Rethinking the nature of intraspecific variability and its consequences on species coexistence

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Abstract

25

26 **Context** Intraspecific variability (IV) has been proposed to explain species coexistence in

27 diverse communities. Assuming, sometimes implicitly, that conspecific individuals can perform

28 differently in the same environment and that IV blurs species differences, previous studies have

29 found contrasting results regarding the effect of IV on species coexistence.

30 **Objective** We aim at showing that the larg IV observed in data does not mean that conspecific

31 individuals are necessarily different in their response to the environment and that the role of

32 high-dimensional environmental variation in determining IV has been largely underestimated in

33 forest plant communities.

34 **Methods and Results** We first used a simulation experiment where an individual attribute is

35 derived from a high-dimensional model, representing "perfect knowledge" of individual

36 response to the environment, to illustrate how a large observed IV can result from "imperfect

37 knowledge" of the environment. Second, using growth data from clonal *Eucalyptus* plantations

38 in Brazil, we estimated a major contribution of the environment in determining individual

39 growth. Third, using tree growth data from long-term tropical forest inventories in French

40 Guiana, Panama and India, we showed that tree growth in tropical forests is structured spatially

41 and that despite a large observed IV at the population level, conspecific individuals perform

42 more similarly locally than compared with heterospecific individuals.

43 **Synthesis** As the number of environmental dimensions that are typically quantified is generally

44 much lower than the actual number of environmental dimensions influencing individual

45 attributes, a great part of observed IV might be misinterpreted as random variation across

46 individuals when in fact it is environmentally-driven. This mis-representation has important

47 consequences for inference about community dynamics. We emphasize that observed IV does not

48 necessarily impact species coexistence *per se* but can reveal species response to high-

49 dimensional environment, which is consistent with niche theory and the observation of the many

50 differences between species in nature.

51

52 **Keywords:** competition; environmental variation; high-dimensional niche; individual variation;

53 intraspecific variability; spatial autocorrelation; spatial heterogeneity; species coexistence

Introduction

Ecological communities are characterized by numerous coexisting species, for instance in grasslands, coral reefs or tropical forests. Understanding how these species stably coexist while competing for the same basic resources, *viz.* light, water, and nutrients (Baraloto et al. 2010), is a longest-standing question in ecology (Gause 1934, Hutchinson 1961, Levine et al. 2017). Although numerous mechanisms have been suggested to contribute to species coexistence (Janzen 1970, Connell 1971, Chesson 2000, Hubbell 2001, Wright 2002, Levine and HilleRisLambers 2009), it is unclear when and to what extent they explain the high species diversity observed in nature (Clark 2010). This is especially true in forests, where tree species coexist while seemingly requiring similar resources in the same location. Astonishingly, a hectare of tropical forest can harbor more than 900 plant species of a diversity of forms and functions (Wilson et al. 2012).

Many theoretical mechanisms that might explain tree species coexistence typically follow the assumption that all conspecific individuals are identical. However, intraspecific variability (IV) in traits, demographic rates or any proxy of performance, henceforth denoted as "attributes", can alter community structure and dynamics (Bolnick et al. 2011). Indeed, large IV has been observed across a number of attributes in plant communities(Albert et al. 2012, Violle et al. 2012). For instance, Siefert et al. 2015 estimated that IV accounted for 25% of the variability in functional traits within plant communities on average, and this proportion was even estimated at 44% in a tropical forest (Poorter et al. 2018). Likewise, IV in growth rates for trees of standardized size, local crowding and terrain slope has been found to account for up to 58% of total growth variability in a tropical forest stand (Le Bec et al. 2015).

76

77 IV, as a pathway for coexistence, has so far not shared the same attention as other mechanisms.

78 This is in part because modeling studies that have explored the effect of IV on species

79 coexistence have yielded contrasting results (Stump et al. 2021). In most theoretical analyses,

80 variability in attributes among conspecific individuals has been included through independent

81 random draws (Lichstein et al. 2007, Hart et al. 2016, Barabás and D'Andrea 2016, Crawford et

82 al. 2019 but see Purves and Vanderwel 2014, Banitz 2019). Similarly, empirical studies typically

83 summarize IV as a variance around species mean attributes (Jung et al. 2010, Albert et al. 2010,

84 Siefert et al. 2015, Poorter et al. 2018). With this representation, IV can increase species niche

85 overlap and blur species differences, sometimes slowing down competitive exclusion in models

86 of community dynamics (Vieilledent et al. 2010, Crawford et al. 2019). However, in some other

87 models, non-linear responses can make such IV beneficial to the superior competitors (*i.e.* the

88 most competitive individuals of the more competitive species), thus accelerating competitive

89 exclusion (*e.g.* Courbaud et al. 2012, Hart et al. 2016). Alternatively, in particular spatial

90 configurations, more precisely when IV is greater in species preferred habitats, it has been shown

91 to foster species coexistence (Uriarte and Menge 2018). Stump et al. (2021) have proposed to

92 reconcile these contrasting results by distinguishing the effect of IV on niche traits (which

93 control individual performance response to environmental conditions) vs. hierarchical traits

94 (which control individual performance independently from environmental conditions). They

95 demonstrated with different simulation models of community dynamics that IV in traits can alter

96 stabilizing mechanisms and fitness differences in a complex way which depends upon the nature

97 of the traits (niche vs. hierarchical) and their response curve, and thus promote or not species

98 coexistence. In all the above examples however, IV, since simulated through independent

99   random draws around species mean attributes, would be caused by differences among

100 individuals that are fully independent of the environment: differences among individuals would

101 remain unchanged even when experiencing exactly the same environmental conditions.

102 Importantly, such simulated IV thus leads to a variation among conspecific individuals that is

103 completely unstructured in space and time. New appreciation of fine-scale environmental

104 heterogeneity and structure as well as species differences in their response to the environment,

105 however, may suggest that this assumption of unstructured IV is rarely met.

106 Novel remote sensing tools such as high-spatial and -temporal resolution airborne LiDAR scans

107 (Tymen et al. 2017, Cushman et al. 2022), intensive soil samplings and metabarcoding (Zinger et

108 al. 2019), and more generally studies on the microclimate (Zellweger et al. 2019) and

109 microhabitats (Baraloto and Couteron 2010) have indeed evidenced strong environmental

110 variation operating at fine scales (*e.g.* cm to meter scales) in many dimensions (Fig. 1). These

111 environmental dimensions can be resources for which species compete (*e.g.* light, water,

112 nutrients) but also all other components that shape the environment locally in space and time

113 (*e.g.* temperature, wind, elevation, slope, soil texture, soil microorganisms *etc.*). In parallel,

114 naturalists and taxonomists have long documented species differences in many aspects of their

115 morphology and life history (Fig. 2). Such differences between species have then been specified

116 and quantified through traits that drive each species response to the environment (species

117 functional traits, Mcgill et al. 2006, Westoby and Wright 2006). Similar to the environment that

118 presents highly-dimensional variation at local scales, these functional species differences spread

119 along many dimensions within communities (Hutchinson 1957, 1959, Baraloto et al. 2010, Kraft

120 et al. 2015, Rüger et al. 2018, Maréchaux et al. 2020, Vleminckx et al. 2021).

121 In this paper, we explore the potential that the role of environmental variation in shaping

122   *observed* IV has been largely underestimated with important consequences on our understanding

123   of the effect of *observed* IV on community dynamics. Indeed, a great part of *observed* IV might

124   emerge from species responses to a high-dimensional environment (Fig. 3): observed differences

125   among individuals of the same species can be caused by the (often poorly quantified) differences

126   in the micro-environment they experience. If so, variation among conspecific individuals would

127   be structured in space and time, and not necessarily by genetic variation. More specifically, we

128   present insights from a simulation experiment, experimental data, and tropical forest inventory

129   data in order to examine three hypotheses (Fig. 4): (i) the large IV observed in natural

130   communities can emerge from heterogeneity in multiple unobserved environmental dimensions;

131   (ii) because environmental variation is structured in space and time, IV is likely to be similarly

132   structured as well, suggesting that it is not appropriate to represent IV as a purely random noise

133   in models; and (iii) since a large observed IV does not necessarily imply that conspecific

134   individuals substantially differ in their fundamental niche, conspecific individuals may still

135   respond more similarly to environment than heterospecific individuals. We therefore call for a

136   reconsideration of the nature and structure of observed IV, which could shed new light on the

137   coexistence conundrum. While we acknowledge the existence of genetically-based individual

138   variations, and that plasticity has a genetic basis (Nicotra et al. 2010, Westerband et al. 2021), we

139   suggest that a substantial part of *observed* IV might result from the higher dimensionality of the

140   species niche than typically observed. Species differences along these many dimensions can lead

141   to multiple local inversions of species hierarchy in an environment varying in space and time,

142   thereby allowing the stable coexistence of numerous species.

143

Theoretical illustration: unobserved environmental dimensions result in large observed IV

146

147 We first conducted a simulation experiment to illustrate how observed intraspecific variability,

148 or "individual effects", can result from variation in unobserved environmental variables (as

149 suggested by (Clark et al. 2007). We generated simulated data of an individual attribute (here

150 tree growth) depending on a certain number of environmental variables varying in space, and

151 then analyzed the simulated data assuming that most of the environmental variables are actually

152 unobserved, as it is typically the case in the field.

153

A "perfect knowledge" simulation model

155 We considered a set of *J* species with *I* individuals each, distributed in a virtual landscape. The

156 environment was assumed to be fully known and defined by *N* environmental variables, X_1 to X_N,

157 that were each randomly and independently generated in the landscape, assuming spatial

158 autocorrelation. Individual location was drawn randomly in a virtual landscape defined by a *C* ×

159 *C* square grid, each cell corresponding to a particular environment (Fig. 5a). Individuals were

160 identical within species (same model parameters for all conspecific individuals), but different

161 between species (different model parameters between heterospecific individuals).

162

163 We considered the following "perfect knowledge" mathematical model, which depicts the exact

164 attribute Y_{ijt} (*e.g.*, growth) of an individual *i* of species *j* given its environment at time *t* (Eq. I,

165   Appendix 1).

166

167    $ln(Y_{ijt}) = \beta_{0,j} + \beta_{1,j} \, ln(X_{1,ijt}) + \beta_{2,j} \, X_{2,ijt} + \ldots + \beta_{N,j} \, X_{N,ijt}$ **(Eq. I)**

168

169   In this model, $\beta_j = [\beta_{0,j}, \ldots, \beta_{N,j}]$ is the vector of parameters defining the response of individuals of

170   species j to the environment. Because conspecific individuals respond similarly to environmental

171   variables, variation in Y_{ijt} among them is only due to differences in the environment where and

172   when each individual is growing. Using this model, we computed the attribute Y of the $I{\times}J$

173   individuals at T dates, assuming that values for some of the environmental variables changed

174   between dates, and thus obtained a simulated dataset $\{Y_{ijt}, X_{1,ijt}, \ldots, X_{N,ijt}\}$ with $N=10$, $I = 300$, $J =$

175   2, $C = 500$ and $T = 2$.

176

An "imperfect knowledge" statistical model

178   Second, we considered an "imperfect knowledge" statistical model for which we assumed that

179   only one explanatory variable X_1 (*e.g.,* light) in the above simulated dataset has been measured

180   among all the environmental drivers that actually determine response variable Y (Eq. II,

181   Appendix 1). This model represents the ecologist's imperfect understanding of attribute Y. The

182   model includes a species fixed effects on the intercept and on the slope ($\beta'_{0,j}$ and $\beta'_{1,j}$) and a

183   random individual effect $b_{0,i}$ on the intercept, $b_{0,i} \sim N(0, \, V_{bj})$, where V_{bj} is the intraspecific

184   variance for species j. We estimated the model parameters based on the simulated dataset

185   introduced above but considering only the first explanatory variable $\{Y_{ijt}, X_{1,ijt}\}$, the remaining

186   "unknown" environmental effects being contained in the model residuals, ε_{ijt}.

187

188 $ln(Y_{ijt}) = [\beta'_{0,j} + b_{0,i}] + \beta'_{1,j} \ln(X_{1,ijt}) + \varepsilon_{ijt}, \varepsilon_{ijt} \sim N(0, V_j)$ **(Eq. II)**

189

Apparent niche overlap and observed intraspecific variability as a result of unobserved environmental variables

192 Despite the fact that conspecific individuals were identical and species responses to environment

193 were different, the variance estimates $\hat{V}_{bj}$ for individual random effects of species j were large,

194 and species responses to the environment overlapped (Fig. 5b). This is due to the contribution of

195 the unmeasured variables $\{X_{2,ijt}, \ldots, X_{N,ijt}\}$ in determining the variation of Y across individuals.

196

197 Since it is driven by spatially autocorrelated variables (Eq. I), the response Y was spatially

198 autocorrelated across conspecific individuals (Fig. 6). This means that two neighboring

199 conspecific individuals have more similar attribute Y than two distant conspecific individuals.

200 Additionally, the variance of Y was lower within than between species: conspecific individuals

201 responded more similarly to the environment than heterospecific individuals did (Fig. 6).

202

203 With this simulation experiment, we simply illustrated that: (i) a high IV can emerge from

204 unobserved environmental dimensions exclusively, (ii) the spatial structure of IV follows the

205 spatial structure of the underlying environmental variables, and (iii) IV does not blur differences

206 between species (Fig. 6) despite apparent niche overlap (Fig 5b).

207

Experimental insights: large observed intraspecific variability in a clonal tree plantation

We then moved from a theoretical to an experimental approach using census data from clonal *Eucalyptus* plantations, where genetic variability among individuals growing within a single same site is controlled. We explore the partitioning of IV between intrinsic (genotypes) and extrinsic sources, which is often infeasible in natural settings, to demonstrate that substantial observed IV can indeed emerge from genetically identical individuals in the field, even when persisting in an apparently homogeneous environment.

An extreme case of controlled genetic and environmental variation

The EUCFLUX experiment (São Paulo state, Brazil) is a clonal trial with a replicated, statistically-sound design (le Maire et al. 2019). It includes 14 genotypes of 5 different *Eucalyptus* species or hybrids of various origins. Each genotype is planted in plots of 100 trees, at a density of 1666 trees per hectare, and replicated spatially in 10 blocks (Fig. 7). The experimental set-up was designed to minimize the variation in environmental factors among blocks, which were separated by less than 1.5 km within a homogeneous 200-ha stand showing small variation in soil properties. Tree diameter at breast height (D) has been measured over 5 complete censuses, spanning 6 years, age at which such plantation is generally harvested (see le Maire et al. 2019 and Appendix 2 for further details on this experimental set-up).

A partitioning of observed variance among individual tree growth

230 We computed annual diameter growth (G) in mm/yr^{-1} for each tree as well as a competition index

231 (C) as the sum of the basal area of the eight direct neighbors of each tree. The dataset included

232 64,125 growth estimates corresponding to 13,531 trees in total. To quantify the relative

233 importance of the different sources of growth variability, we used a statistical hierarchical

234 growth model (Eq. III) including an intercept (β_0), fixed effects of the log-transformed diameter

235 (β_1) and competition index (β_2), and random effects on the intercept of the block ($b_{0,b}$, with $b_{0,b} \sim$

236 $N(0, V_b)$), the genotype ($b_{0,g}$, with $b_{0,g} \sim N(0, V_g)$), the census date ($b_{0,t}$, with $b_{0,t} \sim N(0, V_t)$), and

237 the individual ($b_{0,i}$, with $b_{0,i} \sim N(0, V_i)$). All the data were log-transformed and scaled, and a

238 constant of 1 mm was added to all growth values to avoid undefined logarithms.

239

240 $ln(G+1)_{i,t} = [\beta_0 + b_{0,b} + b_{0,g} + b_{0,t} + b_{0,i}] + \beta_1 \, ln(D)_{i,t} + \beta_2 \, ln(C)_{i,t} + \varepsilon_{i,t}, \, \varepsilon_{i,t} \sim N(0, V)$ (**Eq. III**)

241

242 We used conjugated priors with inverse-gamma distributions (with shape and scale

243 parameters=10^{-3}) for variance parameters, and normal distributions (with mean=0 and

244 variance=1) for mean parameters. The estimation of model parameters was done using a

245 Bayesian approach using Stan software with the brms R package (Bürkner 2017, 2018). We

246 made 10,000 iterations for each MCMC with a burn-in period of 5,000 steps and a thinning rate

247 of one fifth. We obtained 1,000 estimations per parameter and examined the trace plots to check

248 convergence of the MCMC chains.

249

250 We then examined the proportion of the model residual variance (variation of the response

251 variable that is not explained by the covariates) related to each random effect in order to partition

252   the block, genotype, date and individual variances.

253

254   Variation among individuals is not explained by genotype

255   While minor variability was associated with blocks (Table 1), confirming that they are broadly

256   homogeneous by design, the variability associated with extrinsic temporal factors was

257   predominant (Table 1). It reveals that the competition index (C) used in the analysis to

258   encapsulate the effect of progressive canopy closure does not fully encompass all temporal

259   effects.

260   Importantly, the variability between individuals was almost twice as high as the variability

261   between genotypes (Table 1). Hence, even in such an extremely conservative case, where

262   environmental variation in space is minimized and genotypic variability controlled, a large part

263   of measured IV cannot be explained by purely-genetic differences among individuals that would

264   remain independent of the environment as an IV simulated through independent random draws

265   would be. This suggests an underestimated role of environmental micro-heterogeneity in shaping

266   variation among individuals, for instance inevitable spatial variation of biotic and abiotic

267   variables (soil microbiome, pathogens, soil structure and water content, light *etc.*) at fine scales

268   (e.g. cm- to m-scale, hence impacting tree-scale environment, Baraloto and Couteron 2010, Fig.

269   1) as well as potential early manipulations of the young plant, the way it was planted, *etc.*

270

271 ***Empirical insights: observed intraspecific variability is high***

272 ***and spatially structured and does not blur species differences***

273 ***in tropical forests***

274 To test some of our hypotheses in natural communities, we then used data from three long-term

275 tree inventories in tropical forests, from Amazonia (Paracou, French Guiana; Gourlet-Fleury et

276 al. 2004), Central America (Barro Colorado Island, Panama; Losos and Leigh 2004) and South-

277 East Asia (Uppangala, India; Pélissier et al. 2011). More specifically, we inferred observed IV,

278 tested if individual growth showed local spatial autocorrelation, *i.e.* was structured in space, and

279 if conspecific individual growth was more similar than heterospecific individual growth locally.

280 These three sites encompass contrasting climatic conditions (rainfall ranging from 2,600 in BCI

281 to 5,100 mm.y^{-1} in Uppangala), disturbance regimes (incl. various logging experiments in

282 Paracou) and topography (from gentle in BCI to mountainous in Uppangala), making them

283 representative of the global tropical forests. The data from these tropical forest inventories that

284 we used in this paper are summarized in Table 2.

285

286 For all three datasets, annualized growth between two censuses was computed as the difference

287 of DBH ($\geq$ 10 cm) between two consecutive censuses, divided by the time period between those

288 two censuses. Growth estimates < -2 or > 100 mm.y^{-1} as well as individuals from incompletely

289 identified species and individuals and species with a single observation were discarded prior to

290 analysis. Mean annual growth for each individual tree was then computed as the difference of

291 DBH between the first and the last time a tree was measured, divided by the time period between

292   those two measurements.

293

294   **High observed intraspecific variability in tree growth in tropical forests**

295   To quantify the relative importance of intra- vs. inter-specific variability in each site, we used a

296   hierarchical growth model (Eq. IV), including an intercept β_0, a diameter (D) fixed effect β_1, a

297   species random effect b_{0j} (with $b_{0j} \sim N(0, V_b)$) and an individual random effect d_{0i} (with $d_{0i} \sim N(0,$

298    $V_d)$) on the intercept. All data were log-transformed and scaled, and a constant of 2 mm was

299   added to all growth values to avoid undefined logarithms.

300

301    $ln(G_{ijt}+2) = [\beta_0 + b_{0j} + d_{0i}] + \beta_1 \times ln(D_{ijt}) + \varepsilon_{ijt}, \varepsilon_{ijt} \sim N(0,V)$ **(Eq. IV)**

302

303   For Paracou, which has a very large dataset, we sampled 100,000 growth values randomly to

304   perform inference. No sampling was done for Uppangala and BCI. We used priors with inverse-

305   gamma distributions (with shape and scale parameters=10^{-3}) for variance parameters, and normal

306   distributions (with mean=0 and variance=1) for mean parameters. We estimated the inter- and

307   intra-specific growth variability from the variance of the species (V_b) and individual (V_d) random

308   effects, respectively. Model parameters were estimated the same Bayesian approach as for the

309   analysis of the *Eucalyptus* dataset.

310   For the three sites, IV estimated from the growth model (V_d, ranging from 0.41 to 0.66) was of

311   the same order of magnitude as the interspecific variance (V_b, ranging from 0.36 to 0.66) (Table

312   3). Overall, a large share of the variability in tree growth comes from individual effects in the

313   three sites, even after accounting for the effect of diameter on tree growth, showing a high

314 intraspecific variability in growth in these tropical forests.

315

Spatial autocorrelation of individual growth within species at the local scale in tropical forests

318 To test whether individual growth was spatially autocorrelated, we performed in each site, spatial

319 analyses of the mean individual growth values. We chose a conservative approach based on

320 mean individual growth without accounting for the effect of diameter, thus without removing

321 ontogenetic differences and considering the pattern of individual growth as it is in the field. More

322 specifically, we performed Moran's I one-tailed tests as implemented in the *ape* R package

323 (Paradis and Schliep 2019), for pairs of conspecifics less than 100 m apart in the same plot (to

324 avoid capturing the effect of treatment in Paracou and including the spaces between the plots).

325 For the most abundant species, we sampled 3,000 individuals with a uniform probability. We

326 considered only the species with more than five conspecific neighbors less than 100 m-apart in

327 the same plot.

328 Positive spatial autocorrelation in tree growth between conspecifics was significant for 19 to

329 31% of the species in the three sites, representing between 45 and 79% of the total number of

330 individuals (Table 4). Spatial autocorrelation was however much higher in logged plots as

331 compared to unlogged in Paracou, because of a more heterogeneous light environment resulting

332 from logging history (Appendix 3).

Higher similarity of growth within conspecific- than heterospecific individuals

locally in tropical forests

To test if the performance of conspecific individuals was locally more similar than the performance of heterospecific individuals in the three sites, we also used mean individual growth, thus ignoring ontogenetic differences. We computed the mean individual growth semivariance (Baraloto and Couteron 2010) considering either conspecific or heterospecific neighbors within a 100-m radius. In the first case, semivariance was estimated as the mean of the squared difference in individual mean growth for all pairs of conspecific individuals. In the second case, semivariance was estimated as the mean of the squared difference in individual mean growth for all pairs of individuals with an individual of the focal species and one of another species. We considered only the species with more than five individuals, and with more than five heterospecific neighbors within the 100-m neighbohood distance. For each species, we then compared the semivariances between conspecific and heterospecific individuals using a Mann-Whitney test with a 0.05 alpha-risk.

The mean individual growth semivariance appeared significantly higher among heterospecifics than among conspecifics for 42 to 61% of the species in the three sites, representing 58 to 89% of the total number of individuals (Table 5). To control for a potential effect of species abundance on the semivariance estimations, we replicated the analysis by sampling a maximum of ten individuals per species. The results were qualitatively unchanged (Appendix 3).

Discussion

High-dimensional environmental variation leads to large observed intraspecific variability

IV can result from intrinsic differences among individuals or from extrinsic environmental variation, including biotic factors, or interactions of both (Violle et al. 2012, Moran et al. 2016, Westerband et al. 2021). While much emphasis has been placed on genetically-driven IV in studies on coexistence (Booth and Grime 2003, Ehlers et al. 2016, Barabás and D'Andrea 2016), sometimes implicitly through the use of independent random draws across individuals (Lichstein et al. 2007, Hart et al. 2016, Crawford et al. 2019), and although we acknowledge its ecological and evolutionary importance, we here argue that the importance of environmentally-driven IV in natural communities has been underestimated and has radically different consequences for species differences and community assembly. More specifically, we argue that a large part of observed IV can result from high-dimensional environmental variation in space and time.

First, using a simple simulation experiment, we illustrated how environmental variation in unobserved dimensions of the environment can produce large observed IV, although conspecific individuals are clones (Fig. 5). Similarly, the variance partitioning of individual tree growth within a common garden of *Eucalyptus* clones (le Maire et al. 2019) shows that the variance in growth between individuals is about twice as high as the variance between genotypes (Table 1). This reveals that a large part of the observed IV can emerge from environmental variables, even when the variation of the environment was sought to be minimized.

375 Importantly, because IV can emerge from environmental heterogeneity without underlying

376 genetic differences, observed IV does not necessarily imply that conspecific individuals

377 substantially differ in their response to the environment, nor that species niches overlap (Fig. 3).

378 Instead, large observed IV can also reflect the projection of species' high-dimensional niches

379 within a high-dimensional environment that is variable in time and space: conspecific individuals

380 differ with each other because they each thrive in a different micro-environment. In empirically

381 observed data, such IV is therefore the result of projecting a high-dimensional response (*e.g.*,

382 physiological processes), which is controlled by multiple macro- and micro-environmental

383 variables, down to a low-dimensional, integrative response (*e.g.*, annual growth) that is poorly

384 characterized because of an incomplete view of the environmental variables that contribute to it.

385 This reassigns an important part of observed variation among individuals, often perceived as

386 neutral or random since they are seemingly unrelated to the observed dimensions of the

387 environment (Fig. 3, Fig. 5, Table 1), to the classical niche theory (Hutchinson 1957) and is in

388 agreement with natural history observations of individual trait differences that are associated to

389 species-specific ecological strategies.

390

391 The "biodiversity paradox" highlights that a large number of species can coexist while

392 competing for a limited number of resources (Hutchinson 1961). This puzzling question has

393 generally been tackled considering trade-offs along a limited number of niche axes, often

394 corresponding to resources (Tilman 1982, Rees 2001). But if the number of resources may

395 indeed be relatively limited (*e.g.*, light, water, and nutrients for plants), the number of

396 independent environmental factors (*e.g.* microclimatic variables) that drive the performance of

397 individuals for a particular level of resources is not. Environments are known to vary along

398   multiple dimensions at fine scales in space and time (Fig. 1), and in many cases, this variation

399   has been shown to influence individual attributes (*e.g.,* Fortunel et al. 2020).

400

401   Nevertheless, despite technological advances, many of these abiotic and biotic environmental

402   factors are still poorly understood and monitored. As a result, the dimensionality of field

403   observations is typically low compared with the high dimensionality of the environment in

404   nature (Bramer et al. 2018, Estes et al. 2018). The variability in individual attributes due to the

405   variation of unobserved environmental variables therefore remains mostly a black box, and is

406   typically summarized in terms of residual variance in statistical models (Albert et al. 2012,

407   Siefert et al. 2015) or encapsulated into so-called "individual random effects" (Clark et al. 2007).

408   We here emphasize that even in the absence of any intrinsic differences among conspecific

409   individuals, a large IV can emerge from the imperfect characterization of the environment (Fig.

410   3, Fig. 5, Table 1), which varies in a high number of dimensions (Fig. 1).

411

412   **Intraspecific variability is structured in space and time**

413   IV has commonly been perceived and modeled through independent random draws around the

414   species mean in community ecology studies (Lichstein et al. 2007, Courbaud et al. 2012, Hart et

415   al. 2016, Barabás and D'Andrea 2016, Uriarte and Menge 2018). While this representation

416   typically results from a lack of knowledge, with randomness being used as a substitute for more

417   detailed understanding of underlying ecological processes (Clark et al. 2007), it encapsulates

418   strong hypotheses relating to the nature of IV that are rarely discussed. In contrast, we argue here

419   that IV is generally non-random and structured in both space and time.

420

421 At a given time, conspecific individuals that are distributed across space can strongly vary in

422 their attributes (Violle et al. 2012, Siefert et al. 2015, Moran et al. 2016, Poorter et al. 2018).

423 While this spatial IV has often been interpreted as random, *i.e.* implying that conspecific

424 individuals can perform differently within the same environment (Fig. 3c), a large part of this

425 variability appeared in fact structured in space and likely associated with fine-scale spatial

426 changes in the environment (Fig. 3b, Moran et al. 2016). In our illustrative simulation

427 experiment, the attribute of conspecific individuals varies spatially as a result of the

428 environmental variation in space, and the spatial autocorrelation of conspecific attributes reflects

429 the spatial autocorrelation of the environmental variables (Fig. 5, Fig. 6).

430

431 Similarly, data from three long-term forest inventory sites across the tropics revealed spatial

432 autocorrelation in tree diameter growth of conspecific individuals (Table 3), suggesting that IV is

433 strongly driven by the spatial variation of the environment, which is itself highly structured (Fig.

434 1). However, we acknowledge that genetically-driven IV can also be spatially structured, for

435 instance via dispersal patterns or natural selection (Moran et al. 2016). We hypothesize that in

436 that case, attributes would likely be randomly structured in space (Getzin et al. 2014) or

437 correlated at the spatial scale of seed dispersal, typically several tens of meters in tropical forests

438 (Clark et al. 2004, Seidler and Plotkin 2006, Muller-Landau et al. 2008), while environmental

439 variables are typically highly spatially correlated at fine scales (*e.g.* meter scale, Baraloto and

440 Couteron 2010). We also acknowledge that natural selection can happen at fine scales (Marrot et

441 al. 2021), and could thus produce spatially structured IV due to local genetic adaptation.

442 Nevertheless, data documenting genetic variation within species can still reveal higher similarity

443 between conspecifics than heterospecifics locally as well as non-overlapping species niches

444 (Schmitt et al. 2021). Importantly, any local genetic adaptation does not preclude that

445 multidimensional environmental variations generate large observed IV that is structured in space

446 and time and whose consequences cannot be well represented and understood using a random

447 variation around a species mean.

448

449 In communities of sessile organisms such as trees, IV has been commonly structured in space

450 using individual random effects, which vary among conspecific individuals but stay constant

451 through the lifetime of individuals (Clark et al. 2007, Vieilledent et al. 2010). We here argue that

452 while this approach can *reveal* the spatial structure of IV through inference, the use of the

453 resulting estimated standard deviation term to introduce individual variation in simulations of

454 community dynamics is not sufficient to *produce* a spatially structured IV, as we showed is

455 observed in natural communities.

456 Similarly, individual attributes can change over time. Because individuals within a species can

457 be measured at different points in time, as it is often the case when assembling functional trait

458 databases for example (Zanne et al. 2009, Albert et al. 2011, Kattge et al. 2020) this can lead to

459 an observed unstructured IV when characterized by a variance around a species mean (Fig. 3c).

460 But a large part of this observed IV is actually structured in time and associated with temporal

461 changes in the environment. For instance, the temporal storage effect (Chesson and Warner

462 1981), a well-known coexistence mechanism, structures species performance because species are

463 able to "store" growth during favorable timespans to overcome lean times; mast-seeding or

464 masting, which describes periodic and synchronized massive seed production of conspecific

465 individuals, would also result in a temporally structured IV (Koenig and Knops 2005). Temporal

466 variation in individual response within a species can typically be structured with temporal

467 random effects (Clark et al. 2007). Temporal random effects have been used to estimate the

468 inter-annual variability in tree growth (Metcalf et al. 2009, Fortunel et al. 2018) and fecundity

469 (Clark et al. 2007) for example. In all those examples, temporal environmental variation affects

470 conspecific attributes in the same way (Clark 2010).

471

472 We therefore call for a reconsideration of the nature and the way of integrating IV into models of

473 community dynamics. When IV is modeled randomly with a variance around a species mean, it

474 implies that conspecific individuals can perform differently in the exact same environment, thus

475 implying intrinsic differences between conspecific individuals. This type of unstructured IV can

476 result in an overestimated increase in species niche overlap, which blurs species differences (Fig.

477 3a and 3c, Stump et al. 2021). While trait heritability has rarely been considered in studies on the

478 role of IV on coexistence (but see Barabás and D'Andrea 2016), in some studies, the random

479 variation in attributes across conspecific individuals is considered as environmental, because it is

480 not heritable in the model (*e.g.* Lichstein et al. 2007, Moran et al. 2016). However,

481 environmentally-driven IV should be structured in space and time, as the environment is (Fig. 1,

482 Fig. 6). In addition, when IV is randomly distributed among conspecific individuals, similarity

483 among conspecific individuals is systematically underestimated, which is not the case when IV is

484 structured in space and time (Purves and Vanderwel 2014, Banitz 2019), as discussed hereafter.

485

Conspecific individuals respond more similarly than heterospecific individuals locally

Species differ in multiple attributes, responding to a high number of environmental variables (Fig. 2), but often in ways that cannot be readily observed. If observed IV results mainly from high-dimensional environmental variation in space and time rather than from intrinsic differences between conspecific individuals, then for a given environment, conspecific individuals should respond more similarly than heterospecific individuals. This is the case in our illustrative simulation experiment, where the fact that conspecific individuals have exactly the same set of parameters and respond identically to spatial and temporal changes in the environment results in higher inter- than intraspecific variance in the response locally (Fig. 5, Fig. 6).

Corroborating this point of view, pairs of conspecific individuals in 11 North-American temperate forest stands showed higher correlation in their temporal variation of growth rate or fecundity than pairs of heterospecific individuals on average (Clark 2010). This indicates that conspecific individuals responded more similarly to environmental variation in time than individuals of different species. Importantly, these results were obtained in a system with high observed IV (leading to an apparent species niche overlap), where species responded in the same direction to environmental changes (*e.g.* increased tree growth in climatically favorable years). Hence, considering the temporal structure of IV revealed species differences that were not apparent otherwise, since they led to spreading along a high number of dimensions that varied at fine scales (Clark 2010). However, as well highlighted by Stump et al. 2021, these results were often misinterpreted as an evidence that IV fostered coexistence. As another piece of evidence

509   presented here, pairs of spatially proximal conspecific individuals tended to present more similar

510   temporal means in absolute tree growth than pairs of close heterospecific individuals across three

511   large contrasted tropical forest sites (Table 5). This provides new empirical evidence that,

512   although estimated IV can be substantial, conspecific individuals respond more similarly than

513   heterospecific individuals to environmental variation in space.

514

515   A stronger similarity in the response to environment between conspecific than heterospecific

516   individuals locally leads to a stronger concentration of competition within species, which,

517   ultimately, can result in intraspecific competition being greater than interspecific competition, a

518   common driver of stable species coexistence (Lotka 1925, Volterra 1926, Chesson 2000).

519   Because species differ in their response to the environment, environmental variation in space and

520   time leads to local or punctual inversions of species hierarchy in performance (Fig. 3d). As

521   possibilities of hierarchy inversions between species increase rapidly with increasing

522   dimensionality of the environment (Fig. 3b), the high-dimensionality of the environment offers

523   room for the stable coexistence of numerous species (Falster et al. 2017, Rüger et al. 2018). In

524   the end, we therefore argue that a substantial part of IV is not a mechanism for coexistence in

525   itself but can rather be the signature of species differences and environmental variation that allow

526   coexistence: the high-dimensional species differences, which make them respond differently in a

527   high-dimensional environment varying in space and time, can only be observed at the individual

528   scale. In the absence of precise information on the many dimensions across which species differ

529   and environment varies, large observed IV is the evidence of the niche mechanisms enabling

530   species coexistence.

531

532 Recommendations and concluding remarks

533 Most of the theoretical studies that have explored the role of IV in species coexistence so far did

534 so by adding variances around species-specific means, thus considering IV as stochastic, which

535 implies that conspecific individuals perform differently in the same environment. Here, we

536 provide insights suggesting that large observed IV can emerge from environmental heterogeneity

537 and is structured in space and time. We stress that this interpretation has strong consequences on

538 the understanding of the effects of IV on species coexistence: (i) observed IV does not

539 necessarily imply that conspecific individuals are strongly intrinsically different nor that species

540 niches overlap, and (ii) the spatial and temporal structure of observed IV reveals stronger

541 concentration of competition within species locally in space and time, which is a frequent

542 necessary condition for stable species coexistence. We thus call for a reconsideration of the

543 nature of IV and of the way it is integrated in models, by thoroughly distinguishing its sources

544 (intrinsic vs. extrinsic, and their interactions). We acknowledge the existence of genetically-

545 driven IV, potentially due to local adaptation to the microenvironment, and its eco-evolutionary

546 importance, but suggest that multidimensional environmental variation generates a large

547 observed IV that is structured in space and time. We underline that environmentally-driven

548 structured IV has been largely overlooked in previous community ecology studies and has

549 consequences on community dynamics which cannot be represented and understood using a

550 random variation around a species mean. To this end, we recommend that empirical studies

551 explore further the spatio-temporal structure of IV and how it relates to environmental variation

552 along multiple dimensions, and, when possible, assess the relative importance of genetically and

553 environmentally driven IV, for instance by means of common garden experiments. Models of

554 community dynamics should then endeavor to structure IV in space and time so that it reflects

555 the high-dimensional variation in both the environment and species attributes, and not only some

556 intrinsic differences between conspecific individuals (Purves and Vanderwel 2014, Moran et al.

557 2016, Banitz 2019). In both empirical studies and models, this implies that the species attributes

558 are measured at the individual level, localized in space, and repeatedly observed in time.

559 Simultaneously, the monitoring of multiple environmental variables at fine scales in space and

560 time is required in order to better capture their effect on individual attributes (such as

561 physiological or mechanistic traits, Shipley et al. 2016, Brodribb 2017), hence reducing the part

562 of unexplained IV, and ultimately to better characterize the high-dimensionality of species

563 niches. Altogether, these recommendations will enable to better account for species differences

564 that are expressed at the individual level and evidence their impacts on the community dynamics

565 in natura and in silico.

Supplementary information and data access

The appendices and all the code used for this study are available in a GitHub repository (https://github.com/camillegirardtercieux/coexIV) and have been permanently archived on Zenodo (https://doi.org/10.5281/zenodo.5504013).

Appendix 1: Simulation experiment with two species.

Appendix 2: Analysis of an *Eucalyptus* clonal plantation dataset.

Appendix 3: Analysis of tropical forest inventory data.

No new data were used in this study. For access to forest plot inventory data and *Eucalyptus*

589 plantation data used in this study, refer to the data used in Le Bec et al. 2015, Hérault and

590 Piponiot 2018, Condit et al. 2019 and le Maire et al. 2019. However, the analyses and reflections

591 presented here are original.

592

593 **Statements of author roles:**

594 *CGT, IM and GV conceived the initial ideas and coordinated the INTRACO working group. All*

595 *authors contributed to the study design and ideas within the INTRACO working group. CGT led*

596 *the analyses. CGT, IM and GV wrote the first draft of the manuscript, and all authors*

597 *contributed substantially to revisions.*

598

599 **Declaration of Interests**

600 All authors declare that they have no conflict of interest.

59

601

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825 **Table 1: Mean posteriors of the *Eucalyptus* model and their estimation errors and residual**

826 **variance partitioning among the different random effects.**

827

	Intercept (β_0)	Diameter (β_1)	Competition (β_2)	Individual variance (V_i)	Block variance (V_b)	Genetic variance (V_g)	Temporal variance (V_t)	Residual variance (V)
Estimate	-3.70E-02	5.50E-01	-2.70E-01	2.30E-01	5.40E-02	1.30E-01	1.20E+00	5.10E-01
Estimation error	4.60E-01	5.10E-03	8.90E-03	4.10E-03	1.50E-02	2.90E-02	5.70E-01	2.00E-03
Percentage of unexplained variance				10.83%	2.54%	6.12%	56.50%	24.01%

828

829 **Table 2: Features of the three tropical forest data sets used as empirical case studies.**

Site	Rainfall (mm. y⁻¹)	Sampling	Min DBH	Nb of censuses	Periodicity	Disturbance	Topography	Nb of species	Nb of individuals	Data source
Paracou, French Guiana	3,000	15 × 6.25 ha (incl. 12 logged plots)	10 cm	24	1-2 y since 1992	Natural disturbances + selective logging	flat	613	69,548	(Hérault and Piponiot 2018)
BCI, Panama	2,600	50 ha	10 cm	8	5-y since 1980	Natural disturbances	hilly	225	37,224	(Condit et al. 2019)
Uppangala, India	5,100	5,92 ha (4 transects and 3 plots)	9.5 cm	20	1-yr since 1992	Natural disturbances	mountainous	102	3,789	(Le Bec et al. 2015)

Table 3: Mean posteriors of the tropical forest model and their estimation errors and residual variance partitioning among the different random effects.

	Intercept (β_0)	Diameter (β_1)	Species variance (V_b)	Individual variance (V_d)	Residual variance (V)
Paracou					
Estimate	6.70E-02	2.90E-02	4.70E-01	4.60E-01	7.60E-01
Estimation error	2.20E-02	3.80E-03	1.70E-02	3.90E-03	2.30E-03
% Variance			27.81%	27.22%	44.97%
Uppangala					
Estimate	8.40E-02	1.90E-01	3.60E-01	6.60E-01	5.90E-01
Estimation error	4.40E-02	1.20E-02	4.30E-02	8.60E-03	1.90E-03
% Variance			22.36%	40.99%	36.65%
BCI					
Estimate	1.90E-01	-2.20E-02	6.60E-01	4.10E-01	8.10E-01
Estimation error	5.00E-02	4.50E-03	3.50E-02	4.00E-03	2.00E-03
% Variance			35.11%	21.81%	43.09%

834 **Table 4**: **Spatial autocorrelation of the growth of conspecific individuals in three tropical**

835 **forest sites.** Shown are the proportion of species, and of corresponding individuals, in percent,

836 for which individual growth among conspecific individuals is significantly positively spatially

837 autocorrelated. The spatial autocorrelation of individual growth was tested using Moran's I

838 index.

839

	Significant	Not significant
Paracou		
% Species	31.00	69.00
% Individuals	78.90	21.10
Uppangala		
% Species	18.50	81.50
% Individuals	45.30	54.70
BCI		
% Species	20.10	79.90
% Individuals	54.70	45.30

840

841 **Table 5**: **Comparison of local intra- and interspecific variability in individual growth for**

842 **three tropical forest sites**. The variability was estimated with the semivariance and the

843 comparison was performed with a Mann-Whitney's test. The semivariances were computed for

844 all species with > 5 individuals and > 5 heterospecific neighbors within 100 m in the same plot,

845 and considering pairs of individuals that were less than 100 m apart and in the same plot. Shown

846 are the proportion of species, and of corresponding individuals, for which (i) intraspecific

847 variability was significantly lower than interspecific variability, (ii) intraspecific variability was

848 significantly higher than interspecific variability, or (iii) the difference between inter- and

849 intraspecific variabilities was not significant.

850

	Intraspecific variability < Interspecific variability (i)	Intraspecific variability ~ Interspecific variability (ii)	Intraspecific variability > Interspecific variability (iii)
Paracou			
% Species	60.70	40.70	0.67
% Individuals	88.80	10.90	0.28
Uppangala			
% Species	42.20	62.20	4.44
% Individuals	57.70	23.60	18.80
BCI			
% Species	46.10	47.80	3.14
% Individuals	76.00	19.30	4.69

851

852 **Figure 1: High environmental variability at a small spatial scale. (a)** Soil nitrogen content in

853 a 12×12 m plot at Cedar Creek in g.kg⁻¹, (USA), Tilman 1982; **(b)** Carbon in % (left) and

854 aluminum in ppm (right) soil content in a 12-ha (250×500 m) plot at The Nouragues (French

855 Guiana), Zinger et al. 2019; **(c)** Soil water content during mid-dry season of a regular year in

856 MPa in a 50-ha (1000×500 m) forest plot at Barro Colorado Island (Panama), Kupers et al. 2019.

857 Coordinates in m.; **(d)** Canopy height in m and topography (10 m spaced elevation lines) in a 50-

858 ha (2500×2000 m) area at the Nouragues Research Field Station, Tymen et al. 2017. Coordinates

859 in m (UTM 22N).

860
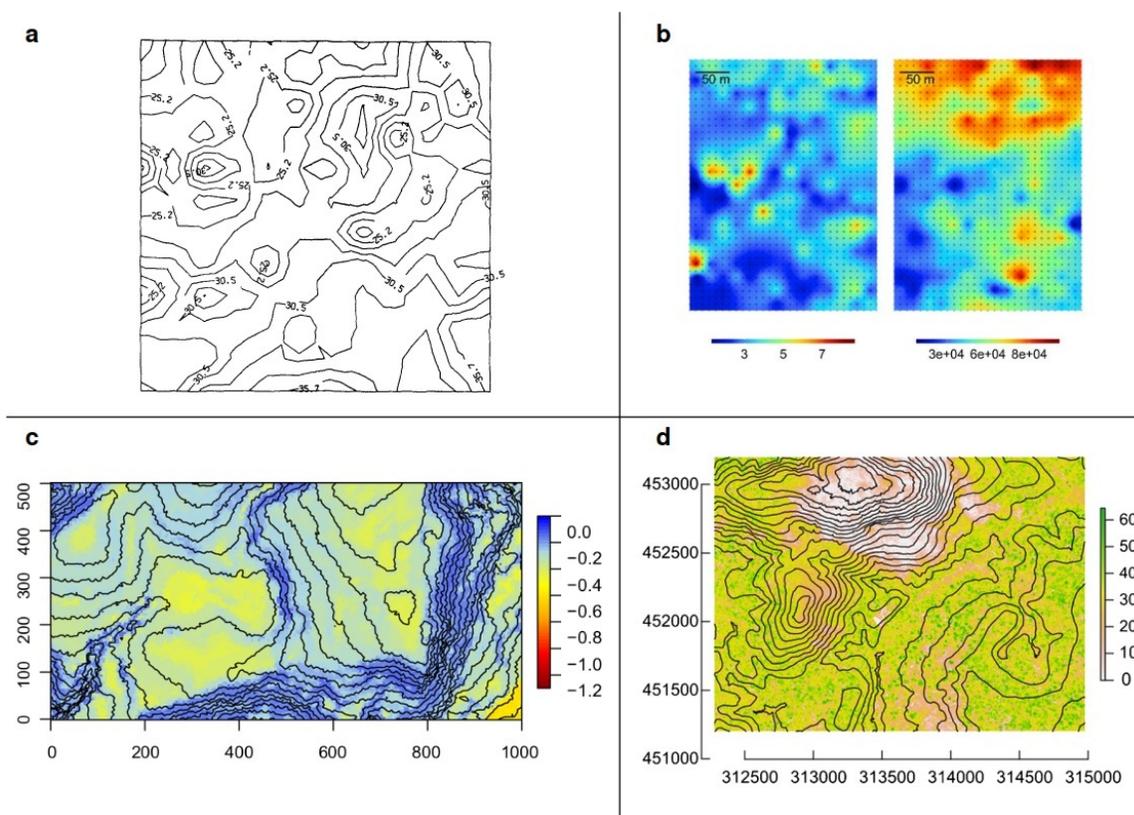
861 **Figure 2: Morphological diversity of tree species illustrating strong differences between**

862 **species. (a)** Diversity of tree species architecture and height in a tropical forest (Hallé et al.

863 1978). Coordinates are in m.; **(b)** Diversity of seed size and shape from 17 tree species of the

864 Fabaceae family in the Peruvian Amazon (Muller-Landau 2003); **(c)** Diversity of leaf size and

865 shape (herbarium of Cayenne, Gonzalez et al. 2021) and of wood aspect (reflecting wood

866 characteristics) and density (Normand et al. 2017) for 12 tree species in French Guiana. Species

867 from top left to bottom right are *Bocoa prouacensis, Zygia racemosa, Vouacapoua americana,*

868 *Eperua falcata, Bagassa guianensis, Hymenolobium excelsum, Mangifera indica, Sterculia*

869 *pruriens, Parkia nitida, Couroupita guianensis, Hura crepitans,* and *Ceiba pentandra.* Black

870 bars next to herbarium samples indicate the scale (10 cm).

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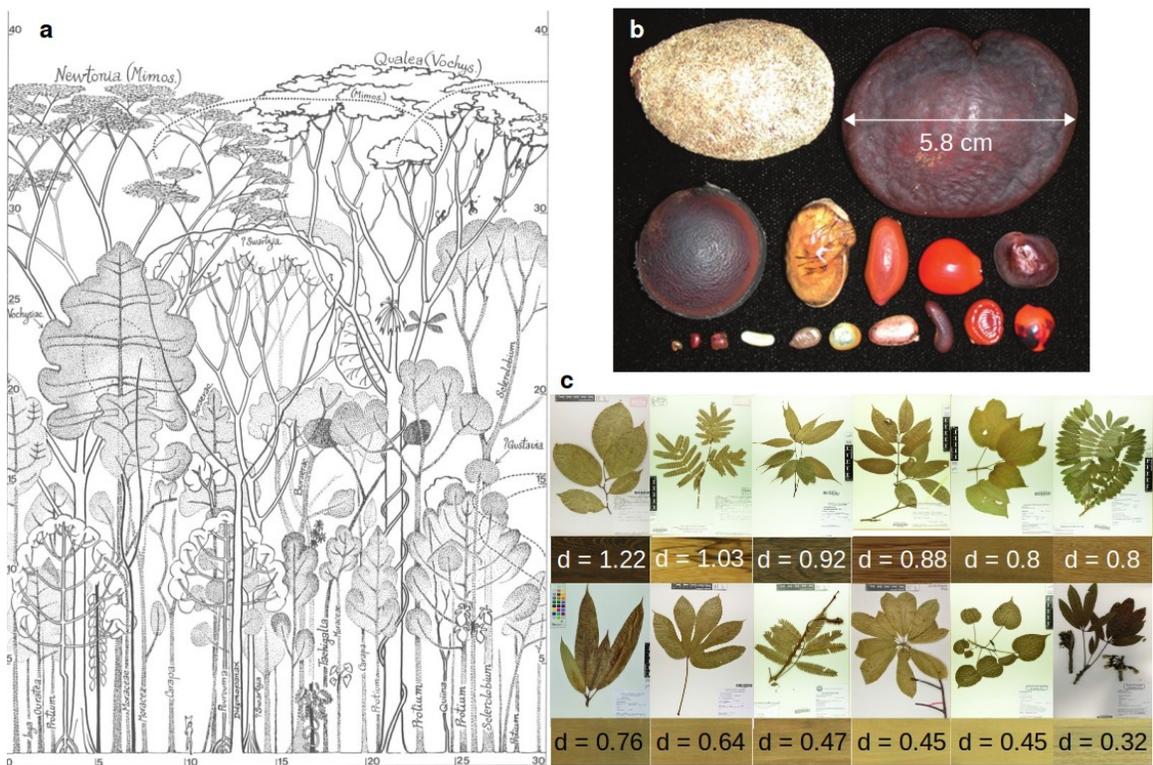
872 **Figure 3**: **Reinterpreting observed intraspecific variability (IV): from niche widening to**

873 **niche projection into a high-dimensional environment.** In **(a)**, within a given environment E0

874 defined along an environmental axis X1 (E0=E(X1,0)), conspecific individuals are identical and

875 have the same performance pA and pB, for species A (blue) and species B (orange). Species A

876 outcompetes species B in E0. Actual measured differences among conspecific individuals,

877 shown in **(c)**, can be interpreted in different ways. First, as conspecific individuals exhibit

878 contrasting attributes in E0, they become more different. This can result in some heterospecific

879 individuals having similar performances: IV would blur species differences. Alternatively, IV

880 measured in E0 results from the variation of unobserved environmental variables (E0=E(X1,0,

881 X2); **(b)**). Contrasting performances among conspecific individuals in E0 do not result from

882 intrinsic differences among them but from differences in the local environment they experience

883 and that was poorly characterized, *i.e.* the number of observed dimensions is lower than the

884 actual number of environmental dimensions. Similarly, although species niches present some

885 overlap when projected on one dimension **(d)**, they do not overlap in the two-dimensional space

886 **(b)**. Moreover, while species A outcompetes species B on average when X1=X1,0, the opposite

887 occurs when X1=X1,1 **(d)**, leading to an inversion of species hierarchy between different

888 environments. Similarly, while species A outcompetes species B in E(X1,0, X2,0), the opposite

889 occurs in E(X1,0, X2,1). Although only two dimensions are shown, species respond to many

890 environmental variables varying in space and time, multiplying the possibilities of niche

891 segregation and hierarchy inversions between species, offering room for species coexistence in a

892 variable high-dimensional environment. The code used to generate this figure is available online.

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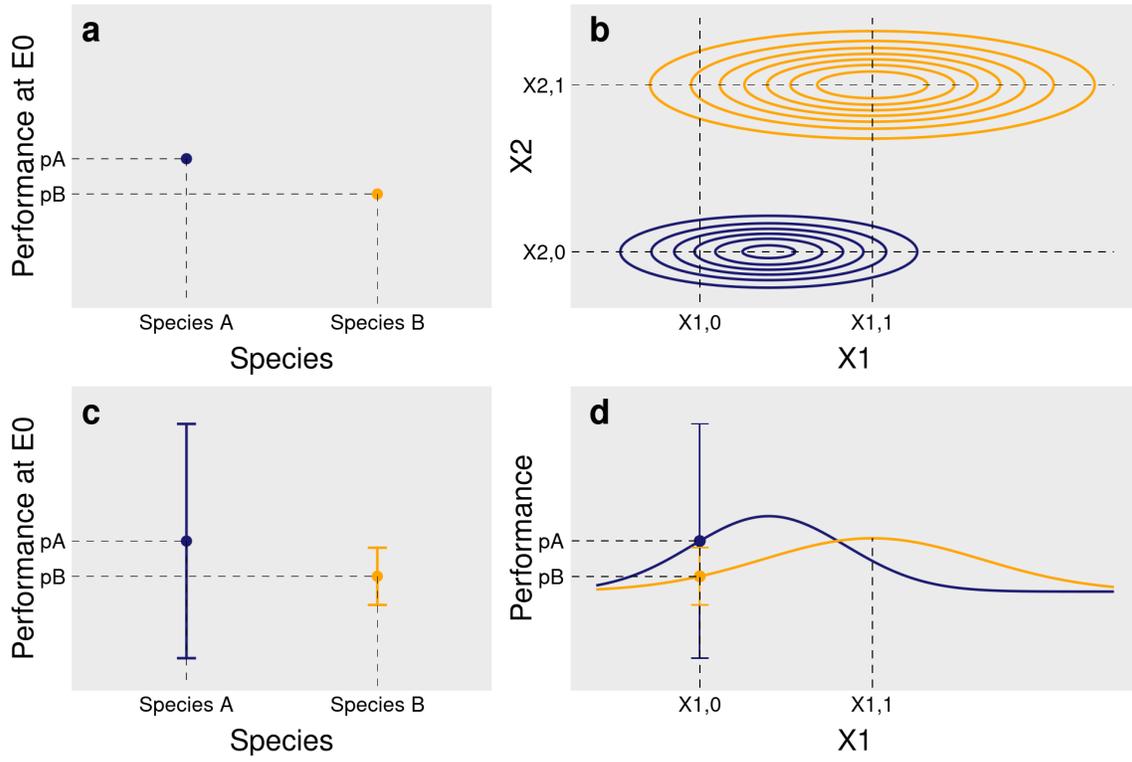
Figure 4: Multiple insights on the nature of IV and its consequences on individual and species differences. We used literature and data analyses of various nature to support the hypothesis that a large part of observed IV can result from multidimensional environmental variations that are spatially and temporally structured rather than by intrinsic and spatio-temporally unstructured differences between conspecific individuals, with radically different consequences on species coexistence.
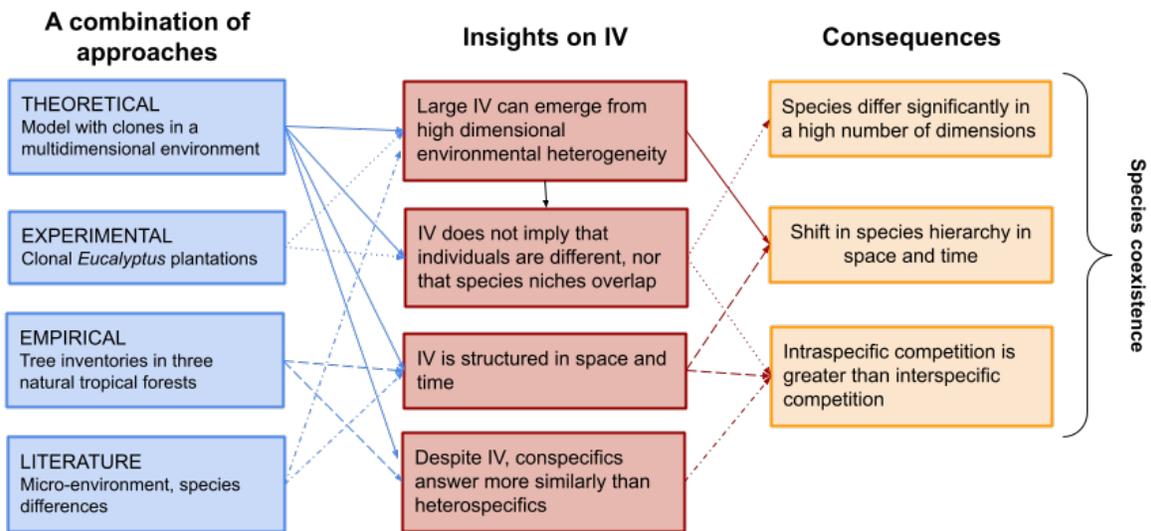
Figure 5: Observed intraspecific variability as a result of the imperfect characterization of the environment. A simulated response variable (Y, *e.g.* growth) is generated for individual clones of two species thriving in a high-dimensional environment. This response variable was first computed as a function of ten environmental variables ("perfect knowledge" model, Eq. I), but is then analyzed using a statistical model that accounts for the unique environmental variable that was assumed to be observed in the field (X_1, *e.g.* light) and includes a random individual effect ("imperfect knowledge" model, Eq. II). The intraspecific variability estimated with these random individual effects is then due to the variation in space and time of the nine unobserved environmental variables. **(a)** Positions of a sample of I=600 individuals from J=2 species in a landscape defined by a square grid of C × C cells (C=500). The background color indicates the value of the observed environmental variable X_1 on each cell at date t. The response Y of each individual, which depends on the environment within each cell (Eq. I), is also indicated by a color scale. **(b)** Response Y as a function of the observed environmental variable X_1 for the two species. Points represent the data $\{Y_{ijt}, X_{1,ijt}\}$. Thick lines represent the predictive posterior means for the two species. The envelopes delimited by two thin lines represent the 95% credible intervals of the predictive posterior marginalized over individuals (taking into account $\hat{V}_{bj}$). The envelopes thus represent the intraspecific variability which is due to the N-1 unobserved environmental variables.
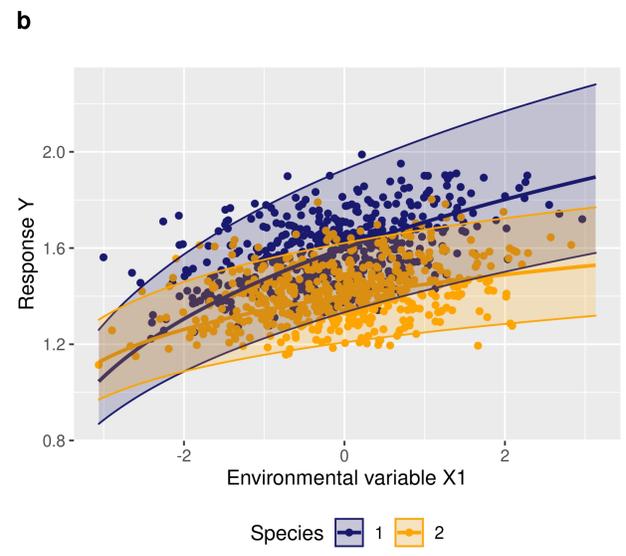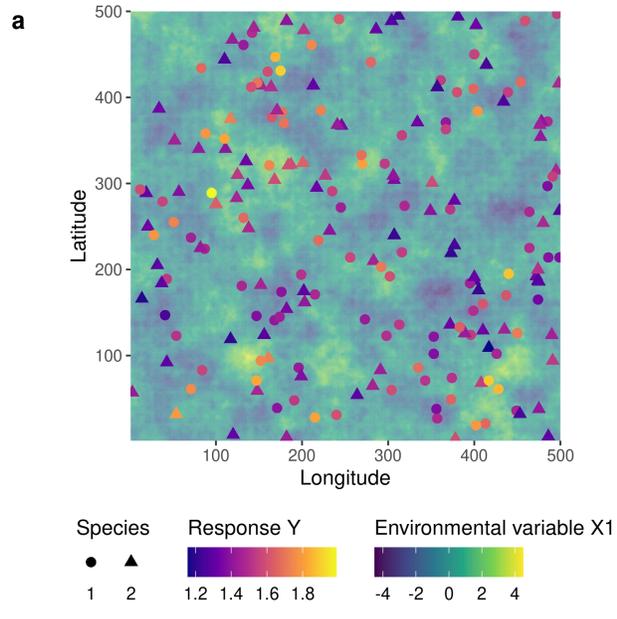
921 **Figure 6: Spatial autocorrelation of attribute Y across individuals within and between**

922 **species (J=2) in a simulation experiment.** This semivariogram represents the semivariance of

923 the individual mean attribute Y as a function of the distance between individuals. The increasing

924 curves evidence spatial autocorrelation in Y (similar results using Moran's I test). The

925 semivariance of all individuals taken together (purple curve) is higher than the semivariance of

926 conspecific individuals for the two species (orange and blue curves), which means that

927 intraspecific variability is lower than interspecific variability.
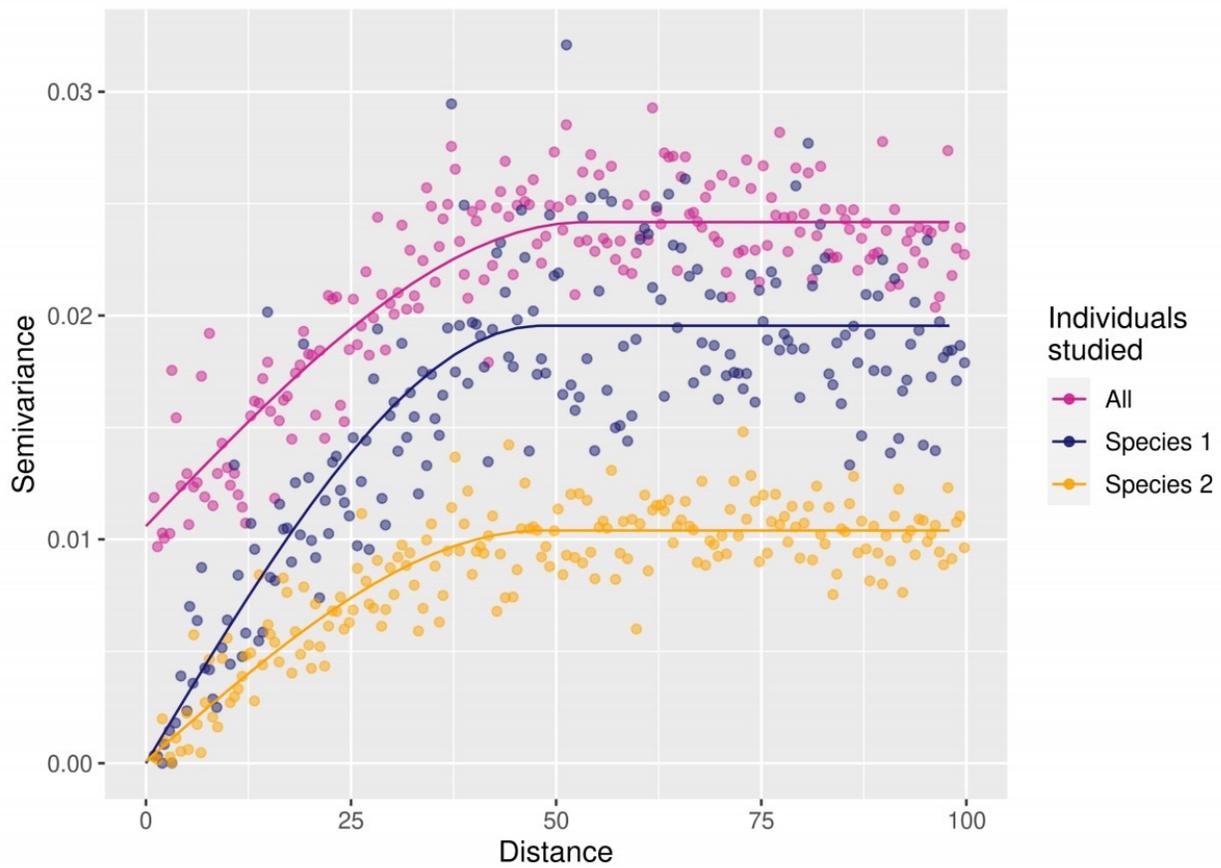
929 **Figure 7: Experimental setup of the EUCFLUX experiment.** The ten blocks **(a)** and the

930 organization of the 16 genotypes within a block **(b)**. In our analyses, two genotypes were

931 discarded because they were obtained from seeds and not clones and therefore included some

932 genetic variability. A more complete figure legend can be found in le Maire et al. 2019.