

1 **A global meta-analysis of the relative extent of intraspecific trait variation in plant**
 2 **communities**

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111 **Abstract**

112 Recent studies have shown that accounting for intraspecific trait variation (ITV) may better
113 address major questions in community ecology. However, a general picture of the relative extent
114 of ITV compared to interspecific trait variation in plant communities is still missing. Here, we
115 conducted a meta-analysis of the relative extent of ITV within and among plant communities
116 worldwide, using a dataset encompassing 629 communities (plots) and 36 functional traits.
117 Overall, ITV accounted for 25% of the total trait variation within communities and 32% of the
118 total trait variation among communities on average. The relative extent of ITV tended to be
119 greater for whole-plant (e.g. plant height) versus organ-level traits and for leaf chemical (e.g. leaf
120 N and P concentration) versus leaf morphological (e.g. leaf area and thickness) traits. The
121 relative amount of ITV decreased with increasing species richness and spatial extent, but did not
122 vary with plant growth form or climate. These results highlight global patterns in the relative
123 importance of ITV in plant communities, providing practical guidelines for when researchers
124 should include ITV in trait-based community and ecosystem studies.

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134 **Introduction**

135 In recent decades, an explosion of research on functional diversity, which measures the values of
136 functional traits and their variation within and among communities, has shed new light on
137 community assembly and ecosystem processes (Weiher & Keddy 1995; Diaz & Cabido 2001;
138 Hooper *et al.* 2005; McGill *et al.* 2006; Kraft *et al.* 2008). By working with functional traits,
139 researchers seek generalizable predictions across organizational and spatial scales (Adler *et al.*
140 2013). The dominant theories and approaches in trait-based community ecology have focused
141 largely on trait differences among species (McGill *et al.* 2006), but there has recently been
142 renewed interest in the role of intraspecific trait variation (ITV) (Bolnick *et al.* 2011; Violle *et al.*
143 2012). This interest is grounded in the observation that functional traits vary at the individual
144 level, and this variation influences the interactions among organisms and between organisms and
145 their environment that ultimately drive the assembly and functioning of communities (Bolnick *et*
146 *al.* 2003; Vellend & Geber 2005). Integrating ITV in community ecology thus has the potential
147 to strengthen understanding of processes operating at the community level and ecosystem levels.

148 Recent studies have demonstrated that accounting for ITV may be critical for answering
149 key questions and making predictions about plant community assembly and ecosystem
150 functioning (Violle *et al.* 2012). Plants often display strong intraspecific variation in functional
151 traits, reflecting both heritable genetic variation and phenotypic plasticity, and this variation
152 influences plant responses to abiotic filters and biotic interactions (Fridley *et al.* 2007; Fridley &
153 Grime 2010), as well as plant effects on ecosystem processes (Crustinger *et al.* 2006; Hughes *et*
154 *al.* 2008). Recent studies have found that consideration of ITV improves the ability of trait-based
155 analyses to make inferences about local community assembly processes (Jung *et al.* 2010; Paine
156 *et al.* 2011; Siefert 2012a). Accounting for ITV has also been shown to improve predictions of

157 outcomes of species interactions (Kraft *et al.* 2014), community responses to spatial and
158 temporal environmental gradients (Lepš *et al.* 2011; Kichenin *et al.* 2013; Jung *et al.* 2014), and
159 ecosystem processes such as productivity and nutrient cycling (Breza *et al.* 2012).

160 Despite the predictive power that may come from considering ITV in plant community
161 studies, a practical limitation is the difficulty of measuring trait values on a large number of
162 individuals per species, particularly in species-rich communities (Baraloto *et al.* 2010). When
163 and how ITV should be incorporated in trait-based ecology studies has thus emerged as an urgent
164 question (Albert *et al.* 2011). Although many factors go into answering this question, a basic
165 consideration is the relative amount of intraspecific compared to interspecific trait variation in
166 the communities being studied. If ITV is large compared to interspecific variation, it is likely to
167 have important ecological consequences and should not be ignored out of hand. Recently,
168 empirical studies have quantified the relative amount of ITV compared to interspecific variation
169 for various plant functional traits and communities (e.g. Jung *et al.* 2010; Messier *et al.* 2010;
170 Lepš *et al.* 2011; Auger & Shipley 2012). This work has shown that the extent of ITV within and
171 among plant communities is often substantial—sometimes similar to or greater than interspecific
172 variation—but highly context-dependent, varying strongly among traits and communities. An
173 improved understanding of the context-dependence of ITV in plant communities is necessary for
174 integrating ITV in trait-based ecology and for understanding its role in ecological processes
175 acting at the community scale and beyond (Albert *et al.* 2011). To address this need, we
176 conducted a global-scale meta-analysis to determine the relative extent of ITV compared to
177 interspecific variation in plant communities and to identify general trends in how ITV varies
178 among traits and study systems.

179 The first aim of our meta-analysis was to make generalizations about how ITV varies
180 among functional traits and broad trait categories. Previous studies examining inter- and
181 intraspecific trait variation in plant communities have found that the relative extent of ITV varies
182 strongly among traits. For example, Hulshof & Swenson (2010), partitioning variation in four
183 leaf traits in a tropical forest in Costa Rica, found that ITV ranged from 36-83% of total trait
184 variance. Our global meta-analysis approach allowed us to identify traits that consistently display
185 high ITV across systems and to test general hypotheses about how ITV varies among trait
186 categories. First, we tested whether the relative extent of ITV differs between traits measured at
187 the whole-plant level (e.g. plant height, plant architecture) and at the organ level (leaves, stems,
188 and roots). Based on plant optimization models (Marks 2007), we expected that traits measured
189 at higher levels of plant integration (i.e. whole-plant traits) should be highly sensitive to the
190 environment and thus display high ITV as a result of local genetic adaptation and phenotypic
191 plasticity. In contrast, we expected organ-level traits to be more strongly conserved and thus vary
192 mostly at the interspecific level (Marks 2007). Then, focusing on leaf traits, we tested whether
193 the relative extent of ITV differed between traits related to leaf chemical composition—e.g.
194 elemental concentrations and ratios—and traits related to leaf morphology—e.g. leaf area, leaf
195 thickness, specific leaf area (SLA), leaf dry matter content (LDMC). Comparative studies have
196 found that leaf nutrient concentrations are highly labile within species, displaying strong plastic
197 responses to resource availability, whereas leaf morphology tends to be more stable (Rozendaal
198 *et al.* 2006; Kazakou *et al.* 2014). We therefore expected leaf chemical traits to show higher
199 relative ITV at the community level than leaf morphological traits.

200 The second aim of this meta-analysis was to examine how ITV varies among
201 communities differing in terms of the dominant growth form, species richness, and climate. First,

202 we asked whether the relative extent of ITV differs between communities consisting of woody
203 versus herbaceous plants. We may expect long-lived (i.e. woody) species to have high
204 ontogenetic variation and express strong phenotypic plasticity to face environmental hazards
205 over their lifetimes, leading to high ITV (Sultan 1987; Borges 2009). Conversely, species with
206 long tissue lifespan may have higher costs or limits to plasticity, and we might thus expect them
207 to express less ITV than fast-growing, ruderal (i.e. herbaceous) species (Maire *et al.* 2013).
208 Second, we tested whether the relative extent of ITV varies with community species richness.
209 Previous work suggests that ITV should be most important in species-poor communities (e.g.
210 MacArthur 1984; Antonovics 1992; Whitham *et al.* 2006), and niche theory predicts that the
211 relative extent of ITV should decrease with increasing species richness (Violle *et al.* 2012).
212 However, few studies have empirically examined this relationship in plant communities, and
213 these have produced conflicting results (Hulshof *et al.* 2013; Le Bagousse-Pinguet *et al.* 2014).
214 Finally, we tested whether the relative extent of ITV varies with climate (temperature and
215 precipitation) on a global scale. Previous research suggests that phenotypic plasticity may be
216 constrained in stressful environments (Valladares *et al.* 2007). If this is true, we expect the
217 relative extent of ITV to decrease with increasing climatic stress (i.e. decreasing temperature and
218 precipitation). Alternatively, several hypotheses predict that unfavorable conditions increase the
219 expression of genetic variability in traits, leading to the opposite pattern (Hoffmann & Merilä
220 1999). Community-level ITV has rarely been measured across broad climatic gradients (but see
221 Hulshof *et al.* 2013), so these hypotheses remain largely untested.

222 Third, we examined how the relative extent of ITV depends on the spatial scale (grain
223 and extent) of observation across studies. Interspecific and intraspecific trait variation are both
224 expected to increase with spatial extent as broader environmental gradients are encountered,

225 leading to turnover of species and genotypes as well as plastic trait responses (Albert *et al.* 2011;
226 Auger & Shipley 2013). However, ITV must saturate at some scale once the entire potential
227 genetic and environmental variation of species is reached. Therefore, the relative contribution of
228 ITV to trait variation among communities is expected to decrease with increasing spatial extent
229 from local to regional and global scales (Albert *et al.* 2011) or with increasing distance along
230 environmental gradients (Auger & Shipley 2013). At the community level, the relationship
231 between spatial grain (plot or sampling unit size) and the relative extent of ITV within
232 communities is more difficult to predict. For example, this relationship may depend on the scale
233 of environmental heterogeneity relative to the size of individual plants, and thus the potential for
234 individuals to express genetic and plastic trait differences across different environments.

235 In assessing the extent and role of ITV in plant communities, it is important to recognize
236 that ITV arises from multiple mechanisms, including heritable genetic variation, phenotypic
237 plasticity, and ontogenetic variation, and these mechanisms will differentially affect whole-plant
238 versus organ-specific traits. While specific sources of variation may be of interest for
239 investigating particular ecological or evolutionary questions, all sources contribute to the trait
240 variation observed in natural communities and potentially influence community assembly and
241 ecosystem processes. Understanding the extent and consequences of ITV at the community level,
242 even if its underlying mechanisms are unknown, is therefore an important step for trait-based
243 ecology (Violle *et al.* 2012). Moreover, partitioning the sources of ITV—for example, using
244 classical methods from quantitative genetics (Vellend *et al.* 2014)—may not be feasible at the
245 community level except in systems dominated by one or few species. In our meta-analysis, we
246 therefore considered all potential sources of ITV and did not attempt to distinguish them. ITV
247 may also be measured at different levels of organization, including within-individual (e.g.

248 variation among leaves within a plant), among-individual, and among-population or site. Here,
249 we focused on ITV at two levels of organization. Specifically, we aimed to quantify 1) the
250 relative contribution of among-individual ITV to the total trait variation within plant
251 communities (within-community analysis), and 2) the relative contribution of among-population
252 ITV to the total variation in mean trait values among plant communities (among-community
253 analysis).

254 Overall, we quantified the relative extent of ITV within and among plant communities
255 using a dataset consisting of 44 studies, encompassing 629 plant communities (plots) worldwide
256 and 36 plant functional traits. Using these data, we conducted a meta-analysis to address two
257 main questions: 1) how does the relative extent of ITV vary among plant functional traits and
258 among broad trait categories? 2) Can variation in the relative extent of ITV among studies be
259 explained by basic properties of the studied communities, including plant growth form, species
260 richness, climate, and spatial scale? By addressing these questions, we provide the broadest and
261 most thorough assessment to date of the importance of ITV to community-level functional
262 diversity. Our findings suggest practical guidelines for when ITV is likely to be substantial in
263 plant communities and therefore important to include in trait-based community and ecosystem
264 studies.

265

266 **Methods**

267 **A global dataset to assess ITV in plant communities**

268 To conduct our meta-analysis, we assembled data from published and unpublished studies by the
269 authors that measured intraspecific trait variation within and among terrestrial, vascular plant
270 communities. Criteria for including a study in the within-community analysis were 1) species

271 composition data including relative abundance for at least one community (defined here as a
272 single plot or sampling unit); and 2) trait measurements on at least five individuals (or all
273 individuals if total was fewer than five) per species per community. Criteria for including a study
274 in the among-community analysis were 1) species composition data including relative abundance
275 for three or more communities; and 2) trait measurements on at least one individual per species
276 per sampled community. For both within- and among-community analyses, we only included
277 studies that measured traits of species that together made up at least 80% of total community
278 abundance (variously measured as cover, density, biomass, or frequency) as recommended in
279 previous studies (Pakeman & Quested 2007). Following typical methods in plant community
280 ecology, many studies focused on a single vegetation layer (e.g. trees or herbs), even if multiple
281 layers were present in the study area. We included these studies in the analysis, acknowledging
282 that they may include only a subset of the vascular vegetation in a given area.

283 Following the trait definition of Violle *et al.* (2007), we included in our dataset
284 morphological and physiological features of plants measurable at the individual level. Further,
285 we sought to include traits known to be related to some aspect of plant functioning, i.e.
286 functional traits. As the goal of this study is to give a general picture of the relative extent of ITV
287 in plant communities, and given the diversity of ecological questions that functional traits can be
288 used to address, we preferred to be inclusive with our selection of traits. Characters such as plant
289 height and canopy dimensions measured at the individual level, for instance, may be viewed as
290 measures of performance rather than indicators of plant strategy in the context of community
291 assembly studies. However, individual variation in such characters still contributes to the
292 standing phenotypic variation within and among communities, with potential consequences for
293 coexistence, ecosystem functioning, and other processes. We conducted analyses with plant

294 height either included or excluded; as both approaches produced similar results, we present only
295 results with height included for completeness.

296 We classified the traits in our dataset by organ (whole-plant, leaf, stem, or root), and leaf
297 traits were in turn categorized as morphological (i.e. related to overall leaf size, shape, density, or
298 mechanical properties) or chemical (i.e. describing leaf chemical composition). To simplify the
299 analysis and allow for generalization, we combined data for closely related traits (e.g. vegetative
300 and reproductive height). A summary of traits included in our dataset and description of their
301 ecological significance are found in Tables S1 and S2 in the Supporting Information.

302 For each study, we collected metadata including geographic coordinates, spatial grain
303 (area of single community, i.e. sampling unit, in m²), spatial extent (maximum geographic
304 distance between communities in km), ecosystem type (tropical or temperate), growth form
305 (woody, herbaceous, or both), and alpha and gamma species richness (mean number of species
306 within communities and total number of species across all communities in a study, respectively).
307 For each study, we extracted mean annual temperature (MAT) and mean annual precipitation
308 (MAP) values from WorldClim (<http://www.worldclim.org>). We also obtained information on
309 sampling design and effort, including the number of communities, percent of total species
310 richness and total community abundance sampled, and number of individuals and populations
311 sampled per species. Studies varied in their methods of selecting individuals and leaves within
312 individuals for trait measurement. Most studies selected individuals randomly, only avoiding
313 damaged or unhealthy individuals, but some studies only included individuals from particular
314 life stages or size classes (e.g. adult trees or saplings), thus reducing ITV association with
315 ontogeny. For leaf traits, some studies selected leaves randomly within each individual, but most
316 studies—following standard trait protocols (Perez-Harguindeguy *et al.* 2013)—selected only

317 young, fully-expanded, outer canopy leaves, thus reducing ITV associated with light
318 environment and leaf age. We included studies with both random and non-random selection of
319 individuals and leaves in our meta-analysis, acknowledging that this may contribute to
320 unexplained variation in ITV among studies and overall underestimation of ITV.

321 Our final dataset consisted of 171 study-trait combinations (cases), representing 33
322 studies and 30 unique traits, with data suitable for the within-community analysis; and 214 trait-
323 study combinations from 37 studies, representing 36 traits, with data suitable for the among-
324 community analysis (see Tables S1, S3). The studies covered a broad geographic range (Fig. 1)
325 and included all major global biomes except deserts. For both datasets, studies measuring woody
326 species were more common than studies of herbaceous or combined woody and herbaceous
327 species. Among plant organs, leaf traits were best represented, followed by whole-plant, stem,
328 and root traits. Leaf morphological traits were better represented than leaf chemical traits. The
329 individual traits with the greatest number of observations were specific leaf area (SLA), plant
330 height, leaf dry matter content (LDMC), leaf thickness, bark thickness, wood density, leaf length,
331 and leaf area (see Table S1).

332 **Data analysis**

333 We used the framework developed by Lepš *et al.* (2011) and de Bello *et al.* (2011) to evaluate
334 the relative contribution of intraspecific trait variation to total within-community (*wITV*) and
335 among-community (*aITV*) trait variance for each trait and study (see Box 1 for details). Our
336 *wITV* metric represents the proportion of total within-community trait variance attributable to
337 ITV. The *aITV* metric represents the relative contribution of intraspecific trait variation versus
338 species turnover to the total among-community variance, with positive values indicating a
339 greater contribution of ITV and negative values indicating a greater contribution of species

340 turnover. Differences in *wITV* and *aITV* among traits and studies could be driven by differences
341 in the absolute extent of interspecific or intraspecific variation, or a combination of the two.
342 Disentangling these sources is an interesting research question (see e.g. Hulshof *et al.* 2013; Le
343 Bagousse-Pinguet *et al.* 2014), but here we focused on the relative rather than absolute extent of
344 ITV, because it allows comparison of multiple traits measured in different units or on different
345 scales, for which comparison of raw variance values would be difficult or impossible.

346 We evaluated the factors influencing the relative extent of ITV within (*wITV*) and among
347 communities (*aITV*) using linear mixed models and an information-theoretic approach (Burnham
348 & Anderson 2002). For each response variable (*wITV* and *aITV*), we performed separate analyses
349 on all traits together (including only traits measured in at least two studies), leaf traits only, and
350 the two most commonly sampled individual traits in our dataset, SLA and plant height. We also
351 performed separate analyses on the dataset divided by growth form (woody or herbaceous) and
352 biome (temperate or tropical).

353 For analyses of all traits and leaf traits, we developed a set of linear mixed models that
354 included trait and study as random effects and all possible combinations of the following fixed
355 effects: mean annual temperature (MAT), mean annual precipitation (MAP), alpha species
356 richness (*wITV* analysis only), gamma species richness (*aITV* analysis only), spatial grain, spatial
357 extent (*aITV* analysis only), growth form, organ (whole-plant, leaf, stem, or root; only for
358 analysis of all traits) and leaf trait category (morphological or chemical; leaf trait analyses only).
359 For analyses of single traits (SLA and plant height), we used simple linear regressions with
360 species richness, grain, extent, and growth form as fixed effects. Species richness and spatial
361 grain and extent were log-transformed to reduce skewness. We excluded models that contained
362 highly correlated ($|r| > 0.5$) predictor variables. The combinations of variables excluded varied

363 among analyses, but in most cases temperature, precipitation, and species richness were
364 positively correlated, and thus no more than one of these predictors was included in each model.
365 Additionally, spatial extent and grain were positively correlated, so no more than one of them
366 was included in each model when analyzing *aITV*.

367 The models were ranked according to the corrected Akaike information criterion (AICc)
368 and their relative support was evaluated with the AICc weight (Burnham & Anderson 2002). We
369 retained a confidence set of models with cumulated AICc weight of 0.95 (Johnson & Omland
370 2004). The relative importance of each fixed effect in the confidence set was calculated as the
371 sum of the Akaike weights over all of the models in which it appeared. We further calculated
372 model averaged estimates of the fixed effects over the confidence set of models (Burnham &
373 Anderson 2002).

374 Finally, to test whether variation in the relative extent of ITV among traits was consistent
375 across organizational scales (within- and among-community), we examined the relationship
376 between mean *wITV* and *aITV* across traits. We calculated the average *wITV* and *aITV* across
377 studies for each trait, using only studies that measured both *wITV* and *aITV* for a given trait. We
378 tested whether mean *wITV* and *aITV* were correlated using reduced major axis regression and a
379 permutation test. All analyses were conducted using R version 3.0.2 (R Core Development Team
380 2012) using packages lme4 (Bates *et al.* 2013) and MuMIn (Bartoń 2013).

381

382 **Results**

383 **Relative extent of ITV within communities**

384 Across all studies and traits, ITV accounted for on average 25% of the total within-community
385 trait variance, with interspecific variance accounting for the remainder (intercept of random

386 effects only model for $wITV = 0.25$; 95% confidence interval = 0.19-0.31). There was
387 considerable variation in the relative extent of ITV among traits and studies, with values ranging
388 from 2 to 67% (Fig. 2a; Table S1). Of the most commonly measured traits, ITV tended to be
389 relatively high for SLA, plant height, leaf N, and LDMC (median $wITV = 25-30\%$; Fig. 2a), and
390 lower for wood density and leaf area, leaf thickness, and leaf length (median $wITV < 20\%$; Fig.
391 2a). There was no effect of any variable relating to sample size or sampling effort on $wITV$.

392 Results of linear mixed model analysis of all traits showed that the relative extent of ITV
393 within communities was negatively related to species richness and greater for whole-plant traits
394 than for leaf traits (Fig. 3a; Appendix S1). The analysis of leaf traits showed that $wITV$ was
395 marginally greater for chemical compared to morphological traits (Fig. 3b). For SLA, $wITV$
396 decreased marginally with increasing MAT (Fig. 3c). For plant height, $wITV$ was negatively
397 related to species richness and decreased marginally with increasing mean annual temperature
398 and precipitation (Fig. 3d).

399 The relative extent of ITV within communities did not differ between studies measuring
400 woody versus herbaceous species (relative importance of growth form = 0.10; Fig. 3), but the
401 effects of species richness, organ, and leaf trait category were all stronger for woody
402 communities (see Appendix S2). There was also a marginal negative effect of MAP on $wITV$ for
403 woody but not for herbaceous communities (Appendix S2). Temperate and tropical communities
404 did not differ in $wITV$ (relative importance of biome = 0), but the effects of species richness and
405 organ were stronger for temperate communities (see Appendix S2). In addition, $wITV$ decreased
406 with increasing spatial grain in temperate but not in tropical communities (Appendix S2).

407 **Relative extent of ITV among communities**

408 Across all studies and traits, ITV accounted for 32% of the total trait variation among
409 communities on average, whereas species turnover accounted for 64% (intercept of random
410 effects model for $aITV = -0.94$; 95% confidence interval = -1.64 to -0.24). For individual traits,
411 there were cases in which the average contribution of ITV was greater than ($aITV > 0$, e.g. leaf
412 N:P; Fig. 2b; Table S1), similar to ($aITV = 0$; e.g. SLA, LDMC, leaf C:N), or much less than that
413 of species turnover ($aITV < 0$; e.g. leaf size traits). Of the commonly measured traits, the relative
414 contribution of ITV was greatest for plant height, bark thickness, and LDMC and least for leaf
415 area, length, and thickness (Fig. 2b; Table S1). The covariation between ITV and species
416 turnover was highly variable but was most often weakly positive (median = 7.7%), indicating
417 that traits tended to vary in the same direction due to ITV and species turnover. Overall, $aITV$
418 was not influenced by any variable related to sample size or sampling effort.

419 The relative extent of ITV among communities was negatively related to spatial grain and
420 extent (Fig. 4a; Appendix S3). The analysis of leaf traits showed that $aITV$ was greater for
421 chemical than morphological traits (Fig. 4b). For SLA, $aITV$ decreased marginally with
422 increasing grain, extent, and precipitation and was lower for studies that included both woody
423 and herbaceous growth forms than for studies with only woody or herbaceous species (Fig. 4c).
424 For plant height, $aITV$ was marginally negatively related to gamma species richness and spatial
425 extent (Fig. 4d).

426 Although growth form (woody versus herbaceous) was not an important factor in
427 explaining $aITV$ when looking at all community types together (relative importance of growth
428 form = 0.06), we found differences in the effects of predictors when analyzing woody and
429 herbaceous communities separately (see Appendix S3). In particular, there was a strong negative
430 effect of precipitation and positive effect of gamma species richness on $aITV$ for herbaceous but

431 not for woody communities (Appendix S4). Similarly, there was no overall difference in *aITV*
432 between temperate and tropical communities (relative importance of biome = 0), but the effects
433 of spatial extent, growth form, and leaf trait category were much stronger for tropical
434 communities (see Appendix S4). In addition, there was a negative effect of temperature on *aITV*
435 in tropical but not temperate communities (Appendix S4).

436 **Relationship between within- and among-community ITV across traits**

437 Mean *wITV* and *aITV* were positively correlated across traits ($R^2 = 0.42$; $P < 0.01$), indicating
438 that traits with a high relative extent of ITV within communities also had high ITV among
439 communities (Fig. 5). Most traits fell near the overall regression line, but some traits (e.g. leaf
440 thickness) were well above the line, indicating relatively higher ITV among than within
441 communities. Conversely, some traits (e.g. leaf carbon concentration and lateral spread) fell well
442 below the regression line, indicating relatively higher ITV within than among communities.

443

444 **Discussion**

445 Our global meta-analysis revealed that ITV often contributes substantially to the total trait
446 variation within and among plant communities but is typically less than interspecific variation.
447 On average, ITV accounted for 25% of total within-community trait variance and 32% of total
448 among-community variance in mean trait values. Below, we discuss general trends in the
449 context-dependence of the relative extent of ITV in plant communities and the implications of
450 these findings for trait-based ecology.

451 **Variation in relative extent of ITV among functional traits**

452 The relative extent of ITV varied strongly among the traits examined in this study, and we
453 identified several general patterns with respect to broad trait categories. First, leaf chemical traits

454 tended to have greater ITV within and among communities compared to leaf morphological
455 traits. This result is in line with previous studies finding high ITV in leaf chemical traits. For
456 example, Kazakou *et al.* (2014), examining leaf trait variation in a common garden experiment
457 and Mediterranean old-fields, found that ITV accounted for >60% of total variation in leaf N, P,
458 and C concentrations. Storage of carbon and nutrients by plants, which depends on element
459 availability in the environment, may explain the high intraspecific variability in leaf chemical
460 composition (Chapin *et al.* 1990), but heritable genetic variability may also contribute to
461 differences among individuals and populations. Our finding that ITV is an important source of
462 variation in leaf chemical traits across community types and biomes worldwide has strong
463 implications for studies of nutrient cycling and decomposition. Leaf chemical traits of plant
464 communities are known to exert a strong influence on nutrient cycling and decomposition rates
465 (Quested *et al.* 2007; Cornwell *et al.* 2008), and intraspecific variability in these traits is likely to
466 play a role in driving spatial and temporal variation in these processes.

467 We also found strong differences in the relative extent of ITV for leaf traits related to
468 different aspects of plant function. ITV within communities was relatively high (25% or more of
469 total community trait variation) for both chemical and morphological traits linked to the leaf
470 economics spectrum (e.g. leaf N and P, SLA, LDMC). This is consistent with previous studies
471 finding extensive ITV in leaf economic traits arising from plastic responses to light, nutrients,
472 and other environmental factors (Meziane & Shipley 1999; Rozendaal *et al.* 2006), as well as
473 genetic variability and ontogenetic variation (Scheepens *et al.* 2010; Vasseur *et al.* 2012; Mason
474 *et al.* 2013). Our finding that leaf economic traits consistently display high ITV within and
475 among communities globally has important implications for trait-based ecology. Leaf economic
476 traits represent a primary axis of functional variation in plants worldwide and are linked to a

477 proposed universal ‘fast-slow’ plant economics spectrum that may help explain individual plant
478 strategies, community assembly, and ecosystem functioning (Reich 2014). The high intraspecific
479 variability in leaf economic traits suggests that ITV may play an important role in community-
480 and ecosystem-level processes and deserves increased consideration in future studies. In contrast
481 to leaf economic traits, ITV was low for traits related to leaf size (area, length, width, thickness),
482 which are typically considered independent of the leaf economics spectrum but have been linked
483 with adaptation to broad climatic gradients (Craine *et al.* 2012). Previous studies have found that
484 leaf size traits have limited plasticity and low ITV relative to the large interspecific variation
485 among co-occurring species (Rozendaal *et al.* 2006). Our findings suggest that species mean trait
486 values are likely to capture the majority of leaf size variation within and among most plant
487 communities worldwide.

488 Finally, we found that within-community ITV tended to be greater for whole-plant traits
489 than for organ-level traits. This result is consistent with predictions of plant optimization models
490 (Marks 2007), which show that variation in whole-plant traits is primarily driven by
491 environment, whereas variation in organ-level traits is more tightly constrained by phylogeny.
492 Since plants grow by iterating terminal modules (organs), and since the rate of accumulation of
493 such modules is partly determined by resource supplies from the environment, ITV is expected
494 to be higher in traits involving several modules (i.e. whole-plant traits) than in traits involving a
495 single terminal module. We were only able to include two whole-plant traits, plant height and
496 lateral spread, in our analysis, and studies measuring additional whole-plant traits are needed to
497 provide more general tests of these predictions. Maximum plant height is considered an
498 important plant strategy indicator that is linked to light acquisition and competitive ability
499 (Westoby 1998; Violle *et al.* 2009). The large ITV in plant height in our meta-analysis may

500 reflect genetic variability in maximum height, but also likely includes large environmental and
501 ontogenetic components, which are less clearly related to plant strategy and community
502 assembly.

503 **Variation in relative extent of ITV with community properties**

504 The relative extent of ITV within communities decreased with increasing species richness across
505 all traits and studies. Post-hoc analysis of our dataset showed that for most traits, this relationship
506 was primarily due to an increase in interspecific variance (and thus total community trait
507 variance) with increasing richness, while ITV remained relatively constant. Few previous studies
508 have examined relationships between species richness and community-level trait variation,
509 particularly ITV, and these have produced conflicting results. For example, Lamanna *et al.*
510 (2014), examining tree assemblages in the New World, found a positive relationship between
511 species richness and total community trait space, which is consistent with our results. Hulshof *et*
512 *al.* (2013), working in woody plant communities along elevational and latitudinal gradients,
513 found a negative relationship between species richness and the ratio of intraspecific to
514 interspecific variance in SLA, suggesting that as species richness increased, species' niches
515 became more tightly packed in trait space, relative to the total space occupied by the community.
516 Similarly, our finding that the relative extent of ITV decreases with increasing species richness
517 indicates that individual species tend to occupy smaller proportions of the total community trait
518 space in more species-rich communities, consistent with niche theory (MacArthur & Levins
519 1967; Violle *et al.* 2012). In contrast, Le Bagousse-Pinguet *et al.* (2014), working in
520 experimental grassland communities, found that ITV and the ratio of ITV to total community
521 trait variance were positively related to species richness, suggesting greater trait overlap between
522 species in more species-rich communities.

523 Our findings highlight the importance of accounting for ITV in species-poor
524 communities, where ITV is more likely to account for a large proportion of total community
525 functional diversity (Fajardo & Piper 2011). Whether ITV should be included in studies of
526 species-rich communities will likely depend on the goals of the study, as well as practical
527 considerations. It is important to recognize that while our results show that the relative extent of
528 ITV tends to decrease with increasing species richness, the absolute extent of ITV does not. In
529 addition, previous work cautions against the use of species mean trait values for estimating
530 community trait means and variances, even in species-rich communities (Baraloto *et al.* 2010).

531 The relative extent of ITV varied surprisingly little with climate or growth form,
532 suggesting that the patterns we observed are generally consistent across global biomes and plant
533 community types. There was a weak tendency for the relative extent of ITV to increase with
534 decreasing mean annual temperature and precipitation, consistent with the hypothesis that
535 expression of genetic and environmental trait variation is increased in stressful conditions
536 (Hoffmann & Merilä 1999). This result should be interpreted with caution, however, as
537 temperature, precipitation, and species richness were positively correlated in our dataset, making
538 it difficult to separate the effects of specific factors. Moreover, while we used mean annual
539 temperature and precipitation as predictors to capture global-scale variation in climate, our
540 dataset encompassed multiple, complex environmental gradients, making broad generalization
541 difficult. Future studies examining patterns of trait variation along specific environmental
542 gradients predicted to influence plant community assembly, or experimentally manipulating
543 these factors, are needed to test hypotheses about the relationship between inter- and intraspecific
544 functional variation and abiotic stress.

545 The relative extent of ITV also did not vary consistently between studies measuring
546 woody versus herbaceous species. ITV was hypothesized either to be higher in longer-lived,
547 woody plants as a result of developmental and plastic variation in response to temporal
548 environmental variation (Sultan 1987; Borges 2009), or lower in such plants because longer
549 tissue lifespan may impose higher costs or limits to plasticity (Maire *et al.* 2013). Our analysis
550 did not support either hypothesis, possibly because both processes were acting and neutralized
551 each other. Confounding differences between woody and herbaceous study systems in our
552 dataset may also have made it difficult to detect general patterns. Comparing the relative extent
553 of ITV in woody versus herbaceous species within specific community types may provide a
554 stronger test of these hypotheses. We note that, while there was no difference in the relative
555 extent of ITV between studies measuring only woody or herbaceous species, ITV tended to be
556 lower in studies that included both growth forms. This result is not surprising, given the large
557 interspecific variation in many traits between woody and herbaceous species, and it suggests that
558 the relative importance of ITV decreases as the taxonomic or functional scope of a study
559 increases.

560 **Relationship between ITV and spatial scale**

561 Consistent with our prediction, the contribution of ITV (relative to that of species turnover) to
562 among-community trait variation tended to decrease with increasing spatial extent—i.e., the
563 maximum distance between sites in a study. This pattern is likely to be driven by the increasing
564 breadth of environmental gradients encountered at larger spatial extents. Increasing
565 environmental gradient breadth leads to increased species turnover and thus interspecific trait
566 variation, but at some point probably exhausts the potential genetic and plastic trait variability of
567 individual species (Albert *et al.* 2011; Auger & Shipley 2013). Previous studies have shown that

568 ITV contributes strongly to changes in community mean trait values along relatively narrow,
569 local-scale environmental gradients (e.g. Jung *et al.* 2010; Pérez-Ramos *et al.* 2012), with species
570 turnover becoming more important as the breadth of environmental gradients increases (Siefert *et*
571 *al.* 2014). Our findings support the use of species mean trait values in functional biogeography
572 studies (Violle *et al.* 2014, 2015) examining relationships between environmental factors and
573 community trait distributions at broad spatial scales, although ITV could still be important in
574 systems dominated by relatively few widely-distributed species (Fajardo & Piper 2011).

575 Spatial grain, defined here as the area of individual sampling units or communities, had
576 an inconsistent effect on the relative amount of ITV within communities. In herbaceous
577 communities, there was a negative relationship between grain and the relative extent of ITV,
578 while in woody communities, the relationship was positive. These contrasting results may relate
579 to differences in the scale on which plants of different size perceive environmental variation.
580 Previous studies have shown that a large proportion of the ITV of herbaceous plant species
581 occurs at relatively fine spatial scales (Albert *et al.* 2010; Siefert 2012b), indicating strong
582 intraspecific trait responses to fine-scale environmental heterogeneity and saturation of ITV with
583 increasing scale. In contrast, larger, woody plants acquire resources across wider areas,
584 integrating over such fine-scale variation (Hutchings *et al.* 2003), so that small plots contain little
585 effective environmental variation and thus low ITV of woody species. With increasing grain
586 size, plots contain more effective environmental variation from the plant perspective, leading to
587 increased ITV (relative to interspecific trait variation). Overall, these results lead us to
588 hypothesize that the relative extent of ITV should be maximized at intermediate grain sizes, with
589 the location of the peak depending on the size of the organisms and scale of environmental
590 heterogeneity in a given study.

591

592

593 **Relationship between within- and among-community ITV across traits**

594 In general, we found that the relative extent of ITV within and among communities was
595 positively correlated across traits. In other words, traits that had relatively high ITV within
596 communities also had high ITV among communities, indicating consistency across levels of
597 organization addressed in plant community ecology studies. The few exceptions to this trend
598 may represent traits for which ITV is primarily driven by factors operating at either within- or
599 among-community scales. For example, lateral spread had the highest relative within-community
600 ITV of any trait in our study, but lower-than-average relative ITV among communities. This may
601 suggest strong intraspecific responses to competition and other biotic interactions occurring
602 within communities, but weak responses to among-community environmental gradients. In
603 contrast, leaf thickness displayed moderate relative ITV among communities but extremely low
604 relative ITV within communities. This is consistent with relatively strong intraspecific responses
605 of leaf thickness to broad-scale climatic gradients, but weak responses to fine-scale biotic
606 interactions.

607 **Limitations**

608 We were able to conduct the broadest assessment to date of the relative extent of ITV in plant
609 communities, but several aspects of our dataset may limit the generality of our findings. First, we
610 had little or no data on several types of potentially important functional traits, including root,
611 reproductive, and phenological traits. Second, several globally important community types (e.g.
612 deserts) and geographic regions (e.g. Africa) were missing or underrepresented. Third, studies
613 varied in the method of selecting individuals and leaves for trait measurement. Notably, many

614 studies selected individuals non-randomly (e.g. mature, healthy-looking individuals growing in
615 full sun) according to established trait sampling protocols (Perez-Harguindeguy *et al.* 2013),
616 which likely resulted in underestimation of ITV. Additional work is needed to better understand
617 the influence of sampling effort and design on the quantification of the absolute and relative
618 amount of ITV within and among communities, but the optimum methods will likely depend on
619 the goals and questions of specific studies.

620 We also recognize, as previously mentioned, that our analysis was unable to distinguish
621 between ITV arising from phenotypic plasticity and heritable genetic differences. We are not
622 aware of any study that has quantified the contributions of these sources to overall trait variation
623 at the community level. Doing so would require a tremendous amount of effort and may only be
624 feasible for communities dominated by one or few species (Grassein *et al.* 2010). We speculate
625 that plastic trait variation is likely to be larger than intraspecific genetic variation for most traits
626 and communities, given the low heritability typically observed for plant functional traits in field
627 conditions (Geber & Griffen 2003), although exceptions certainly exist (see e.g. Donovan *et al.*
628 2010). The consequences of different sources of ITV for community and ecosystem-level
629 processes are little understood. The relative extent of plastic vs. genetic trait variation may have
630 important consequences for community responses to environmental change (Lavergne *et al.*
631 2010), since plastic trait responses are expected to be rapid but limited in scope, whereas
632 adaptive evolutionary responses may be broader in scope but proceed more slowly (Gienapp *et*
633 *al.* 2008). While quantification of the relative amount of ITV in communities as done here is a
634 first necessary step for community ecology, disentangling the extent and consequences of plastic
635 and genetic trait variation at the community and ecosystem levels certainly remains a major
636 challenge for future researchers.

637 **Recommendations for including ITV in trait-based studies**

638 The results of our meta-analysis suggest some general guidelines for when ITV is likely to be
639 substantial and therefore important to consider in plant community and ecosystem studies (Albert
640 *et al.* 2011). First, ITV consistently accounts for a significant proportion of the total within- and
641 among-community trait variation in whole-plant traits and leaf economic traits including leaf
642 chemical traits, SLA, and LDMC; we therefore recommend that researchers consider ITV in
643 studies measuring these traits. As many of these traits have been strongly implicated in
644 community assembly and ecosystem functioning, integrating ITV in future studies should lead to
645 improved understanding of these processes. Second, the decrease in the relative importance of
646 ITV with increasing spatial extent suggests that it is most relevant to consider ITV in studies
647 conducted on local scales and short environmental gradients. Conversely, functional
648 biogeography studies may provide robust broad-scale interpretations without accounting for ITV
649 (Violle *et al.* 2014). Third, the increase in the relative extent of ITV with decreasing species
650 richness emphasizes the need to account for ITV in studies of species-poor communities, in
651 which individual species may fill a large proportion of the total community trait space. Having
652 made these recommendations, we stress that the relative magnitude of ITV is not the only factor
653 determining whether and to what degree ITV will influence ecological processes. Even when
654 ITV is relatively low, it can have large effects at the community level (e.g. Jung *et al.* 2010).
655 Nevertheless, knowing the relative extent of ITV for a given trait and study system is an
656 important step for designing trait-based plant ecology studies, and this information may also
657 provide input for simulations to test the importance of ITV for specific ecological questions
658 (Albert *et al.* 2011).

659 In conclusion, this study provides the first global assessment of the relative extent of ITV
660 in plant communities. Our results confirm that ITV often accounts for a significant proportion of
661 the total functional diversity within and among communities and demonstrate that the relative
662 extent of ITV varies predictably among traits and with species richness and spatial scale. Beyond
663 quantifying the extent of ITV, the next step for trait-based plant community ecology is to more
664 systematically test how this variation influences community and ecosystem processes and
665 dynamics (Enquist *et al.* 2015).

666

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694
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964 **Supporting information**

965 Additional Supporting Information may be downloaded via the online version of this article at
966 Wiley Online Library

967 **Figure Legends**

968

969 **Figure 1.** Locations of studies included in the within-community analysis only (white circles, n
970 = 7), among-community analysis only (grey circles, $n = 11$), and both analyses (black circles, $n =$
971 26).

972

973 **Figure 2.** Boxplots showing relative magnitude of intraspecific trait variation (a) within
974 communities ($wITV$) and (b) among communities ($aITV$) for all traits with at least two
975 observations in our dataset. The number of observations (studies) per trait is indicated above the
976 box. Solid horizontal line indicates overall mean value across all traits. Dashed horizontal line
977 indicates equal magnitude of intraspecific and interspecific trait variation ($wITV = 0.5$; $aITV =$
978 0). Values above dashed line indicate larger intraspecific than interspecific variation and vice
979 versa.

980

981 **Figure 3.** Model averaged coefficient estimates and 95% confidence intervals for fixed effects
982 included in confidence set of models explaining relative extent of intraspecific trait variation
983 within communities ($wITV$). Results are shown for analyses of all traits, leaf traits, specific leaf
984 area (SLA), and plant height. Continuous predictors were standardized (mean = 0, sd = 1) to
985 make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights
986 of models in which a given predictor appears. Results are shown only for predictors with RI >
987 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form
988 (herbaceous, woody, or herbaceous and woody); TC: leaf trait category (chemical or
989 morphological).

990 **Figure 4.** Model averaged coefficient estimates and 95% confidence intervals for fixed effects
991 included in confidence set of models explaining relative extent of intraspecific trait variation

992 among communities (*aITV*). Results are shown for analyses of all traits, leaf traits, specific leaf
993 area (SLA), and plant height. Continuous predictors were standardized (mean = 0, sd = 1) to
994 make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights
995 of models in which a given predictor appears. Results are shown only for predictors with RI >
996 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form
997 (herbaceous, woody, or herbaceous and woody); TC: leaf trait category (chemical or
998 morphological).

999

1000 **Figure 5.** Relationship between relative magnitude of intraspecific trait variation within (*wITV*)
1001 and among (*aITV*) across traits in our dataset. Each point represents the mean *wITV* and *aITV* for
1002 a given trait across the studies in which it was measured. Error bars represent standard error.
1003 Only cases in which a given trait was measured within- and among-communities in the same
1004 study are included in this analysis. Solid line is the ranged major axis regression line.
1005 Significance of the relationship was assessed using a permutation test. BT: bark thickness; H:
1006 plant height; LA: leaf area; LC: leaf C; LCN: leaf C:N; LDMC: leaf dry matter content; LK: leaf
1007 K; LL: leaf length; LP: leaf P; LS: lateral spread; LT: leaf thickness; LW: leaf width; SLA:
1008 specific leaf area; WD: wood density.



Figure 1

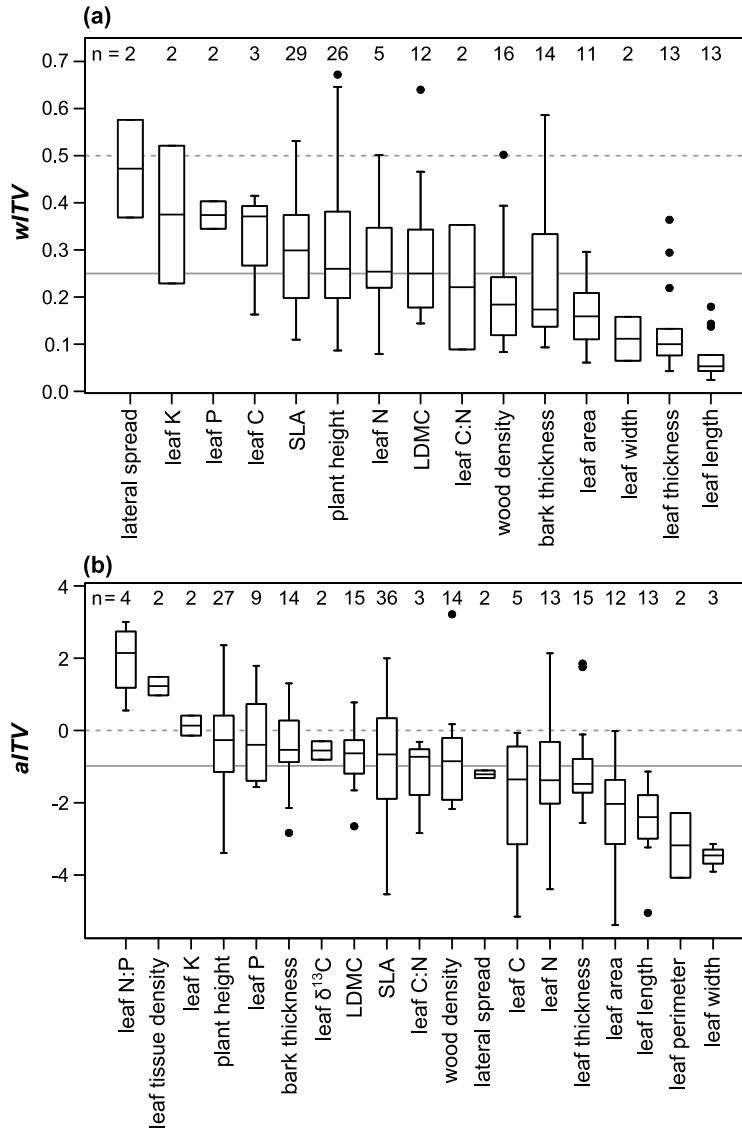


Figure 2

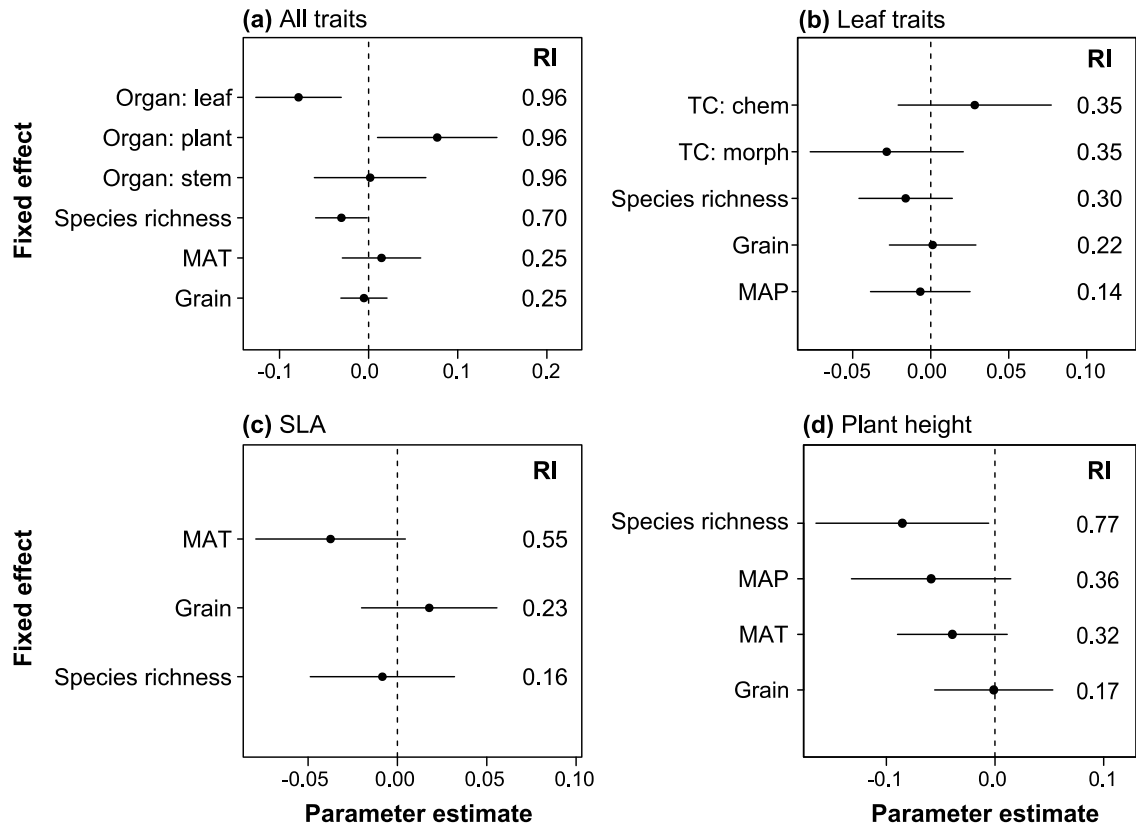


Figure 3

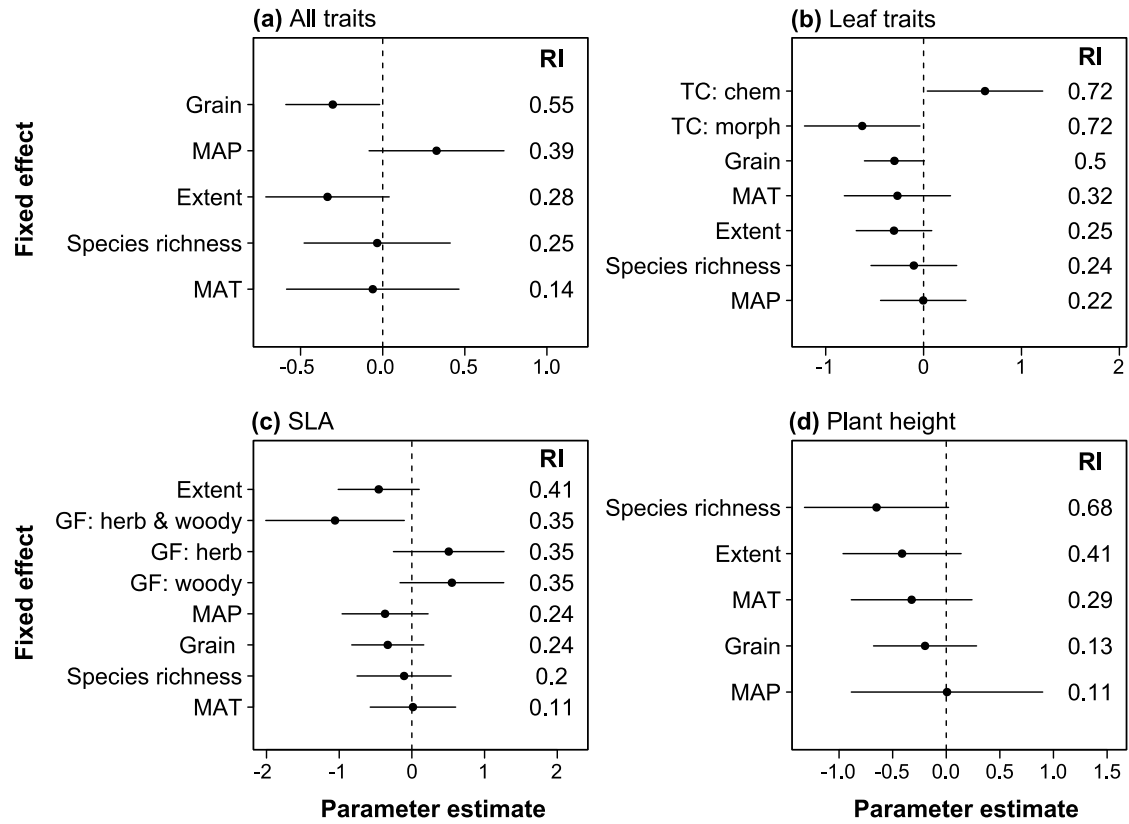


Figure 4

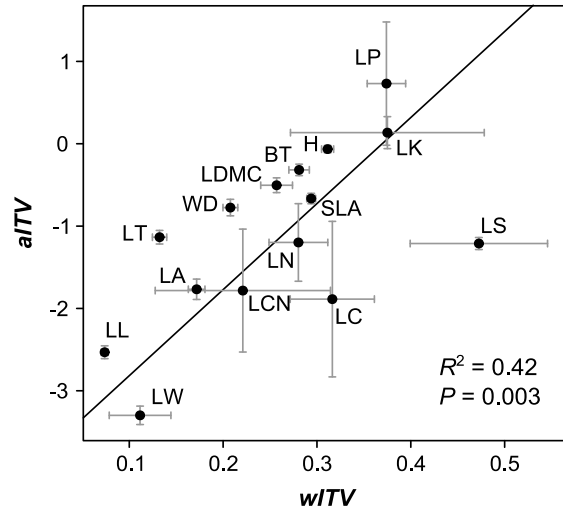


Figure 5

1009 **Box 1: Trait variance partitioning**

1010 **Within-community**

1011 For each community i and each functional trait within a given study, we calculated the
1012 abundance-weighted interspecific and intraspecific trait variance, which sum to the total within-
1013 community trait variance (de Bello *et al.* 2011). We calculated the relative contribution of ITV to
1014 within-community trait variance ($wITV$) of each community as the ratio of the intraspecific trait
1015 variance over the total within-community trait variance:

1016
$$wITV_i = 100 \times \frac{\sum_j p_{ij} \times \frac{1}{N_{ij}} \sum_k (t_{ijk} - t_{ij})^2}{\sum_j p_{ij} \times \left(t_{ij} - \sum_j p_{ij} t_{ij} \right)^2 + \sum_j p_{ij} \times \frac{1}{N_{ij}} \sum_k (t_{ijk} - t_{ij})^2},$$

1017 where p_{ij} is the relative abundance of species j in community i , N_{ij} and t_{ij} are the number of
1018 sampled individuals and the mean trait value, respectively, of species j in community i , and t_{ijk} is
1019 the trait value of individual k in community i belonging to species j . The relative amount of
1020 intraspecific trait variation within communities in each study was then calculated by averaging
1021 $wITV_i$ over the communities.

1022 **Among-community**

1023 The relative contribution of intraspecific variability to among-community trait variance ($aITV$)
1024 was calculated in several steps. For each study, the weighted mean of each trait in each
1025 community i was computed using the community-level species mean trait value (CWM_i) and the
1026 study-level species mean trait value ($CWM_{fixed,i}$). The intraspecific variability effect was
1027 measured as $CWM_{intra,i} = CWM_i - CMW_{fixed,i}$. The sum of squares associated with CWM_i ,
1028 $CWM_{intra,i}$ and $CMW_{fixed,i}$ across communities (SS_{tot} , SS_{intra} and SS_{fixed}) was calculated
1029 using an intercept-only linear model. SS_{tot} represents the total among-community trait variation,

1030 SS_{intra} represents variation due exclusively to intraspecific variability, and SS_{fixed} represents
1031 variation due exclusively to changes in species occurrence and relative abundance (i.e., species
1032 turnover). We then calculated $aITV$ as:

1033
$$aITV = \ln\left(\frac{SS_{intra}}{SS_{fixed}}\right).$$

1034 This provides a symmetric measure of the relative contributions of ITV and species turnover to
1035 the total among-community trait variation, with positive values indicating a larger effect of ITV
1036 and negative values indicating a larger effect of species turnover. We chose to measure ITV
1037 relative to species turnover rather than relative to the total among-community variation because
1038 in some cases, the ITV and species turnover effects oppose each other, potentially resulting in
1039 the total among-community variation approaching zero. The covariation between the effects of
1040 intraspecific variability and species turnover was calculated as:

1041
$$cov = 100 \times \frac{SS_{tot} - SS_{intra} - SS_{fixed}}{SS_{tot}}.$$

1042