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RESEARCH ARTICLE

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Quantifying the role of intra-specific trait variation for allocation and organ-level traits in tropical seedling communities

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Abstract

Questions: Community structure is the outcome of individual-level interactions. Recent work has shown that disaggregating trait information from the species to the individual level can elucidate ecological processes. We aim to integrate trait dispersion analyses across different aggregation levels including a broad range of traits that allow assessment of patterns of variation among co-occurring and non-co-occurring individuals. We ask the following questions: (1) what is the role of intra- and inter-specific dissimilarity within neighbourhoods vs. across neighbourhoods in promoting trait dispersion; (2) how is trait variation partitioned across all individuals in each study system; and (3) are the results consistent across traits and forests?

Location: Puerto Rico and China.

Methods: We measured allocation and organ-level (e.g. specific leaf area) traits on every individual in two seedling censuses in two tropical rain forests. Then, we partitioned trait variation within and across species, considering its impact on patterns of trait dispersion, and quantifying how these outcomes vary depending on whether allocation-related or organ-level traits are considered.

Results: We found an increase in trait dispersion when individual-level traits are considered, reflecting conspecific differentiation for allocation of traits. Organ-level traits, however, do not necessarily promote strong phenotypic displacement within conspecifics. Consistent with this, we found that the majority of variation in allocation of traits was between conspecifics, while most of the variation in organ-level traits was found between species.

Conclusions: Overall, trait displacement occurs within and across neighbourhoods, reflecting differentiation at inter- and intra-specific levels. Also, we identify two major phenotypic groups of variation, allocation and organ-level traits, that constitute two contrasting strategies for response to biotic and abiotic contexts: one highlights ecological differences among individuals, while the other highlights differences among species.

KEYWORDS
China, functional trait dispersion, inter-specific trait variation, intra-specific trait variation, plant communities, Puerto Rico, tropical forest, variance partitioning

1 | INTRODUCTION

Organismal traits are now routinely used in community ecology to test hypotheses regarding community assembly and strategies that favour species establishment (Albert et al., 2012; Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012; McGill, Enquist, Weiher, & Westoby, 2006). The traits that plant ecologists measure are believed to reflect major differences among species with respect to their resource acquisition, defence and reproductive strategies (Grime, 1979; McGill et al., 2006; Swenson, 2013; Westoby, 1998). Thus, the level of similarity in ecological strategies among species is linked to differences in the ecological processes that regulate community structure, dynamics and diversity (Baraloto et al., 2012; Kraft, Valencia, & Ackerly, 2008; Kunstler et al., 2016; Swenson & Enquist, 2009; Weiher & Keddy, 1995). In the recent years, this trait-based approach has explored the role of traits and has increasingly sought to incorporate intra-specific variation (e.g. Paine, Baraloto, Chave, & Hérault, 2011; Siefert et al., 2015; Umaña, Zhang, Cao, Lin, & Swenson, 2015). Such studies allow for a more detailed understanding of individual interactions with the environment and with other species (e.g. Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Paine et al., 2011; Siefert, 2012). Although it is broadly accepted that trait variation across individuals is remarkable (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Bolnick et al., 2011; Violle et al., 2012) – whether as a result of plasticity or genetic variation – there are still many areas where the role of intra-specific variation has not been considered.

Previous studies have incorporated intra-specific trait variation into their research to quantify the degree to which the functional composition or diversity of an assemblage changes when a species' mean trait value is applied to all conspecifics vs. when individual-level trait values are utilized (e.g. Paine et al., 2011; Siefert, 2012). For example, Paine et al. (2011) found that communities were more functionally over-dispersed when individual-level trait data were used instead of species-level mean trait data, the implication being that individuals may be functionally displacing one another in order to locally co-occur. Therefore, disaggregating the trait information from species to individuals improves our understanding of the patterns emerging from interactions at smaller scales.

However, intra-specific trait studies in tree communities conducted at the forest level still have important limitations. First, it remains unknown whether the functional displacement observed when using individual-level data is mainly due to differences between individuals from same species, suggesting strong intra-specific interactions, or whether the increases in trait distance occur at both the intra-specific and inter-specific levels. Second, previous work has not been able to evaluate whether trait differences among individuals are maximized at neighbourhood scales among potentially interacting individuals with respect to local-scale environmental variation (highlighting the predominant role of biotic interactions) or whether trait differences occur at larger scales reflecting trait variation in response to larger-scale gradients in the abiotic environment and highlighting the role of abiotic selection. For example, it is well known that there is important heterogeneity in light and soil nutrients in tropical forests (Chazdon & Fetcher, 1984; Chazdon, Fetcher, Chazdon, & Fetcher, 1984; Harms, Condit, Hubbell, & Foster, 2001; Hubbell, 1999; John et al., 2007; Kapos, Pallant, Bien, & Freskos, 1990). This heterogeneity might drive trait dissimilarities among individuals of the same species that are not necessarily co-occurring but are occupying slightly different environments, locally resulting in a pattern where the entire range of individual-level variation in traits is actually divided in smaller clusters.

The aggregation of trait information among interacting conspecific individuals (i.e. measuring local neighbourhood/plot-level mean trait values) is necessary for tests of hypotheses regarding community assembly in natural settings. Trait data information aggregated at plot level, computed as mean trait values for conspecifics co-occurring locally, provides an additional ecological scale that considers only neighbourhood individuals. First, by comparing plot-level trait dispersion (which considers mean trait values at plot scale, here referred to as "plot level") with individual-level trait dispersion we can obtain three results that will provide novel insights regarding the role of inter- and intra-specific trait dispersion for locally co-occurring individuals: (1a) plot-level dispersion (which only considers inter-specific trait differences) is higher than the individual-level dispersion (which considers intra-specific trait differences), indicating that intra-specific trait dispersion is smaller than inter-specific dispersion; (1b) plot-level dispersion is similar to individual-level dispersion, indicating that intra-specific trait dispersion is similar to inter-specific dispersion; (1c) plot-level dispersion is smaller than individual-level dispersion, indicating that intra-specific dispersion is higher than the inter-specific distance. Second, by comparing site-level trait dispersion (which considers mean trait values for the entire study system) with plot-level trait dispersion we can obtain three results that will highlight the drivers or functional β-diversity: (2a) plot-level dispersion is higher than site-level dispersion, indicating that co-occurring individuals of different species tend to increase the trait distance more than non-co-occurring individuals; (2b) plot- and site-level trait dispersion are similar, suggesting that site-level mean trait values reflect the mean plot level; (2c) plot-level trait dispersion is smaller than site-level trait dispersion, indicating that co-occurring individuals tend to be more similar in traits than non-co-occurring individuals.

The magnitude of intra-specific trait variation might vary depending on the group of traits analysed (Siefert et al., 2015). The most commonly studied functional traits are organ-level traits, such as specific leaf area, wood density, seed mass, etc. (Díaz et al., 2015). However, there are also whole-plant traits that might present different patterns of variation. Theory has proposed that traits that represent higher-order integration have the potential to be more flexible and more strongly linked to performance patterns (Marks, 2007). For example, the two whole-plant traits Siefert et al. (2015) investigated, plant height and spread, were more variable within species than organ-level traits such as specific leaf area. These intriguing results potentially have large implications for our understanding of what axes of plant function are more likely to adjust to local abiotic and biotic contexts that dictate community structure and dynamics.

Here we aim to build on previous intra-specific trait variation research in plant community ecology that investigated trait variation partitioning or the influence of individual-level trait data on patterns of trait dispersion using detailed individual-level phenotype and co-occurrence data for tree seedlings distributed across 200 plots in two tropical forests. We studied trait dispersion at seedling stages, since the high mortality occurring at this early stage has an important impact on community assembly patterns and influences latter ontogenetic stages (Poorter, 2007). We focus our analyses on three relevant scales: individuals, plots (which consider mean trait values at plot level) and site level (which considers mean trait values for the entire study system). Specifically, we ask the following questions: (1) how does the trait dispersion within a community differ when using individual-, plot- or site-level trait values; (2) how is trait variation partitioned across all individuals in each study system and are the results consistent across traits and forests; (3) how do the patterns of trait dispersion at different aggregation levels vary across different trait types?

2 | METHODS

2.1 | Study site and trait measurement

This study was developed in two well-separated tropical rain forests with different land use and natural disturbance histories. The main motivation for using two sites was to evaluate whether, despite the differences in disturbance history and species composition, there are similarities in the patterns of trait dispersion and the role of intra-specific variation across tropical regions. The first study site is located in Xishuangbanna, Yunnan, China (101°34′E, 21°36′N), with mean annual temperature of 21°C and mean annual precipitation of 1,493 mm. This region is characterized by a typical monsoon climate, with two seasons (rainy season from May to Oct, and dry season from Nov to Apr) and soil pH between 4.5 and 5.7 (Cao et al., 2008). We established 218 1 m × 1 m seedling plots arrayed in a regular grid. All freestanding seedlings <50 cm in height were tagged, identified and measured (5% could not be identified and were recorded as clearly distinguishable morpho-species). We observed a mean of seven species and a mean of 15 individuals per plot. The second study site is located in the El Yunque National Forest, Puerto Rico (65°47′W, 18°19′N), where mean annual temperature is 25°C, mean annual precipitation is 3,500 mm, and soils are formed from volcanistic rock (Thompson et al., 2002). We established 200 1 m × 1 m seedling plots. All the procedures to measure seedlings were the same as those described for China, and in total, 3% of the species were determined to morpho-species level. For this study we considered trees, lianas and palms.

All individuals present in the seedling plots were collected in order to measure traits. For each individual we measured fresh leaf area (LA in cm^2), leaf thickness and specific leaf area (SLA), calculated as: SLA = LA/dry leaf mass of one to three healthy fully expanded leaves. In addition to these organ-level traits, we measured five biomass allocation traits: leaf area ratio (LAR), which determines leaf area present per unit plant mass (leaf area/total seedling dry mass), and stem specific length (SSL), which measures length per unit stem mass (stem length/stem dry mass); LAR and SSL are also considered plant-level allocation traits; leaf mass fraction (LMF), which measures the fraction of total plant biomass allocated to leaves (leaf dry mass/total seedling dry mass), stem mass fraction (SMF), which measures the fraction of total plant biomass allocated to stems (stem dry mass/total seedling dry mass), root mass fraction (RMF), which measures the fraction of total plant biomass allocated to stems (root dry mass/total seedling dry mass) (Poorter et al., 2012). For root mass assessments we carefully removed a core of soil around each seedling (about 50-cm depth) to avoid under-sampling, however, fine roots ($\ll$1 mm) were very difficult to handle and were not considered in this study.

2.2 | Quantifying functional dispersion

A major aim of the present study was to evaluate changes in functional dispersion when trait information is represented at different aggregation levels. Specifically, in this work we used three levels: individual, plot and site. The individual-level analyses considered trait values from single individuals. The plot-level analyses were based on the average trait value from conspecific individuals within a 1 m × 1 m plot and represent the local neighbourhood. The site-level analyses were based on species mean values calculated by averaging the trait values of all conspecifics found in all 1 m × 1 m plots.

To measure the functional dispersion, we calculated the abundance-weighted (based on number of individuals) mean Euclidean pair-wise distance (*mpd*) for single log-transformed traits for seedlings co-occurring within each plot, using individual-, plot- and site-level trait data. Given that the *mpd* function from the 'picante' package in R (R Foundation for Statistical Computing, Vienna, Austria) computes the Rao metric instead of *mpd* abundance-weighted (de Bello, Carmona, Lepš, Kovats, & Pärtel, 2016), we used the code presented in Appendix S1. To control for sample size effects we used a null model approach to estimate the standardized effect size (SES) values. The randomization consisted of shuffling the names of species of individuals/plots/sites 999 times in the trait matrix. Thus, our null models randomized trait values but maintained observed patterns of species richness, species abundances and species occupancy rates. Finally we had 999 *mpd* null values for each plot at each scale of trait measurement to compare with the *mpd* observed value. We calculated the SES value by subtracting the mean of the null distribution of *mpd* values from the observed *mpd*, divided by the SD of the null distribution (Swenson, 2014). This SES *mpd* value is the functional dispersion for the plot, where positive values indicate more dispersion than expected and negative values indicate less dispersion than expected. We conducted a Friedman test (for repeated measurements) to assess whether there were significant differences in the SES values calculated for plots using individual-, plot- and site-level trait data. Then we performed a post-hoc test on the Friedman results to determine which pair-wise combinations of levels were significantly different. In addition to the *mpd* abundance-weighted analyses, we performed non-abundance-weighted analyses for individual traits and multivariate trait analyses (Appendix S1). For the multivariate analyses, we performed PCAs for all traits and used the first three orthogonal axes that explained 71% and 73% of the variation for China and Puerto Rico, respectively (Table S1 in Appendix S1).

We also performed analyses using the mean nearest neighbour trait distance metric to evaluate the changes in minimum trait distance across the three aggregation levels (site, plot and individual). This metric calculates the minimum trait distance among all the pairs of co-occurring individuals/species and then takes the mean value. Thus, at the individual level, the minimum distance is likely represented by pairs of conspecifics; while at the plot and site levels, the trait distance between pairs of conspecifics is not explicitly considered. The results and discussion from these analyses are presented in Appendix S2.

2.3 | Quantifying variance partitioning

We assessed variation in individual traits across three nested levels: among species at site level, among species at plot level and among individuals within plots. To accomplish this, we fit GLMs for each trait across the three levels nested in each other with all the traits log10-transformed. We followed the methodology described in Messier, McGill, and Lechowicz (2010) for these analyses. Specifically, we partitioned trait variance across the nested levels to estimate the variance in a trait between individuals in a plot, between species in a plot and between species across the entire site. This was repeated across all traits and at each study site. Lastly, we were interested in whether the amount of variation in a trait explained at one nested level (i.e. individuals within a plot) was correlated in one study site with the variation explained for that trait and level in the other study site across all traits using Pearson correlations. For example, was the amount of variation between individuals in plots high for biomass allocation traits in both sites and the amount of variation between individuals in plots low for organ-level traits in both sites?

3 | RESULTS

3.1 | Functional dispersion

The analyses of individual plots showed that the functional dispersion among co-occurring individuals tended to be higher when trait information was represented at the individual level, compared with species mean level, but comparisons between individual- and plot-level results were not always significantly different (Figures 1 and 2, Tables S2 and S3 in Appendix S1). In particular, for plots located in El Yunque, Puerto Rico, analyses with individual-level traits for the biomass allocation traits LMF, RMF and SMF were significantly different from trait dispersions using plot-level data (Figure 1, Tables S2 and S3 in Appendix S1). Organ-level traits (LA, SLA, leaf thickness) and SSL showed no significantly different trait dispersion when using individual- and plot-level aggregation data (Figure 1, Tables S2 and S3 in Appendix S1). For LAR the differences were not significant at any level. The results for plots located in Xishuangbanna, China, showed that the biomass allocation traits LMF, RMF and SMF were significantly different at the three levels evaluated. LA, SLA, LAR and showed no differences in trait dispersion between plot and individual level. For leaf thickness, the functional dispersion was not significantly different between plot- and site-level results (Figure 2, Tables S2 and S3 in Appendix S1). Differences in trait dispersion for leaf area (Puerto Rico) and SSL (China) were significantly higher when using site-level data than when using individual-level data. The results with a non-abundance-based metric and with PCA trait axes showed the same general pattern found with the abundance-based metric and with individual traits. The results at individual level tended to be higher than plot- and site-level results (Figures S1–S6 in Appendix S1). This

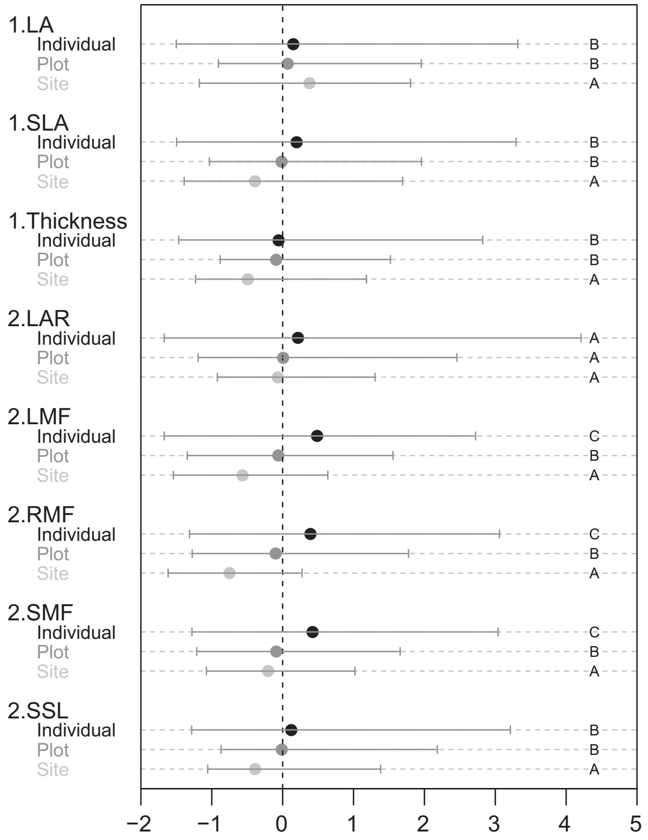

FIGURE 1 Differences in functional dispersion (SES *mpd*) for three ecological levels: individual, plot and site. The *x*-axis represents the SES *mpd* computed at each level. Dots represent the mean values for plots located at El Yunque, Puerto Rico. Trait names with 1 indicate organ-level traits; trait names with 2 indicate biomass allocation traits. LA, leaf area; LAR, leaf area ratio; LMF, leaf mass fraction; RMF, root mass fraction; SLA, specific leaf area; SMF, stem mass fraction; SSL, stem specific length; thickness, leaf thickness. Lines are trait dispersion values for 95% of the plots

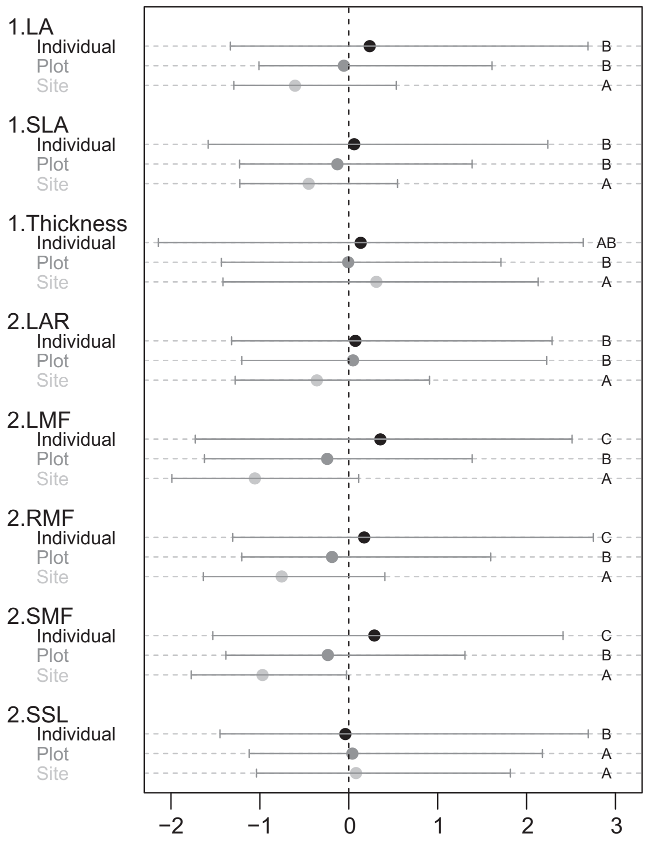

FIGURE 2 Differences in functional dispersion (SES *mpd*) for three ecological levels: individual, plot and site. The *x*-axis represents the SES *mpd* computed at each level. Dots represent mean values for plots located at Xishuangbanna, China. Conventions are as in Figure 1. Lines are the trait dispersion values for 95% of plots

high observed similarity in both types of analyses (abundance and incidence) are likely due to the small community size of the seedling plots, where abundance is not highly variable across species and diversity is limited.

3.2 | Trait variance partitioning

The variance partitioning results showed that differences between species accounted for the most variation in organ-level traits, while individual differences within species explained the highest percentage of variation for biomass allocation-related traits (Figure 3). The Pearson correlation test showed that both sites were highly consistent in the variance partitioning explained for each individual trait (Figure 3). In other words, the amount of variation in a trait explained at the site or individual level in one study site was strongly correlated with the amount of variation explained for these levels in the other site. The results of variance partitioning showed high trait variation between species at plot level, but the amount of variation explained by this level across traits was not consistent across study sites (Figure 3).

4 | DISCUSSION

The importance of trait variation among conspecific individuals is widely appreciated, but frequently it is not quantified in trait-based community ecology (Albert et al., 2012; Bolnick et al., 2011; Violle et al., 2012), particularly in species-rich ecosystems (but see Baraloto et al., 2010; Hulshof & Swenson, 2010; Messier et al., 2010; Messier, Mcgill, Enquist, & Lechowicz, 2016; Hulshof et al., 2013). In this study we evaluated the influence of trait variation on patterns of trait dispersion at three different aggregation levels (site, plot, individual) that allow for further inferences related to the role of inter-specific and intra-specific trait differences among co-occurring and not co-occurring individuals. We found that trait dispersion is high at the intra- and inter-specific levels for biomass allocation traits, but less variable for the other traits assessed. Also, plot- and site-level dispersions were consistently different across all traits, suggesting that intra-specific trait dispersion is patchily distributed across communities, likely related to environmental heterogeneity. In addition, the variance partitioning analyses show that the magnitude of intra-specific trait variation is highly dependent on the type of trait being analysed. Specifically, organ-level traits were usually less variable between individuals in plots and therefore increased trait dispersion to a lesser degree, while biomass allocation traits were generally more variable between individuals and therefore increased trait dispersion to a greater degree.

4.1 | Comparing patterns of functional dispersion for biomass allocation traits and organ-level traits

By comparing the results at site and individual levels, we found that in general functional dispersion within local communities was significantly different, being higher at the individual level and lower at the site level. Previous studies in tropical (Paine et al., 2011) and temperate (Jung et al., 2010) communities have found similar results, indicating that conspecific seedlings tend to increase their differences in ecological strategies within communities. However, these results do not provide enough information on the role of co-occurring vs. non-co-occurring conspecific individuals in driving these patterns in traits dispersion. For further inferences we should consider the results obtained at plot level.

For biomass allocation traits, dispersion within local communities was different at the three levels (site, plot, individual), suggesting that trait dissimilarity across conspecifics is happening within plots and across the forest. First, by comparing site- and plot-level patterns, our results suggest that there is an important variation in traits among non-interacting conspecifics occurring across the different plots studied, indicating an important role of abiotic and biotic characteristics that generate idiosyncratic trait patterns at the plot level. Indeed, light and soil conditions have been found to vary at local scales (Baldeck, Harms, Yavitt, John, Turner, Navarrete et al., 2013; Baldeck, Harms, Yavitt, John, Turner, Valencia et al., 2013; Hubbell, 1999; John et al., 2007; Kapos et al., 1990), promoting variation in ecological strategies from site to site. In addition, the biotic

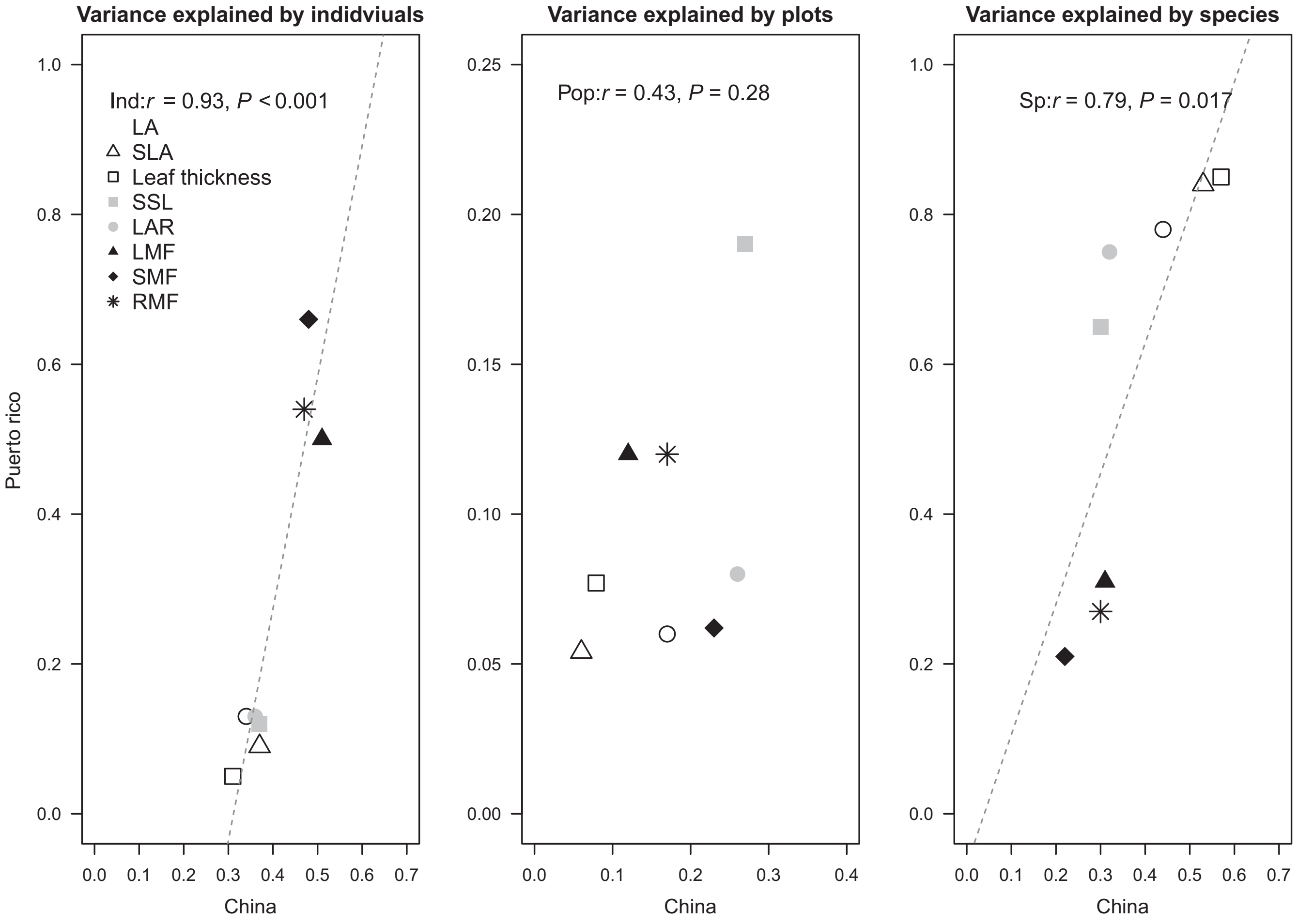

FIGURE 3 Correlation of variance partitioning patterns for each trait between China and Puerto Rico. Left plot shows the correlation for trait variance due to individual differences at each site (China and Puerto Rico). Middle plot shows the correlation for trait variance due to plots differences at each site. Right plot shows correlation for trait variance due to species differences at each site. Empty symbols, organ-level traits; filled grey symbols, plant-level biomass allocation traits; filled black symbols, biomass allocation traits

environment might also vary from plot to plot, promoting trait variation at this small scale (Abakumova, Zobel, Lepik, & Semchenko, 2016). Second, by comparing plot- and individual-level patterns, the results show important trait dispersion among co-occurring conspecifics, which indicates the high variability in biomass allocation strategies occurring at small spatial scales. Combined, the results show that trait dispersion is not homogenously distributed at community level (site level), instead, each plot exhibits particular trait composition, which creates important differences in species mean values at the plot level. Although trait dispersion patterns still provide limited information to infer particular ecological processes assembling these communities and the role of niche differentiation (D'Andrea & Ostling, 2016), we hypothesized that these results could be the outcome of environmental heterogeneity at small spatial scales (i.e. in light availability) that results in spatial clusters of ecological strategies and biomass allocation patterns to maximize resource acquisition.

For organ-level traits, the differences in trait dispersion between individual- and plot-level analyses were attenuated, indicating major constraints in variation. For these traits, co-occurring conspecifics exhibit trait values that are very close to the plot-level mean estimates. This can be interpreted as the result of a spatially dependent pattern where neighbouring individuals are likely closely related (i.e. full or half siblings) and therefore more similar in their traits. Lastly, leaf thickness and SSL (for China) and LAR (for Puerto Rico) showed no significant difference between species and individual levels. The leaf mechanical properties have been shown to be highly flexible and variable among species (Onoda et al., 2011); for SSL and LAR we suggest that these traits might have the potential to be highly variable within and across species, and do not constitute idiosyncratic traits that distinguish the species.

Combining results from the different trait types, our results suggest that trait dispersion could in part be caused through ecological processes acting at plot-level scale and promoting differences in traits between co-occurring individuals. This local trait displacement occurs mainly between heterospecifics, and for some traits it also promotes differentiation between conspecifics (i.e. biomass allocation traits). In addition, the increases in trait dispersion when comparing plot- and site-level results indicate that specific conditions that characterize each of the local neighbourhoods promote trait differentiation across plots. Previous work on trait variation partitioning indicated that while there may be substantial trait variation among individuals locally, trait distribution between communities can be similar (Messier et al., 2010). Here, we show that there is substantial among-community trait differentiation across the different plots for plant communities at early life stages.

The metrics used in this study are related to the *t*-statistic proposed by Violle et al. (2012) based on dispersion ratios. Violle et al. (2012) used trait variances computed at different aggregation levels (hierarchical levels) to evaluate the strength of filtering processes operating at different organization levels. Our *mpd* analyses computed at different aggregation levels should be highly related to this *t*-statistic, and are also useful to enhance the predictive power of trait-based studies into community ecology.

4.2 | Trait variation partitioning for allocation and organ-level traits shows contrasting patterns for species and individuals

In this study we measured two types of functional trait, organ-level traits and biomass allocation traits. Our trait dispersion results show that, in general, biomass allocation traits tend to exhibit higher trait dispersion, in some cases showing significant differences at the three levels considered in this study (i.e. site, plot, individual). In agreement with these results, the variance partitioning analyses show that the percentage of variance in biomass allocation traits is highest among individuals within species than among species at plot level or among species at site level. On the other hand, organ-level traits, such as LA and SLA, and additional (plant-level) traits such as SSL and LAR, tended to exhibit less trait variation at plot level and greater variation among species within plots and across the site. These traits, therefore, generally did not greatly alter the trait dispersion within and among our communities.

When correlating the amount of variation in a trait explained by individuals within a plot in one study site with the amount explained in the other study site, we found a strong relationship (Figure 3). A similarly strong relationship was found when plotting the amount of variation in a trait explained by species differences at site level (Figure 3). However, at plot level (trait values within species co-occurring in the same plot), the correlation was non-significant and the amount of variance explained at this level was overall low. The site- and individual-level results indicate that different trait groups themselves vary in their magnitude of intra-specific variation in a consistent manner across regions, with whole plant biomass allocation traits being more variable and organ-level traits being less variable. Consistent with this, a meta-analysis by Siefert et al. (2015) found similar results, where whole plant traits such as height and spread tended to be more variable at the individual level. Here, we have built on their work by integrating information from additional trait groups related to biomass allocation, plant- and organ-level traits and by sampling all individuals across communities rather than non-randomly selecting a few pristine individuals.

Overall our results show that organ-level traits tend to exhibit higher variance among species than among individuals, as compared to biomass allocation-related traits. These results have important general implications for trait-based plant community ecology. Specifically, the results suggest that biomass allocation-based traits likely have a lower degree of heritability and are more likely to be individually adjusted to the local abiotic and biotic context to promote differentiation and co-occurrence (Marks, 2007), whereas at organ level they are less likely to vary with respect to the local context and are more likely related to where species fall along a broader environmental gradient. Thus, it is tempting to place biomass allocation and organ-level traits into the *alpha* and *beta* trait context of Ackerly and Cornwell (2007). Specifically, biomass allocation may be considered primarily *alpha* traits, where trait variation is largely found within sites rather than across sites, and organ level may be considered primarily *beta* traits where trait variation is largely found across sites. However, our results show that biomass allocation traits increase dispersion both within and across sites, indicating that they do not fall neatly into either an *alpha* or *beta* trait category and are more generally aspects of plant form. Biomass allocation traits are the most likely to adjust to local- and regional-scale environmental variation, whereas organ-level traits are *beta* traits related to regional-scale environmental variation. Thus, future trait-based studies interested in the importance of local intra-specific interactions should place more emphasis on measuring variation in biomass allocation traits within and across species, and future studies interested in interactions driving distributions of species along gradients will need to place equal focus on organ-level and biomass allocation-based traits within and across species.

5 | CONCLUSIONS

It is generally agreed that variation in traits among conspecific individuals has an important role in the maintenance of diversity within ecological communities, but this intra-specific variation frequently goes unmeasured. In this study we have gone one step further by analysing trait dispersion at different scales: first we found that at neighbourhood scales there is important differentiation between heterospecifics and, for some more flexible traits (i.e. biomass allocation traits), also between conspecifics. Second, we found evidence for trait dispersion between non-co-occurring individuals across plots. We have analysed a broad range of different traits, and our results suggest that not all the traits show the same level of variation. Organ-level traits are generally less variable within plots and within species, while biomass allocation-related traits are highly variable within and across plots. This indicates that biomass allocation traits, which are frequently not measured, are highly context-dependent and likely hold a great deal of important information regarding the intra- and inter-specific interactions that drive community structure, dynamics and diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Results for the Friedman test, PCA mean pair-wise abundance and incidence data for China and Puerto Rico

Appendix S2 Results for MNTD analyses

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