	29	28.8	0.1	6.5	1.0	29.1	0.0	10.2	0.5
<i>Nectandra reticulata</i>		1.4	1.4	2.1	2.9	6.5	4.4	37.5	3.6	16.5	2.3	4.5	1.4	1.4	1.4	1.4	88.7	27	27.3	0.2	6.1	2.4	27.9	0.1	13.4	4.4
<i>Perrottetia sessiliflora</i>		7.0	7.1	7.2	7.3	7.4	7.3	8.6	8.1	43.6	8.4	11.1	7.2	7.2	0.0	7.1	144.5	29	29.0	0.0	13.3	2.7	29.2	0.0	16.1	3.6

<i>Pourouma bicolor</i>	2.5	2.7	3.4	4.5	6.0	6.0	6.6	5.4	5.6	4.5	5.2	2.8	2.7	1.2	2.6	61.6	27	27.6	0.4	1.4	0.3	28.9	0.1	1.9	0.2
<i>Rauvolfia leptophylla</i>	5.9	6.1	7.9	8.3	13.6	11.3	25.2	11.4	71.9	13.0	189.2	12.1	52.5	6.1	6.6	441.0	31	30.4	0.1	12.7	1.4	30.7	0.1	17.8	2.0
<i>Sapium laurifolium</i>	2.5	2.5	2.7	2.8	3.2	2.9	4.8	3.5	35.2	4.2	13.5	2.8	3.1	2.6	2.6	88.9	29	29.1	0.2	10.4	3.9	29.3	0.2	13.0	3.6
<i>Tachigali setifera</i>	0.8	1.3	3.5	1.5	2.7	1.5	6.0	4.1	53.3	4.6	17.6	2.0	2.6	0.9	0.9	103.4	29	29.1	0.1	7.8	1.0	29.5	0.1	9.9	1.5
<i>Tapirira guianensis</i>	2.2	2.2	2.4	2.4	2.8	2.5	3.7	2.9	14.9	3.2	28.2	3.8	12.2	2.2	2.3	88.1	31	30.3	0.5	11.8	1.4	30.6	0.3	15.1	0.6
<i>Tapirira obtusa</i>	1.0	1.1	1.3	1.4	1.8	1.7	4.6	4.0	112.0	8.6	117.4	6.6	23.6	0.7	1.1	287.0	31	29.8	0.2	12.0	1.6	30.0	0.1	13.8	1.3
<i>Turpinia occidentalis</i>	2.3	5.9	6.5	7.2	9.9	9.3	17.1	8.7	17.5	7.5	14.4	6.2	6.3	3.7	6.3	128.7	29	28.2	0.4	6.6	3.6	28.9	0.2	8.1	3.6
<i>Virola sebifera</i>	2.0	2.0	2.1	2.3	2.7	2.7	3.9	2.8	8.6	2.6	6.0	2.1	2.1	0.0	2.0	44.0	29	28.8	0.1	4.7	0.9	29.4	0.1	7.4	1.6
<i>Vismia glaziovii</i>	0.0	1.0	1.0	1.9	3.3	3.0	19.7	11.4	292.2	8.4	36.1	0.3	0.4	0.0	0.0	378.7	29	29.0	0.1	12.1	3.8	29.2	0.1	13.8	3.5

Mean	2.3	2.8	3.2	3.4	5.7	4.6	13.0	8.2	68.6	8.8	39.0	4.2	8.2	1.6	2.5	176.0		28.9		7.8		29.4		10.2	
σ	0.2	0.2	0.3	0.3	0.7	0.6	2.1	1.6	13.6	1.5	6.9	0.5	1.4	0.2	0.3	23.4		0.1		0.6		0.1		0.6	

San Pedro I

<i>Alchornea latifolia</i>	4.5	4.7	5.0	5.0	5.9	5.0	13.6	7.8	128.6	10.3	43.7	5.8	8.5	2.1	5.0	255.7	29	28.2	0.7	6.8	5.0	29.5	0.0	7.9	4.9
<i>Alzatea verticillata</i>	4.8	4.9	5.9	5.7	10.1	7.1	63.8	20.2	121.1	10.4	25.9	4.0	5.6	3.4	4.8	297.8	29	28.5	0.1	9.9	1.8	28.6	0.1	11.4	2.3
<i>Caryocar pallidum</i>	3.3	4.0	5.0	6.7	6.9	5.7	15.3	9.2	140.8	23.3	330.5	26.2	72.7	4.3	5.7	659.6	31	30.6	0.2	9.0	1.0	30.7	0.2	10.4	1.2
<i>Cecropia angustifolia</i>	2.8	3.1	3.6	4.2	4.4	3.9	8.0	6.1	108.3	9.8	135.5	6.4	18.0	1.4	2.9	318.4	31	30.1	0.1	14.5	2.7	30.2	0.0	17.1	2.8
<i>Chrysophyllum sp. 9745</i>	0.0	0.8	3.5	1.6	11.4	9.3	71.9	19.0	118.8	4.6	52.5	1.3	2.5	0.1	0.1	297.3	29	28.7	0.2	8.8	2.1	28.9	0.1	11.4	2.3
<i>Clusia elliptica</i>	0.0	0.5	4.3	2.2	11.5	4.6	31.7	20.3	338.5	20.3	299.7	7.6	27.0	0.4	0.7	769.3	29	29.9	0.2	13.5	2.4	30.0	0.1	14.8	2.6
<i>Clusia thurifera</i>	2.5	3.3	6.5	5.4	7.8	4.9	14.5	10.0	178.4	10.7	195.0	5.4	20.2	2.2	2.6	469.1	31	29.7	0.2	19.2	7.6	30.0	0.2	30.9	13.1
<i>Cyathea sp. 28406</i>	5.4	5.5	5.7	6.0	6.1	5.9	6.0	5.6	6.6	5.5	6.1	3.9	5.7	0.0	5.5	79.3	29	27.8	0.6	3.0	0.9	29.6	0.3	6.8	1.7
<i>Dendropanax tessmannii</i>	0.0	0.6	0.4	0.8	1.0	2.7	8.2	12.4	277.5	22.6	474.1	11.2	43.3	0.3	0.4	855.5	31	30.3	0.1	16.0	2.0	30.3	0.1	17.2	2.0
<i>Elaeagia mariae</i>	0.0	0.8	0.8	0.9	1.8	1.9	19.8	6.8	26.8	2.2	11.6	0.7	1.5	0.0	0.7	76.4	29	28.8	0.2	8.0	0.6	28.9	0.1	9.4	0.8
<i>Ficus americana</i>	3.6	3.9	4.5	5.1	9.6	11.7	34.6	38.7	206.3	24.4	94.0	8.4	12.5	3.4	3.5	464.2	29	29.3	0.1	4.9	0.4	29.5	0.2	5.5	0.3
<i>Gutteria glauca</i>	0.0	0.5	0.6	0.7	0.9	1.2	2.0	1.6	5.5	1.1	2.5	0.1	0.2	0.0	0.0	16.8	29	28.5	0.3	2.5	0.2	29.2	0.1	3.7	0.3
<i>Hedyosmum cuatrecasazum</i>	8.7	8.7	8.9	9.0	9.1	9.3	9.6	8.8	9.3	8.7	9.0	8.8	5.6	0.0	8.9	122.2	27	27.2	0.8	2.0	0.3	28.6	0.4	3.5	0.2
<i>Helicostylis towarensis</i>	11.1	11.3	11.8	12.2	12.3	11.9	12.1	13.4	13.9	14.5	13.5	11.8	11.5	0.0	11.5	172.7	30	28.4	0.4	1.1	0.1	29.6	0.0	1.1	0.1
<i>Ilex gabrielleana</i>	4.4	4.6	4.9	5.2	7.8	5.5	30.8	9.1	222.6	10.1	121.3	5.5	8.7	4.3	4.7	449.6	29	29.5	0.1	25.7	5.5	29.5	0.1	31.0	5.7
<i>Inga feuillei</i>	4.3	4.3	4.5	4.4	4.7	4.4	5.2	5.7	51.4	5.5	5.6	4.3	4.4	0.0	4.4	113.1	29	28.9	na	16.1	na	29.0	na	17.9	na
<i>Inga killipiana</i>	2.9	3.0	3.2	3.3	3.6	3.4	4.5	4.2	22.0	5.5	17.5	3.7	3.8	2.9	3.0	86.6	29	29.3	0.6	6.6	0.5	29.6	0.4	9.1	2.2
<i>Lissocarpa sp. 5077</i>	8.2	8.3	8.5	8.6	8.8	8.9	10.3	9.8	16.9	13.2	45.0	24.7	66.2	13.8	12.6	263.9	31	31.9	0.3	3.7	0.3	31.8	0.3	4.9	1.0
<i>Lissocarpa sp. 9727</i>	5.7	5.9	6.1	6.3	6.5	6.4	7.5	6.6	14.5	9.5	38.6	28.4	96.0	14.2	15.7	267.7	31	32.2	na	3.8	na	32.1	na	4.8	na
<i>Meriania sp. 28275</i>	3.1	3.4	4.2	4.7	5.7	5.5	10.8	6.3	25.2	3.8	5.1	3.0	3.0	0.0	3.1	86.8	29	27.9	0.2	4.4	1.0	28.7	0.0	8.0	1.5
<i>Mezilaurus campaucola</i>	3.9	3.9	4.1	4.8	4.8	5.5	34.4	9.5	114.6	8.7	37.5	4.0	0.0	0.0	5.2	240.9	29	29.0	na	13.0	na	29.0	na	16.1	na
<i>Ocotea cernua</i>	6.1	6.2	6.3	6.4	7.5	7.0	33.7	8.1	26.4	8.1	17.6	6.2	6.3	0.0	6.1	152.0	27	28.4	0.1	9.9	1.5	28.6	0.2	13.2	0.8
<i>Ocotea sp. 28289</i>	5.1	5.1	5.3	5.3	6.0	5.7	29.6	6.9	44.0	7.5	22.0	5.4	5.3	0.0	7.8	160.9	29	29.0	na	15.8	na	28.9	na	17.7	na
<i>Parinari occidentalis</i>	5.2	5.5	5.8	6.2	6.3	5.9	8.7	8.1	189.0	11.9	71.0	5.9	7.0	3.0	5.3	344.8	29	29.3	0.1	16.5	6.0	29.5	0.1	19.8	6.9
<i>Pouteria torta</i>	4.4	4.6	4.9	4.8	4.9	4.8	7.2	8.7	126.0	11.6	133.7	8.6	16.5	1.0	5.5	347.0	31	30.2	0.3	15.6	2.3	30.3	0.3	16.8	2.5
<i>Protium glabrescens</i>	3.3	3.3	3.6	3.5	12.4	4.0	62.1	9.1	206.4	10.4	36.1	4.0	4.1	0.0	4.3	366.4	29	28.8	na	21.1	na	28.9	na	21.7	na
<i>Protium montanum</i>	3.2	9.9	5.9	19.3	17.5	75.6	45.0	39.4	210.4	11.9	116.0	4.9	5.5	2.3	2.8	569.5	29	29.1	0.1	20.6	0.4	29.4	0.1	24.6	2.0

<i>Prunus sp. 28301</i>	7.7	7.9	8.4	8.7	10.9	9.2	38.6	14.5	266.2	16.7	160.0	10.1	12.9	7.7	9.0	588.5	29	29.5	na	21.2	na	29.6	na	24.3	na
<i>Retrophyllum rospigliosii</i>	4.4	4.4	4.5	4.5	4.8	4.7	13.6	7.1	31.2	6.2	10.2	4.6	4.7	0.0	4.5	109.5	29	28.8	na	8.1	na	28.9	na	9.0	na
<i>Tapirira guianensis</i>	2.2	2.3	2.9	2.6	3.1	2.7	8.9	5.8	98.0	9.7	189.5	11.5	54.1	2.4	2.4	398.0	31	30.5	0.1	14.4	2.0	30.6	0.1	15.5	1.9
<i>Weinmannia pinnata</i>	3.9	4.0	4.1	4.1	4.3	4.4	14.1	10.3	53.0	6.4	8.4	4.0	4.0	2.2	4.3	131.4	29	28.7	0.1	6.0	0.9	28.8	0.1	6.5	0.8
Mean	3.0	3.6	4.2	4.6	6.6	7.6	22.0	11.9	118.9	10.6	111.3	6.9	17.0	1.7	3.6	333.4		29.2		10.4		29.6		12.5	
σ	0.3	0.4	0.3	0.6	0.7	2.3	2.6	1.4	13.3	0.8	16.9	0.8	2.8	0.3	0.4	31.8		0.1		0.7		0.1		0.9	
Trocha Union IV																									
<i>Alchornea grandiflora</i>	4.7	4.7	5.2	5.4	6.1	6.0	7.5	8.7	73.8	10.7	41.1	5.6	5.7	1.1	4.8	191.0	29	29.4	0.1	7.7	1.1	29.7	0.1	9.4	1.2
<i>Cinchona calisaya</i>	4.5	4.5	6.8	6.7	7.1	6.8	8.7	7.1	10.7	7.0	9.0	3.8	3.8	0.0	4.8	91.3	29	28.9	0.2	8.7	0.9	29.1	0.1	11.0	1.4
<i>Clusia alata</i>	2.3	2.3	5.5	3.9	10.3	5.8	23.3	21.2	685.7	17.0	199.7	4.3	12.4	2.3	2.6	998.6	29	29.3	0.2	22.6	4.8	29.4	0.1	24.7	4.6
<i>Clusia sp. 28522</i>	4.8	3.5	10.4	5.0	16.4	5.6	22.8	18.2	438.0	11.3	105.6	4.2	7.8	1.5	3.5	658.5	29	29.1	0.1	20.5	3.7	29.3	0.1	23.4	4.2
<i>Cyathea delgadii</i>	4.6	4.6	4.7	4.6	5.0	4.8	5.9	4.8	9.0	4.7	6.6	0.0	5.8	3.5	4.0	72.7	29	29.3	0.2	11.9	2.5	29.7	0.1	21.9	2.6
<i>Freziera karsteniana</i>	2.5	2.5	2.7	3.3	4.3	4.8	11.3	6.4	124.1	10.7	220.7	9.0	78.0	3.7	9.4	493.2	31	30.7	0.1	18.3	0.9	30.7	0.1	22.6	1.4
<i>Gordonia fruticosa</i>	4.9	4.9	5.4	5.2	5.6	5.3	6.2	5.5	26.2	6.0	23.1	5.2	5.2	0.0	5.0	113.6	29	29.6	0.1	14.6	0.7	29.8	0.0	20.3	1.6
<i>Hedyosmum goudotianum</i>	7.9	7.9	8.2	8.1	9.0	8.8	37.8	16.5	381.7	10.8	12.4	0.0	5.5	3.0	5.6	523.2	29	28.8	0.0	31.4	1.1	28.9	0.0	35.2	1.2
<i>Miconia madisonii</i>	3.7	4.2	4.9	4.6	5.1	5.2	6.0	5.6	7.3	4.3	4.7	2.8	3.0	1.7	3.8	67.0	29	27.2	0.3	2.0	0.4	28.7	0.1	3.2	0.6
<i>Miconia sp. 28578</i>	11.2	11.1	15.0	11.5	13.4	11.3	13.7	11.6	20.0	11.5	15.8	11.6	12.7	0.0	11.3	181.5	29	28.1	na	10.5	na	29.6	na	11.1	na
<i>Myrsine andina</i>	2.7	2.7	5.2	2.9	6.8	4.8	17.4	21.4	452.3	31.6	474.4	9.0	28.9	2.7	2.7	1065.6	31	30.0	0.1	17.2	1.4	30.0	0.1	17.8	1.4
<i>Myrsine coriacea</i>	2.6	2.5	3.9	3.5	37.5	8.3	179.8	23.7	936.3	30.7	286.7	5.6	12.5	2.2	2.6	1538.5	29	29.1	0.1	24.4	2.3	29.2	0.1	26.9	2.2
<i>Ocotea glabriflora</i>	2.7	2.8	3.6	4.1	4.1	3.8	4.3	3.7	5.5	3.2	4.0	1.2	1.2	0.0	2.3	46.4	29	27.0	0.4	2.4	0.5	28.8	0.1	4.8	1.0
<i>Ocotea sp. 9607</i>	2.1	2.1	4.8	3.4	19.2	4.6	60.2	3.7	25.1	2.7	4.9	1.7	1.7	0.0	2.1	138.4	27	27.3	0.2	15.0	1.3	27.9	0.2	33.0	4.6
<i>Prunus integrifolia</i>	2.2	2.2	2.7	2.3	5.8	3.2	52.9	24.7	734.0	26.4	291.2	9.1	12.2	1.6	2.6	1173.1	29	29.5	0.1	21.0	1.8	29.5	0.1	21.7	1.9
<i>Ternstroemia brachypoda</i>	2.4	2.4	2.6	2.5	3.0	2.8	20.5	9.1	254.2	13.9	90.9	6.8	18.3	2.8	4.2	436.4	29	29.5	0.1	15.6	0.8	29.5	0.1	16.5	0.8
<i>Weinmannia bangii</i>	5.5	5.6	6.1	5.7	13.8	8.1	322.9	23.4	752.7	25.5	489.9	8.6	13.6	0.5	6.4	1688.3	29	29.2	0.1	32.4	3.3	29.2	0.1	34.7	3.3
<i>Weinmannia reticulata</i>	5.2	6.7	7.0	6.9	7.2	7.1	8.5	8.0	13.8	8.8	11.0	6.9	6.9	1.9	7.2	113.0	29	29.2	0.3	3.9	0.7	29.4	0.1	4.2	0.6
Mean	3.9	4.0	5.5	4.7	10.2	5.8	48.6	12.8	297.3	13.5	137.6	5.0	13.3	1.7	4.4	568.1		28.9		15.8		29.3		19.4	
σ	0.3	0.3	0.3	0.3	1.2	0.3	12.9	1.1	45.4	1.3	24.3	0.4	2.3	0.2	0.3	79.7		0.1		1.1		0.1		1.3	
Esperanza																									
<i>Anthurium sp.</i>	0.0	1.1	4.3	1.9	7.1	5.2	17.4	7.8	189.6	18.3	171.1	8.2	14.8	0.3	0.2	447.4	29	29.8	0.1	10.0	1.2	29.9	0.1	11.6	1.0
<i>Cavendishia bracteata</i>	17.7	17.7	18.3	17.5	20.3	17.9	29.4	0.0	42.1	20.4	78.4	20.9	37.6	18.3	29.3	385.8	31	30.7	na	16.1	na	30.6	na	18.2	na
<i>Clusia alata</i>	4.0	4.2	10.5	6.9	18.9	8.7	41.1	27.5	765.5	21.4	220.8	6.1	12.0	3.9	4.2	1155.7	29	29.2	0.0	22.5	2.4	29.4	0.0	25.6	2.2
<i>Clusia elliptica</i>	6.1	6.2	8.0	7.1	11.6	10.2	31.2	30.7	581.7	18.0	215.6	9.2	16.3	5.4	6.7	964.0	29	29.2	0.1	17.8	6.3	29.3	0.1	19.6	6.6
<i>Clusia sp. 28086</i>	0.0	1.3	17.6	7.7	30.0	10.3	33.3	33.1	358.8	10.6	73.4	1.2	2.3	0.2	0.4	580.1	29	28.8	0.1	9.1	2.5	29.2	0.1	11.3	2.6
<i>Cyathea sp. 28406</i>	0.0	0.1	0.2	0.2	0.7	1.2	2.2	2.4	3.9	1.3	1.6	0.5	0.0	0.0	0.0	14.3	29	28.4	0.1	1.5	0.2	28.8	0.1	1.8	0.2
<i>Elaphoglossum sp.</i>	0.0	0.1	0.1	0.2	0.6	0.8	1.4	0.9	1.8	0.6	0.7	0.2	0.4	0.1	0.2	8.0	29	28.6	0.2	1.9	0.0	29.0	0.1	2.6	0.2
<i>Hedyosmum angustifolium</i>	9.7	9.8	19.5	13.3	27.5	17.0	37.7	43.9	658.9	20.8	201.3	6.0	11.5	6.6	9.9	1093.3	29	26.6	0.2	2.0	0.3	28.5	0.2	11.4	2.0
<i>Hedyosmum cuatrecasazum</i>	13.9	13.9	14.5	14.7	16.0	16.0	25.7	16.2	57.8	14.3	14.5	0.0	0.0	0.0	14.0	231.3	29	28.3	na	9.9	na	28.6	na	19.7	na

<i>Meliosma frondosa</i>	0.0	1.1	1.2	3.9	5.5	6.4	40.4	11.3	43.1	5.4	18.5	1.0	1.1	0.1	0.1	139.0	29	28.4	0.2	3.9	0.6	28.6	0.2	5.8	1.1
<i>Miconia micropetala</i>	0.0	0.9	1.5	2.7	3.6	4.7	11.7	7.4	43.1	5.3	19.8	1.0	1.2	0.1	0.1	103.0	29	28.8	0.2	4.9	1.0	29.1	0.2	6.3	0.9
<i>Myrsine coriacea</i>	2.7	2.4	4.6	6.0	30.2	17.2	120.3	37.2	621.3	25.5	257.9	5.7	13.7	2.7	2.8	1150.4	29	29.2	0.1	13.6	2.1	29.3	0.1	16.9	2.4
<i>Oreopanax sp. 9624</i>	0.0	4.2	7.4	3.5	5.3	3.9	7.6	3.7	51.7	3.5	3.1	0.4	0.3	0.1	0.1	94.7	29	27.6	0.4	4.5	1.0	28.7	0.1	7.3	1.9
<i>Palicourea sp.</i>	0.0	0.2	0.6	0.5	2.1	2.0	7.2	4.7	36.6	4.5	32.0	2.5	4.7	0.2	0.2	97.9	29	29.4	0.4	5.3	1.4	29.9	0.2	6.2	1.6
<i>Pentacalia sp. 28009</i>	12.4	12.4	13.0	12.5	17.0	16.0	22.9	23.8	34.0	41.6	73.9	16.8	16.6	8.7	14.2	335.7	31	29.8	0.0	2.3	0.6	30.1	0.1	2.3	0.6
<i>Pentacalia sp. 28150</i>	19.3	19.5	20.5	20.3	20.7	20.2	20.5	19.6	22.6	19.4	20.3	0.0	0.0	0.0	19.5	242.3	29	30.3	na	20.7	na	30.4	na	25.0	na
<i>Prunus integrifolia</i>	3.2	3.2	4.6	3.8	10.7	4.7	57.1	16.0	399.8	13.6	137.5	5.1	6.5	2.8	2.8	671.4	29	29.2	0.1	21.2	2.6	29.3	0.1	23.2	2.8
<i>Schefflera allocotantha</i>	0.0	5.2	46.0	19.7	56.8	6.8	13.9	4.2	16.4	1.9	2.5	0.9	0.8	0.2	0.2	175.4	29	25.2	0.4	4.5	0.9	28.4	0.0	5.3	1.9
<i>Symplocos reflexa</i>	0.0	1.4	1.2	1.8	2.5	5.5	9.6	14.5	73.0	4.5	117.5	3.1	53.8	0.2	0.2	288.9	31	30.6	0.1	9.7	2.0	30.7	0.1	13.0	2.7
<i>Weinmannia bangii</i>	0.0	0.2	0.4	0.4	3.0	8.8	82.1	12.9	186.8	3.7	16.4	0.4	0.4	0.1	0.1	315.7	29	28.8	0.2	10.9	1.2	28.9	0.2	16.5	3.3
Mean	2.9	3.6	7.9	5.8	14.4	8.8	39.9	18.2	277.3	12.9	103.3	4.2	9.1	2.2	3.3	513.8		28.8		9.9		29.3		12.7	
σ	0.6	0.5	1.4	0.7	2.1	0.8	6.2	2.1	45.9	1.6	15.6	0.6	1.5	0.5	0.7	70.1		0.1		0.9		0.1		1.0	
Acjanaco																									
<i>Clethra cuneata</i>	7.6	7.7	19.3	9.9	105.2	17.5	350.7	32.4	1047.9	20.2	204.4	9.2	11.6	7.3	8.2	1859.2	29	28.4	0.2	31.2	2.2	28.8	0.1	40.8	3.0
<i>Hedyosmum sp. 28204</i>	10.5	10.2	118.6	14.4	99.0	12.1	33.3	8.0	11.2	7.8	12.2	0.9	9.8	0.9	11.2	360.0	27	25.1	0.3	18.7	5.1	27.8	0.2	131.3	70.8
<i>Miconia setulosa</i>	5.3	5.5	7.9	7.5	7.4	6.5	10.4	6.3	12.8	5.5	6.9	0.9	4.5	0.0	5.8	93.1	29	27.2	0.3	4.0	0.6	28.6	0.1	9.4	1.7
<i>Miconia sp. 28227</i>	4.6	5.4	6.4	6.4	6.3	5.4	12.8	5.3	12.9	4.6	6.1	4.4	4.5	0.0	5.0	90.1	29	27.2	na	4.5	na	28.3	na	15.9	na
<i>Miconia sp. 6363</i>	7.0	7.0	12.3	7.7	14.9	7.5	15.4	7.8	34.2	7.5	12.5	1.0	7.2	0.0	7.7	149.8	29	27.8	0.9	16.8	1.6	28.7	0.3	37.8	14.2
<i>Myrsine pelucida</i>	5.2	5.2	6.2	5.2	6.2	7.2	12.9	13.7	247.1	15.1	95.0	6.2	8.1	0.0	5.3	438.4	29	29.4	na	15.7	na	29.5	na	17.4	na
<i>Pentacalia oronocensis</i>	5.4	5.5	6.7	9.6	9.5	24.0	15.6	21.3	58.2	14.5	133.7	7.8	15.2	5.7	6.8	339.3	31	29.7	na	4.1	na	30.2	na	7.3	na
<i>Persea ferruginea</i>	2.3	7.7	18.3	13.4	16.0	11.1	13.4	2.4	3.3	1.9	2.1	1.2	2.1	0.5	2.1	97.8	27	24.7	0.1	2.0	0.4	27.6	0.1	27.3	6.3
<i>Polylepis pauta</i>	6.1	5.7	15.8	6.1	8.9	7.2	21.9	6.7	44.0	6.6	91.4	7.4	122.2	5.7	7.5	363.1	31	30.9	0.2	33.8	3.9	31.3	0.2	54.5	4.6
<i>Symplocos baehni</i>	3.5	3.5	4.2	3.9	5.7	10.7	36.0	9.8	282.5	10.4	306.1	7.4	56.7	3.5	3.7	747.7	31	30.1	0.1	30.6	3.6	30.1	0.1	37.8	2.4
<i>Symplocos quitensis</i>	7.2	7.3	8.1	7.9	8.4	7.9	9.1	8.6	13.4	7.6	11.7	7.3	8.1	1.6	8.1	122.3	29	28.7	0.2	4.5	0.5	29.6	0.0	6.7	0.8
<i>Weinmannia fagaroides</i>	5.5	5.7	8.9	6.8	22.9	14.3	667.2	22.2	397.8	14.0	121.6	5.7	5.9	1.9	5.9	1306.3	29	28.1	0.2	30.4	2.8	28.2	0.1	42.1	3.2
Mean	6.0	6.6	22.5	8.5	30.4	10.6	121.3	11.7	198.6	9.2	84.9	4.7	24.3	2.3	6.6	548.1		27.9		18.1		29.0		40.7	
σ	0.5	0.5	9.6	0.7	8.3	1.0	39.7	1.7	61.9	1.0	17.4	0.6	5.9	0.4	0.6	110.9		0.3		2.0		0.2		8.5	

C_{max} : Modal chain length

ACL: Average Chain Length

CPI: Carbon Preference Index

Table S2 Tukey's Honest Significant Difference significance table for the *n*-alkane load by lamina area (KMA).

Site	TAM-06	TAM-05	PAN-02	PAN-03	SPD-02	SPD-01	TRU-04	ESP-01	ACJ-01
TAM-06		<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	*	****	****	****
TAM-05	<i>ns</i>		<i>ns</i>	<i>ns</i>	<i>ns</i>	*	****	****	****
PAN-02	<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	<i>ns</i>	****	****	****
PAN-03	<i>ns</i>	<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	****	****	****
SPD-02	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>		*	****	****	****
SPD-01	*	*	<i>ns</i>	<i>ns</i>	*		<i>ns</i>	****	**
TRU-04	****	****	****	****	****	<i>ns</i>		*	<i>ns</i>
ESP-01	****	****	****	****	****	****	*		<i>ns</i>
ACJ-01	****	****	****	****	****	**	<i>ns</i>	<i>ns</i>	

ns: Not significant

*: $p \leq 0.05$

** : $p \leq 0.01$

****: $p \leq 0.0001$

Table S3 Tukey's Honest Significant Difference significance table for the average chain length (ACL) of *n*-alkanes.

Site	TAM-06	TAM-05	PAN-02	PAN-03	SPD-02	SPD-01	TRU-04	ESP-01	ACJ-01
TAM-06		<i>ns</i>	<i>ns</i>	<i>ns</i>	****	**	****	****	****
TAM-05	<i>ns</i>		<i>ns</i>	<i>ns</i>	****	****	****	****	****
PAN-02	<i>ns</i>	<i>ns</i>		<i>ns</i>	**	<i>ns</i>	*	***	****
PAN-03	<i>ns</i>	<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	<i>ns</i>	*	****
SPD-02	****	****	**	<i>ns</i>		<i>ns</i>	<i>ns</i>	<i>ns</i>	****
SPD-01	**	****	<i>ns</i>	<i>ns</i>	<i>ns</i>		<i>ns</i>	<i>ns</i>	****
TRU-04	****	****	*	<i>ns</i>	<i>ns</i>	<i>ns</i>		<i>ns</i>	****
ESP-01	****	****	***	*	<i>ns</i>	<i>ns</i>	<i>ns</i>		****
ACJ-01	****	****	****	****	****	****	****	****	

ns: Not significant

*: $p \leq 0.05$

** : $p \leq 0.01$

***: $p \leq 0.001$

****: $p \leq 0.0001$