

# Modelling responses of western Amazonian palms to soil nutrients

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## Summary

**1.** Understanding the responses of individual plant species along different edaphic gradients is a key question in ecology, with implications to community assembly, functioning of forest ecosystems, niche theory and conservation planning. In tropical rain forests, responses to soil nutrients have been described only for a handful of species. Even abundant and conspicuous components of the forest, such as the palms (Arecaceae), remain largely unknown in this respect.

**2.** We inventoried all palm species and analysed soil chemistry in 96 sites across western Amazonia to (i) assess the relative importance of some micronutrients vs. macronutrients as drivers of patterns in palm species composition, (ii) model the response shapes of 61 palm taxa and of canopy vs. understorey palms along gradients of selected soil nutrients, (iii) determine if the response shapes of conspecific palm varieties differ in relation to the most important observed soil nutrient and (iv) assess if the rank order of the most abundant canopy species changes along edaphic gradients.

**3.** Patterns in palm species composition were best explained by Mehlich-III extractable exchangeable bases (Ca, K, Mg) and phosphorus (P), with the different palm species clearly separating along the soil cation concentration gradient. All 61 palm taxa exhibited statistical responses along soil nutrient gradients. Response shapes in relation to exchangeable bases varied among bimodal skewed (51% of species), unimodal skewed (47%) and monotonic (2%).

**4.** There were no significant differences between canopy vs. understorey species in their mean response shapes to the exchangeable bases, but canopy species had significantly higher mean optimum value for soil P and greater mean niche width along the Ca, K, Mg, P and boron (B) gradients. Varieties of the same species of *Bactris*, *Desmoncus* and *Geonoma* generally had different response shapes and different optima for the exchangeable bases.

**5. Synthesis.** Among the soil variables we studied, macronutrients (especially exchangeable bases and P) emerged as more important than micronutrients in predicting species abundances in palm communities of western Amazonian non-inundated forests. Non-Gaussian responses were predominant, conspecific palm varieties exhibited different response types, and the rank order of dominance of canopy palms varied along the gradients of exchangeable bases and P. Together, these findings advance niche theory about palms and may be used for generating better predictive models of palm species distributions and for experimental studies that search for the physiological mechanisms underlying inter- and intra-specific trade-offs along edaphic gradients.

**Key-words:** Arecaceae, ecological response curves, exchangeable bases, gradient analysis, Huisman–Olf–Fresco models, phosphorus, plant community ecology, resource gradients, tropical forest, tropical soils

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## Introduction

Understanding how the occurrence and abundance of a species vary along environmental gradients is a fundamental goal of ecology, as the question is directly derivable from the concepts of niche (Hutchinson 1957) and gradient analysis (Whittaker 1956). Although in tropical rain forests the importance of soil factors as controls of plant species composition at the community level is well-established (Phillips *et al.* 2003; Tuomisto, Ruokolainen & Yli-Halla 2003; Kristiansen *et al.* 2012), the responses of individual species along soil nutrient gradients remain largely unknown (but see Tuomisto 2006; Condit *et al.* 2013; Zuquim *et al.* 2014).

Here, we investigate how the abundances of a large number of Amazonian palm species vary along different soil nutrient gradients. Palms are in many ways an important component of tropical rain forests and, therefore, a well-suited model group for this purpose. There are 2400 species of palms on Earth, 730 of these are tropical American and 152 grow in Amazonia (Henderson 1995). Amazonian palms are key providers of ecosystem services to indigenous and local communities (Cámara-Leret *et al.* 2014), and many species are commercialised both locally and internationally (Brokamp *et al.* 2011). Amazonian palm communities are remarkable both in terms of local species density, which often reaches 30–40 species ha<sup>-1</sup>, and in stem density, which may reach 8000 stems ha<sup>-1</sup> (Balslev *et al.* 2011). Furthermore, palms are disproportionately well represented among the dominant Amazonian tree species (Pitman *et al.* 2001; ter Steege *et al.* 2013).

Clarifying a species' response along environmental gradients (i.e. determining its environmental niche) is of theoretical, methodological and practical importance. First, understanding the niche requirements of plants is important for understanding community assembly and the functioning of forest ecosystems, including why some species are abundant and others are rare at a site. Species that are oligarchic (Pitman *et al.* 2001) or hyperdominant (ter Steege *et al.* 2013) should, in principle, exhibit flatter responses along environmental gradients than subdominant species, yet cross-taxon studies are still remarkably scant. Second, response shape affects the applicability of ordination methods. Canonical correspondence analysis is one of the most widely used ordination methods and one of its basic assumptions is that species responses are Gaussian (ter Braak 1986). Non-Gaussian responses (e.g. skewed or bimodal) may occur when interspecific competition displaces the mode from the physiological optimum (Austin 1976), but even physiological responses may be non-Gaussian (Austin & Austin 1980). There is evidence that non-Gaussian distributions are frequent or even predominant in plant communities (Austin 1976; Minchin 1989). In the tropics, skewed response curves have been found for various plant groups: thistles along soil nutrient gradients in Australia (Austin *et al.* 1985), trees along P gradients in Cameroon and Panama (Garlan *et al.* 1986; Condit *et al.* 2013) and *Polybotrya* ferns along edaphic gradients in Amazonia (Tuomisto 2006). Third, knowledge of species

responses to environmental factors has practical implications for, e.g. enhancing simulation models about climate change impacts on vegetation (Austin *et al.* 1994), predicting species' abundances and occurrences based on environmental data (Bongers *et al.* 1999), predicting environmental conditions on the basis of floristic inventories (Sirén, Tuomisto & Navarrete 2013) and generating better floristic maps for conservation planning (Zuquim *et al.* 2014).

The high richness and density of Amazonian palm communities largely results from the high diversity of understorey species of the genera *Geonoma* and *Bactris* (Balslev *et al.* 2011). Species in these genera may exhibit great morphological variation. Subspecific varieties are readily recognised in some areas, but in others morphological differentiation is not possible due to intermediate forms (Henderson 2000, 2011). Conspecific varieties of *Geonoma* and *Bactris* often co-occur in the same habitat (Costa *et al.* 2009), but whether their coexistence can be explained by edaphic niche partitioning or even sympatric divergent evolution via habitat specialisation (Savolainen *et al.* 2006) remains unknown. Antagonistic patterns in topographic preferences among some understorey palm species have been documented in individual sites (Svenning 1999), but such patterns are not consistent across sites (Vormisto, Tuomisto & Oksanen 2004). While reproductive isolation for some of the nine *Geonoma macrostachys* morphotypes has been confirmed (Listabarth 1993), establishing genetic distinctness at regional scales is problematic (Roncal, Francisco-Ortega & Lewis 2007). Henderson (2011) highlighted three hypotheses, which are not mutually exclusive, to explain the distribution of polymorphic palm species: refugia, rapid expansion (Cronk 1998) and resource polymorphism (Smith & Skúlason 1996). The three conditions *sensu* Smith & Skúlason (1996) that promote resource polymorphism and that may lead to divergent evolution are found in Amazonia: (i) unoccupied edaphic niches, which arise from river dynamics, tectonics or volcanism (Salo *et al.* 1986; Hoorn *et al.* 2010), (ii) high habitat heterogeneity (Tuomisto *et al.* 1995) and (iii) relaxation of interspecific competition, which occurs in the form of differences in phenology and pollinator spectrum (Listabarth 1993). In *Geonoma*, these resource polymorphisms 'may represent an intermediate step in sympatric speciation' (Henderson 2011, p. 22).

Earlier studies in lowland tropical rain forests have suggested that soil P may be the most important nutrient-limiting tree growth (Vitousek 1984), although other nutrients (e.g. N and K) may be colimiting (Mirmanto *et al.* 1999; Wright *et al.* 2011; Alvarez-Clare, Mack & Brooks 2013; Fisher *et al.* 2013). Research in Central America has suggested that palm distributions are best explained by exchangeable bases, P and N (Clark *et al.* 1995; Andersen, Turner & Dalling 2010; Baribault, Kobe & Finley 2012), and tree distributions by P and to a lesser degree Ca (Condit *et al.* 2013). On the other hand, several studies on Amazonian trees, ferns and Melastomataceae have found that exchangeable bases explain compositional differences better than P does (Phillips *et al.* 2003; Tuomisto, Ruokolainen & Yli-Halla 2003; Tuomisto *et al.* 2003). Furthermore, a niche breadth analysis of trees in

three large (25–50 ha) Neotropical tree plots (John *et al.* 2007) suggested that both exchangeable bases and several micronutrients can be more important controllers of tree species distributions than P. It has even been proposed that B may be a uniquely important soil gradient for tropical plants, as its concentration seems to range from severe scarcity to toxicity (Steidinger 2015).

Widespread palm species in Amazonia tend to be tall and have wide tolerances to soil fertility (Ruokolainen & Vormisto 2000). At local scales, different canopy species may exhibit different responses to soil fertility. For example, *Oenocarpus bataua* was found to be more abundant in poor soils and *Iriartea deltoidea* in rich soils in a study in Ecuador (Korning *et al.* 1994). In a landscape-scale study in Costa Rica, *Euterpe* and *Prestoea* showed opposite edaphic associations, whereas *Iriartea* and *Socratea* showed reciprocal density variation in two soil types (Clark *et al.* 1995). Although illuminating, single-site studies only sample a fraction of the environmental gradient that species experience in their entire geographic ranges, so broader-scale approaches are needed to unravel species responses properly.

Our objective is to contribute to our understanding on soil–plant relationships in tropical rain forests. We do so by modelling the statistical responses of selected palm species to soil nutrients and by investigating if soil nutrient availability could drive the assembly and composition of palm communities in western Amazonian *terra firme* rain forests. We address these questions using a large floristic and soil data set collected in 96 transects across five countries. Specifically, we ask (i) what is the relative importance of some micronutrients vs. macronutrients in explaining dissimilarity in palm species composition between sites; (ii) what are the response shapes of 61 western Amazonian palm taxa and of understorey vs. canopy palms to soil nutrients, and which is the most important nutrient out of those analysed; (iii) whether varieties within the same palm species differ in their response shapes to the most important soil nutrient and (iv) whether the rank order of abundance of the most abundant canopy species varies in accordance with their inferred preferences for soil nutrients. This is, to our knowledge, the first study to investigate the response shapes of a large number of Amazonian palm taxa in relation to individual soil nutrients. We address 61 palm taxa (c. 40% of the Amazonian palm flora), including conspecific pairs of varieties belonging to three diverse genera (*Bactris*, *Desmoncus* and *Geonoma*).

## Materials and methods

### FIELD SAMPLING AND SOIL ANALYSIS

During 1995–2012 we collected data on palm species distribution and abundance in nine regions in western Amazonia (Fig. 1) (Aarhus University Palm Transect Database, doi: 10.15468/r5hujc). We used satellite images and field observations to place 96 transects in *terra firme*, i.e. non-inundated terrain that appeared to have old-growth forest cover and homogeneous geomorphology. Each transect was 5 m × 500 m in size. Geographical location was recorded in

Universal Transverse Mercator coordinates at the mid-point of each transect using a handheld GPS.

In each 5 m × 5 m subunit, we identified and counted all palm individuals of all life-history stages (seedlings, juveniles, subadults and adults). Ramets of clonal and multistemmed species were counted as separate individuals. Individuals were determined to the lowest possible taxonomic level, i.e. variety in *Bactris* and *Geonoma*, and subspecies in *Desmoncus*, and this classification was maintained in the analyses. We unified nomenclature according to the World Checklist of Palms (Govaerts & Dransfield 2005). Voucher specimens were collected and deposited in national herbaria in Bogotá (COL), Iquitos (AMAZ), La Paz (UMSA), Lima (USM), Manaus (INPA) and Quito (QCA), with duplicates from all regions in Aarhus (AAU) (herbarium acronyms according to Thiers 2015).

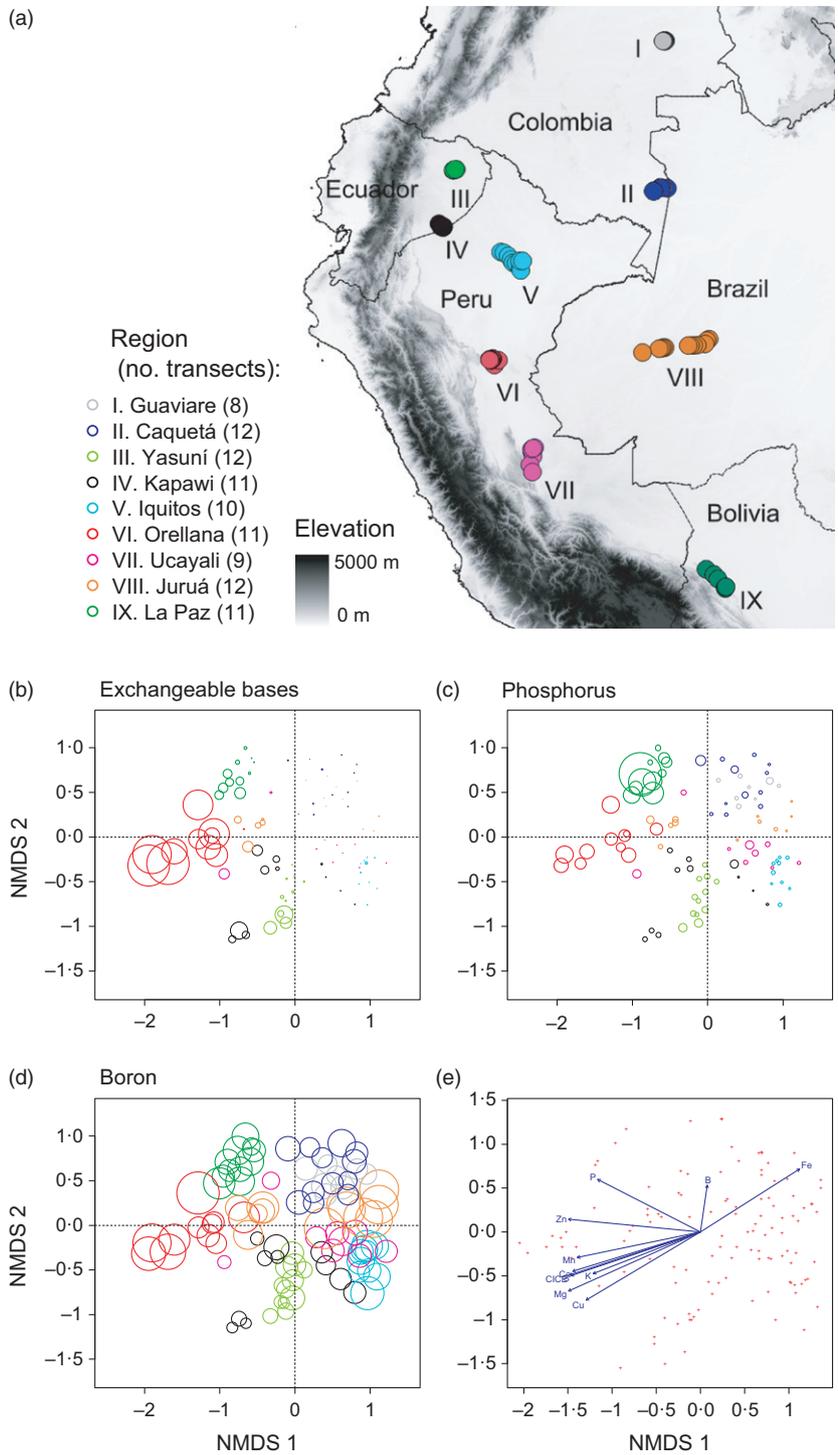
Soil samples were collected in each transect at the beginning, middle and end, corresponding generally to subunits 1, 50 and 100. In total, 275 soil samples were analysed. Due to the loss of some soil samples, 12 transects had only two soil samples, and one transect had only one sample. In the data analyses, we used transect-wise means of the laboratory analysis results.

Each soil sample was bulked from five topsoil subsamples (0–10 cm depth below the organic layer; c. 0.5 dm<sup>3</sup> per sample) distributed at the corners and the centre within a subunit. Roots and stones were removed and the samples were air dried in the field and stored in cotton bags or plastic bottles. The soil samples were analysed at the Agronomic Research Centre of the University of Costa Rica. Nutrients were extracted in Mehlich-III solution (Mehlich 1984) and then analysed for macronutrients (Ca, K, Mg, P, S) and micronutrients (B, Cu, Fe, Mn, Zn) using inductively coupled plasma-optical emission spectrometry. The Mehlich-III method was selected because it is a multielement extraction method designed to reflect the actual plant nutrient availability across a wide range of soil properties with reaction ranging from acid to basic (Soil Survey Staff 2014). We did not include nitrogen (N) in our analyses because N is a volatile element and it was not possible to standardise the storage conditions and time between the collection and analysis of the soil samples. However, earlier studies have suggested that N limitation is more important in montane than in lowland tropical rain forests (Vitousek & Matson 1988; Andersen, Turner & Dalling 2010), and that P limitation may be more important in the lowlands (Vitousek 1984; Aragão *et al.* 2009; Quesada *et al.* 2009).

### DATA ANALYSES

Floristic similarity between transects was calculated with the equation  $2W/(A+B)$ , where W is the shared palm abundance between two transects, A is the total abundance of all palm species in the first transect and B the total abundance in the second transect. This equation corresponds to the Sørensen index when applied to presence–absence data and to the Steinhaus index when applied to abundance data (Legendre & Legendre 2012). Here, we used the number of stems as a measure of species abundance. The equation  $\text{Dissimilarity} = 1 - \text{Similarity}$  was used when dissimilarity values were needed.

To assess species compositional patterns, we subjected the abundance-based dissimilarity matrix to non-metric multidimensional scaling (NMDS). This maps the between-site floristic dissimilarity values into an ordination space with a predefined number of dimensions (Minchin 1987). We produced a two-dimensional ordination using the *metaMDS* function in the R package *VEGAN* (Oksanen *et al.* 2016), and projected soil variables as vectors onto the ordination using the



**Fig. 1.** (a) Map of northwestern South America showing the locations of the 96 sampled transects and their division to nine regions. (b–e) Non-metric multidimensional scaling (NMDS) of the transects on the basis of the dissimilarity of their palm floras (as measured with the Steinhaus index). Stress value = 0.204. The diameter of the circles is proportional to the mean log-transformed concentration of Mehlich-III extractable, (b) exchangeable bases (Ca+K+Mg), (c) phosphorus, and (d) boron. Colours refer to the nine geographical regions shown in (a). (e) The NMDS ordination with a *posteriori* projection of soil variables with arrowheads indicating the strength of correlation between the soil variable and NMDS axes 1 and 2. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

*envfit* function. We calculated squared correlation coefficients ( $R^2$ ) for each predictor in relation to the NMDS axes and determined their significance with a Monte Carlo permutation test using 999 random permutations.

Mantel tests were run to find out whether dissimilarity in species composition correlated with dissimilarity in soil nutrient concentration. These analyses were done in parallel using presence–absence and abundance data to assess to what degree taking species abundances into account affects the results. Euclidean distance matrices were computed for all soil variables together and for each of them individually. All soil variables were log-transformed prior to

computing the Euclidean distances. Before combining soil variables into one distance matrix, each variable was standardised to zero mean and unit variance. To control for spatial autocorrelation and thereby avoid inflating the apparent importance of the environmental variables included in the analyses, we also ran partial Mantel tests, where the correlation with logarithmically transformed geographical distances was partialled out before calculating the correlation between floristic and edaphic dissimilarities. Spatial autocorrelation in floristic data emerges because dispersal of seeds is spatially restricted, which makes geographically close sites floristically more similar to each other than sites that are located further apart. This distance decay in

similarity is expected to be approximately logarithmic (Hubbell 2001). Environmental variables are often spatially autocorrelated as well, both those that were included in the analyses and those that were not. Therefore, geographical distances can also serve as surrogates for differences in unmeasured environmental variables. The standardised form of the Mantel statistic ( $r_M$ ) was used, which is equivalent to the Pearson correlation coefficient between two dissimilarity matrices. In all cases, we established the statistical significance of each correlation at the  $P < 0.001$  level with a Monte Carlo permutation test using 999 random permutations. All analyses were made using the *mantel* function in the R package *VEGAN* (Oksanen *et al.* 2016).

Species' responses along environmental gradients have been tested with a variety of methods. Here, we focus on the Huisman–Olf–Fresco (HOF) models and extended HOF models (eHOF) because they have been found to perform well for parametric questions of shape (Oksanen & Minchin 2002). HOF models (Huisman, Olf & Fresco 1993) are logistic regression models of hierarchically increasing complexity. They test statistically whether a response is flat (model I), or significantly monotonic (II), plateau (III), symmetric unimodal (IV) or skewed unimodal (V). Importantly, HOF models provide reliable estimates of the niche properties of species that differ in abundance (Lawesson & Oksanen 2002). Extended HOF models (eHOF) further allow testing for bimodal responses with either two equal optima (model VI) or two unequal optima (VII) (Jansen & Oksanen 2013).

We fitted the seven hierarchical logistic regression models to the palm species abundance data using the R package *eHOF* (Jansen & Oksanen 2013) and selected the most appropriate model according to the Akaike Information Criterion corrected for small samples (AICc) and a bootstrap approach (999 permutations) to guarantee model stability. The change in palm species abundance along each log-transformed soil nutrient gradient was analysed for all palm taxa that occurred in at least 10 transects. The soil variables were log transformed before analysis because a unit change in nutrient availability is likely more important for plants when the nutrient is scarce than when it is abundant. The species optima and niche widths along each soil nutrient gradient were derived from the eHOF models. We tested for statistical differences between the mean optimum response of canopy vs. understorey palms to soil nutrients using Welch's *t*-test for unpaired samples. This test was also used to test for statistical differences between palms with no skew, positive or negative skewed responses to soil nutrients. All statistical analyses were conducted in R 3.1.3 (R Development Core Team, 2015).

## Results

### GENERAL FLORISTIC AND EDAPHIC PATTERNS

About 100 300 palm individuals, representing 118 taxa, were found in the 96 inventoried transects (Table S1, Supporting Information). Each transect contained 195–2904 individuals (mean  $\pm$  SD:  $1045 \pm 553$ ) and 8–36 taxa ( $19 \pm 6$ ) (Table S2). Species accumulation curves showed a clear tendency to level off in all transects (Fig. S1), indicating that the 500-m-long transects were adequate to sample local palm species composition in western Amazonia. The most frequent species were *Euterpe precatoria*, *Socratea exorrhiza* and *O. bataua*, each of which was present in at least 75 transects and in all nine regions (Table S3). The most abundant species were *O. bataua* and *Lepidocaryum tenue*, each with over 14 000 individuals. Sixteen taxa were found in only one

transect and 61 taxa were present in at least 10 transects. Pair-wise floristic similarity values between transects ranged from 0.00 to 0.96 (mean = 0.35) when calculated with presence–absence data (Sørensen index) and from 0.00 to 0.92 (mean = 0.15) when calculated with abundance data (Steinhaus index).

The concentration of Mehlich-III extractable macronutrients varied greatly among regions and transects (Table 1, Fig. 1b–e). The concentration of exchangeable bases (Ca, K, Mg) varied 400-fold and was mainly determined by Ca, which accounted for 14–93% (mean = 51%) of the sum. Phosphorus concentration varied 30-fold. Micronutrient concentrations also varied greatly among transects: B concentrations varied four-fold, Fe 10-fold, Cu 30-fold, Zn 60-fold and Mn c. 1800-fold. Correlation values of environmental vectors with the NMDS axes showed that palm species composition and abundance were strongly related to the gradients of all soil variables except B (Fig. 1e, Table S4). Concentration of B was only weakly correlated with the other soil variables ( $r = 0.19$  or below), except with Fe ( $r = 0.61$ ) and S ( $r = 0.63$ ). Phosphorus correlated moderately with the other soil variables ( $0.35 \leq r \leq 0.57$ ) but strongly with Zn ( $r = 0.77$ ). The remaining soil variables (Ca, Cu, K, Mg, Mn, S, Zn and Fe) correlated moderately-to-strongly with each other ( $0.43 \leq r \leq 0.87$ ; Fig. S2, Table S5).

### MANTEL AND PARTIAL MANTEL TESTS

The matrix correlation between overall edaphic and floristic dissimilarity was 0.64 when presence–absence data were used, and 0.49 when abundance data were used ( $P < 0.001$  in both cases) (Table S6). All correlations between floristic difference and difference in individual edaphic variables were statistically significant for both presence–absence data and abundance data. In all cases, presence/absence data yielded higher correlation coefficients than abundance data did. Sum of bases, Ca and Mg yielded the highest correlation coefficients ( $r_M = 0.57$ – $0.58$  for presence–absence,  $r_M = 0.42$ – $0.45$  for abundance data). Mn, Cu, S and Zn yielded intermediate correlations ( $r_M = 0.47$ – $0.52$  for presence–absence,  $r_M = 0.32$ – $0.38$  for abundance data), and B, K, Fe and P yielded the lowest (but still significant) correlations ( $r_M = 0.20$ – $0.39$  for presence–absence,  $r_M = 0.12$ – $0.30$  for abundance data). Correlations between floristic and geographic dissimilarity matrices were statistically significant ( $r_M = 0.62$  for both presence–absence and abundance data). Dissimilarities in all soil variables were also correlated with the log-transformed geographical distances, but the correlations were relatively low ( $r_M = 0.09$ – $0.25$ ). All correlations between floristic and edaphic distance matrices remained statistically significant after removing the effect of log-transformed geographic distance with partial Mantel tests, and were, hence, not merely due to spatial autocorrelation in the data.

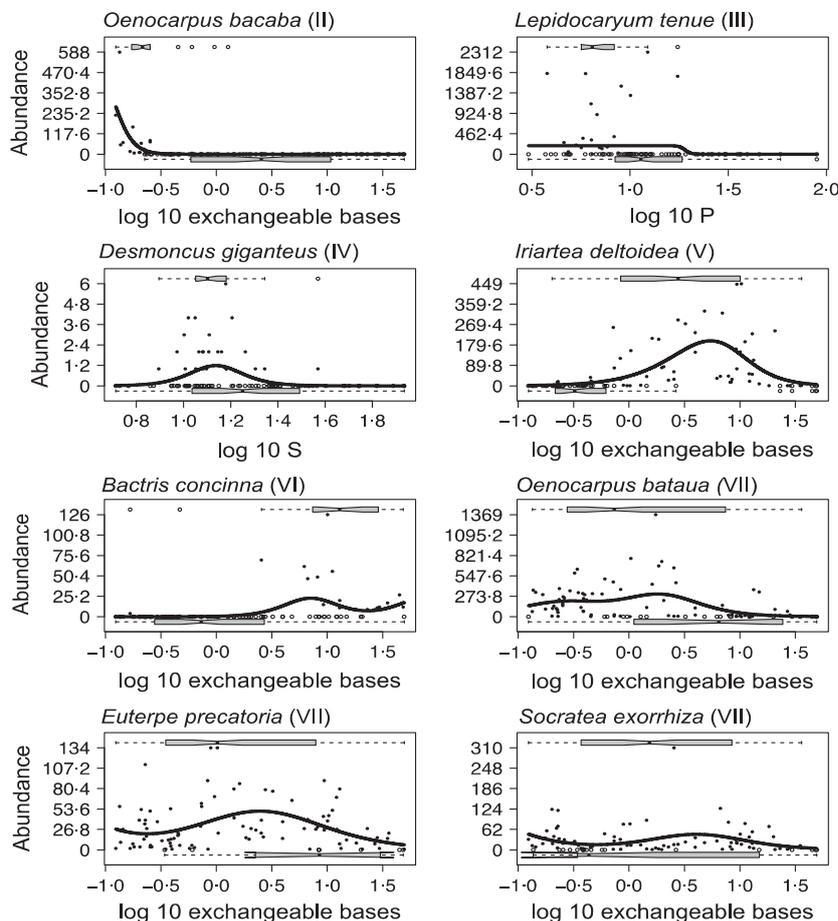
### RESPONSE SHAPES

All 61 palm taxa responded to soil nutrients, as assessed with eHOF models (Fig. 2, Fig. S3, Table S7). The most frequent response shape was bimodal with unequal optima (51% of

**Table 1.** Means and ranges of soil (a) macronutrients and (b) micronutrients in nine regions in western Amazonia. For geographical locations, see Fig. 1

Site	Exchangeable bases (Ca+K+Mg)	Ca	K	Mg	P	S
<b>(a) Macronutrients</b>						
1. Guaviare	0.19 (0.13–0.25)	0.07 (0.05–0.09)	0.05 (0.03–0.08)	0.07 (0.04–0.09)	8.24 (4.75–14.49)	12.32 (7.23–16.02)
2. Caquetá	0.71 (0.12–1.44)	0.33 (0.06–0.84)	0.25 (0.03–0.42)	0.14 (0.04–0.41)	9.32 (4.8–21.56)	9.80 (5.17–12.77)
3. Yasuní	5.95 (0.72–20.71)	4.30 (0.31–15.92)	0.14 (0.11–0.20)	1.50 (0.3–4.64)	12.00 (9.41–17.64)	26.75 (20.18–37.12)
4. Kapawi	6.77 (0.57–20.12)	4.80 (0.23–15.28)	0.35 (0.14–0.83)	1.61 (0.2–4.17)	9.30 (3.04–16.84)	20.14 (12.51–34.19)
5. Iquitos	0.57 (0.24–2.65)	0.23 (0.07–1.50)	0.17 (0.09–0.24)	0.18 (0.06–0.99)	6.27 (4.61–8.30)	10.92 (7.47–16.07)
6. Orellana	31.02 (1.45–49.40)	26.48 (0.7–42.87)	0.48 (0.18–0.81)	4.07 (0.56–7.63)	27.04 (13.03–36.56)	58.83 (19.51–86.06)
7. Ucayali	1.93 (0.37–12.23)	1.22 (0.09–8.76)	0.19 (0.15–0.25)	0.52 (0.1–3.23)	10.73 (5.94–17.74)	12.93 (10.25–23.02)
8. Juruá	3.17 (0.17–12.93)	2.27 (0.06–9.99)	0.12 (0.05–0.25)	0.78 (0.06–2.69)	7.93 (3.71–15.77)	14.76 (8.87–24.75)
9. La Paz	6.86 (0.74–12.95)	4.96 (0.2–10.35)	0.27 (0.15–0.49)	1.64 (0.39–4.09)	34.55 (10.49–89.27)	26.66 (9.42–55.55)
Mean (range)	6.60 (0.12–49.39)	5.16 (0.05–42.87)	0.23 (0.03–0.83)	1.21 (0.04–7.63)	14.12 (3.04–89.27)	21.89 (5.17–86.06)
Site	B	Cu	Fe	Mn	Zn	
<b>(b) Micronutrients</b>						
1. Guaviare	0.47 (0.41–0.54)	0.41 (0.19–0.62)	323.50 (282.82–373.44)	1.24 (0.23–2.01)	0.29 (0.14–0.42)	
2. Caquetá	0.48 (0.4–0.59)	0.51 (0.21–2.29)	327.62 (257.79–431.43)	2.54 (0.31–17.36)	1.09 (0.2–4.80)	
3. Yasuní	0.39 (0.24–0.52)	0.89 (0.46–1.45)	257.73 (118.67–363.16)	121.94 (16.2–308.12)	1.88 (1.02–3.39)	
4. Kapawi	0.37 (0.23–0.54)	2.85 (1.45–4.66)	197.83 (64.31–326.61)	78.93 (3.8–248.45)	1.95 (0.8–3.96)	
5. Iquitos	0.57 (0.45–0.72)	0.31 (0.22–0.71)	395.91 (325.85–424.17)	2.64 (0.29–16.51)	0.55 (0.26–0.84)	
6. Orellana	0.62 (0.42–0.91)	2.66 (0.41–5.26)	184.88 (108.57–507.98)	230.46 (37.76–422.43)	4.02 (1.92–7.21)	
7. Ucayali	0.47 (0.29–0.61)	0.73 (0.28–2.35)	349.49 (171.48–481.79)	15.09 (1.29–95.8)	0.94 (0.46–2.23)	
8. Juruá	0.71 (0.4–0.87)	0.43 (0.16–1.01)	513.36 (244.45–643.36)	96.94 (0.63–370.38)	1.68 (0.38–4.43)	
9. La Paz	0.54 (0.38–0.68)	1.37 (0.53–2.03)	300.94 (182.24–438.82)	150.57 (50.32–268.27)	4.03 (1.31–8.40)	
Mean (range)	0.51 (0.23–0.91)	1.15 (0.16–5.26)	316.64 (64.31–643.36)	82.17 (0.23–422.43)	1.89 (0.14–8.40)	

Concentration of exchangeable bases, Ca, K and Mg in  $\text{cmol}_c \text{kg}^{-1}$ . Concentrations of all other elements in  $\text{mg kg}^{-1}$ .



**Fig. 2.** Examples of different response shapes of palms to soil nutrients, fitted using extended Huisman–Olf–Fresco models (eHOF): (II) monotonic, (III) plateau, (IV) unimodal symmetric, (V) unimodal skewed, (VI) bimodal with two equal optima and (VII) bimodal with unequal optima. Roman numerals in parenthesis indicate the most appropriate eHOF model selected according to the Akaike Information Criterion corrected for small samples sizes and a bootstrap approach (999 permutations). The lower horizontal boxplot ( $y = 0$ ) represents absences and the upper boxplot represents occurrences of the respective species along the gradient. All species showed some response, so eHOF model I (no response) is not shown.

palm taxa), followed by unimodal skewed (47%); monotonic responses were rare (2%) and unimodal symmetric (i.e. Gaussian) or plateau were not found at all (Table S8). No differences in response shapes were found among the different age classes within taxa (i.e. seedlings, juveniles and adults; data not shown). Among unimodal skewed responses, species with a negative skew had significantly higher mean optima for exchangeable bases than those with a positive skew (Fig. S4).

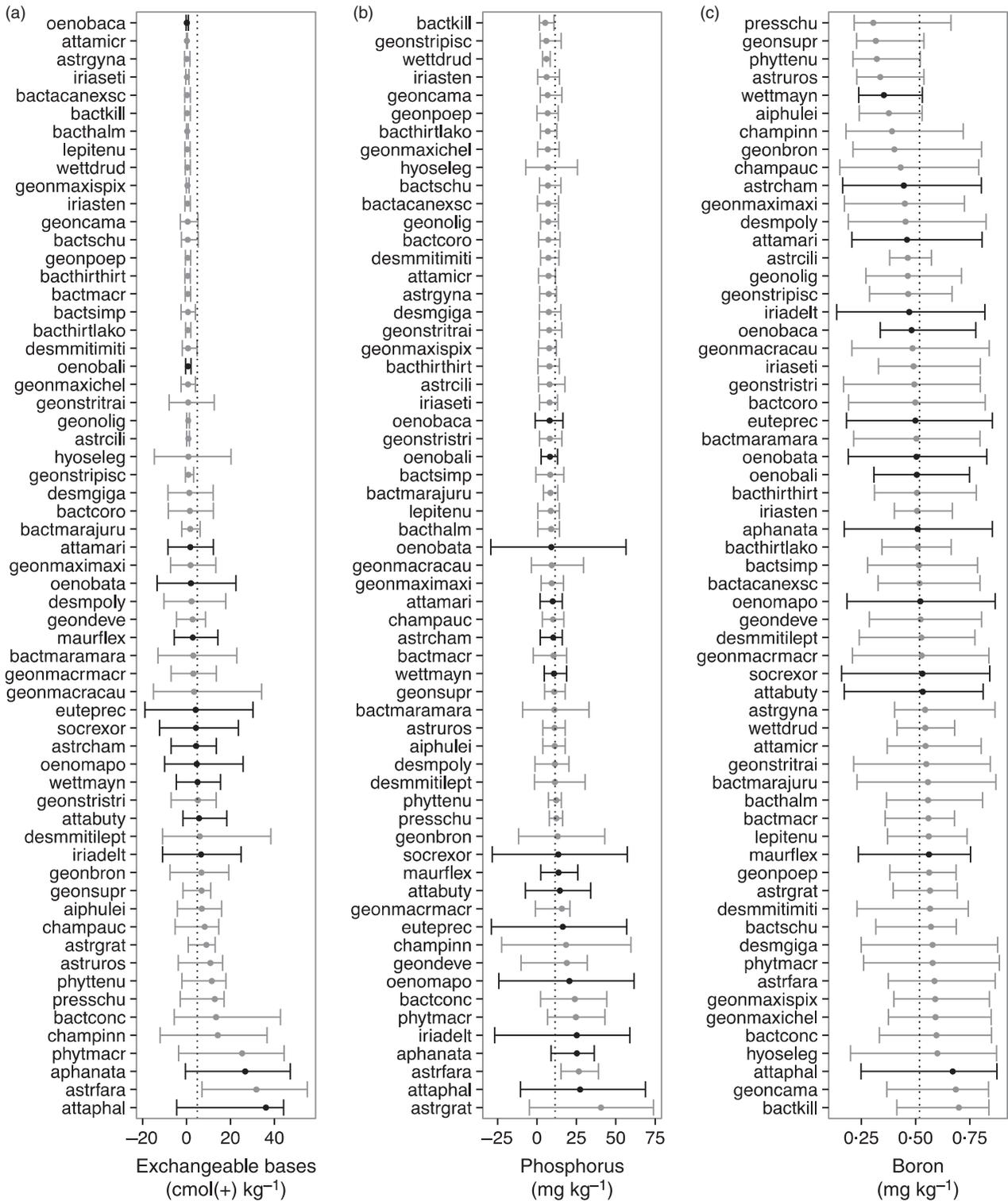
There were 14 canopy and 47 understorey species with  $\geq 10$  occurrences in our sample (Table S8). Among canopy palms, the most common response shape was bimodal with unequal optima (57%), followed by unimodal skewed (29%) and bimodal with equal optima (7%). In understorey palms, unimodal skewed responses were predominant (53%), followed by bimodal with unequal optima (43%).

#### DISTRIBUTION ALONG EDAPHIC GRADIENTS

Most palm taxa had broad and overlapping realised niches along the different soil nutrient gradients (Fig. 3, Table S9). About 54% of all taxa had optima in the low end of the exchangeable bases gradient (Fig. 3a). Species typically growing in white sand forests (i.e. *Astrocaryum gynacanthum*, *Attalea microcarpa*, *Iriartella setigera* and *Oenocarpus bacaba*) exhibited the lowest optima for exchangeable bases. Palms with intermediate optima for exchangeable bases included *Attalea maripa*, *E. precatória* and *O. bataua*, whereas palms with high optima included *Aphandra natalia*, *Attalea phalerata* and *Phytelephas*

*macrocarpa*. The mean optimum of canopy palms was statistically indistinguishable from the mean optimum of understorey palms for both exchangeable bases and B. In contrast, canopy palms had significantly higher mean optimum for P and larger mean niche width along the exchangeable bases, P and B gradients than understorey palms did (Fig. 4).

Most conspecific varieties of *Bactris*, *Desmoncus* and *Geonoma* differed in their response shape along the exchangeable bases gradient (Fig. 5). For example, *Bactris hirta* var. *hirta* exhibited a bimodal response with unequal optima and was most abundant in soils of intermediate concentration of extractable bases, whereas *B. hirta* var. *lakoi* showed a unimodal skewed response and was most abundant in base-poor soils (Fig. 5a). A similar difference was seen between conspecific varieties of *G. macrostachys* (Fig. 5g and j). Model selection in both cases was robust, as evidenced by the large difference in explanatory power (AICc) between the best and the next-best model (Table S10). In contrast, differences in explanatory power between models were small in *Bactris maraja* var. *maraja* (Fig. 5e) and *Desmoncus mitis* subsp. *mitis* (Fig. 5f). Still, for *D. mitis* subsp. *mitis* both the best (IV) and next-best (V) model were different than the best model of *D. mitis* subsp. *leptospadix* (VII). In both *Geonoma maxima* and *Geonoma stricta*, two conspecific varieties showed bimodal responses with unequal optima centred at the intermediate to base-rich soils, and one variety had a skewed response and an optimum in base-poor soils. Some of the conspecific varieties never

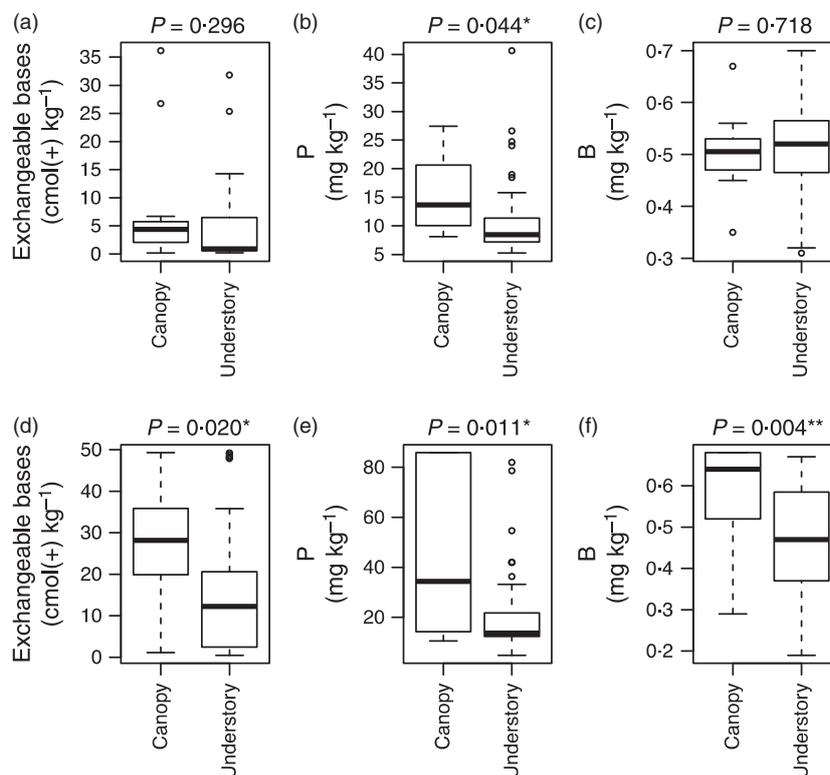


**Fig. 3.** The optimum and range of 61 western Amazonian palm taxa for (a) exchangeable bases (Ca+K+Mg), (b) phosphorus and (c) boron. The vertical grey dashed line in each figure indicates the mean optimum. Black horizontal lines indicate canopy palms; grey horizontal lines indicate understory palms. For unabbreviated species names see Table S9.

occurred in the same transect, whereas others could be found together in up to 19 transects (Table S11).

The four most abundant canopy palms in our sample (*E. precatatoria*, *I. deltoidea*, *O. bataua* and *S. exorrhiza*) also had the widest niches along the exchangeable bases and P gradients

(Fig. 3, Table S9). Typically, *O. bataua* was the most abundant canopy palm in soils of low-to-moderate concentration of exchangeable bases and P. Its abundance decreased sharply in the more fertile soils, where other canopy palms and especially *I. deltoidea* replaced it as dominant (Fig. 6).



**Fig. 4.** Comparison of the optima (a–c) and ranges (d–f) of canopy vs. understory palms in response to (a, d) exchangeable bases (Ca+K+Mg), (b, e) phosphorus and (c, f) boron. Significance was tested using Welch's *t*-test for unpaired samples. \* $P < 0.05$ ; \*\* $P < 0.01$ .

## Discussion

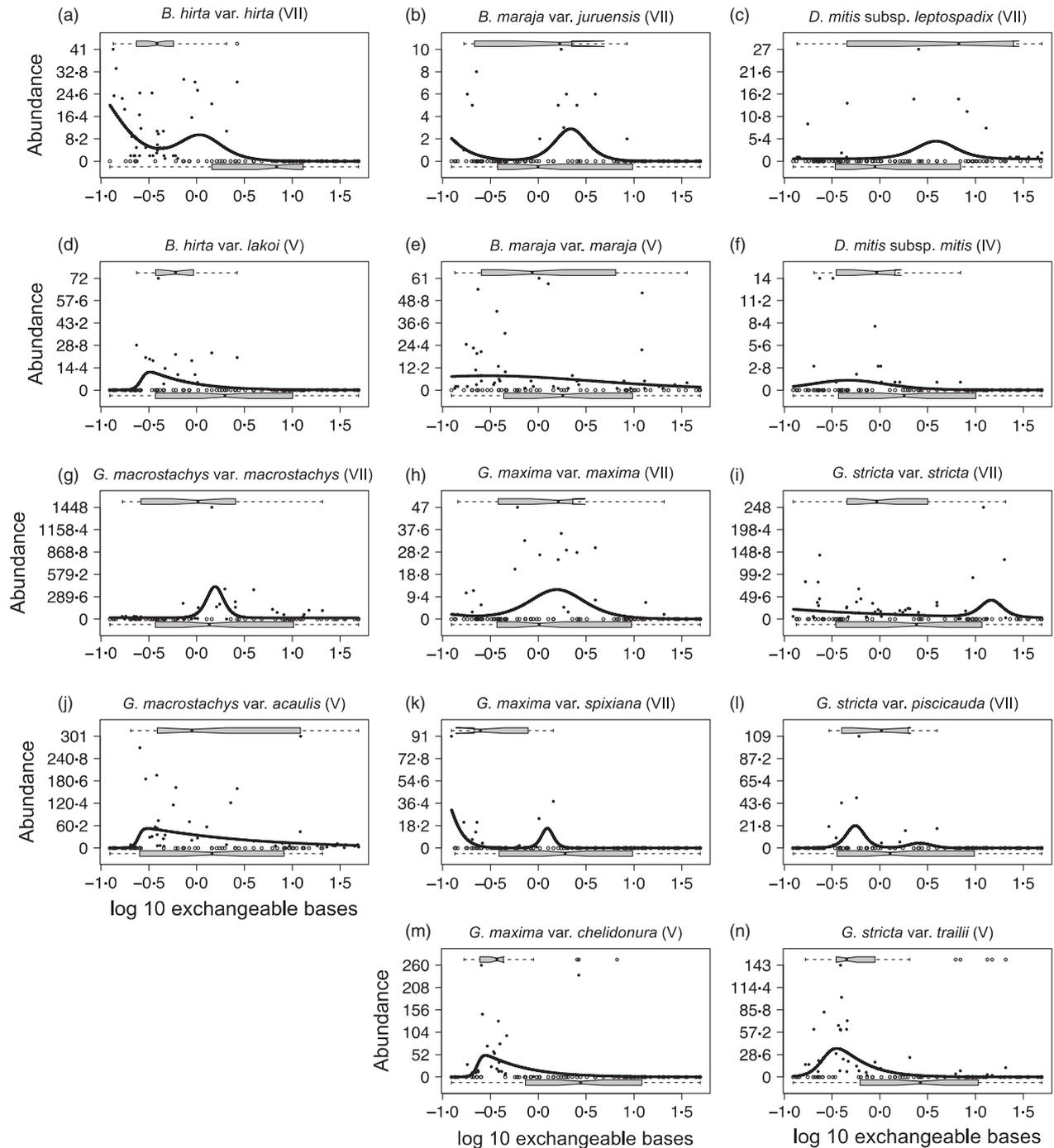
Our large database on palm inventories has allowed us, for the first time, to model and compare the response curves of 61 Amazonian *terra firme* palm taxa along soil nutrient gradients. Our results support the general hypothesis that palm species distribution patterns and community composition are driven by soil nutrients. The specific results can be summarised as follows: (i) concentration of exchangeable bases was the most important soil gradient (out of those analysed) in explaining palm species occurrences and abundances in *terra firme* palm communities, (ii) the modelled species responses to soil nutrients were generally skewed rather than Gaussian, (iii) canopy palms had greater tolerances than understory palms for all nutrients analysed and also higher P optima, (iv) different conspecific palm varieties exhibited different response types to soil nutrients and (v) the rank order in dominance of the most abundant canopy palms changed along the exchangeable bases gradient. Below we discuss each of these observations separately.

### EFFECT OF SOIL EXCHANGEABLE BASES, P AND B ON FLORISTIC COMPOSITION

The range of soil macronutrient concentrations in our study area is comparable with the overall range documented in western Amazonia (Clinebell *et al.* 1995; Tuomisto & Ruokolainen 1998; Quesada *et al.* 2010), and thus reflects well the great edaphic heterogeneity of *terra firme* forests of the western Amazon basin (Tuomisto, Ruokolainen & Yli-Halla 2003). The floristic composition of palm communities in our sample was clearly related to the concentration of exchangeable bases, in

agreement with earlier studies on trees, ferns, Melastomataceae and palms in the area (Tuomisto *et al.* 1995; Phillips *et al.* 2003; Tuomisto, Ruokolainen & Yli-Halla 2003; John *et al.* 2007; Ruokolainen *et al.* 2007), as well as earlier studies on palms in montane forests of Panama (Andersen, Turner & Dalling 2010). Phosphorus was also important in explaining the floristic patterns visible in the NMDS ordination, but not quite as important as exchangeable bases. This is in contrast with the widely held view that P is the most important nutrient for explaining floristic patterns in tropical rain forests (Vitousek 1984; Sollins 1998; Baribault, Kobe & Finley 2012; Condit *et al.* 2013). The relatively modest role that we found for B goes even more strongly against the predicted pattern (Steidinger 2015), although even B did provide some additional explanatory power. One obvious complication in interpreting the results related to P is that the laboratory methods vary considerably (Wuenscher *et al.* 2015), and it is not clear which of them gives the most reliable estimate of P availability to plants.

Our mechanistic understanding of lowland Amazonian palm–soil associations is limited because the few experimental studies that have focused on palms were made in lowland rain forests of Costa Rica (Alvarez-Clare, Mack & Brooks 2013) or in montane rain forest of Panama (Andersen *et al.* 2010; Andersen & Turner 2013; Andersen, Turner & Dalling 2014), which share few species with Amazonia. Large-scale nutrient addition experiments with canopy trees and one palm species (*S. exorrhiza*) have shown that positive growth responses to the addition of P in lowland rain forests vary among taxa and size classes (Alvarez-Clare, Mack & Brooks 2013). Other experiments have found that understory palm distributions along a N gradient correspond to N uptake rates

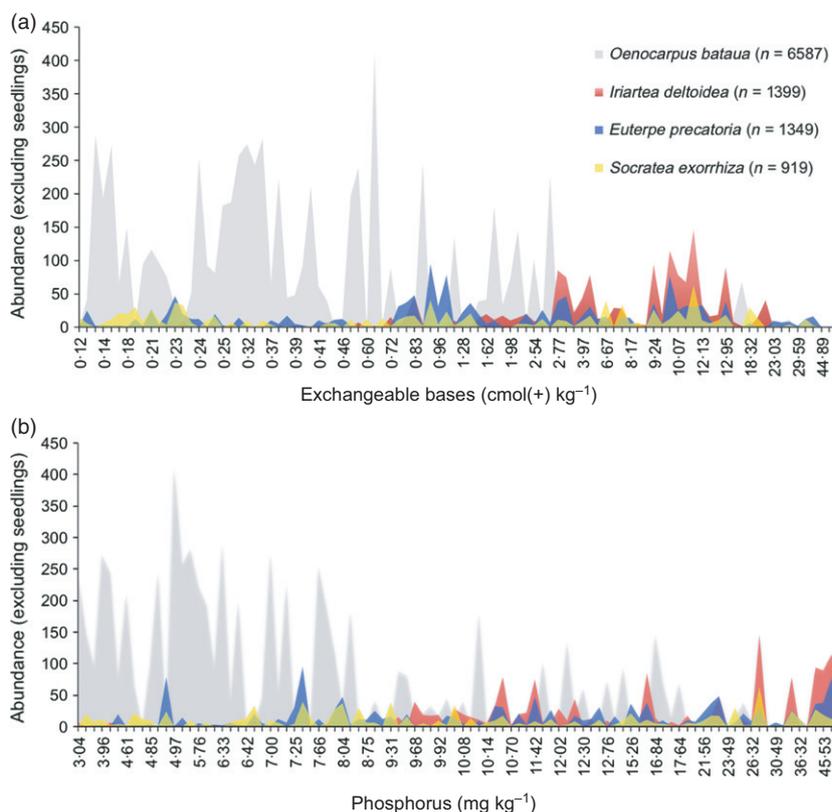


**Fig. 5.** Response shapes of conspecific palm varieties or subspecies to exchangeable bases fitted using extended Huisman–Olf–Fresco models: (a, d) *Bactris hirta* (var. *hirta*, var. *lakoi*), (b, e) *Bactris maraja* (var. *juruensis*, var. *maraja*), (c, f) *Desmoncus mitis* (subsp. *leptospadix*, subsp. *mitis*), (g, j) *Geonoma macrostachys* (var. *macrostachys*, var. *acaulis*), (h, k, m) *Geonoma maxima* (var. *maxima*, var. *spixiana*, var. *chelidonura*) and (i, l, n) *Geonoma stricta* (var. *stricta*, var. *piscicauda*, var. *trailii*). For description of eHOF models, see Fig. 2. For model selection results, see Table S10.

rather than preferences for different soil N forms in lower montane forests (Andersen & Turner 2013). These findings serve as a reminder that multiple elements may be limiting to palms (Baribault, Kobe & Finley 2012), including macronutrients that we did not measure (e.g. N). The situation can be further complicated by nutrient interactions (Townsend *et al.* 2011; Wright *et al.* 2011) and unmeasured micronutrients (Barron *et al.* 2009).

#### SKewed Responses

No taxon had a flat response curve (eHOF type I model) for any of the soil variables. On physiological grounds, there is reason to expect a unimodal response shape, but this may be asymmetric (Whittaker 1956; Austin 1976, 1990). For example, an asymmetric response arises if a species' yield increases progressively from low to medium nutrient concentrations, but



**Fig. 6.** Abundance of four canopy palms in 96 transects in western Amazonia. The transects are ranked according to the concentration of (a) exchangeable bases (Ca+K+Mg) and (b) phosphorus in their soils. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

then decreases rapidly at excessive nutrient concentrations (Austin & Austin 1980). Indeed, skewed physiological responses to environmental factors have often been found (Austin *et al.* 2009). Of course, observational field data can hardly ever reflect the physiological response to a single soil variable exactly. Species abundances in nature are affected by multiple factors simultaneously and, depending on their covariance patterns, it may be analytically difficult or impossible to discern their separate effects. Furthermore, many important factors are inherently difficult to measure (e.g. interactions with other species, dispersal history).

Interspecific competition is one of the factors that might change the shape of the realised response curve relative to the physiological response curve (Austin 1976). In particular, competition between species may lead to a bimodal response, if a (specialist) species can out-compete another (more generalist) species at the middle of a gradient but not at its extremes (Ellenberg & Mueller-Dombois 1974). On the other hand, there is experimental evidence that competition does not necessarily have any effect on response shapes (Austin & Austin 1980). In our data, taxa with a unimodal response with negative skew along the exchangeable bases gradient had higher optima than species with a positive skew, and few species had optima in the intermediate portion of the exchangeable bases gradient. This is in agreement with the prediction that the change in species abundance along an environmental gradient is more gradual when it is caused by competition than when it is caused by the limits of physiological tolerance (Ellenberg & Mueller-Dombois 1974).

Overall, we believe that the response shapes modelled here provide meaningful approximations of the species'

physiological responses, at least for the most important variables such as exchangeable bases and P. These elements are essential in various physiological processes, such as in activating enzymes, as secondary messengers and as key components of nucleic acids and chlorophyll (Maathuis 2009). Most species were geographically widespread and occurred in areas where different kinds of soils are available (Table S3), and in the separate regions each species was consistently concentrated to the same part of the edaphic gradient (Fig. S5). This pattern is unlikely to emerge unless there is a real causal relationship behind it. Because large sampling gaps still exist in western Amazonia (Schulman, Toivonen & Ruokolainen 2007), our models of palm species' responses along edaphic gradients may be useful to predict palm community composition in unsampled sites on the basis of edaphic information and satellite imagery (cf. Tuomisto *et al.* 2003), and to predict edaphic site conditions using quantitative species lists (cf. Sirén, Tuomisto & Navarrete 2013; Zuquim *et al.* 2014).

#### CANOPY VS. UNDERSTOREY RESPONSES

Bimodal response with unequal optima was the most commonly modelled response in canopy palms, whereas unimodal skewed responses were most common in understorey palms. If bimodal response results from competitive effects (a better adapted species displaces another species from intermediate conditions), then these results can be interpreted to suggest that canopy species might be experiencing stronger interspecific competition for exchangeable bases (or another resource correlated with them) than understorey palms.

Non-biological explanations are also possible. In particular, a bimodal response may emerge as a result of strongly biased sampling, where the middle part of a gradient is poorly represented (Austin, Cunningham & Fleming 1984). This is not likely to have been the case in our data, however. Most canopy palms with bimodal responses had intermediate-to-high optima for exchangeable bases (Fig. 3), and this part of the gradient was relatively evenly sampled, although not quite as densely as the relatively poor soils (Fig. S6). Even though the extremely nutrient-poor soils were under-sampled (no white sand forests were included in our sample), increasing the sampling of this forest type would only affect a few species with very low optima for exchangeable bases (i.e. *O. bacaba*, *O. balickii*). It is more likely that the bimodal responses emerged because transects representing optimal values for a taxon along one environmental gradient had less suitable values for it along another gradient, which would affect the response shape along the first gradient (Austin, Cunningham & Fleming 1984). The differences we observed among canopy vs. understorey palms resemble results obtained in montane forests in Tasmania, where different structural groups of plants (trees, shrubs, pteridophytes) showed different distributions of modes and different frequency distributions of modal abundances (Minchin 1989). In any case, our results conform to the view that bimodal responses are widespread (Austin 1985) (Ellenberg & Mueller-Dombois 1974), and underscores the importance of extended HOF models to test for them (Jansen & Oksanen 2013).

Canopy palms had significantly greater tolerances to exchangeable bases, P and B than understorey palms did. This agrees with an earlier result that large palms tend to be more habitat generalists than small palms (Ruokolainen & Vormisto 2000). Such size-related differences in habitat specificity have been suggested to exist among tropical rain forest trees as well (Webb *et al.* 1967; Duque *et al.* 2002; Chust *et al.* 2006), although size-dependent differences in data quality may affect the observed patterns (Jones, Tuomisto & Olivas 2008). It is intriguing that our models suggest canopy palms to exhibit a significantly higher mean optimum response to soil P but not to exchangeable bases or B when compared to understorey palms. This may suggest that canopy palms are less efficient in extracting P from P-poor soils than understorey palms are, or that canopy palms are better competitors than understorey palms on P-rich soils, but experimental studies are needed to test this. Below-ground physiological measurements that test the hypothesis of resource partitioning for soil P (*cf.* Turner 2008) would also allow assessing whether canopy palms exploit different available forms of P than understorey palms do, and whether canopy and understorey palms differ in their soil P uptake rates and absolute demands (*cf.* Andersen & Turner 2013).

#### MODELLLED RESPONSE SHAPES OF UNDERSTOREY CONSPECIFIC PALMS

The observed differences in response shape among conspecific taxa seem to agree with the niche diversification hypothesis, or that 'diversity is maintained by the total number and range of habitats and the degree of specialisation of species to parts of

that range' (Connell 1978). Similarly, previous studies in the Amazon basin have found evidence for opposing patterns in topographic or edaphic preferences among species of understorey palms (Svenning 1999), *Passiflora* climbers (Gentry 1981), *Clidemia* climbers (Schulman, Koivunen & Ruokolainen 2004), Burseraceae trees (Fine *et al.* 2005) and *Adiantum* and *Polybotrya* ferns (Tuomisto, Poulsen & Moran 1998; Tuomisto 2006). Our study differs from these in that we show some pairs of conspecific varieties in *Geonoma*, *Bactris* and *Desmoncus* to exhibit different response shapes along soil nutrient gradients. Previously, such an ecological differentiation has been reported between two Amazonian varieties of *Lindsaea lancea*, but these may actually represent different species (Tuomisto 1998).

Differences in the modelled response shape were evident between some conspecific palm varieties (within *B. hirta*, *G. macrostachys*, *G. maxima*, *G. stricta*), but not between others (*B. maraja*, *D. mitis*). Both *G. macrostachys* var. *macrostachys* and var. *acaulis* are widespread in lowland forests and they were recognised by Henderson as distinct varieties (Henderson 1995). Roncal, Francisco-Ortega & Lewis (2007) later found genetic differences between both varieties in some sites, but not in others, and lack of genetic distinctness at the regional scale led these authors to question Henderson's varieties. Still, both varieties were kept as distinct morphotypes in the most recent taxonomic treatment of *Geonoma*, which recognises nine different morphotypes (Henderson 2011). Topographical preferences of var. *macrostachys* and var. *acaulis* have been found to vary from site to site, which may be because topography is an indirect environmental gradient, and more direct ones (such as soil nutrient content) may have different patterns along topographical gradients in different sites (Vormisto, Tuomisto & Oksanen 2004; Roncal 2006). Direct factors for plant growth, such as the mineral nutrients we measured, seem more consistent in explaining the edaphic distributions of taxa.

Overall, our result that some intraspecific morphotypes showed differential niche use partially supports the resource polymorphism hypothesis of Smith & Skúlason (1996). One caveat is that our soil sampling was not directed at specific taxa, as soils were collected at the beginning, middle and end of each transect. Because edaphic heterogeneity in Amazonia is high even at local scales, more detailed soil sampling strategies (i.e. within a 0.5-m radius of palm individuals (Roncal 2006) and at several depths) could advance the understanding about edaphic niches further.

#### HYPERDOMINANT CANOPY PALMS

The four most abundant canopy palms in our western Amazonian sample (Fig. 6) are also among the ten most abundant species in the entire Amazon basin (ter Steege *et al.* 2013). Our data show that these hyperdominants have non-random distributions not only in relation to broad forest type categories (ter Steege *et al.* 2013) but also along the gradients of soil exchangeable bases and P. *Oenocarpus bataua* was the most abundant canopy palm in soils of low-to-intermediate concentration of exchangeable bases and P, but in more base- and P-rich soils it was consistently replaced as dominant by

the other canopy species, in particular *I. deltoidea*. As *O. bataua* was recorded in every one of the nine regions, and *I. deltoidea* in eight of them (Table S3), the difference between the two in modelled soil optimum is more likely to reflect a true physiological difference than the effects of spatially clustered sampling in combination with limited geographical distribution or other historical chance events. Indeed, experimental studies in Costa Rica have related basal area increment of palms (including *I. deltoidea*) with soil base cation and P concentration, supporting the notion that these can be limiting resources (Baribault, Kobe & Finley 2012).

Habitat specialisation appears to be a general property of many Amazonian tree species even within non-inundated forests (Phillips *et al.* 2003). A landscape-scale study in Costa Rica found reciprocal density relationships of canopy palm species (*S. exorrhiza* and *I. deltoidea*), but this could partly have been influenced by selective logging (Clark *et al.* 1995). In parts of the Amazon basin, pre-Columbian soil amendments (*terra preta do indio*) are decisive for soil nutrient availability today (Glaser & Birk 2012). It is conceivable that effects related to ancient logging and soil nutrient amendments may still influence floristic composition and species responses, not only at the local scale as shown by Quintero-Vallejo *et al.* (2015) but also at a regional scale. Future studies on the physiological mechanisms underlying inter- or infra-specific trade-offs along edaphic gradients should attempt to encompass *terra preta* as an important confounding factor, but also clarify the anthropogenic influence on present-day palm distributions in Amazonia.

## Authors' contributions

All authors conceived and designed the study. Performed the fieldwork: H.B. and R.C.-L. Analysed the data: R.C.-L., H.T., H.B., K.R. and S.M.K. Wrote the paper: R.C.-L. All authors discussed the results and commented on the manuscript. The authors declare no competing interests.

## Acknowledgements

We wish to thank Birgitte Kretzschmar Tagesen who assisted us in locating and handling soil samples, Flavia Bertsch and her laboratory (Universidad de Costa Rica) for conducting all soil analyses and our colleagues at the Section for Ecoinformatics & Biodiversity (Aarhus University) and the Amazon Research Team (University of Turku) for valuable advice. We thank James Ross, Nina Wurzbarger, Amy Austin and four anonymous reviewers for suggestions to improve this work. This work was supported by the Danish Council for Independent Research – Natural Sciences (grant no. 4181-00158 to H.B.), the European Community (FP7 grant no. 212631 to H.B.) and the Academy of Finland (grants to H.T.).

## Data accessibility

Palm transect data: doi: 10.15468/r5hujc (Aarhus University Palm Transect Database, Department of Bioscience, Aarhus University 2016). Soil nutrient data: uploaded as online supporting information.

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Received 18 August 2016; accepted 9 November 2016  
Handling Editor: Nina Wurzbarger

## Supporting Information

Details of electronic Supporting Information are provided below.

**Fig. S1.** Palm species accumulation curves per transect, shown for all nine regions in the western Amazon basin.

**Fig. S2.** Relationships between other soil variables and exchangeable bases (Ca+Mg+K) in 96 transects in the western Amazon basin.

**Fig. S3.** Responses of 61 palm taxa to exchangeable bases (Ca+Mg+K), phosphorus, and boron, fitted using extended Huisman–Olf–Fresco models: (II) monotonic (red), (III) plateau (green), (IV) symmetric (blue), (V) unimodal skewed (brown), (VI) bimodal with two equal optima (magenta) and (VII) bimodal with unequal optima (pink).

**Fig. S4.** (a) Optimum response of 61 palm taxa to exchangeable bases in the western Amazon basin.

**Fig. S5.** Palm abundance as a function of the concentration of exchangeable bases in the soil, for species found in less than half of the regions.

**Fig. S6.** Soil cation concentration in 96 transects in the western Amazon basin.

**Table S1.** Frequency (number of transects) and abundance (number of individuals) of 118 palm taxa in 96 transects in western Amazonia.

**Table S2.** Means and ranges of the total abundance (number of individuals) and richness (number of taxa) of palms in nine regions sampled in western Amazonia.

**Table S3.** Abundance (number of individuals per region) and overall frequency (number of regions) of 61 palm taxa in nine regions in western Amazonia.

**Table S4.** Direction cosines and squared coefficients of soil variables fitted onto the Non-Metric Multidimensional Scaling (NMDS) ordination space of 96 palm communities in western Amazonia.

**Table S5.** Linear Pearson correlation coefficients between soil properties as measured in 96 transects in western Amazonia.

**Table S6.** (A) Mantel test results between floristic and edaphic dissimilarities ( $r_M$  is the Pearson correlation between the two) in 96 transects in western Amazonia, and corresponding partial Mantel test results where the effect of logarithmically transformed geographic distances has been partialled out.

**Table S7.** Response shapes of 61 western Amazonian palm taxa along soil nutrient gradients as fitted using extended Huisman–Olf–Fresco models and abundance data: (II) monotonic, (III) plateau, (IV) unimodal symmetric, (V) unimodal skewed, (VI) bimodal with two equal optima and (VII) bimodal with unequal optima.

**Table S8.** Percentage of western Amazonian palm taxa ( $n = 61$ ) with different response shapes to (A) macronutrients and (B) micronutrients, and percentage of (C) canopy ( $n = 14$ ) and understorey palms ( $n = 47$ ) with different response shapes along the exchangeable bases (Ca+K+Mg) gradient.

**Table S9.** Ranges, means and optimum values of selected log-transformed soil nutrients as modelled with abundance data for 61 western Amazonian palm taxa: (a) exchangeable bases (Ca+Mg+K), (b) phosphorus and (c) boron.

**Table S10.** The best and next-best eHOF models for the abundance responses of conspecific palm varieties or subspecies along the gradient of soil exchangeable base concentration (Ca+K+Mg).

**Table S11.** Number of transects where conspecific subspecies and varieties of palms co-occur and their mean abundances over the transects where they co-occur.

**Data S1.** Supporting information (soil nutrient data).