Niche breadth of Amazonian trees increases with niche optimum across broad edaphic gradients

Jason Vleminckx, Oscar Valverde Barrantes, Claire Fortunel, C. E. Timothy Paine, David Bauman, Julien Engel, Pascal Petronelli, Nállarett Dávila, Marcos Rios, Elvis Harry Valderrama Sandoval, et al.

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Author list and affiliation

Jason Vleminckx[1,2,3], Oscar Valverde Barrantes[2,4], Claire Fortunel[5], C.E. Timothy Paine[6], David Bauman[5,7], Julien Engel[4,5], Pascal Petronelli[8], Nállarett Dávila[9†], Marcos Rios[9], Elvis Harry Valderrama Sandoval[10], Italo Mesones[11], Elodie Allié[8,12], Jean-Yves Goret[12], Freddie C. Draper[13], Juan Ernesto Guevara Andino[14], Solène Béroujon[15], Paul V. A. Fine[16], Christopher Baraloto[2,4,12]

1. Yale Institute For Biospheric Studies (YIBS), Yale University, New Haven, CT, USA. ORCID: 0000-0001-7557-0866.
2. Department of Biological Sciences and Institute of Environment, Florida International Univ., FL, USA.
3. Plant Ecology and Biogeochemistry lab, Faculty of Sciences, Université Libre de Bruxelles, Brussels, Belgium.
4. International Center for Tropical Botany, Dept of Biological Sciences, Florida International Univ., Miami, FL, USA.
5. AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.
6. Environmental and Rural Science, Univ. of New England, Armidale, New South Wales, Australia.

† This author is deceased

7. Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK.
8. CIRAD, UMR Ecologie des Forêts de Guyane, AgroParisTech, Univ. De Guyane, Univ. Des Antilles, Kourou Cedex, France.
9. Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru, Avenida José A. Quiñones km 2.5, Iquitos, Loreto Perú.
10. Facultad de Ciencias Biológicas, Universidad Nacional de la Amazonía Peruana, Iquitos, Loreto, Perú.
11. Department of Integrative Biology and University and Jepson Herbaria, University of California, Berkeley, 3040 Valley Life Sciences Building 3140, Berkeley, California 94720-3140 USA.
12. INRAe, UMR Ecologie de Forêts de Guyane, AgroParisTech, CIRAD, INRA, Univ. de Guyane, Univ. des Antilles, Kourou Cedex, France.
13. Center for Global Discovery and Conservation Science, Arizona State University, 1001 South McAllister Avenue Tempe, Tempe, Arizona 85287 USA.
14. Field Museum of Natural History, Chicago, IL, USA. ORCID: 0000-0002-5433-6218.
15. EcoFoG, UMR Ecologie des Forêts de Guyane, AgroParisTech, Univ. de Guyane, Univ. des Antilles, Kourou Cedex, France.

Corresponding author: Jason Vleminckx (email: jasvlx86@gmail.com).

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2. Abstract

Understanding how biotic interactions and environmental filtering mediated by soil properties shape plant community assembly is a major challenge in ecology, especially when studying complex and hyper-diverse ecosystems like tropical forests. To shed light on the influence of both factors, we examined how the edaphic optimum of species (their niche position) relates to their edaphic range (their niche breadth) along different environmental gradients, and how this translates into functional strategies.

Here we test four scenarios describing the shape of the niche breadth – niche position relationship, including one neutral scenario and three scenarios proposing different relative influences of abiotic and biotic factors on community assembly along a soil resource gradient. To do so, we used soil concentration data for five key nutrients (N, P, Ca, Mg and K), along with accurate measurements of 14 leaf, stem and root traits for 246 tree species inventoried in 101 plots located across Eastern (French Guiana) and Western (Peru) Amazonia.

We found that species niche breadth increased linearly with species niche position along each soil nutrient gradient. This increase was associated with more resource acquisitive traits in the leaves and the roots for soil N, Ca, Mg and K concentration, while it was negatively associated with wood density for soil P concentration. These observations agreed with one of our hypothetical scenarios in which species with resource conservation traits are confined to the most nutrient-depleted soils (abiotic filter), but they are outperformed by faster-growing species on more fertile conditions (biotic filter). Our results refine and strengthen support for niche theories of species assembly, while providing an integrated approach to improve forest management policies.

3. Main text

Introduction

A major interest among plant community and evolutionary biologists is to better understand how environmental filtering and biotic interactions shape community assembly. Many studies examining the determinants of plant β-diversity have emphasized the role of abiotic conditions, such as soil properties, through filtering processes related to species resource acquisition strategies and tolerance to drought and toxicity (Condit et al. 2013, Kraft et al. 2015, Vleminckx et al. 2017, Van Breugel et al. 2019). Several theories have suggested that hyperdiverse communities such as tropical forests also experience strong biotic interactions, mediated by intense inter-specific competition for resources and enemy attacks (Schemske 2009, Fine 2006, 2013). Over time, these biotic interactions would have resulted in the local coexistence of species displaying narrower species niches (Dobzhansky 1950, Pianka 1966, MacArthur 1969).

Habitat heterogeneity remains a major determinant of species turn-over in tropical forests. In the Amazon, for instance, white-sand habitats show extremely nutrient-depleted conditions that select for species investing into costly but well-defended tissues (e.g. thick leaves, hard wood), which render these species less competitive on relatively more fertile conditions (the growth-defense trade-off; Fine et al. 2006, 2010). Species relative investment in costly tissues should therefore reflect their optimum along a resource availability gradient. This optimum should correlate well with the range of resource availability a species can tolerate, under the assumption that poor-soil specialists are poor competitors in fertile conditions and are thereby confined to more restricted niches than faster-growing, rich-soil specialists. Therefore, comparing the range and optimum of species along a steep resource availability gradient would help to determine whether conservative species with a high degree of specialization for poor soil conditions exhibit narrower niches than acquisitive species that

grow faster and are more competitive in fertile soils (assuming that no other processes are becoming important across a broad gradient in soil fertility). Such a comparison would address a major concern that most studies may overstate the role of abiotic filtering as a community assembly rule because they fail to consider the potential influence of biotic processes (Kraft et al. 2014). Additionally, examining how species range and optimum align with different functional strategies may help to identify adaptive trade-offs that delimit species' niches. Despite the rapid accumulation of plant functional trait data from diverse ecosystems, few studies have attempted to link tree species range, optimum, and functional traits (but see Treurnicht et al. [2019] for Fynbos plant communities of the Cape Floristic Region).

Species niche range and optimum relate to the two fundamental parameters proposed by Hutchinson in his hypervolume model (1957), which has provided one of the most successful mechanistic constructs of the ecological niche concept. The niche range is commonly referred to as “niche breadth”, “niche width”, “niche size”, or “ecological amplitude” (Carscadden et al. 2020). Following the Hutchinson’s concept of the niche, the niche breadth determines the range of environmental conditions that a species can tolerate and the range of resources that it uses (the potential, or fundamental niche), a range that in reality is more contracted due to antagonistic interactions mediated by competition for resources, natural enemies, or dispersal barriers (the realized, or observed niche) (Malanson, Westman & Yan 1992; McGill et al. 2006; Kraft et al. 2014). The niche optimum represents the set of environmental conditions where the fitness of a species is highest, as reflected by growth rate, reproduction success, survival, population size or distribution range (Sexton et al. 2017). This parameter can be assessed by calculating the niche position, which can be defined as the average, or median value of an environmental variable where the species occurs, or sometimes as the marginality of this average value compared to the community mean (Roughgarden 1974). The niche position is generally used as a proxy for the niche optimum, since the “true” optimal conditions for a

122 species is generally unknown (as its “true” niche breadth) or only estimated via habitat
123 suitability models (Zuquim et al. 2019). Most studies examine species distributions across only
124 a portion of their geographic and environmental ranges (Sheth et al. 2020), with sampling
125 protocols that are rarely explicitly designed to cover an exhaustive representation of the habitat
126 heterogeneity occurring within a study area, or to provide an equilibrated sampling effort across
127 contrasted habitat conditions.

128 We can propose at least four hypothetical scenarios predicting the shape of niche
129 breadth-position relationships along a gradient of soil nutrient availability (Fig. 1). The
130 relationship between realized species niche breadth and niche position, as well as with their
131 traits, can be illustrated using Gaussian-like curves for simplicity, as in the classic resource
132 utilization model of McArthur (1958) (Fig. 1a), even though actual distributions may follow
133 other forms (Le Bagousse-Pinguet et al. 2017). These curves can be translated into values
134 describing the relationship of niche breadth plotted against niche position (Fig. 1b).

135 In the first scenario, species niche breadth varies randomly across species, regardless of
136 their niche position along a gradient of soil resource availability. This pattern would arise if
137 species were competitively equivalent on any level of that specific soil resource availability,
138 i.e. if species edaphic distribution is only driven by stochastic and dispersal processes. In that
139 sense, this scenario is consistent in its outcome with Hubbell’s neutral theory (2001). In the
140 second scenario, poor soil resources select for species investing in protection against physical
141 and biological damages, to the detriment of growth, which would render these species
142 increasingly less competitive when soil fertility increases. In this case, niche breadth should
143 increase with niche position, and the strength (slope) of this relationship should reflect how
144 much the cost of adaptation to nutrient-poor soils restricts the ability of conservative species to
145 compete with more acquisitive species and establish in more fertile habitats. This scenario is
146 consistent with previous studies showing that poor-soil specialists exhibit resource conservation

147 strategies (e.g. durable tissues with slow turnover), whereas species preferring more fertile soils
148 are characterized by resource acquisitive traits (e.g. cheap tissues with high turnover) (Fine et
149 al. 2006, Pinho et al. 2017, Poorter et al. 2018). Scenario 3 is similar to the second scenario,
150 except that the soil nutrient is not limiting for any species beyond a certain threshold, above
151 which the nutrient availability does not impact fitness anymore. Niche breadth therefore tends
152 to reach a plateau. Such a pattern has rarely been emphasized but see Steidinger (2015) for soil
153 calcium concentration optimum in Panama, which stabilizes and shows a trend consistent with
154 scenario 3. In the fourth scenario, the increase of potential niche breadth as soil resource
155 availability becomes less limiting is counter-balanced by a greater "species packing", i.e. a
156 constriction of species' realized niches (MacArthur 1969) resulting from stronger competition
157 for resources. In this scenario, niche breadth increases with soil resource availability optima,
158 up to a certain intermediate level of soil fertility, then decreases as a consequence of species
159 packing, forming a bell-shaped curve.

160 To further shed light on the goodness-of-fit of each scenario to real species assemblages,
161 we may also inquire whether niche breadth-position relationships show consistent patterns
162 along decoupled environmental gradients, and whether the same functional trade-offs align
163 along each gradient. Environmental axes may covary, or vary independently from each other,
164 either because they are spatially structured at different spatial scales (e.g. climate vs
165 microhabitat variables), or in the case of soil properties because they are influenced by different
166 pedological or biogeochemical processes. For instance, some key soil nutrients like base cation
167 (e.g. calcium, magnesium, potassium) are known to covary, as their concentrations depend on
168 common chemical and geological conditions (e.g. soil acidity, nature of the bedrock). Other
169 soil variables, notably anionic nutrients (e.g. PO_4^{3-}, NO_3^{2-}), may display decoupled spatial
170 variations, as they undergo different chemical constraints (e.g. P immobilization) or different
171 biogeochemical processes (e.g. N-fixation, nitrification) (Hedin et al. 2009, Vleminckx et al.

2015, Quesada et al. 2010). Whether we observe similar niche breadth-position relationships along decoupled environmental dimensions, or whether niche breadth and niche position are influenced by the same resource use traits along those environmental dimensions, are key questions to improve our understanding of community assembly mechanisms. However, these questions remain poorly examined (Futuyma and Moreno 1988, Sultan et al. 1998, Carscadden et al. 2020).

The "world-wide plant economics spectrum hypothesis" (Reich 2014) suggests that fast-slow economics spectra would be consistently observed along decoupled soil fertility gradients, with resource conservation traits being selected on nutrient-depleted soils in general. Although some evidence has supported this hypothesis (Poorter et al. 2018), previous studies have also shown that tree communities display decoupled trait syndromes across leaf, stem and roots (Baraloto et al. 2010, Fortunel et al. 2012, Laughlin 2014, Vleminckx et al. 2021, Asefa et al. 2022). These decoupled wood and leaf economic traits have been shown to respond to similar fertility gradients in tropical forests (Fortunel et al 2014, Vleminckx et al. 2021). Yet, to date there has been no attempt to integrate niche breadth data to examine how individual nutrient availability gradients potentially determine species edaphic ranges, and whether decoupled traits align with the same fertility gradients.

Here, we address these questions using a unique dataset of 246 tree species inventoried in 101 plots located across Eastern (French Guiana) and Western (Peru) Amazonia, together with accurate measurements of 14 leaf, stem and root traits. We first examine whether species niche breadth and niche position, taken separately, are aligned or decoupled among five soil nutrient availability gradients (N, P, Ca, Mg and K). Second, we examine how well the four scenarios presented in Fig. 1 match the observed niche breadth-position relationship along each soil gradient. We address the following specific questions:

(1) How are species niche breadth and position associated among the different soil nutrient gradients?

(2) How well do our four scenarios (Fig. 1) fit the niche breadth-position relationship?

(3) Are decoupled niche breadth and position dimensions associated with different plant functional strategies?

Methods

Study areas

We established a nested experimental design with replicated plots in habitats displaying contrasting soil conditions, characteristic of lowland Amazonian forests – white-sand (WS), Terra Firme (TF) and seasonally flooded forests (SF) (Fortunel et al. 2014, Baraloto et al. 2021) – at both regional (c.100 km) and basin-wide (2500 km) distances. A total of 101 0.1-ha plots were inventoried between 2008 and 2018 in ten subregions of tropical moist forest in French Guiana (hereafter FG; 63 plots) and between 2008 and 2011 in three subregions in Peru (38 plots) (Fig. 2). French Guiana forests stand on an old Precambrian tableland, with old, highly weathered and nutrient-depleted soils (Gourlet-Fleury et al. 2004). Mean annual rainfall across inventory subregions ranges between 2160 and 3130 mm (http://www.worldclim.com/) and is distributed seasonally throughout the year. The wet season stretches from December to July and is usually interrupted in February or March by a short dry period, while the dry season occurs from August to November with monthly rainfall never exceeding 100 mm. Mean temperature oscillates between 23.0 and 26.6°C with low seasonal variation (Gourlet-Fleury et al. 2004). Elevation among subregions ranged from 42 to 529 m. Forests from the Western Amazon in Peru cover heterogeneous soil conditions consequent to the combined impact of marine incursions, the Andean uplift, and the weathering of volcanic sediments (Hoorn et al. 2010). Mean annual rainfall varies between 2405 and 2750 mm, whereas mean temperature ranges

220 from 26.3°C to 26.7°C (http://www.worldclim.com/), and elevation from 95 to 173 m. The
221 study areas are further detailed in Baraloto et al. (2021).

222 **Tree species inventories**

223 Trees were inventoried following a modified version of the Gentry plots proposed by Phillips
224 et al. (2003) and described by Baraloto et al. (2013). Each plot consisted of ten parallel 50 m-
225 long transects departing perpendicularly from a main 180 m-long central line, successively in
226 alternate directions every 20 m along the line (a schematic illustration of a plot is provided in
227 Appendix S1: Figure S1). All stems with a circumference ≥ 8 cm at 1.3 m above the ground
228 (2.5 cm DBH) were inventoried over a two-meter width along each transect. At least one
229 individual of every putatively-distinct taxon encountered was collected in the field to create
230 plot-level voucher collections. In rare cases (0.2% of all stems sampled), no identification was
231 achieved nor could vouchers be collected due to lack of leaves or obstructed canopies. The plot
232 level vouchers were meticulously sorted so that independent distinct taxa had at least one
233 collection in each plot. Further sorting resulted in standardized project type collections for all
234 distinct taxa which were identified at regional herbaria for the Peru (AMAZ) and French Guiana
235 (CAY) collections. We then further standardized and resolved vouchers from both these
236 collections during a five-month period at the herbarium of the Missouri Botanical Garden (MO),
237 such that any unnamed, putative novel species was compared to other congeners from the other
238 region (Baraloto et al. 2021). At the end, we provided a full detail of all project vouchers
239 describing our standardized inventories (vouchers and/or photos are available for loan upon
240 request). Species diversity was characterized in each subregion using species richness, as well
241 as the effective number of species expected from 1000 random samplings of 2 individuals to
242 weight for species abundance (Dauby & Hardy 2011) (Table 1).

243 **Soil data**

244 We collected bulked soil cores at 0–15 cm depth at ten regularly spaced positions along the
245 central line of the plot (Appendix S1: Figure S1). The ten cores were mixed into a 500 g sample
246 that was dried to constant mass (at 25°C) and sieved (2 mm mesh). Samples from were shipped
247 to the University of California, Davis DANR laboratory for physical and chemical analyses (see
248 Baraloto et al. 2011 for full protocol details). The bioavailability of three base cations (Ca, Mg,
249 K) and P, and the total soil nitrogen concentration (N) were then quantified for each soil sample,
250 following a protocol described in details Baraloto et al. (2011). We lack data on other soil
251 variables like soil pH and soil Al, Mn and Fe concentration to evaluate the impact of soil acidity
252 and toxicity on species niches. The mean and the standard deviation of each soil variable in
253 each habitat and each study region (Peru and French Guiana, separately) is shown in Table 2.
254 The distribution of plot values for each soil variable within each edaphic habitat (SF, TF and
255 WS), and a test of comparison (Wilcoxon-Mann-Withney) of these values across habitats for
256 each soil variable are shown in supplementary information (Appendix S2: Figure S1). As a
257 complementary information, we also show the projection of plots and soil variables in a
258 Principal Component Analysis (PCA) (see details in Appendix S3: Figure S1).

259 **Functional trait data**

260 We used data for 14 chemical and morphological traits related to resource use and structural
261 defense, comprising ten leaf, two stem and two fine root traits: Leaf thickness and toughness,
262 SLA, Leaf C, N, P, Ca, Mg and K concentration, leaf ^{13}C, sapwood-specific gravity, trunk bark
263 thickness, fine root tissue density and fine root specific root length (SRL). The unit and
264 functional role of each trait, along with additional information on trait sampling locations are
265 provided as online supplementary information (Vleminckx et al. 2023). These functional data
266 were obtained from accurate trait measurements from Peruvian and French Guianan samples
267 collected for 8345 individuals from 1625 species in 371 genera, 78 families and 26 orders

covering the Rosidae, Asteridae and early eudicots (Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021). Missing trait data ranged from 34.96% for leaf thickness up to 74.17% for root SRL (see Table S2 in Vleminckx et al. 2021). Missing values were imputed using a Bayesian hierarchical matrix factorization method (BHMF), based on taxonomic information and co-variation among traits (Fazayeli et al. 2014; see Vleminckx et al. 2021 for details). All these traits reflect species economics spectrum potentially associated to soil nutrient availability levels, or intrinsic water-use efficiency (Leaf ^{13}C) (Baraloto et al. 2010).

Data analysis

Niche breadth and niche position data

Species abundance at the plot level was calculated after weighting each tree by the logarithm of its basal area, to take into account that later life stages are likely to be more representative of the influence of habitat conditions on species distributions, whereas the assembly rules of younger trees can be more stochastic (Vleminckx et al. 2015). We then calculated the niche breadth and the niche position of each of the 246 species that were present in at least three subregions (i.e., areas comprising plots), across each of the five soil nutrients (N, P, Ca, Mg and K). For each soil variable, the niche position of each species corresponded to the median of the soil variable calculated among plots where the species was found (weighting each plot according to the abundance of the species). The niche breadth was calculated as the interquartile range (25-75%) of values for the soil variable. The 25-75% range was chosen to provide robust niche breadth values that were weakly sensitive to outliers (Steidinger 2015). Calculations using a 20-80% and a 15-85% range provided highly consistent results that did not modify our interpretations. Prior to any subsequent analysis, niche breadth and niche position values were normalized (using a Box-Cox transformation) and standardized (z-score transformation). We then detrended niche breadth values to remove any potential

biased inflation of these values induced by the effects of: (i) the total abundance of each species across all plots, (ii) the number of subregions and (iii) plots in which each species is present, and (iv) their regional distribution (i.e. dummy variable columns indicating whether each species is present in one region, i.e. Western or Eastern Amazon, or both regions). This detrending was performed by using the residuals of a linear regression of niche breadth against these effects (see details in Appendix S4).

Niche breadth and niche position correlations among soil variables

To specifically address question 1, we performed a PCA on the species niche breadth values corresponding to the different soil nutrients, and the same PCA for species niche position values. We then tested whether the Pearson correlations of niche breadth and niche position among the five soil nutrients were statistically significant. Correlations were considered significant when they were lower or higher than the 2.5-97.5% quantiles of correlation values obtained after randomizing each nutrient concentration values at the plot level and recalculating niche breadth and niche position, while preserving the multi-scale spatial structure of each nutrient within each study region (Peru and French Guiana), independently. To do so, we used Moran Spectral Randomization (MSR, Wagner and Dray 2015), a procedure that allows considering multiscale spatial autocorrelation structures for any type of quantitative variable, based on spatially weighted connectivity information among sampling points (i.e. the 101 plots in our case). This information was obtained from an optimized procedure used to choose a spatial weighted matrix and select a subset of Moran's eigenvector maps (MEMs, Dray et al. 2006), following Bauman et al. (2018a,b), using the R package 'adespatial' (Dray et al. 2022). MEMs are spatial eigenvectors that model multi-scale spatial structures in any type of numerical variable. We tested a minimum spanning tree configuration and a Gabriel's graph to model connectivity among plots, which have been shown appropriate to accurately modeling structures even when dealing with nested and irregular sampling designs such as ours (Bauman

et al. 2018a). The spatial weighted connectivity information from the best MEM model (i.e., the eigenvector combination that best described the spatial structures in the soils nutrients' concentration, based on a forward selection with double stopping criterion) is then used in a spatially constrained randomization algorithm in the MSR method to reproduce variables that accurately mimic the observed spatial structures of the randomized variable(s).

Species in each PCA graph were also characterized by their affinity for each of the three habitats, by calculating and testing their indicator value (indval), following Dufrêne & Legendre (1997). This allowed combining quantitative soil information with qualitative visualization of three well-defined and contrasted habitats of the Amazon region (white-sand, terra firme and seasonally flooded).

Relationship between niche optimum, niche breadth and traits for each soil nutrient

To address question 2, we plotted the niche breadth of species against their niche position values, for each soil variable. The linear and non-linear relationships between niche breadth and niche position were fitted using Bayesian regression models. The posterior distributions of the slope coefficients of interest were summarized through the median and 95% posterior credibility interval. The linear and non-linear (quadratic) slope coefficient distributions were fitted (Bayesian updating) using a quadratic approximation (McElreath 2020). The shape of the niche breadth-position associations and the importance of the linear and quadratic coefficients were used to verify which scenario in Fig. 1 best fits the observed niche breadth-position relationship, for each soil nutrient. Coefficient values were considered as clearly positive or negative whenever at least 95% of their posterior mass probability was positive or negative (i.e., did not encompass zero). Scenarios 2 and 3 predict positive values for the linear coefficient and non-important values for scenarios 1 and 4. Scenarios 3 and 4 predict negative values for the quadratic coefficient, while the latter is expected to be non-important for scenarios 1 and 2.

To address question 3, we performed a variation partitioning to quantify, for each soil variable, the fraction (adjusted R^2) of species niche breadth variation explained purely by their niche position and by their functional traits. We then tested the significance of each fraction by testing whether the observed fraction (adjusted R^2 values) was higher than 95% of null values obtained with the MSR method described above. If the observed adjusted R^2 value quantifying the effect of all traits combined was higher than 95 % of the 4999 adjusted R^2 values obtained with the MSR procedure, than we performed a forward selection to identify the traits that significantly explained niche breadth variation (Blanchet et al. 2008).

Prior to the variation partitioning, we verified whether niche breadth values were influenced by phylogeny. Phylogeny was modelled using a matrix of dummy variables assigning "1" for each species (lines) in their corresponding genus and family (in columns), and "0" for non-matching taxa. The phylogenetic effect was then tested using a residuals permutation test (Anderson and Legendre 1999), which showed no significant effect for any soil variable (Appendix S5: Table S1).

All analyses described in the methods were performed in the R statistical environment (R Development Core Team, 2022). We provide the soil, tree inventory and trait data, along with our R script in the online repository folder: https://doi.org/10.7910/DVN/VWAJYR. References for the R packages used are detailed in the R code.

Results

Correlation of niche breadths and positions among soil variables

The two PCAs performed on niche breadth and niche position values showed highly consistent patterns of variables' projection, revealing a strong relationship between these two niche parameters (Procrustes correlation = 0.587; $P <= 0.001$; MSR test; Fig. 3). There was a strong coordination of species niche breadth and position for soil cations (Ca, Mg and K) and to a lesser extent for N. Increasing niche breadth and position values for N, Ca, Mg and K

aligned well with increasingly acquisitive functional traits such as higher leaf N concentration (Fig. 3). Soil P concentration showed a clear decoupling of niche breadth and position values compared to the other nutrients (Fig. 3). Species significantly indicative of seasonally flooded and terra firme habitats displayed significantly higher niche breadth and niche position, as well as higher leaf N and P concentration for soil N, Ca, Mg and K concentration, compared to white-sand specialists, (Appendix S6: Figure S1, and Appendix S7: Figure S1; for sample size details, see Appendix S8: Figure S1). The following analyses examine in more details the relationship between niche breadth, niche position and functional traits for each soil nutrient.

Functional strategies associated with niche breadth and position

Species niche breadth was positively associated with niche position for each of the five soil nutrients (Fig. 4). No clear negative quadratic term was detected for niche position, indicating that relationships were mostly linear and consistent with scenario 2 (Fig. 1). The niche breadth-position linear relationship was the strongest for soil Ca concentration (R^2 value = 45.1%), followed by soil N (40.2%), P (26.2%) and K (18.2%) concentration. The effect of functional traits on niche breadth nearly entirely co-varied with the effect of niche position. In other words, we did not observe any trait explaining species niche breadth alone. Niche breadth and position values were not significantly explained by the genus and family identity of species for any soil variable ($R^2 < 1\%$; Appendix S5: Table S1).

Functional traits contributed to species niche breadth ($P \leq 0.05$; MSR test) for soil N ($R^2 = 3.7\%$) and Ca (12.4%) concentration, with high niche breadth values for these two soil nutrients being associated with more resource acquisitive strategies among species, in particular higher SLA, Leaf N and Ca concentrations, and higher fine root SRL (Fig. 4). The Pearson correlations between each individual trait and species niche breadth for soil N, Ca, Mg and P concentration are shown in supplementary material (Appendix S9: Figure S1). Species niche

393 breadth for soil K concentration was not significantly explained by functional traits (Fig. 4).
394 Results obtained with soil Mg concentration were consistent with the ones obtained with soil
395 Ca concentration (Appendix S10: Figure S1). Functional traits less clearly explained the niche
396 breadth of soil P (R^2=1.9%), although sapwood density was retained by the forward selection
397 procedure, with species distributed on the most P-depleted soils showing denser wood than on
398 less P-limiting conditions.

399 **Discussion**

400 Niche properties, characterized by species range (niche breadth) and optimum (niche position)
401 along soil nutrient gradients, were coordinated among soil N, Ca, Mg and K, but not soil P
402 (Fig. 3). The decoupling of species niches between soil P concentration and the other nutrients
403 was associated with different functional strategies (Fig. 4). Our results suggest that species
404 undergo increasing abiotic constraints that favor costly resource conservation strategies when
405 soil fertility decreases. These abiotic constraints decrease with increasing soil fertility,
406 allowing species exhibiting more resource acquisitive traits to occupy increasingly larger
407 niches, in line with scenario 2 (Fig. 1).

408 ***Costly poor-soil adaptations limit species edaphic ranges***

409 We found a strong positive and linear increase of species niche breadth with their niche
410 position, for each soil nutrient (Fig. 3, 4), in contrast with predictions from scenario 1. The
411 quadratic term of the niche breadth-position relationship was never clearly different from zero
412 and always positive, which invalidated scenarios 3 and 4 and provided support for scenario 2.
413 Although our sampling may not have captured the full edaphic distribution for every species,
414 the gradients that we measured and the care with which we effected taxonomic determinations,
415 represent a nearly complete picture for most of these species' distributions (Quesada et al. 2010,
416 Baraloto et al. 2021), such that additional sampling would be unlikely to change the present
417 results. It is also worth noting that the way we accounted for spatial distribution disparities

among species in the analyses strongly limited the potential influences of spatial biases related to the statistical design (Taylor 1961).

Species distributed on the most N and Ca-depleted soils had lower leaf nutrient concentrations, in particular N and Ca, while also showing relatively low SLA (Fig. 4, Appendix S7: Figure S1), indicating resource conservation strategies (Fortunel et al. 2014). These species also displayed relatively low niche breadth values, which may suggest that their resource conservation traits confine them to these poor soil conditions (generally white-sands), and exclude them from the more fertile terra firme and seasonally flooded soils.

The positive association between species niche breadth for soil Ca concentration and SRL may reflect the existence of a fast-slow trade-off associated with soil fertility conditions, with poor soils occupied by species investing in longer roots with lower tissue quality, possibly associated with higher uptake capacity in more competitive environments. Our results may suggest that soil Ca limitation has had more influence than the four other soil nutrients studied here on fine root evolutionary history and is consistent with previous manipulative studies in tropical Amazonian forests (Wurzburger & Wright 2015). Nevertheless, root traits were generally poor predictors of niche breadth, possibly because of the multiple alternatives that plants use for nutrient capture, including investments in mycorrhizal associations, that make possible a wide spectrum of trait syndromes in the same soil conditions (Valverde-Barrantes et al. 2017).

The niche breadth-position relationship was significantly positive but relatively weaker for soil K concentration (R^2 = 18.2%) than for soil Ca, N and P concentration (≥ 26.2%; Fig. 4). Yet, niche position and niche breadth for soil K concentration did not show any significant association with any functional trait, contrary to the three other soil nutrients. Thus, while our results suggest that K may indeed limit primary productivity, which is consistent with previous studies in lowland tropical forests (Wright et al. 2011, Baribault et al. 2012, Santiago et al.

443 2012), they also nuance the idea that single functional traits reflect edaphic adaptations among
444 tree species. The decoupling of fast-slow economic spectra reported among Amazonian tree
445 communities (Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021) may partly
446 introduce statistical noise when testing a signal between a single trait and a soil variable, and
447 thus partly explains the weak predictive power of traits on species niche breadth.

448 The marked niche breadth-position relationship observed for soil P (R^2 = 26.2%) was
449 highly decoupled from the other four soil nutrients (Fig. 3, 4). This pattern was consistent with
450 the orthogonality between soil P variation and the four other soil nutrients (Appendix S3: Figure
451 S1). This orthogonality supports previous evidence that soil P availability often varies
452 independently from cationic nutrients (Ca, Mg, K) or can even be higher on cation-poor sandy
453 soils, due to the immobilization of P into Al oxyhydroxide complex forms in more fertile,
454 clayey tropical soils (Walker & Syers 1976, Vleminckx et al. 2015, Turner 2018, Cunha et al.
455 2022). In fact, P availability was even higher on white-sand forests than on the other edaphic
456 habitats in Peru (Table 2), whereas the reverse pattern was observed in French Guiana. Yet, the
457 overall niche breadth-position correlation remained strongly positive, even when considering
458 the disparities of habitat differences for P availability across regions.

459 The decoupling of niche dimensions between soil P and the other four soil nutrients was
460 associated with different functional dimensions. More specifically, species preferences for terra
461 firme and seasonally flooded soils, which contained the highest soil N and cation
462 concentrations, were mostly reflected by acquisitive traits in the leaves, whereas species whose
463 optimum was on low P availability soils tended to have denser wood. The latter signal was
464 weak but nevertheless significant (Fig. 4), and while further studies are needed to verify
465 consistent patterns, it may partly explain the decoupling of traits that has previously been
466 reported among leaf and woody aboveground organs when measured across broad edaphic
467 gradients (Baraloto et al. 2010, Fortunel et al. 2014, Vleminckx et al. 2021).

In parallel with using combinations of forward-selected traits in the variation partitioning, we also followed the approach of previous studies which examined the association between functional strategies and species niche parameters by using multivariate functional variables (Kraft et al. 2015, Muscarella et al. 2016, Pistón et al. 2019). This multivariate trait approach was generally less predictive than the forward-selected trait approach shown in Fig. 4 (for more details, see Appendix S11: Figure S1 and Figure S2).

The overall effect of functional traits on niche breadth variation co-varied with the effect of niche position (Fig. 4). This suggests that the resource use traits studied here mostly reflect species edaphic optima and not their range of resource use. It is also worth noting that intra-specific trait variation may have partly limited the detection of niche-trait association at the species level (Zuleta et al. 2022), but we lack enough trait measurements across habitats for each species to have more accurate insights.

Finally, the absence of genus or family-level signal on niche breadth and position (Appendix S5: Table S1) may suggest that various edaphic niches have evolved multiple times within many different genera and families, which is consistent with recent reports (Fine and Baraloto 2016, Baraloto et al. 2021).

Our results provide further support for the determinant role of soil properties in shaping tree species assembly in tropical forests (Russo et al. 2005, Condit et al. 2013, Vleminckx et al. 2017, Wright et al. 2019, Umaña et al. 2021), while they also provide indirect support to the hypothesis that the strength of abiotic filtering, here mediated by soil nutrient contents, determines the degree of species habitat specialization, i.e. to what extent species are confined to smaller niches because of their costly investments in resource conservation that would potentially make them less competitive in more fertile habitats. Definitive evidence of competitive exclusion would further require adding a temporal dimension to these analyses – i.e. tree demography –, for instance relating tree growth or mortality responses to the interplay

493 of soil, traits, and the functional similarity of the neighborhood (Fortunel et al. 2016, Muledi et
494 al. 2020, Rozendaal et al. 2020). Such dynamics data unfortunately remain too scarce in the
495 tropics for accurate characterization of demographic parameters for many species across the
496 breadth of their distribution ranges, emphasizing the need for continued efforts towards
497 establishing and monitoring long-term permanent sample plots in the tropics (Blundo et al.
498 2021, Davies et al. 2021).

499 Here, we did not investigate the possibility that the steep nutrient gradient occurring
500 across habitat may overlap with a gradient of forest dynamics. Canopy disturbance and forest
501 turnover rate are likely greater in the most fertile habitats (Baraloto et al. 2011, Baker et al.
502 2014), with more productive tree communities exhibiting more acquisitive traits (e.g., high
503 SLA, low leaf thickness…) for soil nutrients and light (Fortunel et al. 2014, Vleminckx et al.
504 2020, 2021). A greater light extinction profile is also expected on fertile soils (Russo et al.
505 2012), which may limit the competitiveness of fast-growing species in the understory, although
506 this effect might be compensated by lower air evaporative demand and thermal constraints
507 (Vinod et al. 2022) in the more shaded vegetation strata. Accurate gap dynamics history and
508 light availability data will need to be better studied to further examine how light and soil nutrient
509 gradients interact to influence niche parameters.

510

511 ***Implications regarding forest conservation and tree responses to climate change***

512 Species adapted to poor soil conditions likely have large potential edaphic niches
513 compared to their realized one, as they could in theory thrive on a much wider range of soil
514 fertilities in the absence of faster-growing competitors, unlike species with higher niche fertility
515 optimum whose realized and fundamental niches are expected to be more packed. The costly
516 resource conservation traits displayed by poor-soil specialists are likely to exclude them from
517 more fertile habitats, explaining the disparities between their realized and fundamental niches.

These adaptations might also allow these species to extend their tolerance to other environmental constraints such as water deficiency (Baraloto et al. 2010), which occurs more frequently on highly drained white-sands than on terra firme or seasonally flooded soils. This would potentially render white-sand tree communities more resilient to more prolonged dry seasons and temperature increases predicted by climate models, predictions that are particularly threatening in the North-Eastern Amazon (Fortunel et al. 2014, Guevara et al. 2016, Esquivel-Muelbert et al. 2018, IPCC 2022). These results could also pave the way for developing more evidence-based forest restoration management plans, for instance by improving the selection of tree species that would be able to establish in a wide range of environmental conditions. Further investigations of the interplay of species niche breadth, niche position and functional strategies for complementary key edaphic and climatic niche dimensions and across different tropical regions and spatial scales will be urgently needed to better predict how the current context of rapid environmental changes is likely to affect tropical forest species composition and associated ecosystem functions.

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5. Author Contributions

C.B. and P.V.A.F. were co-principal investigators for the projects that supported this research. The collection and identification of tree species was coordinated by C.B and P.V.A.F., with help of J.E., P.P., N.D., M.R., E.V., I.M., J.G., C.F., E.A., T.P., A.D., J-Y.G., O.V.B., F.D. and J.V. J.V., C.F., O.V.B. and C.B. led the trait data collection in French Guiana and Peru. J.V. analyzed the data, with help from D.B. with Bayesian analyses. J.V. led the writing of the manuscript. C.B., O.V.B., C.F. and D.B. commented on early versions of the manuscript. All authors contributed to the preparation of the final manuscript.

6. Conflict of Interest Statement

The authors declare no conflict of interest

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9. Tables

Table 1. Summary of key descriptors of study regions, subregions and habitats. NrP = Number of plots; AR = Altitudinal Range (in m); MAR = Mean Annual Rainfall (in mm); MAT = Mean Annual Temperature (in °C). NrSp = mean number of species per plot; ENS_2 = mean (calculated at the plot level) Effective Number of Species expected from 1000 random samplings (with replacement) of two individuals. The three last lines of each region represent the same information for each habitat. Numbers in parenthesis correspond to the standard deviation of the mean.

	NrP	AR	MAR	MAT	NrSp	ENS2
French Guiana	64	42-529	2157-3129	23.0-26.6	80.3 (3.6)	48.6 (5.2)
Saül-Limonade	12	196-253	2421	24.6	66.1 (4.2)	24.4 (4.5)
Trinité	6	126-320	2671	25.1	112.8 (11.7)	77.8 (14.0)
Itoupé	3	521-529	2530	23.0	79.7 (6.9)	30.1 (7.0)
Mitaraka	9	317-347	2157	24.9	70.8 (10.7)	66.1 (17.2)
Laussat	10	49-57	2402	26.2	74.1 (3.7)	28.0 (4.0)
Nouragues	8	108-345	3328	24.8	86.9 (14.0)	68.0 (20.5)
Petite montagne Tortue	9	47-136	3729	25.4	95.0 (10.5)	66.3 (17.0)
Centre Spatial Guyanais	4	43-63	2932	25.8	76.0 (9.2)	25.3 (5.1)
Kaw	2	254-282	3720	24.5	96.0 (6.0)	73.9 (18.5)
Suriname	2	196-229	2241	26.6	38.5 (3.5)	10.1 (6.3)
Terra Firme	20	45-347	2775	25.2	95.5 (4.4)	70.8 (7.6)
Seasonally Flooded	35	43-529	2723	24.9	64.7 (5.2)	24.5 (4.2)
White Sand	10	39-345	2908	25.7	59.5 (5.6)	21.1 (4.7)
Peru	38	95-173	2405-2750	26.3-26.7	101.4 (4.99)	61.2 (6.7)
Morona	6	143-173	2405	26.7	108.2 (6.0)	89.4 (17.2)
North Loreto	18	105-149	2750	26.3	101.6 (8.7)	59.9 (10.5)
South Loreto	14	95-139	2499	26.8	98.3 (7.5)	50.7 (9.0)
Terra Firme	11	95-158	2597	26.6	128.8 (5.6)	101.6 (9.6)
Seasonally Flooded	13	106-156	2636	26.5	87.7 (6.1)	53.4 (9.2)
White Sand	14	106-173	2625	26.6	86.7 (7.8)	29.8 (5.0)

799 **Table 2**. Mean (± standard deviation) of each soil variable in each habitat (SF = Seasonally
800 Flooded; TF = Terra Firme; WS = White-Sand) and each study region (French Guiana and
801 Peru).

	French Guiana			**Peru**		
Habitat	**SF**	**TF**	**WS**	**SF**	**TF**	**WS**
TN (%)	2.29 (3.25)	1.65 (1.35)	0.17 (0.22)	0.23 (0.09)	0.14 (0.05)	0.07 (0.06)
Avail. P (mg/kg)	10.78 (15.51)	5.07 (5.81)	3.67 (4.11)	7.4 (5.75)	2.25 (1.54)	8.4 (8.01)
Ca (mg/kg)	1.26 (2.37)	0.53 (1.02)	0.16 (0.17)	5.96 (7.23)	0.84 (2.58)	0.04 (0.03)
Mg (mg/kg)	0.81 (0.92)	0.32 (0.31)	0.22 (0.24)	1.35 (1.45)	0.31 (0.6)	0.05 (0.04)
K (mg/kg)	0.13 (0.11)	0.1 (0.04)	0.05 (0.05)	0.18 (0.07)	0.06 (0.02)	0.06 (0.03)

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10. Figure captions

Figure.1 (a) Hypothetical scenarios describing species frequency distributions (realized niches) along a gradient of increasing soil nutrient availability, using Gaussian curves for simplicity. (b) Translation of these scenarios into niche breadth – niche positions graphs, showing species and predicted functional strategies with symbols.

Figure 2. Geographical distribution of the 13 subregions in the Amazon (red rectangles), showing the position of the plots (yellow cross symbols) within the two study regions (Peru and French Guiana).

Figure 3. Projection of species and soil variables on axes 1-2 of a principal component analysis (PCA) performed on niche breadth (a) and niche position (b) values. The grey rectangle that connects both PCA graphs shows the Procrustes correlation quantifying the matching of soil variables and species projections between the two PCAs ($P \leq 0.001$; MSR test). The histograms show the relative eigenvalues of each PCA axis (only the first axis in each PCA expressed more variation than expected under a broken stick model). Symbols in the graphs indicate whether species are significantly indicative of one of the three habitats (seasonally flooded, terra firme, or white-sand specialist) or not (generalist). Tables at the bottom show the Pearson correlations of niche breadth (c) and niche position (d) values among soil variables. The significant correlations (*t*-test of Pearson's moment correlation) are indicated in blue (grey values were not significant).

Figure 4. Niche breadth–niche position relationship among the 246 species, for each of four soil nutrients. Values indicated along x and y axes corresponded to back-transformed niche breadth and niche position values, respectively. Traits significantly explained niche breadth variation for N, Ca, and P. For these three nutrients, the Venn diagram on the right of the niche breadth-position graph shows the relative linear contribution (adjusted R^2 from a variation partitioning analysis) of niche position alone, traits alone, and the joint influence of niche

position and traits. Individual traits that significantly explained niche breadth variation (i.e., the traits selected from a forward selection procedure, which was performed if the overall effect of traits was significant when using the MSR testing procedure; see methods for details) were indicated on the right of the Venn diagram, with colors indicating whether correlations were positive (blue) or negative (red) between niche breadth and the trait. Symbols indicate whether species are significantly indicative (significant indval) of one of the three habitats (see the legend panel at the bottom right of the figure). The two grey regions in each graph represent two different 95% Bayesian plausible intervals for predicted niche breadth values. The narrow interval shows the distribution of estimated mean niche breadth values, while the wide interval corresponds to the region in which the non-linear model expects to find 95% of actual niche breadth values at each niche position value. The equation in each graph shows the median of the Bayesian credibility interval for the linear and quadratic coefficients and the intercept. Significant coefficients (i.e., at least 95% of estimated posterior coefficient values being positive) were emphasized in bold. No significant quadratic effects were found for traits. Asterisks in the Venn diagrams indicate significant adjusted R^2 values quantifying the relative effect of niche position alone, traits alone and the co-variation of both niche position and traits, according to the MSR testing procedure (see methods): ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$.

11. Figures

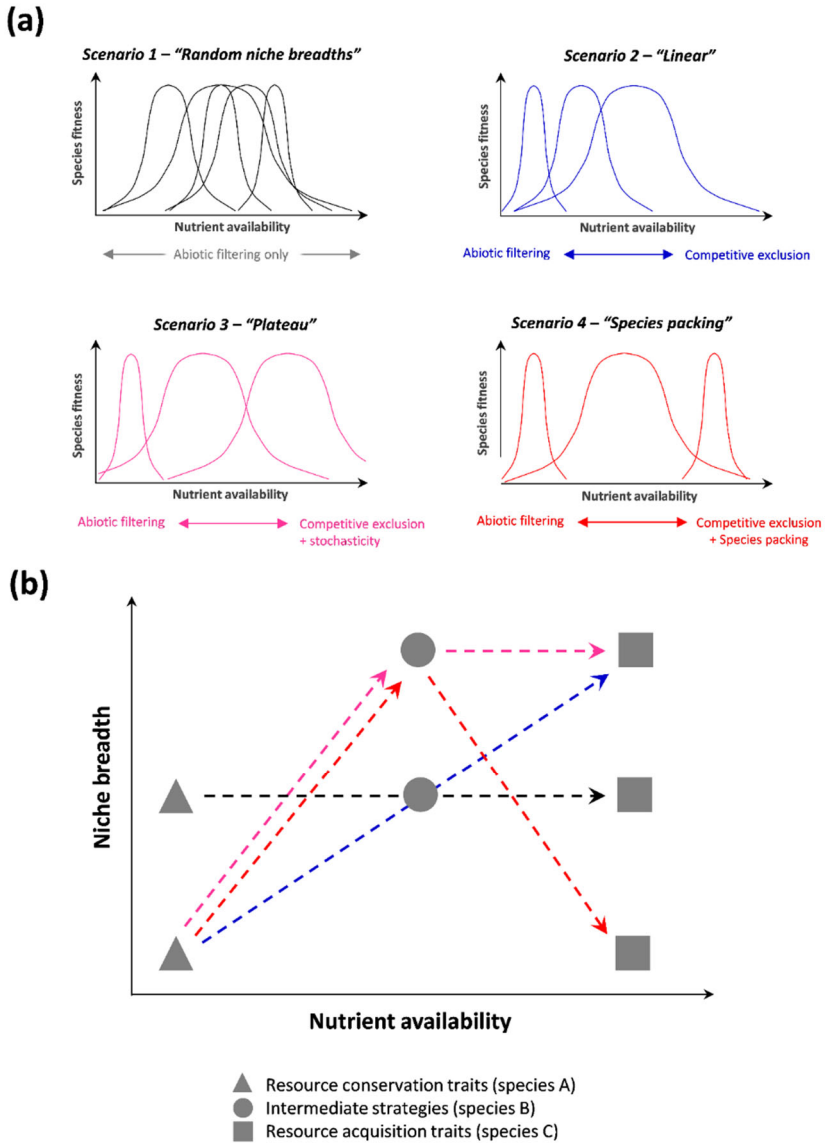
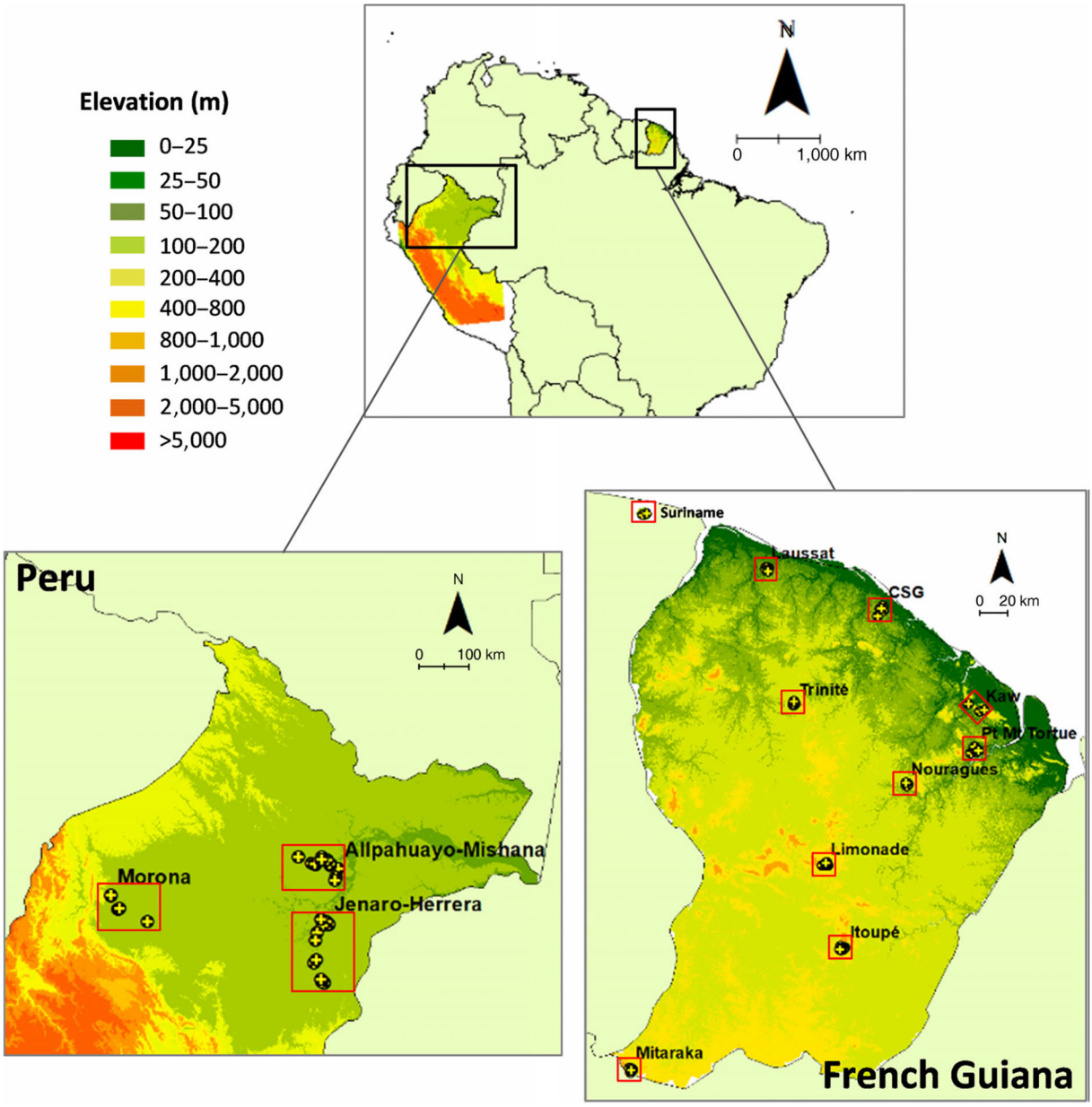


Figure.1



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856 **Figure 2.**

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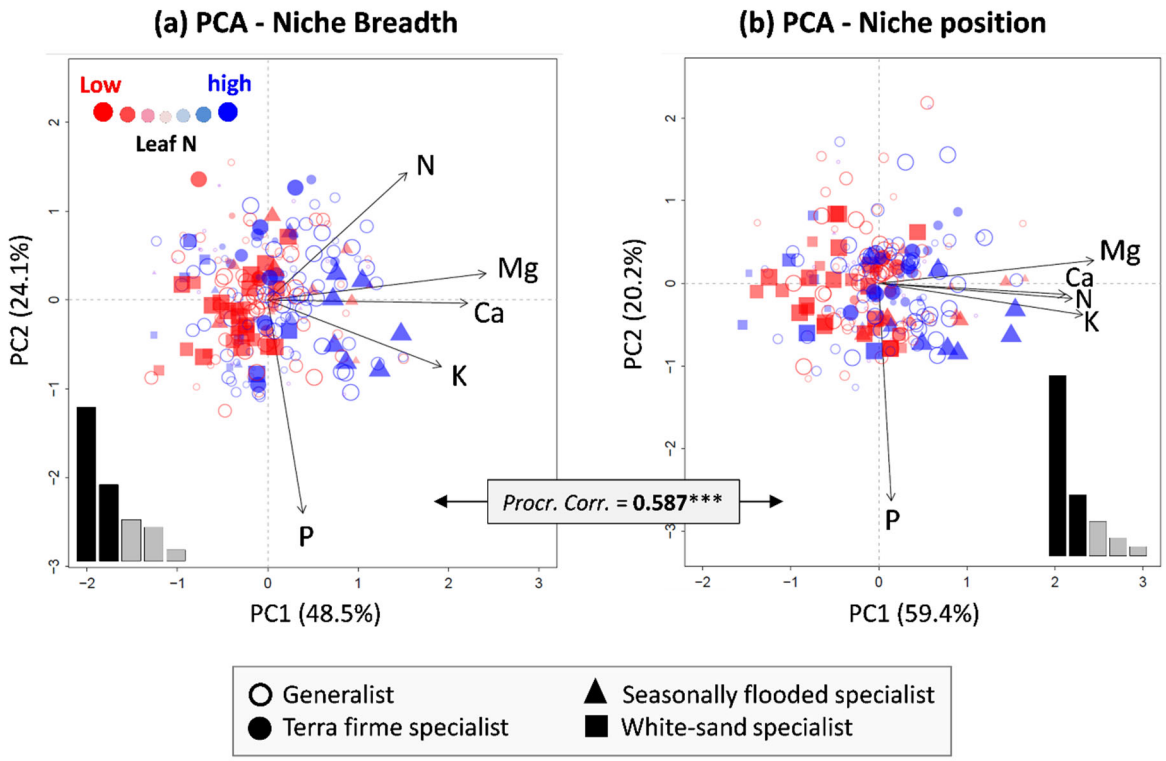

(c) Niche breath correlations

	N	Ca	Mg	K
Ca	0.34			
Mg	0.45	0.77		
K	0.27	0.38	0.55	
P	-0.20	0.12	-0.01	0.23

(d) Niche position correlations

	N	Ca	Mg	K
Ca	0.50			
Mg	0.64	0.74		
K	0.72	0.54	0.75	
P	0.09	0.11	-0.03	0.17

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861 **Figure 3.**

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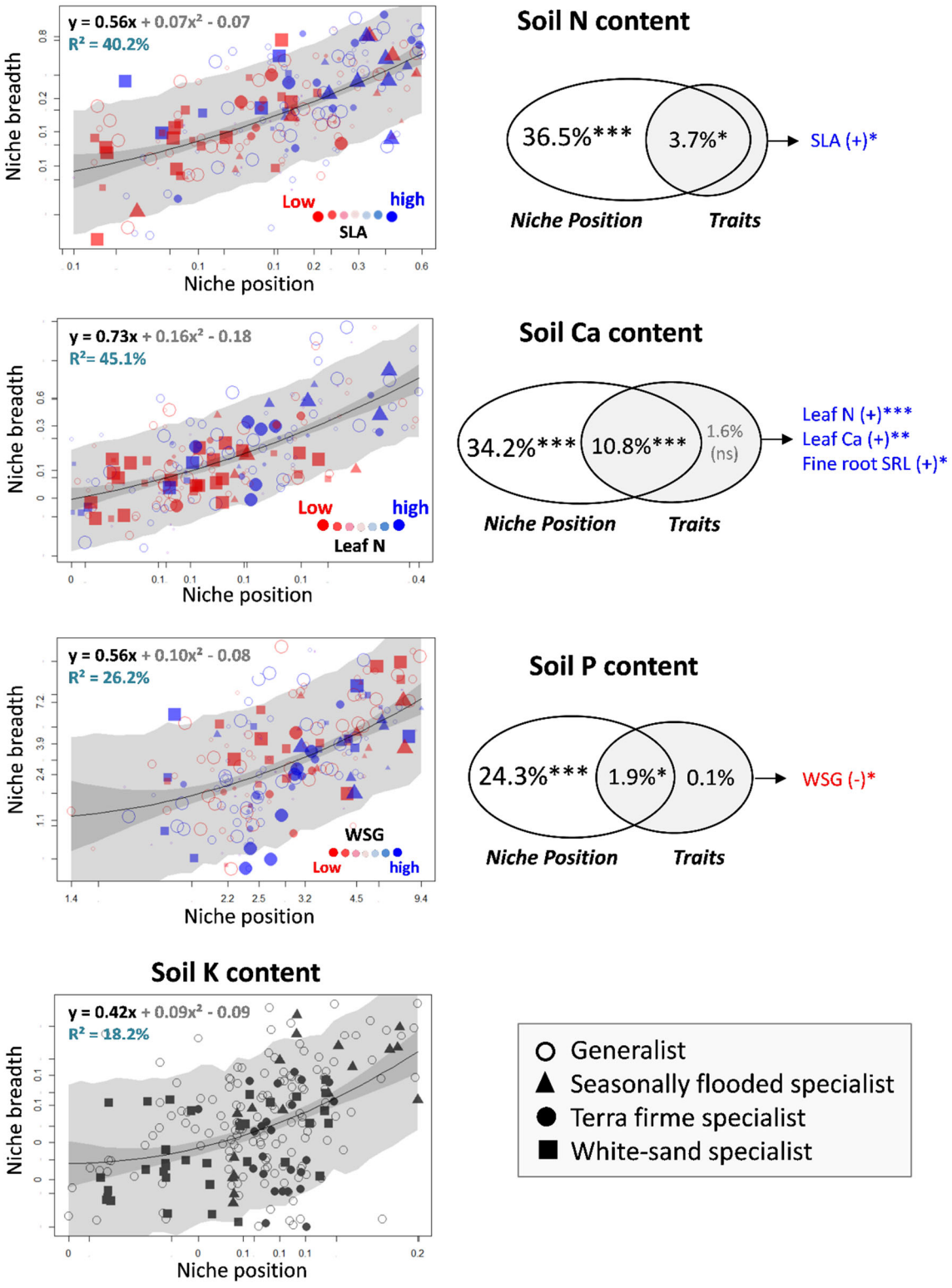
y = 0.56x + 0.07x² - 0.07
R² = 40.2%
Niche breadth
Niche position
Low
high
SLA
Soil N content
36.5%***
3.7%*
SLA (+)*
Niche Position
Traits
y = 0.73x + 0.16x² - 0.18
R²= 45.1%
Leaf N
Soil Ca content
34.2%***
10.8%***
1.6%
(ns)
Leaf N (+)***
Leaf Ca (+)**
Fine root SRL (+)*
y = 0.56x + 0.10x² - 0.08
R² = 26.2%
WSG
Soil P content
24.3%***
1.9%*
0.1%
WSG (-)*
Soil K content
y = 0.42x + 0.09x² - 0.09
R² = 18.2%
Generalist
Seasonally flooded specialist
Terra firme specialist
White-sand specialist

Figure 4.