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

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7   **Author list and affiliation**

8   Jason Vleminckx[1,2,3], Oscar Valverde Barrantes[2,4], Claire Fortunel[5], C.E. Timothy Paine[6],

9   David Bauman[5,7], Julien Engel[4,5], Pascal Petronelli[8], Nállarett Dávila[9†], Marcos Rios[9], Elvis

10   Harry Valderrama Sandoval[10], Italo Mesones[11], Elodie Allié[8,12], Jean-Yves Goret[12], Freddie C.

11   Draper[13], Juan Ernesto Guevara Andino[14], Solène Béroujon[15], Paul V. A. Fine[16], Christopher

12   Baraloto[2,4,12]

13

14   1. Yale Institute For Biospheric Studies (YIBS), Yale University, New Haven, CT, USA.

15   ORCID: 0000-0001-7557-0866.

16   2. Department of Biological Sciences and Institute of Environment, Florida International Univ.,

17   FL, USA.

18   3. Plant Ecology and Biogeochemistry lab, Faculty of Sciences, Université Libre de Bruxelles,

19   Brussels, Belgium.

20   4. International Center for Tropical Botany, Dept of Biological Sciences, Florida International

21   Univ., Miami, FL, USA.

22   5. AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations),

23   Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

24   6. Environmental and Rural Science, Univ. of New England, Armidale, New South Wales,

25   Australia.

† This author is deceased

26   7. Environmental Change Institute, School of Geography and the Environment, University of

27   Oxford, Oxford, UK.

28   8. CIRAD, UMR Ecologie des Forêts de Guyane, AgroParisTech, Univ. De Guyane, Univ. Des

29   Antilles, Kourou Cedex, France.

30   9. Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru, Avenida José A.

31   Quiñones km 2.5, Iquitos, Loreto Perú.

32   10. Facultad de Ciencias Biológicas, Universidad Nacional de la Amazonía Peruana, Iquitos,

33   Loreto, Perú.

34   11. Department of Integrative Biology and University and Jepson Herbaria, University of

35   California, Berkeley, 3040 Valley Life Sciences Building 3140, Berkeley, California

36   94720-3140 USA.

37   12. INRAe, UMR Ecologie de Forêts de Guyane, AgroParisTech, CIRAD, INRA, Univ. de

38   Guyane, Univ. des Antilles, Kourou Cedex, France.

39   13. Center for Global Discovery and Conservation Science, Arizona State University, 1001

40   South McAllister Avenue Tempe, Tempe, Arizona 85287 USA.

41   14. Field Museum of Natural History, Chicago, IL, USA. ORCID: 0000-0002-5433-6218.

42   15. EcoFoG, UMR Ecologie des Forêts de Guyane, AgroParisTech, Univ. de Guyane, Univ.

43   des Antilles, Kourou Cedex, France.

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

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.

73   **Introduction**

74   A major interest among plant community and evolutionary biologists is to better

75   understand how environmental filtering and biotic interactions shape community assembly.

76   Many studies examining the determinants of plant β-diversity have emphasized the role of

77   abiotic conditions, such as soil properties, through filtering processes related to species resource

78   acquisition strategies and tolerance to drought and toxicity (Condit et al. 2013, Kraft et al. 2015,

79   Vleminckx et al. 2017, Van Breugel et al. 2019). Several theories have suggested that

80   hyperdiverse communities such as tropical forests also experience strong biotic interactions,

81   mediated by intense inter-specific competition for resources and enemy attacks (Schemske

82   2009, Fine 2006, 2013). Over time, these biotic interactions would have resulted in the local

83   coexistence of species displaying narrower species niches (Dobzhansky 1950, Pianka 1966,

84   MacArthur 1969).

85   Habitat heterogeneity remains a major determinant of species turn-over in tropical

86   forests. In the Amazon, for instance, white-sand habitats show extremely nutrient-depleted

87   conditions that select for species investing into costly but well-defended tissues (e.g. thick

88   leaves, hard wood), which render these species less competitive on relatively more fertile

89   conditions (the growth-defense trade-off; Fine et al. 2006, 2010). Species relative investment

90   in costly tissues should therefore reflect their optimum along a resource availability gradient.

91   This optimum should correlate well with the range of resource availability a species can

92   tolerate, under the assumption that poor-soil specialists are poor competitors in fertile

93   conditions and are thereby confined to more restricted niches than faster-growing, rich-soil

94   specialists. Therefore, comparing the range and optimum of species along a steep resource

95   availability gradient would help to determine whether conservative species with a high degree

96   of specialization for poor soil conditions exhibit narrower niches than acquisitive species that

97   grow faster and are more competitive in fertile soils (assuming that no other processes are

98   becoming important across a broad gradient in soil fertility). Such a comparison would address

99   a major concern that most studies may overstate the role of abiotic filtering as a community

100 assembly rule because they fail to consider the potential influence of biotic processes (Kraft et

101 al. 2014). Additionally, examining how species range and optimum align with different

102 functional strategies may help to identify adaptive trade-offs that delimit species' niches.

103 Despite the rapid accumulation of plant functional trait data from diverse ecosystems, few

104 studies have attempted to link tree species range, optimum, and functional traits (but see

105 Treurnicht et al. [2019] for Fynbos plant communities of the Cape Floristic Region).

106   Species niche range and optimum relate to the two fundamental parameters proposed by

107 Hutchinson in his hypervolume model (1957), which has provided one of the most successful

108 mechanistic constructs of the ecological niche concept. The niche range is commonly referred

109 to as "niche breadth", "niche width", "niche size", or "ecological amplitude" (Carscadden et al.

110 2020). Following the Hutchinson's concept of the niche, the niche breadth determines the range

111 of environmental conditions that a species can tolerate and the range of resources that it uses

112 (the potential, or fundamental niche), a range that in reality is more contracted due to

113 antagonistic interactions mediated by competition for resources, natural enemies, or dispersal

114 barriers (the realized, or observed niche) (Malanson, Westman & Yan 1992; McGill et al. 2006;

115 Kraft et al. 2014). The niche optimum represents the set of environmental conditions where the

116 fitness of a species is highest, as reflected by growth rate, reproduction success, survival,

117 population size or distribution range (Sexton et al. 2017). This parameter can be assessed by

118 calculating the niche position, which can be defined as the average, or median value of an

119 environmental variable where the species occurs, or sometimes as the marginality of this

120 average value compared to the community mean (Roughgarden 1974). The niche position is

121 generally used as a proxy for the niche optimum, since the "true" optimal conditions for a

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

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

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

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

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

172   2015, Quesada et al. 2010). Whether we observe similar niche breadth-position relationships

173   along decoupled environmental dimensions, or whether niche breadth and niche position are

174   influenced by the same resource use traits along those environmental dimensions, are key

175   questions to improve our understanding of community assembly mechanisms. However, these

176   questions remain poorly examined (Futuyma and Moreno 1988, Sultan et al. 1998, Carscadden

177   et al. 2020).

178   The "world-wide plant economics spectrum hypothesis" (Reich 2014) suggests that fast-

179   slow economics spectra would be consistently observed along decoupled soil fertility gradients,

180   with resource conservation traits being selected on nutrient-depleted soils in general. Although

181   some evidence has supported this hypothesis (Poorter et al. 2018), previous studies have also

182   shown that tree communities display decoupled trait syndromes across leaf, stem and roots

183   (Baraloto et al. 2010, Fortunel et al. 2012, Laughlin 2014, Vleminckx et al. 2021, Asefa et al.

184   2022). These decoupled wood and leaf economic traits have been shown to respond to similar

185   fertility gradients in tropical forests (Fortunel et al 2014, Vleminckx et al. 2021). Yet, to date

186   there has been no attempt to integrate niche breadth data to examine how individual nutrient

187   availability gradients potentially determine species edaphic ranges, and whether decoupled

188   traits align with the same fertility gradients.

189   Here, we address these questions using a unique dataset of 246 tree species inventoried

190   in 101 plots located across Eastern (French Guiana) and Western (Peru) Amazonia, together

191   with accurate measurements of 14 leaf, stem and root traits. We first examine whether species

192   niche breadth and niche position, taken separately, are aligned or decoupled among five soil

193   nutrient availability gradients (N, P, Ca, Mg and K). Second, we examine how well the four

194   scenarios presented in Fig. 1 match the observed niche breadth-position relationship along each

195   soil gradient. We address the following specific questions:

196   (1) How are species niche breadth and position associated among the different soil

197   nutrient gradients?

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

199   (3) Are decoupled niche breadth and position dimensions associated with different plant

200   functional strategies?

201   **Methods**

202   **Study areas**

203   We established a nested experimental design with replicated plots in habitats displaying

204   contrasting soil conditions, characteristic of lowland Amazonian forests – white-sand (WS),

205   Terra Firme (TF) and seasonally flooded forests (SF) (Fortunel et al. 2014, Baraloto et al. 2021)

206   – at both regional (c.100 km) and basin-wide (2500 km) distances. A total of 101 0.1-ha plots

207   were inventoried between 2008 and 2018 in ten subregions of tropical moist forest in French

208   Guiana (hereafter FG; 63 plots) and between 2008 and 2011 in three subregions in Peru (38

209   plots) (Fig. 2). French Guiana forests stand on an old Precambrian tableland, with old, highly

210   weathered and nutrient-depleted soils (Gourlet-Fleury et al. 2004). Mean annual rainfall across

211   inventory subregions ranges between 2160 and 3130 mm (http://www.worldclim.com/) and is

212   distributed seasonally throughout the year. The wet season stretches from December to July and

213   is usually interrupted in February or March by a short dry period, while the dry season occurs

214   from August to November with monthly rainfall never exceeding 100 mm. Mean temperature

215   oscillates between 23.0 and 26.6°C with low seasonal variation (Gourlet-Fleury et al. 2004).

216   Elevation among subregions ranged from 42 to 529 m. Forests from the Western Amazon in

217   Peru cover heterogeneous soil conditions consequent to the combined impact of marine

218   incursions, the Andean uplift, and the weathering of volcanic sediments (Hoorn et al. 2010).

219   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).

Soil data

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

Functional trait data

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

268   covering the Rosidae, Asteridae and early eudicots (Baraloto et al. 2010, Fortunel et al. 2012,

269   Vleminckx et al. 2021). Missing trait data ranged from 34.96% for leaf thickness up to 74.17%

270   for root SRL (see Table S2 in Vleminckx et al. 2021). Missing values were imputed using a

271   Bayesian hierarchical matrix factorization method (BHMF), based on taxonomic information

272   and co-variation among traits (Fazayeli et al. 2014; see Vleminckx et al. 2021 for details). All

273   these traits reflect species economics spectrum potentially associated to soil nutrient availability

274   levels, or intrinsic water-use efficiency (Leaf ^{13}C) (Baraloto et al. 2010).

275

276   **Data analysis**

277   _Niche breadth and niche position data_

278   Species abundance at the plot level was calculated after weighting each tree by the

279   logarithm of its basal area, to take into account that later life stages are likely to be more

280   representative of the influence of habitat conditions on species distributions, whereas the

281   assembly rules of younger trees can be more stochastic (Vleminckx et al. 2015). We then

282   calculated the niche breadth and the niche position of each of the 246 species that were present

283   in at least three subregions (i.e., areas comprising plots), across each of the five soil nutrients

284   (N, P, Ca, Mg and K). For each soil variable, the niche position of each species corresponded

285   to the median of the soil variable calculated among plots where the species was found

286   (weighting each plot according to the abundance of the species). The niche breadth was

287   calculated as the interquartile range (25-75%) of values for the soil variable. The 25-75% range

288   was chosen to provide robust niche breadth values that were weakly sensitive to outliers

289   (Steidinger 2015). Calculations using a 20-80% and a 15-85% range provided highly consistent

290   results that did not modify our interpretations. Prior to any subsequent analysis, niche breadth

291   and niche position values were normalized (using a Box-Cox transformation) and standardized

292   (z-score transformation). We then detrended niche breadth values to remove any potential

293 biased inflation of these values induced by the effects of: (i) the total abundance of each species

294 across all plots, (ii) the number of subregions and (iii) plots in which each species is present,

295 and (iv) their regional distribution (i.e. dummy variable columns indicating whether each

296 species is present in one region, i.e. Western or Eastern Amazon, or both regions). This

297 detrending was performed by using the residuals of a linear regression of niche breadth against

298 these effects (see details in Appendix S4).

299 *Niche breadth and niche position correlations among soil variables*

300   To specifically address question 1, we performed a PCA on the species niche breadth

301 values corresponding to the different soil nutrients, and the same PCA for species niche position

302 values. We then tested whether the Pearson correlations of niche breadth and niche position

303 among the five soil nutrients were statistically significant. Correlations were considered

304 significant when they were lower or higher than the 2.5-97.5% quantiles of correlation values

305 obtained after randomizing each nutrient concentration values at the plot level and recalculating

306 niche breadth and niche position, while preserving the multi-scale spatial structure of each

307 nutrient within each study region (Peru and French Guiana), independently. To do so, we used

308 Moran Spectral Randomization (MSR, Wagner and Dray 2015), a procedure that allows

309 considering multiscale spatial autocorrelation structures for any type of quantitative variable,

310 based on spatially weighted connectivity information among sampling points (i.e. the 101 plots

311 in our case). This information was obtained from an optimized procedure used to choose a

312 spatial weighted matrix and select a subset of Moran's eigenvector maps (MEMs, Dray et al.

313 2006), following Bauman et al. (2018a,b), using the R package 'adespatial' (Dray et al. 2022).

314 MEMs are spatial eigenvectors that model multi-scale spatial structures in any type of

315 numerical variable. We tested a minimum spanning tree configuration and a Gabriel's graph to

316 model connectivity among plots, which have been shown appropriate to accurately modeling

317 structures even when dealing with nested and irregular sampling designs such as ours (Bauman

318   et al. 2018a). The spatial weighted connectivity information from the best MEM model (i.e.,

319   the eigenvector combination that best described the spatial structures in the soils nutrients'

320   concentration, based on a forward selection with double stopping criterion) is then used in a

321   spatially constrained randomization algorithm in the MSR method to reproduce variables that

322   accurately mimic the observed spatial structures of the randomized variable(s).

323   Species in each PCA graph were also characterized by their affinity for each of the three

324   habitats, by calculating and testing their indicator value (indval), following Dufrêne & Legendre

325   (1997). This allowed combining quantitative soil information with qualitative visualization of

326   three well-defined and contrasted habitats of the Amazon region (white-sand, terra firme and

327   seasonally flooded).

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

329   To address question 2, we plotted the niche breadth of species against their niche

330   position values, for each soil variable. The linear and non-linear relationships between niche

331   breadth and niche position were fitted using Bayesian regression models. The posterior

332   distributions of the slope coefficients of interest were summarized through the median and 95%

333   posterior credibility interval. The linear and non-linear (quadratic) slope coefficient

334   distributions were fitted (Bayesian updating) using a quadratic approximation (McElreath

335   2020). The shape of the niche breadth-position associations and the importance of the linear

336   and quadratic coefficients were used to verify which scenario in Fig. 1 best fits the observed

337   niche breadth-position relationship, for each soil nutrient. Coefficient values were considered

338   as clearly positive or negative whenever at least 95% of their posterior mass probability was

339   positive or negative (i.e., did not encompass zero). Scenarios 2 and 3 predict positive values for

340   the linear coefficient and non-important values for scenarios 1 and 4. Scenarios 3 and 4 predict

341   negative values for the quadratic coefficient, while the latter is expected to be non-important

342   for scenarios 1 and 2.

343　　　　To address question 3, we performed a variation partitioning to quantify, for each soil

344　　variable, the fraction (adjusted R²) of species niche breadth variation explained purely by their

345　　niche position and by their functional traits. We then tested the significance of each fraction by

346　　testing whether the observed fraction (adjusted R² values) was higher than 95% of null values

347　　obtained with the MSR method described above. If the observed adjusted R² value quantifying

348　　the effect of all traits combined was higher than 95 % of the 4999 adjusted R² values obtained

349　　with the MSR procedure, than we performed a forward selection to identify the traits that

350　　significantly explained niche breadth variation (Blanchet et al. 2008).

351　　　　Prior to the variation partitioning, we verified whether niche breadth values were

352　　influenced by phylogeny. Phylogeny was modelled using a matrix of dummy variables

353　　assigning "1" for each species (lines) in their corresponding genus and family (in columns), and

354　　"0" for non-matching taxa. The phylogenetic effect was then tested using a residuals

355　　permutation test (Anderson and Legendre 1999), which showed no significant effect for any

356　　soil variable (Appendix S5: Table S1).

357　　　　All analyses described in the methods were performed in the R statistical environment

358　　(R Development Core Team, 2022). We provide the soil, tree inventory and trait data, along

359　　with our R script in the online repository folder: https://doi.org/10.7910/DVN/VWAJYR.

360　　References for the R packages used are detailed in the R code.

361　**Results**

362　***Correlation of niche breadths and positions among soil variables***

363　　　　The two PCAs performed on niche breadth and niche position values showed highly

364　　consistent patterns of variables' projection, revealing a strong relationship between these two

365　　niche parameters (Procrustes correlation = 0.587; $P <= 0.001$; MSR test; Fig. 3). There was a

366　　strong coordination of species niche breadth and position for soil cations (Ca, Mg and K) and

367　　to a lesser extent for N. Increasing niche breadth and position values for N, Ca, Mg and K

368   aligned well with increasingly acquisitive functional traits such as higher leaf N concentration

369   (Fig. 3). Soil P concentration showed a clear decoupling of niche breadth and position values

370   compared to the other nutrients (Fig. 3). Species significantly indicative of seasonally flooded

371   and terra firme habitats displayed significantly higher niche breadth and niche position, as well

372   as higher leaf N and P concentration for soil N, Ca, Mg and K concentration, compared to white-

373   sand specialists, (Appendix S6: Figure S1, and Appendix S7: Figure S1; for sample size details,

374   see Appendix S8: Figure S1). The following analyses examine in more details the relationship

375   between niche breadth, niche position and functional traits for each soil nutrient.

376

377   *__Functional strategies associated with niche breadth and position__*

378   Species niche breadth was positively associated with niche position for each of the five

379   soil nutrients (Fig. 4). No clear negative quadratic term was detected for niche position,

380   indicating that relationships were mostly linear and consistent with scenario 2 (Fig. 1). The

381   niche breadth-position linear relationship was the strongest for soil Ca concentration (R^2 value

382   = 45.1%), followed by soil N (40.2%), P (26.2%) and K (18.2%) concentration. The effect of

383   functional traits on niche breadth nearly entirely co-varied with the effect of niche position. In

384   other words, we did not observe any trait explaining species niche breadth alone. Niche breadth

385   and position values were not significantly explained by the genus and family identity of species

386   for any soil variable ($R^2 < 1\%$; Appendix S5: Table S1).

387   Functional traits contributed to species niche breadth ($P \leq 0.05$; MSR test) for soil N

388   ($R^2 = 3.7\%$) and Ca (12.4%) concentration, with high niche breadth values for these two soil

389   nutrients being associated with more resource acquisitive strategies among species, in particular

390   higher SLA, Leaf N and Ca concentrations, and higher fine root SRL (Fig. 4). The Pearson

391   correlations between each individual trait and species niche breadth for soil N, Ca, Mg and P

392   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

418   among species in the analyses strongly limited the potential influences of spatial biases related

419   to the statistical design (Taylor 1961).

420   Species distributed on the most N and Ca-depleted soils had lower leaf nutrient

421   concentrations, in particular N and Ca, while also showing relatively low SLA (Fig. 4,

422   Appendix S7: Figure S1), indicating resource conservation strategies (Fortunel et al. 2014).

423   These species also displayed relatively low niche breadth values, which may suggest that their

424   resource conservation traits confine them to these poor soil conditions (generally white-sands),

425   and exclude them from the more fertile terra firme and seasonally flooded soils.

426   The positive association between species niche breadth for soil Ca concentration and

427   SRL may reflect the existence of a fast-slow trade-off associated with soil fertility conditions,

428   with poor soils occupied by species investing in longer roots with lower tissue quality, possibly

429   associated with higher uptake capacity in more competitive environments. Our results may

430   suggest that soil Ca limitation has had more influence than the four other soil nutrients studied

431   here on fine root evolutionary history and is consistent with previous manipulative studies in

432   tropical Amazonian forests (Wurzburger & Wright 2015). Nevertheless, root traits were

433   generally poor predictors of niche breadth, possibly because of the multiple alternatives that

434   plants use for nutrient capture, including investments in mycorrhizal associations, that make

435   possible a wide spectrum of trait syndromes in the same soil conditions (Valverde-Barrantes et

436   al. 2017).

437   The niche breadth-position relationship was significantly positive but relatively weaker

438   for soil K concentration (R^2 = 18.2%) than for soil Ca, N and P concentration ($\geq$ 26.2%; Fig.

439   4). Yet, niche position and niche breadth for soil K concentration did not show any significant

440   association with any functional trait, contrary to the three other soil nutrients. Thus, while our

441   results suggest that K may indeed limit primary productivity, which is consistent with previous

442   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

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

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

Implications regarding forest conservation and tree responses to climate change

Species adapted to poor soil conditions likely have large potential edaphic niches compared to their realized one, as they could in theory thrive on a much wider range of soil fertilities in the absence of faster-growing competitors, unlike species with higher niche fertility optimum whose realized and fundamental niches are expected to be more packed. The costly resource conservation traits displayed by poor-soil specialists are likely to exclude them from 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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790   **Table 1**. Summary of key descriptors of study regions, subregions and habitats. NrP = Number

791   of plots; AR = Altitudinal Range (in m); MAR = Mean Annual Rainfall (in mm); MAT = Mean

792   Annual Temperature (in °C). NrSp = mean number of species per plot; ENS2 = mean (calculated

793   at the plot level) Effective Number of Species expected from 1000 random samplings (with

794   replacement) of two individuals. The three last lines of each region represent the same

795   information for each habitat. Numbers in parenthesis correspond to the standard deviation of

796   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)

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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).

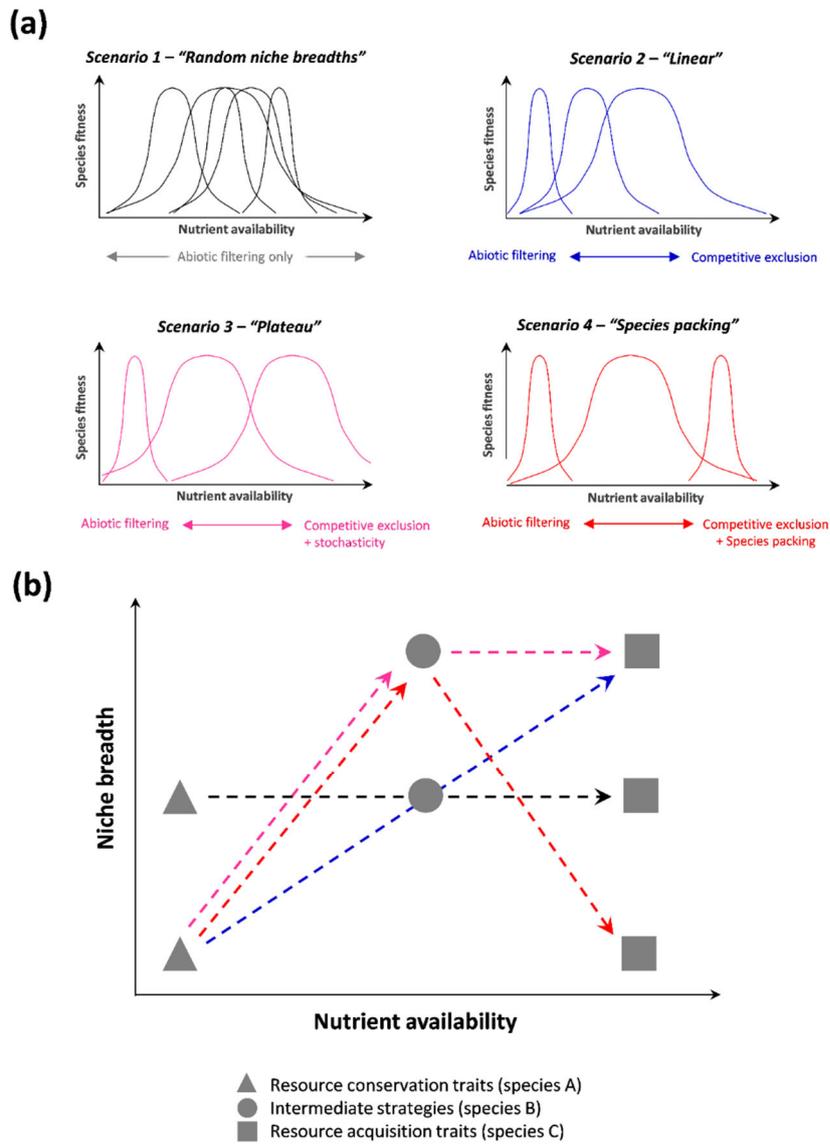| Habitat	French Guiana			Peru		
	SF	TF	WS	SF	TF	WS
TN (%)	2.29 (3.25)	1.65 (1.35)	0.17 (0.22)	0.23 (0.09)	0.14 (0.05)	0.07 (0.06)
Avail. P (mg/kg)	10.78 (15.51)	5.07 (5.81)	3.67 (4.11)	7.4 (5.75)	2.25 (1.54)	8.4 (8.01)
Ca (mg/kg)	1.26 (2.37)	0.53 (1.02)	0.16 (0.17)	5.96 (7.23)	0.84 (2.58)	0.04 (0.03)
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

806   **Figure.1** (a) Hypothetical scenarios describing species frequency distributions (realized niches)

807   along a gradient of increasing soil nutrient availability, using Gaussian curves for simplicity.

808   (b) Translation of these scenarios into niche breadth – niche positions graphs, showing species

809   and predicted functional strategies with symbols.

810   **Figure 2.** Geographical distribution of the 13 subregions in the Amazon (red rectangles),

811   showing the position of the plots (yellow cross symbols) within the two study regions (Peru and
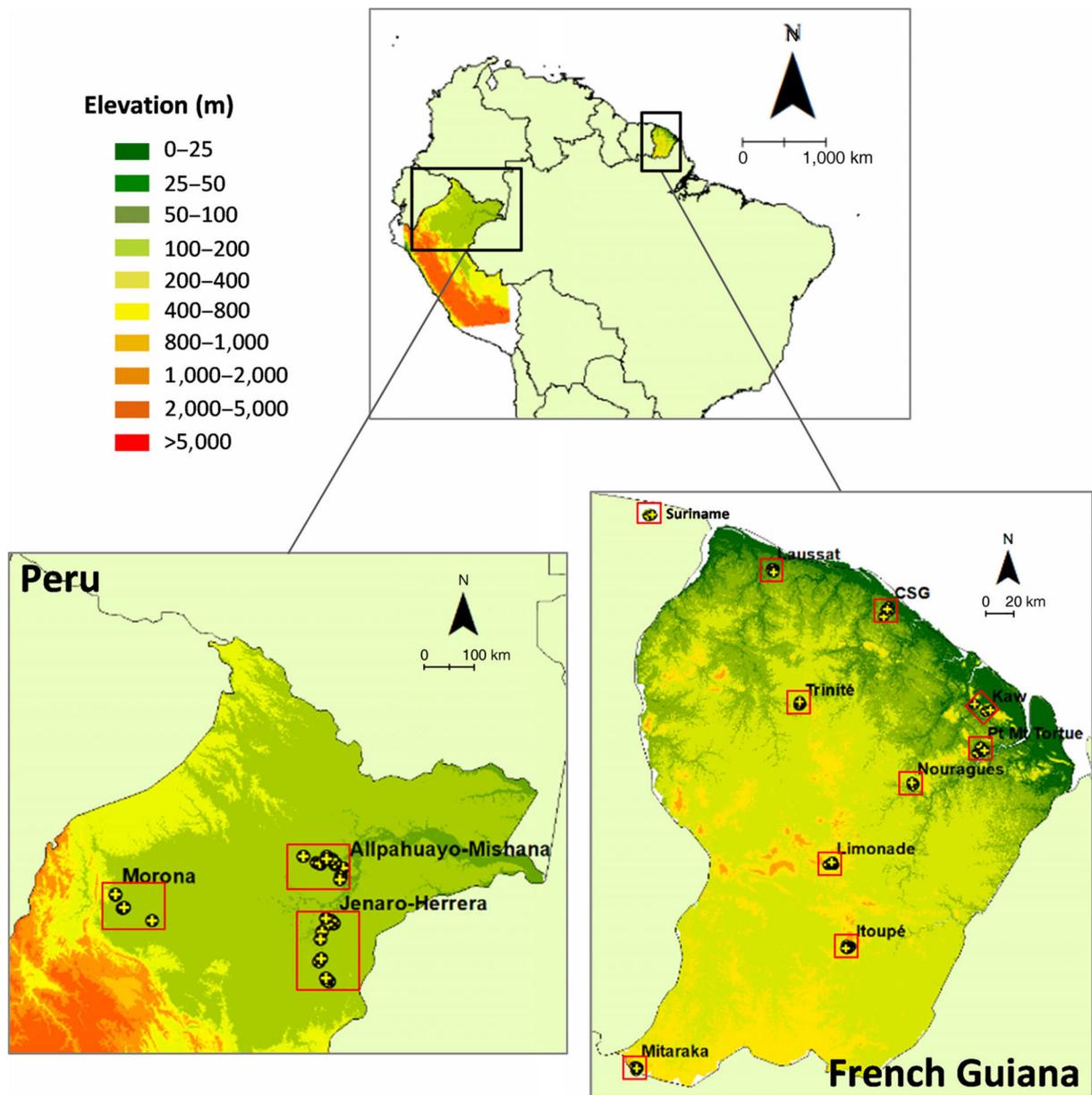
812   French Guiana).

813   **Figure 3.** Projection of species and soil variables on axes 1-2 of a principal component analysis

814   (PCA) performed on niche breadth (a) and niche position (b) values. The grey rectangle that

815   connects both PCA graphs shows the Procrustes correlation quantifying the matching of soil

816   variables and species projections between the two PCAs ($P \leq 0.001$; MSR test). The histograms

817   show the relative eigenvalues of each PCA axis (only the first axis in each PCA expressed more

818   variation than expected under a broken stick model). Symbols in the graphs indicate whether

819   species are significantly indicative of one of the three habitats (seasonally flooded, terra firme,

820   or white-sand specialist) or not (generalist). Tables at the bottom show the Pearson correlations

821   of niche breadth (c) and niche position (d) values among soil variables. The significant

822   correlations (t-test of Pearson's moment correlation) are indicated in blue (grey values were not

823   significant).

824   **Figure 4.** Niche breadth–niche position relationship among the 246 species, for each of four

825   soil nutrients. Values indicated along x and y axes corresponded to back-transformed niche

826   breadth and niche position values, respectively. Traits significantly explained niche breadth

827   variation for N, Ca, and P. For these three nutrients, the Venn diagram on the right of the niche

828   breadth-position graph shows the relative linear contribution (adjusted R^2 from a variation

829   partitioning analysis) of niche position alone, traits alone, and the joint influence of niche

830   position and traits. Individual traits that significantly explained niche breadth variation (i.e., the

831   traits selected from a forward selection procedure, which was performed if the overall effect of

832   traits was significant when using the MSR testing procedure; see methods for details) were

833   indicated on the right of the Venn diagram, with colors indicating whether correlations were

834   positive (blue) or negative (red) between niche breadth and the trait. Symbols indicate whether

835   species are significantly indicative (significant indval) of one of the three habitats (see the

836   legend panel at the bottom right of the figure). The two grey regions in each graph represent

837   two different 95% Bayesian plausible intervals for predicted niche breadth values. The narrow

838   interval shows the distribution of estimated mean niche breadth values, while the wide interval

839   corresponds to the region in which the non-linear model expects to find 95% of actual niche

840   breadth values at each niche position value. The equation in each graph shows the median of

841   the Bayesian credibility interval for the linear and quadratic coefficients and the intercept.

842   Significant coefficients (i.e., at least 95% of estimated posterior coefficient values being

843   positive) were emphasized in bold. No significant quadratic effects were found for traits.

844   Asterisks in the Venn diagrams indicate significant adjusted R^2 values quantifying the relative

845   effect of niche position alone, traits alone and the co-variation of both niche position and traits,

846   according to the MSR testing procedure (see methods): ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$.
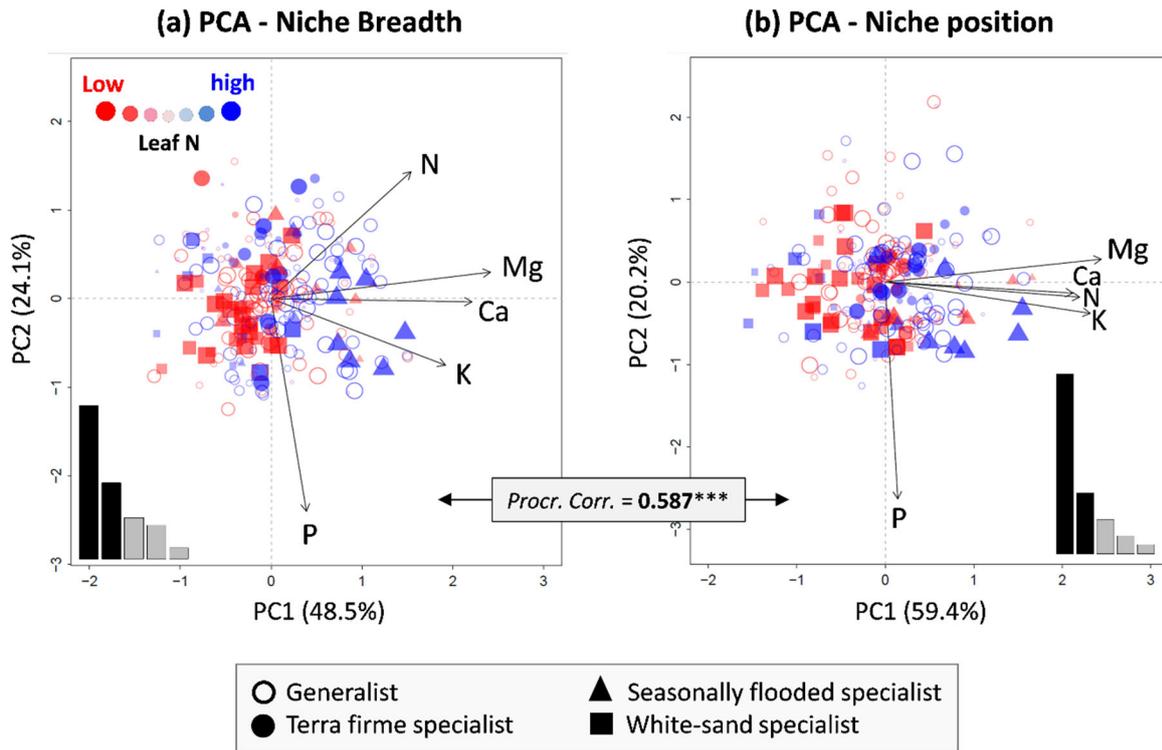
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848   11. Figures

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(a)

Scenario 1 – "Random niche breadths"

Scenario 2 – "Linear"

Scenario 3 – "Plateau"

Scenario 4 – "Species packing"

(b)

▲ Resource conservation traits (species A)
● Intermediate strategies (species B)
■ Resource acquisition traits (species C)

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851   **Figure.1**

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Figure 2.

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(a) PCA - Niche Breadth

(b) PCA - Niche position

Procr. Corr. = **0.587***

○ Generalist   ▲ Seasonally flooded specialist
● Terra firme specialist   ■ White-sand specialist

(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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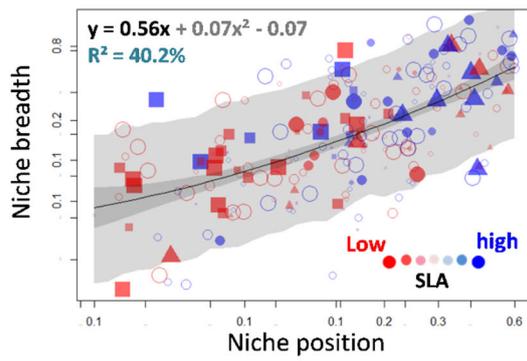
Soil N content
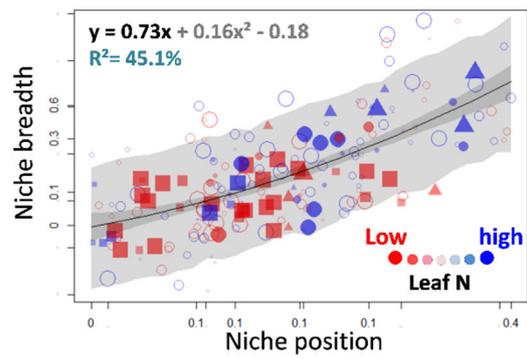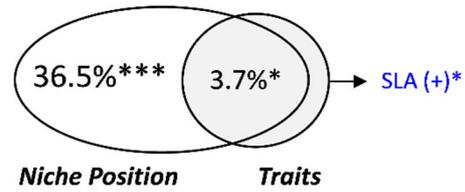
Soil Ca content
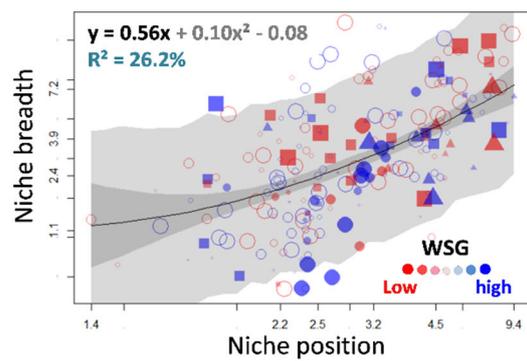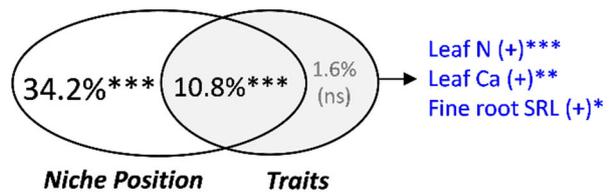
Soil P content

Soil K content

863

864   **Figure 4.**

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