REVIEW AND SYNTHESIS

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

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Abstract

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

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INTRODUCTION

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

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

Accounting for ITV has also been shown to improve predictions of outcomes of species interactions (Kraft et al. 2014), community responses to spatial and temporal environmental gradients (Lepš et al. 2011; Kichenin et al. 2013; Jung et al. 2014) and ecosystem processes such as productivity and nutrient cycling (Breza et al. 2012).

Despite the predictive power that may come from considering ITV in plant community studies, a practical limitation is the difficulty of measuring trait values on a large number of individuals per species, particularly in species-rich communities (Baraloto et al. 2010). When and how ITV should be incorporated in trait-based ecology studies has thus emerged as an urgent question (Albert et al. 2011). Although many factors go into answering this question, a basic consideration is the relative amount of intraspecific compared to interspecific trait variation in the communities being studied. If ITV is large compared to interspecific variation, it is likely to have important ecological consequences and should not be ignored out of hand. Recently, empirical studies have quantified the relative amount of ITV compared to interspecific variation for various plant functional traits and communities (e.g. Jung et al. 2010; Messier et al. 2010; Lepš et al. 2011; Auger & Shipley 2013). This work has shown that the extent of ITV within and among plant communities is often substantial – sometimes similar to or greater than interspecific variation – but highly context-dependent, varying strongly among traits and communities. An improved understanding of the context-dependence of ITV in plant communities is necessary for integrating ITV in trait-based ecology and for understanding its role in ecological processes acting at the community scale and beyond (Albert et al. 2011). To address this need, we conducted a global-scale meta-analysis to determine the relative extent of ITV compared to interspecific variation in plant communities and to identify general trends in how ITV varies among traits and study systems.

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

The second aim of this meta-analysis was to examine how ITV varies among communities differing in terms of the dominant growth form, species richness and climate. First, we asked whether the relative extent of ITV differs between communities consisting of woody vs. herbaceous plants. We may expect long-lived (i.e. woody) species to have high ontogenetic variation and express strong phenotypic plasticity to face environmental hazards over their lifetimes, leading to high ITV (Sultan 1987; Borges 2009). Conversely, species with long tissue lifespan may have higher costs or limits to plasticity, and we might thus expect them to express less ITV than fast-growing, ruderal (i.e. herbaceous) species (Maire et al. 2013). Second, we tested whether the relative extent of ITV varies with community species richness. Previous work suggests that ITV should be most important in species-poor communities (e.g. MacArthur 1972; Antonovics 1992; Whitham et al. 2006), and niche theory predicts that the relative extent of ITV should decrease with increasing species richness (Violle et al. 2012). However, few studies have empirically examined this relationship in plant communities, and these have produced conflicting results (Hulshof et al. 2013; Le Bagousse-Pinguet et al. 2014). Finally, we tested whether the relative extent of ITV varies with climate (temperature and precipitation) on a global scale. Previous research suggests that phenotypic plasticity may be constrained in stressful environments (Valladares et al. 2007). If this is true, we expect the relative extent of ITV to decrease with increasing climatic stress (i.e. decreasing temperature and precipitation). Alternatively, several hypotheses predict that unfavourable conditions increase the expression of genetic variability in traits, leading to the opposite pattern (Hoffmann & Merilä 1999). Community-level ITV has rarely been measured across broad climatic gradients (but see Hulshof et al. 2013), so these hypotheses remain largely untested.

Third, we examined how the relative extent of ITV depends on the spatial scale (grain and extent) of observation across studies. Interspecific and intraspecific trait variation are both expected to increase with spatial extent as broader environmental gradients are encountered, leading to turnover of species and genotypes as well as plastic trait responses (Albert et al. 2011; Auger & Shipley 2013). However, ITV must saturate at some scale once the entire potential genetic and environmental variation in species is reached. Therefore, the relative contribution of ITV to trait variation among communities is expected to decrease with increasing spatial extent from local to regional and global scales (Albert et al. 2011) or with increasing distance along environmental gradients (Auger & Shipley 2013). At the community level, the relationship between spatial grain (plot or sampling unit size) and the relative extent of ITV within communities is more difficult to predict. For example, this relationship may depend on the scale of environmental heterogeneity relative to the size of individual plants, and thus the potential for individuals to express genetic and plastic trait differences across different environments.

In assessing the extent and role of ITV in plant communities, it is important to recognise that ITV arises from multiple mechanisms, including heritable genetic variation, phenotypic plasticity and ontogenetic variation, and these mechanisms will differentially affect whole-plant vs. organ-specific traits. While specific sources of variation may be of interest for investigating particular ecological or evolutionary questions, all sources contribute to the trait variation observed in natural communities and potentially influence community assembly and ecosystem processes. Understanding the extent and consequences of ITV at the community level, even if its underlying mechanisms remain unknown, is therefore an important step for trait-based ecology (Violle et al. 2012). Moreover, partitioning the sources of ITV – for example using classical methods from quantitative genetics (Vellend et al. 2014) – may not be feasible at the community level except in systems dominated by one or few species. In our meta-analysis, we therefore considered all potential sources of ITV and did not attempt to distinguish them. ITV may also be measured at different levels of organisation, including within-individual (e.g. variation among leaves within a plant), among-individual and among-population or site. Here, we focused on ITV at two levels of organisation. Specifically, we aimed to quantify (1) the relative contribution of among-individual ITV to the total trait variation within plant communities (within-community analysis), and (2) the relative contribution of among-population ITV to the total variation in mean trait values among plant communities (among-community analysis).

Overall, we quantified the relative extent of ITV within and among plant communities using a data set consisting of

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

METHODS

A global data set to assess ITV in plant communities

To conduct our meta-analysis, we assembled data from published and unpublished studies by the authors that measured intraspecific trait variation within and among terrestrial, vascular plant communities. Criteria for including a study in the within-community analysis were (1) species composition data including relative abundance for at least one community (defined here as a single plot or sampling unit); and (2) trait measurements on at least five individuals (or all individuals if total was fewer than five) per species per community. Criteria for including a study in the among-community analysis were (1) species composition data including relative abundance for three or more communities; and (2) trait measurements on at least one individual per species per sampled community. For both within- and among-community analyses, we only included studies that measured traits of species that together made up at least 80% of total community abundance (variously measured as cover, density, biomass or frequency)

as recommended in previous studies (Pakeman & Quested 2007). Following typical methods in plant community ecology, many studies focused on a single vegetation layer (e.g. trees or herbs), even if multiple layers were present in the study area. We included these studies in the analysis, acknowledging that they may include only a subset of the vascular vegetation in a given area.

Following the trait definition of Violle *et al.* (2007), we included in our data set morphological and physiological features of plants measurable at the individual level. Furthermore, we sought to include traits known to be related to some aspect of plant functioning, i.e. functional traits. As the goal of this study was to give a general picture of the relative extent of ITV in plant communities, and given the diversity of ecological questions that functional traits can be used to address, we preferred to be inclusive with our selection of traits. Characters such as plant height and canopy dimensions measured at the individual level, for instance, may be viewed as measures of performance rather than indicators of plant strategy in the context of community assembly studies. However, individual variation in such characters still contributes to the standing phenotypic variation within and among communities, with potential consequences for coexistence, ecosystem functioning and other processes. We conducted analyses with plant height either included or excluded; as both approaches produced similar results, we present only results with height included for completeness.

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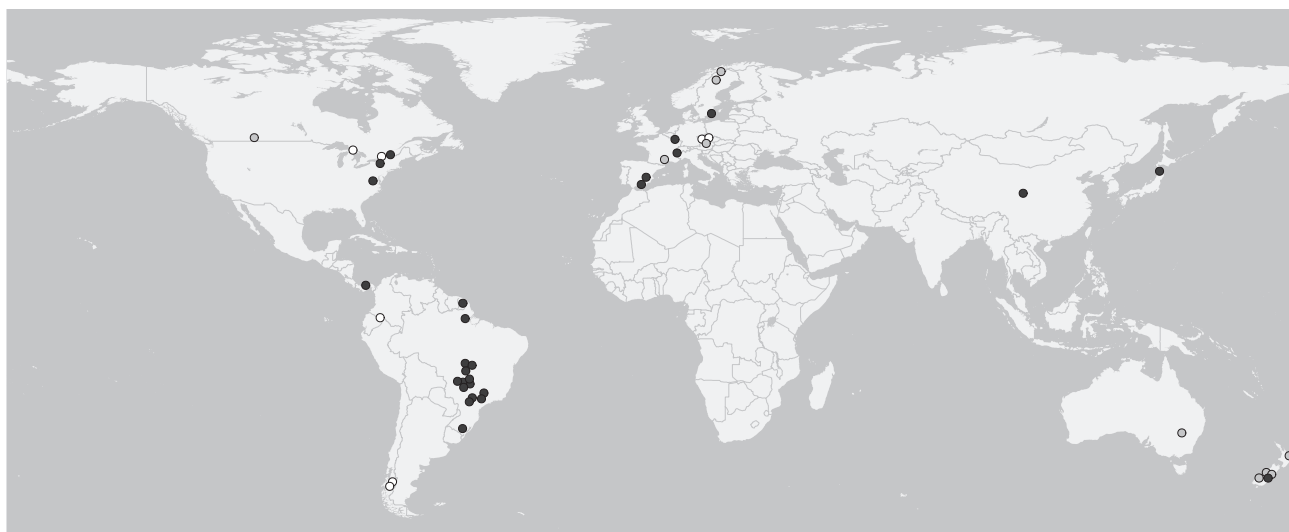

Figure 1 Locations of studies included in the within-community analysis only (white circles, *n* = 7), among-community analysis only (grey circles, *n* = 11) and both analyses (black circles, *n* = 26).

For each study, we collected metadata including geographic coordinates, spatial grain (area of single community, i.e. sampling unit, in m²), spatial extent (maximum geographic distance between communities in km), ecosystem type (tropical or temperate), growth form (woody, herbaceous or both) and alpha and gamma species richness (mean number of species within communities and total number of species across all communities in a study respectively). For each study, we extracted mean annual temperature (MAT) and mean annual precipitation (MAP) values from WorldClim (http://www.worldclim.org). We also obtained information on sampling design and effort, including the number of communities, percent of total species richness and total community abundance sampled and number of individuals and populations sampled per species. Studies varied in their methods of selecting individuals and leaves within individuals for trait measure-ment. Most studies selected individuals randomly, only avoiding damaged or unhealthy individuals, but some studies only included individuals from particular life stages or size classes (e.g. adult trees or saplings), thus reducing ITV association with ontogeny. For leaf traits, some studies selected leaves randomly within each individual, but most studies – following standard trait protocols (Pérez-Harguindeguy et al. 2013) – selected only young, fully expanded, outer canopy leaves, thus reducing ITV associated with light environment and leaf age. We included studies with both random and non-random selection of individuals and leaves in our meta-analysis, acknowledging that this may contribute to unexplained variation in ITV among studies and overall underestimation of ITV.

Our final data set consisted of 171 study-trait combinations (cases), representing 33 studies and 30 unique traits, with data

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Box 1 Trait variance partitioning

WITHIN-COMMUNITY

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

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

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

AMONG-COMMUNITY

The relative contribution of intraspecific variability to among-community trait variance (aITV) was calculated in several steps. For each study, the weighted mean of each trait in each community i was computed using the community-level species mean trait value (CWM$_i$) and the study-level species mean trait value (CWMfixed$_i$). The intraspecific variability effect was measured as CWMintra$_i$ = CWM$_i$ – CMWfixed$_i$. The sum of squares associated with CWM$_i$, CWMintra$_i$ and CMWfixed$_i$ across communities (SS$_{tot}$, SS$_{intra}$ and SS$_{fixed}$) was calculated using an intercept-only linear model. SS$_{tot}$ represents the total among-community trait variation, SS$_{intra}$ represents variation due exclusively to intraspecific variability and SS$_{fixed}$ represents variation due exclusively to changes in species occurrence and relative abundance (i.e. species turnover). We then calculated aITV as:

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

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

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

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

Data analysis

We used the framework developed by Lepš *et al.* (2011) and de Bello *et al.* (2011) to evaluate the relative contribution of intraspecific trait variation to total within-community (*wITV*) and among-community (*aITV*) trait variance for each trait and study (see Box 1 for details). Our *wITV* metric represents the proportion of total within-community trait variance attributable to ITV. The *aITV* metric represents the relative contribution of intraspecific trait variation vs. species turnover to the total among-community variance, with positive values indicating a greater contribution of ITV and negative values indicating a greater contribution of species turnover. Differences in *wITV* and *aITV* among traits and studies could be driven by differences in the absolute extent of interspecific or intraspecific variation, or a combination of the two. Disentangling these sources is an interesting research question (see, e.g. Hulshof *et al.* 2013; Le Bagousse-Pinguet *et al.* 2014), but here we focused on the relative rather than absolute extent of ITV, because it allows comparison of multiple traits measured in different units or on different scales, for which comparison of raw variance values would be difficult or impossible.

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

For analyses of all traits and leaf traits, we developed a set of linear mixed models that included trait and study as random effects and all possible combinations of the following fixed effects: mean annual temperature (MAT), mean annual precipitation (MAP), alpha species richness (*wITV* analysis only), gamma species richness (*aITV* analysis only), spatial grain, spatial extent (*aITV* analysis only), growth form, organ (whole-plant, leaf, stem or root; only for analysis of all traits) and leaf trait category (morphological or chemical; leaf trait analyses only). For analyses of single traits (SLA and plant height), we used simple linear regressions with species rich-
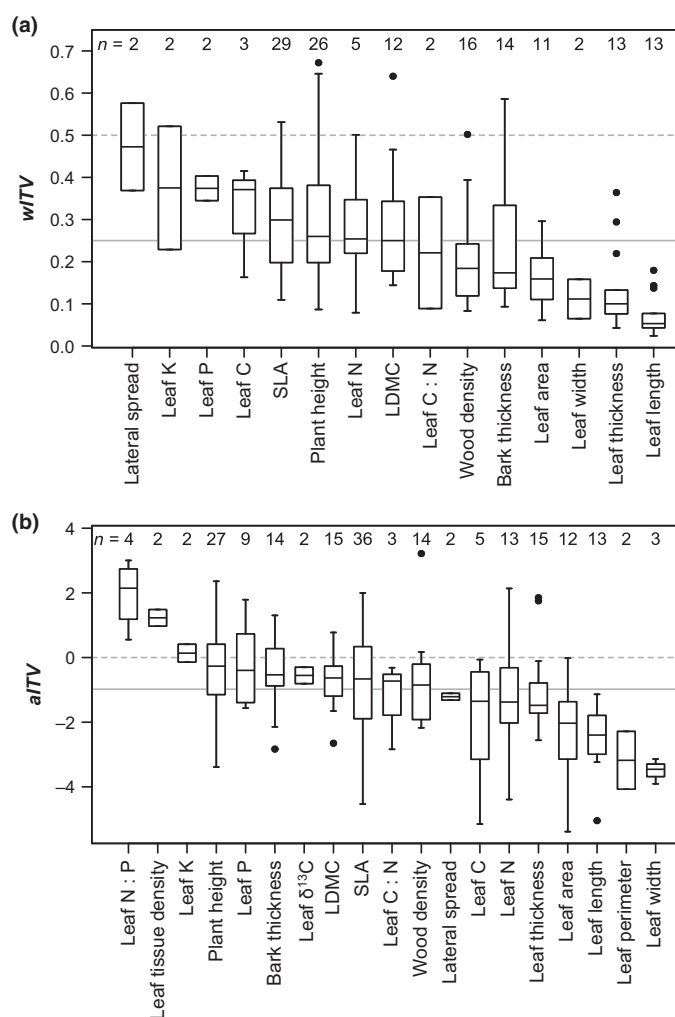

Figure 2 Boxplots showing relative magnitude of intraspecific trait variation (a) within communities (*wITV*) and (b) among communities (*aITV*) for all traits with at least two observations in our data set. The number of observations (studies) per trait is indicated above the box (total number of studies: 33 for *wITV*; 37 for *aITV*). Solid horizontal line indicates overall mean value across all traits. Dashed horizontal line indicates equal magnitude of intraspecific and interspecific trait variation (*wITV* = 0.5; *aITV* = 0). Values above dashed line indicate larger intraspecific than interspecific variation and vice versa.

ness, grain, extent and growth form as fixed effects. Species richness and spatial grain and extent were log-transformed to reduce skewness. We excluded models that contained highly correlated ($|r| > 0.5$) predictor variables. The combinations of variables excluded varied among analyses, but in most cases temperature, precipitation and species richness were positively correlated, and thus no more than one of these predictors was included in each model. In addition, spatial extent and grain were positively correlated, so no more than one of them was included in each model when analysing *aITV*.

The models were ranked according to the corrected Akaike information criterion (AICc) and their relative support was evaluated with the AICc weight (Burnham & Anderson 2002). We retained a confidence set of models with cumulated AICc weight of 0.95 (Johnson & Omland 2004). The relative importance of each fixed effect in the confidence set was calculated
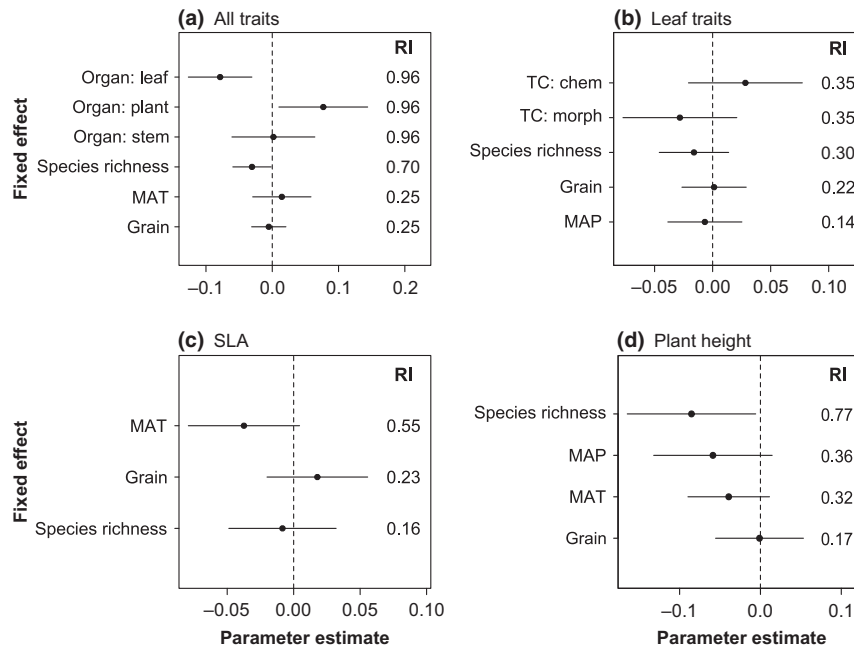
Figure 3 Model averaged coefficient estimates and 95% confidence intervals for fixed effects included in confidence set of models explaining relative extent of intraspecific trait variation within communities (*wITV*). Results are shown for analyses of all traits, leaf traits, specific leaf area (SLA) and plant height. Continuous predictors were standardised (mean = 0, SD = 1) to make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form (herbaceous, woody, or herbaceous and woody); TC: leaf trait category (chemical or morphological).

as the sum of the Akaike weights over all of the models in which it appeared. We further calculated model averaged estimates of the fixed effects over the confidence set of models (Burnham & Anderson 2002).

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

RESULTS

Relative extent of ITV within communities

Across all studies and traits, ITV accounted for on average 25% of the total within-community trait variance, with interspecific variance accounting for the remainder (intercept of random effects only model for *wITV* = 0.25; 95% confidence interval = 0.19–0.31). There was considerable variation in the relative extent of ITV among traits and studies, with values ranging from 2 to 67% (Fig. 2a; Table S1). Of the most commonly measured traits, ITV tended to be relatively high for SLA, plant height, leaf N and LDMC (median *wITV* = 25–30%; Fig. 2a), and lower for wood density and leaf area, leaf thickness and leaf length (median *wITV* < 20%;

Fig. 2a). There was no effect of any variable relating to sample size or sampling effort on *wITV*.

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

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

Relative extent of ITV among communities

Across all studies and traits, ITV accounted for 32% of the total trait variation among communities on average, whereas
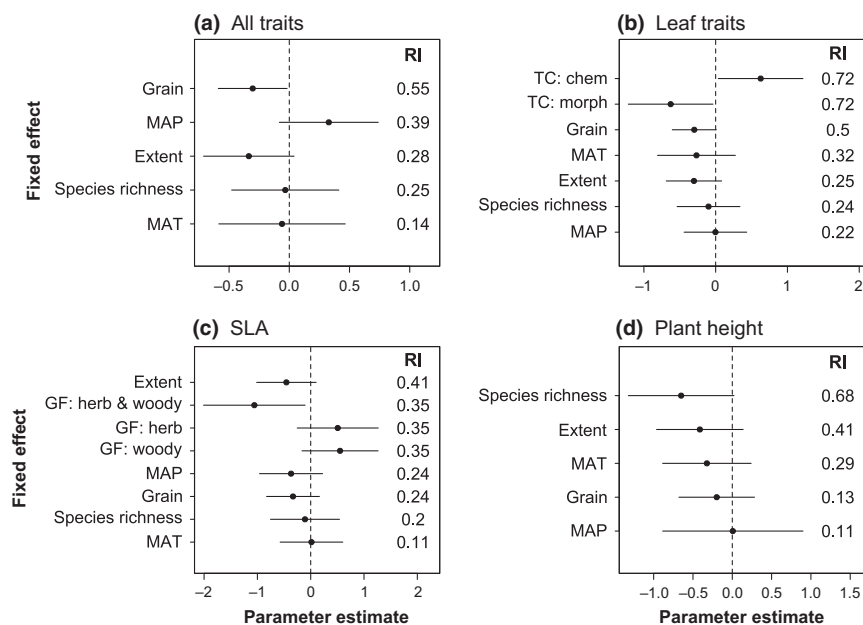
Figure 4 Model averaged coefficient estimates and 95% confidence intervals for fixed effects included in confidence set of models explaining relative extent of intraspecific trait variation among communities (*aITV*). Results are shown for analyses of all traits, leaf traits, specific leaf area (SLA) and plant height. Continuous predictors were standardised (mean = 0, SD = 1) to make magnitude of coefficients comparable. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with RI > 0.10. MAT: mean annual temperature; MAP: mean annual precipitation; GF: growth form (herbaceous, woody or herbaceous and woody); TC: leaf trait category (chemical or morphological).

species turnover accounted for 64% (intercept of random effects model for *aITV* = −0.94; 95% confidence interval = −1.64 to −0.24). For individual traits, there were cases in which the average contribution of ITV was greater than (*aITV* > 0, e.g. leaf N:P; Fig. 2b; Table S1), similar to (*aITV* = 0; e.g. SLA, LDMC, leaf C:N), or much less than that of species turnover (*aITV* < 0; e.g. leaf size traits). Of the commonly measured traits, the relative contribution of ITV was greatest for plant height, bark thickness and LDMC and least for leaf area, length and thickness (Fig. 2b; Table S1). The covariation between ITV and species turnover was highly variable, but was most often weakly positive (median = 7.7%), indicating that traits tended to vary in the same direction due to ITV and species turnover. Overall, *aITV* was not influenced by any variable related to sample size or sampling effort.

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

Although growth form (woody vs. herbaceous) was not an important factor in explaining *aITV* when looking at all community types together (relative importance of growth form = 0.06), we found differences in the effects of predictors when analysing woody and herbaceous communities separately (see Appendix S3). In particular, there was a strong
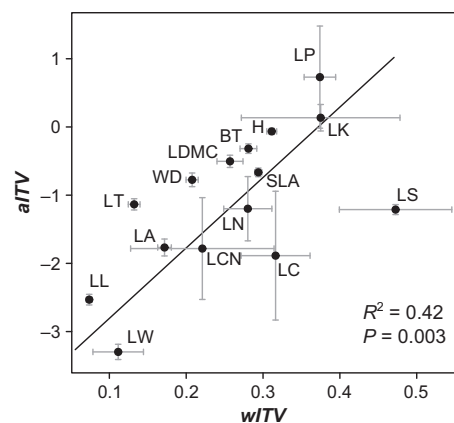

Figure 5 Relationship between relative magnitude of intraspecific trait variation within (*wITV*) and among (*aITV*) communities across traits in our data set. Each point represents the mean *wITV* and *aITV* for a given trait across the studies in which it was measured. Error bars represent standard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

negative effect of precipitation and positive effect of gamma species richness on *aITV* for herbaceous but not for woody communities (Appendix S4). Similarly, there was no overall difference in *aITV* between temperate and tropical communities (relative importance of biome = 0), but the effects of spatial extent, growth form and leaf trait category were

much stronger for tropical communities (see Appendix S4). In addition, there was a negative effect of temperature on *aITV* in tropical but not temperate communities (Appendix S4).

Relationship between within- and among-community ITV across traits

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

DISCUSSION

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

Variation in relative extent of ITV among functional traits

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

We also found strong differences in the relative extent of ITV for leaf traits related to different aspects of plant function. ITV within communities was relatively high (25% or

more of total community trait variation) for both chemical and morphological traits linked to the leaf economics spectrum (e.g. leaf N and P, SLA, LDMC). This is consistent with previous studies finding extensive ITV in leaf economic traits arising from plastic responses to light, nutrients and other environmental factors (Meziane & Shipley 1999; Rozendaal *et al.* 2006), as well as genetic variability and ontogenetic variation (Scheepens *et al.* 2010; Vasseur *et al.* 2012; Mason *et al.* 2013). Our finding that leaf economic traits consistently display high ITV within and among communities globally has important implications for trait-based ecology. Leaf economic traits represent a primary axis of functional variation in plants worldwide and are linked to a proposed universal 'fast-slow' plant economics spectrum that may help explain individual plant strategies, community assembly and ecosystem functioning (Reich 2014). The high intraspecific variability in leaf economic traits suggests that ITV may play an important role in community- and ecosystem-level processes and deserves increased consideration in future studies. In contrast to leaf economic traits, ITV was low for traits related to leaf size (area, length, width, thickness), which are typically considered independent of the leaf economics spectrum but have been linked with adaptation to broad climatic gradients (Craine *et al.* 2012). Previous studies have found that leaf size traits have limited plasticity and low ITV relative to the large interspecific variation among co-occurring species (Rozendaal *et al.* 2006). Our findings suggest that species mean trait values are likely to capture the majority of leaf size variation within and among most plant communities worldwide.

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

Variation in relative extent of ITV with community properties

The relative extent of ITV within communities decreased with increasing species richness across all traits and studies. *Post hoc* analysis of our data set showed that for most traits, this relationship was primarily due to an increase in interspecific

variance (and thus total community trait variance) with increasing richness, while ITV remained relatively constant. Few previous studies have examined relationships between species richness and community-level trait variation, particularly ITV, and these have produced conflicting results. For example Lamanna *et al.* (2014), examining tree assemblages in the New World, found a positive relationship between species richness and total community trait space, which is consistent with our results. Hulshof *et al.* (2013), working in woody plant communities along elevational and latitudinal gradients, found a negative relationship between species richness and the ratio of intraspecific to interspecific variance in SLA, suggesting that as species richness increased, species' niches became more tightly packed in trait space, relative to the total space occupied by the community. Similarly, our finding that the relative extent of ITV decreases with increasing species richness indicates that individual species tend to occupy smaller proportions of the total community trait space in more species-rich communities, consistent with niche theory (MacArthur & Levins 1967; Violle *et al.* 2012). In contrast, Le Bagousse-Pinguet *et al.* (2014), working in experimental grassland communities, found that ITV and the ratio of ITV to total community trait variance were positively related to species richness, suggesting greater trait overlap between species in more species-rich communities.

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

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

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

Relationship between ITV and spatial scale

Consistent with our prediction, the contribution of ITV (relative to that of species turnover) to among-community trait variation tended to decrease with increasing spatial extent – i.e. the maximum distance between sites in a study. This pattern is likely to be driven by the increasing breadth of environmental gradients encountered at larger spatial extents. Increasing environmental gradient breadth leads to increased species turnover and thus interspecific trait variation, but at some point probably exhausts the potential genetic and plastic trait variability in individual species (Albert *et al.* 2011; Auger & Shipley 2013). Previous studies have shown that ITV contributes strongly to changes in community mean trait values along relatively narrow, local-scale environmental gradients (e.g. Jung *et al.* 2010; Pérez-Ramos *et al.* 2012), with species turnover becoming more important as the breadth of environmental gradients increases (Siefert *et al.* 2014). Our findings support the use of species mean trait values in functional biogeography studies (Violle *et al.* 2014, 2015) examining relationships between environmental factors and community trait distributions at broad spatial scales, although ITV could still be important in systems dominated by relatively few widely distributed species (Fajardo & Piper 2011).

Spatial grain, defined here as the area of individual sampling units or communities, had an inconsistent effect on the relative amount of ITV within communities. In herbaceous communities, there was a negative relationship between grain and the relative extent of ITV, while in woody communities, the relationship was positive. These contrasting results may relate to differences in the scale on which plants of different size perceive environmental variation. Previous studies have shown that a large proportion of the ITV of herbaceous plant species occurs at relatively fine spatial scales (Albert *et al.* 2010; Siefert 2012b), indicating strong intraspecific trait responses to fine-scale environmental heterogeneity and

saturation of ITV with increasing scale. In contrast, larger, woody plants acquire resources across wider areas, integrating over such fine-scale variation (Hutchings *et al.* 2003), so that small plots contain little effective environmental variation and thus low ITV of woody species. With increasing grain size, plots contain more effective environmental variation from the plant perspective, leading to increased ITV (relative to interspecific trait variation). Overall, these results lead us to hypothesise that the relative extent of ITV should be maximised at intermediate grain sizes, with the location of the peak depending on the size of the organisms and scale of environmental heterogeneity in a given study.

Relationship between within- and among-community ITV across traits

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

Limitations

We were able to conduct the broadest assessment to date of the relative extent of ITV in plant communities, but several aspects of our data set may limit the generality of our findings. First, we had little or no data on several types of potentially important functional traits, including root, reproductive and phenological traits. Second, several globally important community types (e.g. deserts) and geographic regions (e.g. Africa) were missing or underrepresented. Third, studies varied in the method of selecting individuals and leaves for trait measurement. Notably, many studies selected individuals non-randomly (e.g. mature, healthy-looking individuals growing in full sun) according to established trait sampling protocols (Pérez-Harguindeguy *et al.* 2013), which likely resulted in underestimation of ITV. Additional work is needed to better understand the influence of sampling effort and design on the quantification of the absolute and relative amount of ITV within and among communities, but the optimum methods will likely depend on the goals and questions of specific studies.

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

Recommendations for including ITV in trait-based studies

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

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

AUTHORSHIP

AS conceived of and designed the study. All authors collected and analysed data. AS and LC conducted the meta-analysis. AS, CV, LC, CA and AT wrote the first draft of the manuscript, and all authors contributed to revisions.

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