Intraspecific trait variation and species functional turnover in successional tropical forests: assessing gap-filling for community weighted means

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Abstract

Accounting for intraspecific trait variation (ITV) is central to plant ecology and crucial for vegetation modeling efforts. ITV can be substantial; however, it remains unclear how ITV influences community-weighted mean (CWM) trait estimates. We use leaf and root trait data from 423 trees of 72 species from 15 Angiosperm families in combination with community data from 164 small plots comprising 582 species to evaluate the contribution of ITV to CWMs, comparing unlogged, primary forest to selectively-logged and clear-cut secondary forest. We examine the effect of gap-filling missing trait values via phylogenetic generalized linear modeling (PhyloPars) on CWMs. For six of seven traits, ITV negatively covaried with species turnover to generate larger CWM differences than observed if ITV was not integrated. For example, plot average CWM specific leaf area was 10.7 and 10.4 m² kg⁻¹ for primary and secondary forest, not accounting for ITV, but shifted to 9.8 and 11.1 m² kg⁻¹ after doing so. Specific root length showed a similar trend. Our results from 72-species assemblages were supported by the results from the gap-filled analysis using the entire community, where the contribution of ITV to CWMs ranged from 25 to 75%, with nearly all trait variation due to forest type attributable to ITV. Therefore, CWM trait estimates became more-conservative with forest age, whereas ITV for many traits showed an acquisitive shift, and because of negative covariation between ITV and species turnover, forest age-related CWM differences increased. Differences were unaffected, if not strengthened, by gap-filling incomplete functional trait matrices.

Introduction

Plant functional traits broadly scale along a fast-slow axis related to plant life-history variation and demographic rates (Díaz et al. 2016, Reich, 2014, Wright et al. 2010). For example, the most broadly measured plant functional traits distill to two main axes of functional variation – one related to leaf economics (e.g., specific leaf area – SLA, leaf nitrogen) and another related to whole plant size (Díaz et al. 2016). Despite this, there is substantial functional redundancy among plant taxa (i.e., within communities, Pillar et al. 2013) and considerable functional trait variation within taxa (i.e., intraspecific trait variation, hereafter ITV, Siefert et al. 2015) that muddles trends, for example weakening trait-demography relationships (Poorter et al. 2018a, Yang et al. 2018). Additionally, a portion of ITV is due to the environment; thus, properly accounting for ITV across quantified environmental gradients can reveal trait-environment relationships (Bruehlheide et al. 2018, Craven et al. 2018) and drivers of variance among them (Hofhansl et al. 2021).

Functional trait variation also has implications for plant fitness and how species partition environmental resources within niche space (Laughlin et al. 2020, Laughlin and Messier 2015, Kunstler et al. 2016). Thus, at the community level, functional traits have popularly been used to infer community shifts in plant resource-acquisition strategies across environmental gradients (e.g., environmental filtering, community assembly, Escudero and Valladares, 2016). For example, in tropical forests, functional diversity accounts for differences in forest productivity more so than taxonomic diversity (van der Sande et al. 2018), richness (Rosenfield and Müller, 2020), or forest dynamics in space and time, especially regarding forest succession (Letcher et al. 2015, Lohbeck et al. 2012, Muscarella et al. 2016a, Hogan et al. 2018). Moreover, it is far easier to infer plant community dynamics or plant-environment relationships from a functional trait perspective than through changes in individual species or community (i.e., multivariate) demographics (Poorter et al. 2018a, Poorter et al. 2018b). This trend is exacerbated with increasing plant community richness (Baraloto et al. 2010). In hyper diverse tropical forests, where there can be tens or hundreds of species within genera, using a functional trait perspective often uncovers environmental associations between functional plant strategies (e.g., Kraft et al. 2008), trends which

would be obscured by a traditional taxonomic approach. Moreover, when functional trait studies in hyper diverse tropical forests couple a functional perspective to phylogenetic data, patterns of inference can be strengthened (Baraloto et al. 2012). However, most of these studies use species-level trait data, ignoring ITV. Hence, there is motivation to understand whether incorporating ITV strengthens our ability to infer plant community-environment relationships (Violle et al. 2012, Siefert et al. 2015). This is of particular importance at the community scale because functional traits are used to inform the plant functional types or benchmark aggregate ecosystem functions in forest demography or ecosystem models, which predict tropical forest responses to global change (Fisher et al. 2018, Powell et al. 2018, Warren et al. 2015, Xu and Trugman, 2021).

Conceptually, ITV arises because of genetic variation among individuals, the environment, and the interaction between the two (Siefert et al. 2015, Bolnick et al. 2011). Accounting for ITV is labor-intensive, requiring extensive trait sampling of individuals; however, ITV is central to the ideological reconciliation of ecological and evolutionary frameworks. On the one hand, ecological frameworks seek to account for ITV in predicting community attributes or ecosystem properties, yet on the other, the evolutionary perspective seeks to better understand how natural selection shapes communities, ecosystems, and their constituent biota (Bolnick et al. 2011, Turcotte and Levine, 2016, Violle et al. 2012). Studies seeking to account for ITV in plant communities have traditionally looked at ITV between populations, communities, and ecosystems (e.g., Albert et al. 2010). Few studies have looked at ITV across successional or environmental gradients in tropical forests; moreover, none have sought to assess how such variation scales up to influence estimates of community-weighted mean (CWM) trait patterns.

The lack of studies aimed at quantifying the contribution of ITV to CWM trait patterns is likely due to the laborious undertaking of measuring the functional traits for individuals and the community composition across environmental or successional gradients (Paine et al. 2011). This is particularly difficult in tropical forests, where large trees and high levels of diversity complicate trait sampling (Baraloto et al. 2010). Methodological approaches that have looked for ways around this issue by gap-filling or imputing trait values for missing taxa are a potential solution. Still, each imputation approach has its assumptions, and some are more useful than others (reviewed by Swenson 2014). One of the first proposed methods was multiple imputation chained equations (MICE, van Buuren and Groothuis-Oudshoorn 2010); however, this method has since been shown to be flawed for several reasons, perhaps the most-supreme of which, in the context of plant functional traits, is a lack of phylogenetic consideration (Penone et al. 2014). Two of the next most-desirable methods include Bayesian hierarchical probabilistic matrix factorization (BHPMF, Schrodte et al. 2015), which can use a hierarchical taxonomic structure (e.g., genera within families within orders) to infer phylogenetic structure in the imputation of missing trait values, and PhyloPars (Bruggeman et al. 2009, Goolsby et al. 2017), which uses phylogenetic generalized linear models (pGLM) to impute missing trait values, thereby directly accounting for species relatedness via branch lengths. A recent study compared the three methods, concluding that PhyloPars outperforms MICE and BHPMF for trait imputation (Johnson et al. 2021).

Forest communities typically move from acquisitive to conservative functional composition as species composition changes with forest succession (Christensen and Peet 1984, Letcher et al. 2015, Lohbeck et al. 2013, Muscarella et al. 2016a, Swenson et al. 2012, Garnier et al. 2004). Thus, CWM functional trait values shift toward traits associated with species conservativeness (or slow life-history strategy, e.g., SLA and higher wood density – WD), partly because of turnover in community composition alone (Chazdon et al. 2010). The contribution of ITV in a successional context is less well understood; however, contributions can be substantial. For example, ITV of key leaf traits (i.e., leaf area, SLA, leaf nitrogen content, and leaf phosphorus content) accounted for >25% to

about 75% of the variation in CWM leaf trait values in a temperate rainforest in Chile (Fajardo and Siefert 2018). Root functional traits are of interest because they are abstruse and ecologically complex (Bardgett et al. 2014, Laliberté, 2017), rarely studied in the context of ITV, and control ecosystem function via the flow of nutrients and water through trees (Freschet et al. 2020). Thus, understanding how CWM root traits vary in the context of environmental variation and forest age is potentially key to modeling the functioning of tropical forests into the future (Bardgett et al. 2014, McCormack et al. 2017, Warren et al. 2015),

Few studies have examined how CWM patterns in root traits change with forest succession and how they may be different or similar to leaf traits. A recent study from a temperate forest that used BHMPF to gap-fill missing root trait data (Caplan et al. 2019) found that CWMs shifted toward conservative root strategies (thicker diameters, lower specific root length, higher root tissue density, and lower root nitrogen content) with increasing forest age and that acquisitive (e.g., pioneer) species and invasive species with acquisitive root strategies were able to persist in disturbed communities. A different study sampled a strong edaphic chronosequence in temperate rainforest in New Zealand and found that ITV in root traits showed similar patterns to CWM patterns in root functional traits (Holdaway et al. 2011). The differences in these two studies highlight the need for more studies that quantify the degree to which soil environment-structured variation, forest succession-driven variation, and other ITV sources have on influencing CWM estimates of root functional traits. Here we use root and leaf trait data collected in a paired sampling design along a 6.6-km transect in a tropical forest in Hainan, China, to scale up trait measurements to the community level using a complementary network of small vegetation plots (Xu et al. 2015a, Xu et al. 2015b)

Specifically, we address two research questions: 1) to what extent do species turnover (i.e., changes in community composition because of forest age and environmental filtering effects), ITV, and their covariation influence community-weighted mean functional trait estimates? 2) how sensitive are these patterns to phylogenetic trait imputation for missing taxa (i.e., gap-filling of missing trait data). *Concerning question 1, we expected that changes in plant community composition and species relative abundances (i.e., species turnover) with forest age would influence estimates of community-weighted traits to a greater degree than ITV because the magnitude of interspecific trait variation would be more important if ITV were substantial. For question 2, the testable null hypothesis is no difference in the relative contributions of species turnover and ITV between using directly measured and imputed functional trait data. Accepting the null hypothesis here would validate trait imputation methods and provide a way forward for future functional trait measurement strategies.*

Materials And Methods

Study site: Jianfengling, Hainan Island, China

The Jianfengling forest reserve (JFL), in Hainan, China (18°23'–18°15'N, 108°36'–109°05'E, Fig. 1) is a 47,200 ha mountainous forest with a history of logging and forest resource extraction that dates back to 1957, where about two-thirds of the area was either clear-cut or selectively-logged, meaning 30-40% of large timber-valuable trees were extracted (Xu et al. 2015b, Zhou 1995). All logging ceased in 1994 under a state-wide (Hainan Island only) logging ban, followed by a Chinese national logging ban in 1998 (Wenhua 2004, Zhou 1995). The reserve encompasses several ecological life zones of vegetation, from tropical semi-deciduous monsoon forest at the lower elevations to mossy high elevation forest, with evergreen-monsoon forest dominated by Podocarpaceae intermixed throughout at elevations < 1000 m (Huang et al. 1995). The most common vegetation life zone is tropical montane rain forest (per the Holdridge life zone classification), which occurs at elevations between 600

and 1100 m. It is characterized by a mix of palms and broadleaf evergreen trees that reach an average canopy height of 18 m (Jin et al. 2013).

JFL has a tropical monsoon climate with seasonal rainfall, where the wet season occurs between May and October (Zeng 1995). Cumulative annual rainfall over the last 30 years at JFL has averaged 2700 mm (Wu 1995). The soils are derived from porphyritic granite and are classified as lateritic and humic yellow soils (Wu 1995). They are infertile, leached tropical soils with an exchangeable base content of 30 mL per kg and some aluminum accumulation. Nutrient supplies in these soils are principally derived from the surface accumulation of organic matter, with rates of mineral and organic matter cycling in the soils being slower than other tropical soils (e.g., latisols, Wu 1995).

Root and leaf functional trait data

Functional traits were collected from May to July 2017. Saplings (i.e., trees >1m tall, but less than <10 cm diameter at 1.3m) of 72 species from 15 selected Angiosperm families, comprising 423 saplings (roughly 6 per species), were measured for leaf and root functional traits. Trait collection from saplings was done systematically along a 6.6 km transect that spanned primary and secondary forest with logging history (Fig. 1, see Hogan et al. 2020 for further details). Three leaves and five fine root systems (i.e., those containing 3-4 root orders, per McCormack et al. 2015) per sapling were collected, washed, scanned, dried, and weighed following standard trait measurement protocols. Scanned images were analyzed using leaf and root image analysis software (WinFolia 2007b and WinRhizo 2016, Regent Instruments, Quebec, Canada) for morphological traits. For each individual sapling, trait values were averaged across the three leaf and five root samples analyzed.

These individual-level trait data can be condensed to a few axes of key morphological variation among roots and leaves. A principal components analysis (Hogan et al. 2020) showed that three leaf traits – leaf area, specific leaf area (SLA), and leaf thickness, and four root traits – root system average diameter, specific root length (SRL), root tissue density (RTD), and root branching intensity (RBI) accounted for most of the two to three dimensional above and belowground trait variation among individuals. Therefore, we also focus on those seven traits in these analyses.

The network of small plots

We integrate data from a network of small plots previously established in the JFL forest reserve (Xu et al. 2015a, Xu et al. 2015b). Between August 2007 and June 2009, a network of 164 1/16th-ha (25m × 25m) plots were established in the JFL reserve (Xu et al. 2015b, Fig. 1). The plots span the local variability in vegetative life-zones and range in altitude from 259 to 1135 m. Roughly one-third (52 of 164) of the small plots are in old-growth forest, with no record or visible evidence of logging in the last 200 years (Xu et al. 2015b). The remainder of the plots (112) are in forest that was either selectively logged or clear cut, with human land-use ceasing between 20 and 56 years ago (see Table 1 in Xu et al. 2015b). Selective-logging practices in the area typically result in the removal of 30-40% of the mature stems ≥ 40 cm in diameter of commercially valuable timber species (Xu et al. 2015b, Zhou 1995). In each of the 164 small plots, all free-standing stems ≥ 2.5 cm in diameter at 1.3 m height were mapped, measured, and identified to species.

Data analyses: the network of small plots and Lepš' Intraspecific variability effects

In the interest of scaling up our functional trait measurements from individual trees along the gradient to the scope of the JFL forest reserve using tree community data from the network of small plots, we used an assemblage (i.e., partial community) – weighted mean approach, with basal area species weights. We call this an assemblage-weighted mean (AWM) in lieu of the classical community-weighted mean (CWM) because we could not measure traits for all species found in the plant communities. However, we did employ a sampling design that controlled for plant lineage, targeting species from 15 families across the Angiosperm phylogeny. This sampling design targeted families representing the functional variation in root morphologies across the angiosperm phylogeny and sampled many individuals within each species (average of 6) to assess ITV, where ITV was found to be structured across forest types (Hogan et al. 2020). Species for which we sampled functional traits accounted for 12.4% of species (72 of 580) and 37 % of stems (20,673 of 65,144) in the network of small plots. Basal area (measured in August 2007 to June 2009) in the array of small plots ranged from 16.7 to 77.8 m² ha⁻¹, averaging 44.2 m² ha⁻¹. The basal area of species in those plots for which functional traits were sampled along the 6.6 km gradient was between <1 and 42.3, averaging 18.4 m² ha⁻¹. Thus, the proportion of plot basal area for which there was trait coverage ranged from <1 to 82.3%, averaging 43.6%.

For each of the seven traits of interest, using mean trait values from all individuals for each species sampled along the transect (x_{ij}), we calculated AWMs for each plot. We term these the fixed averages (after Lepš et al. 2011), thus:

$$\text{fixed average} = \sum_{i=1}^S p_i x_i,$$

where p_i is the basal area fraction of that species within the plot (i.e., the community weight). For the AWMs, species weights were calculated after removing all species for which trait data were not sampled; this was necessary as weights must sum to one. We then calculated AWM trait values for each plot using habitat-specific trait values for each species ($x_{i_habitat}$). For example, for plots in secondary forests, trait values from saplings sampled in secondary forest. We term these the specific averages (again after Lepš et al. 2011), as such

$$\text{specific average} = \sum_{i=1}^S p_i x_{i_habitat}.$$

The intraspecific variability effects for the assemblages were calculated as the difference between the fixed and specific averages. Two-way analyses of variance (ANOVAs) assuming homoscedasticity were conducted with respect to each of the seven functional traits chosen. Then using the sum of squares of these tests, the variance in trait values was decomposed into intraspecific and community (i.e., species turnover) portions and their covariation (i.e., interaction). This was done using the ‘trait flex ANOVA’ function (see supplemental material of Lepš et al. 2011) in R v.3.5.0 (R Core Team, 2018)

2.4.2 Data analyses: gap-filling traits and validation of assemblage-weighted means

To validate the results regarding intraspecific variability effects using AWMs, we employed an approach to gap-fill trait data for unsampled taxa. As we have explained, PhyloPars (Bruggeman et al. 2009) appears to be one of the best tools available for gap filling functional traits (Penone et al. 2014, Johnson et al. 2021). Additionally, due to the high degree of phylogenetic-conservatism in certain root traits (e.g., root diameter), PhyloPars is particularly appropriate. It uses a pGLM that calculates phylogenetic covariance of taxa from a Brownian motion model of

trait evolution. Parameter estimates from the phylogenetic and functional trait variance-covariance matrix are then used to estimate missing data values.

A rudimentary phylogeny for all 582 taxa in the network of small plots was obtained from Phylomatic v3 (www.phylodiversity.net/phyloomatic, Webb and Donoghue, 2005), using the 'slik2015' base tree, which contains the most comprehensive phylogenetic skeleton for tropical trees to date (Slik et al. 2018). Wood density (WD) was used as an additional trait in the pGLM, in that we wanted to have one trait that was imputed for all taxa. WD is a highly phylogenetically-conserved trait (Kraft et al. 2010, Swenson and Enquist, 2007), which can be used in the pGLM to constrain modeled trait values for taxa and clades with no trait data. WD values were obtained from the global database of WD values (Chave et al. 2009, Zanne et al. 2009) where available, and the CTFS Forest-GEO WD database (<http://ctfs.si.edu/Public/Datasets/CTFSWoodDensity/>) via the 'BIOMASS' package ('getWoodDensity' function, Réjou-Méchain et al. 2017). Where species WD values were unavailable, values from a higher taxonomic classification (e.g. genus or family) were used (see Online Resource 3).

WD data was combined with three separate incomplete trait matrices, one using fixed trait values (x_i i.e., species mean values for all individuals measured along the transect), and two habitat-specific matrices ($x_{i_habitat}$), with the habitats being secondary and primary forest, as delineated along the sampling transect (see Hogan et al. 2020). pGLMs were fit separately to each incomplete trait matrix and predicted to complete them for all 582 taxa using PhyloPars (<http://zeus.few.vu.nl/programs/phylopars>, Bruggeman et al. 2009) and the Phylomatic-generated phylogeny. For the model setting in PhyloPars, we allowed for correlated evolution of the different traits, but did not allow for intraspecific variation in the models because, in our case, the separate fitting of the pGLMs accounts for this. We then used the gap-filled trait matrices and basal area species weights (p_i) of species in the small plots to recalculate fixed and specific averages (i.e., weighted means) for each plot. We re-ran the trait flex ANOVAs, comparing the AWM analysis, using only the species for which we measured functional traits (i.e., 72 species), to the CWM analysis, which used the PhyloPars-imputed trait data for all 580 species in the communities of the small plots.

Results

Linking the transect to the network of small plots – species forest-type preferences and soils comparison

Of the 72 species that were sampled for functional traits along the 6.6 km transect, plot community composition showed that 65% of them (47 species) preferred primary forest. In comparison, the remainder (25 species) favored plots in secondary forest (Fig. 2). The basal area in primary and secondary forest plots was roughly equal, averaging $40.5 (\pm 0.2, \text{standard error}) \text{ m}^2 \text{ ha}^{-1}$ for small plots in primary forest and $42.7 (\pm 0.2) \text{ m}^2 \text{ ha}^{-1}$ for those in secondary forest. Soils in secondary forest were significantly finer in texture than soils from the primary forest (t (% sand: $F_{1,298} = 63.9, p < .001$, % silt: $F_{1,298} = 53.8, p < .001$, % clay: $F_{1,298} = 38.5, p < .001$) and significantly less acidic (average pH of 2.5:1 soil in water of 4.39 vs. 4.27, $F_{1,298} = 14.1, p < .001$). Soils in the secondary forest had significantly greater total exchangeable base content ($F_{1,298} = 35.7, p < .001$), effective cation exchange capacity ($F_{1,298} = 11.62, p < .001$), and base saturation ($F_{1,298} = 22.5, p < .001$) than the soils in the primary forest. These trends from the soils of the transect mirrored trends in soil properties between small plots in secondary and primary forests (Online Resource 1). Thus, the range of variability in soil conditions between the transect and the network of small plots was similar, making comparisons between functional trait measurements from the transect to the community composition of the network of small plots unbiased relative to the soil environment.

Estimates of assemblage-weighted trait values – fixed vs. specific means

Our analytical approach involved calculating AWM estimates of functional traits using all data irrespective of forest type (i.e., fixed means) and using only data from each forest type (i.e., specific means, see complete analyses in Online Resource 2). Fixed AWM values for leaf functional traits differed drastically from specific AWMs (Table 1, Fig. 3). For example, plot average fixed AWMs for leaf area were 77.5 cm² and 78.2 cm² (a 0.7 cm² difference) for secondary and primary forest, respectively. Those estimates shifted to 70.5 cm² and 81.5 cm² (a difference of 11 cm²) for specific AWMs (Fig. 3A). Fixed AWM estimates for SLA were 10.7 and 10.4 m² kg⁻¹ for small plots in primary and secondary forest, respectively. In contrast, specific AWM estimates for SLA showed a greater difference between forest types, being 9.3 and 10.8 m² kg⁻¹ for small plots in primary and secondary forest, respectively, (Fig. 3B). The trend for leaf thickness was similar to those for leaf area and SLA. AWM differences were not significantly different for fixed averages but were for specific averages (Table 1), being about 0.02 mm greater in secondary forest than in primary forest (Fig. 3C).

Similarly, for root functional traits, fixed AWM values were similar and statistically indistinguishable (in all cases) between primary and secondary forest plots. At the same time, specific AWMs showed apparent and often statistically significant differences (Fig. 4). For example, fixed and specific AWMs for average root system diameter (Fig. 4A) showed an opposite trend, with fixed estimates being slightly (<0.01 mm) more narrow in primary than secondary forest, but with specific estimates being marginally thicker (0.03 mm) in primary than secondary forest. For both the fixed and specific AWMs for root diameter, these differences were not significant (Table 1). Fixed AWMs for SRL, the belowground analog to SLA, were 4.85 m g⁻¹ in primary forest plots and 5.00 m g⁻¹ in secondary forest plots, while the specific CWM estimates for SRL were 3.91 m g⁻¹ in primary forest plots and 5.11 m g⁻¹ in secondary forest plots (Fig. 4B). The difference of specific AWMs for SRL between secondary and primary forest plots was 1.11 m g⁻¹ instead of a difference of 0.15 m g⁻¹ for fixed AWMs for SRL. These differences went from being statistically non-significant for the fixed AWM comparison by forest type to significant for the specific AWMs (Table 1). The results for RTD were similar to those for average root system diameter (Fig. 4C). Fixed AWMs for RTD showed a decreasing trend from primary to secondary forest, with roots being about 0.02 g cm⁻³ less dense in secondary than primary forest. Specific AWMs for RTD showed the opposing trend, with AWMs for RTD being about 0.3 g cm⁻³ denser in secondary than in primary forest. Differences between fixed AWMs were not statistically different, but the difference between specific AWMs were statistically significant (Table 1). Lastly, AWM RBI showed no significant differences when specific means were compared across forest types, with values averaging about 1.97 root tips cm⁻¹ (Figure 4D, Table 1). However, fixed AWM RBI values were statistically different, averaging 1.73 tips cm⁻¹ in primary forest plots and 2.13 tips cm⁻¹ in secondary forest plots (Fig. 4D), a weighted-mean difference of 0.4 tips cm⁻¹.

In summary, the only difference in fixed AWM values by forest type for or any of the seven functional traits considered was for RBI (Table 1, Figs. 3 and 4), but statistical differences in specific AWM trait estimates occurred for all traits except for root diameter, which had a marginally significant difference ($p = .08$, Table 1). Even when differences between specific AWMs between forest types were not statistically significant, they were always greater than differences in fixed AWMs. In some cases, they were also different in sign (i.e., for SLA, leaf thickness, root diameter, and SRL, Figs. 3 and 4).

Comparing assemblage-weighted means to community-weighted means – evaluating pGLM-imputed trait values

Trends in CWM means confirmed the results of the AWM analyses. Like the AWM analysis, the pattern of having larger differences in habitat-specific means than for fixed means between forest types was consistent across all leaf (Fig. 3) and root (Fig. 4) CWMs using pGLM-imputed trait matrices. When pGLM-imputed functional trait matrices for the entire community were used, the variability among weighted trait estimates for plots decreased (i.e. 95% confidence interval breadth contracted). This decrease in estimate variability led to more statistically significant differences for specific CWMs relative to specific AWMs (Table 2). For leaf traits (leaf area, SLA, and leaf thickness), no qualitative difference emerged from CWMs using pGLM-imputed trait data for taxa, versus only measured trait data (Fig. 3, Table 2). The only noticeable difference between the AWM and CWM values in Fig. 3 is that pGLM-imputed CWM values for SLA were translated about $1 \text{ m}^2 \text{ kg}^{-1}$ greater across the fixed and specific means for both forest types. Additionally, the difference between fixed CWMs for RBI was not statistically significant (Table 2), where it was for the fixed AWMs for RBI (Table 1). Also, the difference in specific CWMs for root diameter was statistically significant (Table 2), where the difference between AWMs was marginally significant (Table 1).

Comparing AWMs to CWMs for root traits, we see similar patterns. Using AWMs resulted in no differences between fixed and specific estimates for root diameter (Fig 4A). However, when the pGLM-imputed data were used, the specific estimates for root diameter increased slightly for primary forest and decreased for secondary forest, creating a statistically significant difference between forest-types (Table 2). For the three other root traits (SRL, RTD, and RBI), differences were accentuated slightly, as pGLM-imputed functional trait matrices were used (Fig. 4 B, C, D). This discrepancy in forest-type weighted-trait estimates resulted more from ITV with environment than from species turnover among plots (Table 2, Fig. 5). In many cases, for example for SLA, root diameter, SRL, and RTD, ITV and species turnover had negative covariance values (Table 4, Table S4), meaning that beta diversity in species composition drives weighted-trait values one way (in our case, usually slightly toward the conservative end of the plant economics spectrum, but not always), while ITV with environment causes shifts in the opposite direction (in our case, roots morphologies became more conservative while leaf morphologies were more acquisitive from primary to secondary forest, Hogan et al. 2020).

Interspecific variability effects – the relative effect of ITV and turnover on weighted-mean trait estimates

Results from the interspecific variability effects from AWMs (Table 1) and CWMs (Table 2) can be used to infer the relative contribution of ITV and species turnover by forest type to functional trait variability. They can also be compared to understand the effect of pGLM gap-filling on the relative contribution of ITV and species turnover by forest type to functional trait variability. Between the AWM and CWM analyses, ITV and species turnover had similar contributions to total functional trait variance for the seven traits considered (Fig 5, left panel). The relative contribution of ITV in explaining the trait variation due to forest type increased markedly from the AWMs to CWMs (Fig. 5, middle panel). This decrease came as the contribution of ITV to trait-flex ANOVA error decreased from the AWM analysis to the CWM analysis (Fig. 5, right panel). For example, when using only measured data (i.e., the AWM analysis), the total relative contribution of forest type for leaf area, SLA, and leaf thickness was 5, 11, and 15 percent, respectively (Fig. 5). The relative contribution of forest-type for those three leaf traits increased to 26, 24, and 19 percent, respectively, when pGLM-imputed trait matrices were used in the CWM analysis (Fig. 5). Nearly all this variation was due to ITV and not to species turnover (i.e., β -diversity, relative contributions < 1%) among the small vegetation plots. Moreover, the relative contribution of forest type to functional trait variation in root diameter, SRL, RTD, and RBI was 2, 19, 4, and 49 percent (Table 4), respectively,

using only directly-measured functional traits (i.e., AWMs). In contrast, the relative contribution to forest-type increased to 12, 24, 9, and 77 percent, respectively, when using pGLM-imputed data (i.e., CWMs).

Overall, the trait-flex ANOVA model were strikingly similar between the AWM analysis and the CWM analysis (Fig. 5). For each of the seven traits considered, the trait flex ANOVA models had comparable total explanatory power (Fig. 5, left panel). Considering total weighted-mean trait variation, five traits (SRL, SLA, root system diameter, leaf thickness, and leaf area) showed negative covariation for the AWM trait-flex ANOVAs. For the CWM analysis, only three traits (SRL, root system diameter, and leaf area) showed negative covariation in relation to total trait variation. However, the magnitude of their negative covariation increased. For weighted-mean trait variation due to forest type, both the AWM and CWM analysis were mostly attributable to ITV and not to turnover, although the magnitude differed slightly, with small differences in ITV and species turnover covariation (Fig. 5, middle panel). Lastly, trait flex ANOVA model errors were comparable between AWM and CWM analyses. The general pattern is that the error associate with ITV decreased when using data from the entire plant community (i.e., pGLM-imputed complete functional trait matrices as opposed to the 72 species assemblages). The magnitude of error attributable to species turnover and the covariation between ITV and species turnover was similar between AWM and CWM models (Fig. 5, right panel).

Discussion

The utility of functional perspectives to species-rich tropical forests

The application of functional perspectives (Keddy 1992, Westoby and Wright 2006) to understand the ecology of plants in relation to environmental variation is a promising way to reduce complex and subtle changes in species composition and variation in functional composition of communities into ecologically meaningful information. This has been demonstrated regarding patterns of community assembly (Baraloto et al. 2012, Kraft et al. 2008, Laughlin, 2014, Spasojevic and Suding, 2012) and their underlying variability in plant traits (Letcher et al. 2015, Muscarella et al. 2016b). The data used in this study confirm that ITV in tropical tree communities is substantial (Hogan et al. 2020), which has a consequence for CWM trait estimates (Baraloto et al. 2010, Muscarella and Uriarte, 2016). ITV has been shown to account for vital ecological differences among species, such as rates of photosynthesis and growth (Shipley et al. 2006, Wright et al. 2010), intrinsic rates of population growth (Adler et al. 2014), or variation in ecosystem productivity (Lohbeck et al. 2013, Poorter et al. 2017, van der Sande et al. 2018)

Yet, there has been a burgeoning in examining the role of ITV in functional ecology (i.e., ecologically accounting for species trait variance rather than the mean trait values; Siefert et al. 2015, Violle et al. 2012, Hulshof and Swenson 2010). Undoubtedly, some amount of ITV is related to environmental variation, but difficulty exists in quantifying dimensions of niche space or specific ecosystem properties that systematically relate to this variation (Lavorel and Garnier 2002, Shipley et al. 2016). Furthermore, there is the possibility of genetic variation and genetic environment interactive effects (Kunstler et al. 2016, Soliveres et al. 2014, Yang et al. 2018). Whether to focus on interspecific or intraspecific trait variation, the two approaches employ drastically different sampling designs (Baraloto et al. 2010). On the one hand, diversity-differences are favored by a focus in among taxa trait variation. On the other, when ITV is the focus, sampling effort is maximized for one to a few species potentially at the expense of diversity-driven differences. In the tropics, the costs of this trade-off are particularly acute, as species diversity and environmental variation are both extensive. A second practical difficulty arises in that species compositional differences are often confounded with environmental variation (i.e., environmental

filtering), making it challenging to assess ITV for all taxa, especially less-common ones. Despite this, Lepš et al. (2011) propose a middle-of-the-road solution that appeals, group trait sampling by *a priori* ecological classification (i.e., measure habitat or experimental-treatment specific trait values). This approach proved useful in assessing how fertilization and mowing shape the functional traits of European grasslands (Lepš 1999, Lepš et al. 2011).

We employed a similar approach to assess how environmental variation in resource availability (i.e., soil nutrient content and light availability, see Hogan et al. 2020), roughly summarized by the successional progression of a forest (Odum 1969, Christensen and Peet 1984, Guariguata and Ostertag 2001, Chazdon et al. 2010) leads to functional and compositional community change. In our case, the principal axis of environmental variation, irrespective of compositional differences among forest-types, was a gradient in soil fertility and texture, with soil texture and fertility decreasing along the transect from more-secondary to primary forest (Online Resource 1, Hogan et al. 2020). ITV along this gradient was consistent and measured 7 cm² for leaf area, 0.8 m² kg⁻¹ for SLA, 0.4 mm for root diameter, 0.35 m g⁻¹ for SRL, and 0.3 tips cm⁻¹, on average (Hogan et al. 2020). Additionally, there was considerable interfamilial variation among the taxa, which were preselected to collect a range in root functional strategies. We carefully sampled leaves and roots from individual juvenile trees that spanned environmental variation in soil environment and forest type. These considerations led to the trait data being well suited to scale to the community level using the forest demography data from the network of small plots (Online Resource 1, Xu et al. 2015a, Xu et al. 2015b). Thus, the middle-of-the-road solution proposed by Lepš et al. (2011) of structuring functional trait sampling across known environmental variability is useful when carefully applied to forests, as well.

Consequences of ITV for CWM estimation with tropical forest successional status

On one-hand interpreting, CWM patterns of trait variation can help interpret ecological processes shaping community assembly from regional species pools (i.e., environmental filtering of species or even phenotypes) (Kraft et al. 2008, Muscarella and Uriarte, 2016, Spasojevic et al. 2016). On the other, they are gross generalizations of the aggregate function of species assemblages that may or may not reflect broader forest-level or ecosystem functioning (e.g., total photosynthetic, nutrient uptake, or biomass production capacity of a stand; Warren et al. 2015, Fisher et al. 2018). Their accuracy depends on proper estimates of species traits in relation to the environment, which must account for both among and within species variation (Violle et al. 2012, Shipley et al. 2016, Yang et al. 2018). Measuring the morphology of all the plants within a community may one day be feasible but is currently not possible. Yet, the ability to accurately estimate trait values (e.g., leaf area, or more so even, belowground traits like root-tip abundance) is critical to accurately modeling how vegetation will respond to future changes in the biosphere (Warren et al. 2015, McCormack et al. 2017).

Scaling up trait measurements from along the JFL gradient to the forest using data from a network of small plots revealed that ITV compounded with compositional differences (i.e., species basal area weights) to create discrepancies in community-weighted trait values concerning forest successional status. That is, specific weighted-means were much more different than fixed weighted-means, which was consistent for both the AWM and CWM analyses. These differences would not have been detected had we not sampled functional traits along an environmental gradient consistent with the environmental variation found in the network of small plots (Figs. 3 and 4). This is due to the negative covariation of ITV and compositional turnover for most (six of seven) of the traits examined (for either the AWM or CWM analysis, Fig. 5). For example, along the JFL gradient, we measured a

plant lineage-consistent decrease of about 0.35 m g^{-1} in root-system SRL from secondary to primary forest (Hogan et al. 2020). Accounting for such ITV, the specific mean difference in SRL between primary and secondary plots was 1.11 m g^{-1} for the AWMs and about 0.65 m g^{-1} when pGLM-imputed data were used (Fig 4B). Covariation between ITV and species turnover was positive for the assemblage-weighted mean estimate but was negative for the more-complete analysis (Fig. 5). Regardless, like SRL, the difference in CWM trait estimates exceeded the magnitude of ITV measured across the JFL gradient (Hogan et al. 2020). This is because ITV compounds with β -diversity to move CWM trait values toward the conservative end of the plant economics spectrum (Tables 1 and 2, Figs. 3 and 4) as species composition shifts toward more conservative species in older forest (Lohbeck et al. 2013, Letcher et al. 2015, Muscarella and Uriarte, 2016, Spasojevic et al. 2016).

Several studies have reported negative covariation between species turnover and ITV for a variety of functional traits (grass leaf traits in response to mowing and leaf nitrogen in response to fertilization: Lepš et al. 2011, leaf traits: Fajardo and Siefert, 2018, leaf traits: Kichenin et al. 2013, SLA, leaf phosphorus, leaf thickness: Derroire et al. 2018, plant height and leaf traits excepting SLA: Zuo et al. 2017). Negative trait covariances between drivers of trait variability (e.g., ITV because of environment or disturbance, and species turnover in our case) confer resistance in the change of CWM trait values to a single driver because the effect of one driver limits the trait response to the other driver. This dampening can be understood in the context of the portfolio effect (Schindler et al. 2015), where negative covariance between system components (e.g., drivers of community trait variation) leads to dampened dynamics at higher-order levels (e.g., the community) (Bolnick et al. 2011). On the other hand, positive covariation between species turnover and ITV has been found in some other studies from an equal variety of traits (leaf nitrogen: Kichenin et al. 2013, leaf area, leaf dry matter content, leaf nitrogen: Derroire et al. 2018, SLA: Zuo et al. 2017). The idiosyncrasy of these results points to the context-dependency in the covariation of ITV in decomposing the functional trait variation of plant communities (Kichenin et al. 2013). In the AWM analysis we conducted, we found slight negative covariation for SLA, RTD, root system diameter, leaf thickness, and leaf area (Fig. 5). Extending the analysis to the entire community using pGLM-imputed functional trait matrices created some minor variation in these patterns. The sign of the covariation because of forest type changed for three of the seven traits (leaf area, leaf thickness, and SRL). Thus, although these changes were small, trait covariation seems sensitive to the assemblage of species for which functional traits are measured, potentially pointing to the role of species-specific responses in CWM trait patterns (Muscarella and Uriarte 2016).

With respect to tropical forests, differing patterns in the contribution of ITV versus species turnover and their covariation and may emerge for wet and dry tropical forests (Poorter et al. 2019). We report more negative than positive covariation in ITV and specie turnover in CWM trait estimates. However, positive covariation of ITV and turnover was reported for most leaf traits in the Guanacaste dry forest of Costa Rica (Derroire et al. 2018). Additionally, Zuo et al. (2017) found positive covariation between trait variation because of species turnover and ITV for several leaf traits, excepting SLA, in dune grassland communities in Mongolia.

Patterns of β -diversity among sampled communities in relation to the functional uniqueness of the species contributing to those patterns (i.e., those lost or gained across assemblages) (Spasojevic et al. 2016) drives the covariation of the drivers of trait variability within and across plant communities. In communities with high levels of functional redundancy, such as tropical forests, responses may be muted as individual species play a less significant role in driving overall patterns (Baraloto et al. 2010, Laughlin, 2014, Umaña et al. 2017).

Conclusions

In response to our first research question on whether species turnover is a more significant contributor to variation CWM trait values than ITV, for six of seven traits (i.e., all traits except RBI), species turnover outweighed the contribution of ITV in explaining functional trait variation. However, trait variation due to forest type was nearly entirely explained by ITV, which was consistent across all root and leaf functional traits. This likely reflects both functional trait variation maximized by the sampling design because of forest type and actual ITV among tropical trees. Concerning our second research question, on the sensitivity of patterns of CWMs to gap-filling via phylogenetic trait imputation, we find support for the PhyloPars method, which is in congruence with some recent work (Johnson et al. 2021). Inference was not unchanged quantitatively by trait imputation (i.e., accepting the null hypothesis as outlined in the introduction), however patterns were strikingly similar (i.e., changed very little qualitatively). This result speaks to the need to create ecologically relevant designs for the sampling of plant functional traits (Baraloto et al. 2010, Lepš et al. 2011) that capture ITV efficiently relative to measurement labor. The approach we demonstrate here accounts for trait variation across the community using phylogenetic sampling, as well as for ITV across gradients of environmental variation, like soil fertility, texture, and forest age. Its application captured important variability in CWM trait estimates with land-use driven variation in tropical forest tree communities, which would have been overlooked using traditional analyses with single, fixed trait values for species.

List Of Abbreviations

AWM: assemblage (i.e., partial community)-weighted mean

CWM: community-weighted mean

ITV: intraspecific trait variation

JFL: Jianfengling

pGLM: phylogenetic generalized linear model

RBI: root branching intensity (in tips cm^{-1})

RTD: root tissue density (in g cm^{-3})

SLA: specific leaf area (in $\text{m}^2 \text{kg}^{-1}$)

SRL: specific root length (in g m^{-1})

WD: wood density (in g cm^{-3})

Declarations

Authors' contributions statement: JAH and CB designed the study, JAH and HX collected the data, JAH analyzed the data and wrote the manuscript. All authors contributed intellectually and aided in the editing of manuscript drafts.

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Data Availability: The functional trait data used in this study are archived on figshare: <https://doi.org/10.6084/m9.figshare.7996328.v4>

References

- Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, 111:740-745
- Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* 98:604-613
- Baraloto C, Hardy OJ, Paine CET, Dexter KG, Cruaud C, Dunning LT, Gonzalez MA, Molino JF, Sabatier D, Savolainen V (2012) Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology* 100:690-701
- Baraloto C, Paine CET, Patiño S, Bonal D, Hérault B, Chave J (2010) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology* 24:208-216
- Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* 29:692-699
- Bolnick D, Amarasekare P, Araújo M, Bürger R, Levine J, Novak M, Rudolf V, Schreiber S, Urban M, Vasseur D (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183-92
- Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, Jansen F, Kattge J, Pillar VD, Schrodte F, Mahecha MD, Peet RK, Sandel B, van Bodegom P, Altman J, Alvarez-Dávila E, Arfin Khan MAS, Attorre F, Aubin I, Baraloto C, Barroso JG, Bauters M, Bergmeier E, Biurrun I, Bjorkman AD,

Blonder B, Čarni A, Cayuela L, Černý T, Cornelissen JHC, Craven D, Dainese M, Derroire G, De Sanctis M, Díaz S, Doležal J, Farfan-Rios W, Feldpausch TR, Fenton NJ, Garnier E, Guerin GR, Gutiérrez AG, Haider S, Hattab T, Henry G, Hérault B, Higuchi P, Hölzel N, Homeier J, Jentsch A, Jürgens N, Kącki Z, Karger DN, Kessler M, Kleyer M, Knollová I, Korolyuk AY, Kühn I, Laughlin DC, Lens F, Loos J, Louault F, Lyubenova MI, Malhi Y, Marcenò C, Mencuccini M, Müller JV, Munzinger J, Myers-Smith IH, Neill DA, Niinemets Ü, Orwin KH, Ozinga WA, Penuelas J, Pérez-Haase A, Petřík P, Phillips OL, Pärtel M, Reich PB, Römermann C, Rodrigues AV, Sabatini FM, Sardans J, Schmidt M, Seidler G, Silva Espejo JE, Silveira M, Smyth A, Sporbert M, Svenning JC, Tang Z, Thomas R, Tsiripidis I, Vassilev K, Violle C, Virtanen R, Weiher, E, et al. (2018) Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* 2:1906-1917

Bruggeman J, Heringa J, Brandt BW (2009) PhyloPars: estimation of missing parameter values using phylogeny. *Nucleic Acids Research* 37:W179-W184

Caplan JS, Meiners SJ, Flores-Moreno H, McCormack ML (2019) Fine-root traits are linked to species dynamics in a successional plant community. *Ecology* 100:e02588

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351-366

Chazdon RL, Finegan B, Capers RS, Salgado-Negret B, Casanoves F, Boukili V, Norden N (2010) Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. *Biotropica* 42:31-40

Christensen NL, Peet RK (1984) Convergence during secondary forest succession. *Journal of Ecology* 72:25-36

Craven D, Eisenhauer N, Pearse WD, Hautier Y, Isbell F, Roscher C, Bahn M, Beierkuhnlein C, Bönisch G, Buchmann N, Byun C, Catford JA, Cerabolini BEL, Cornelissen JHC, Craine JM, De Luca E, Ebeling A, Griffin JN, Hector A, Hines J, Jentsch A, Kattge J, Kreyling, J, Lanta V, Lemoine N, Meyer ST, Minden V, Onipchenko V, Polley HW, Reich PB, van Ruijven J, Schamp B, Smith MD, Soudzilovskaia NA, Tilman D, Weigelt A, Wilsey B, Manning, P (2018) Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution* 2:1579-1587

Derroire G, Powers JS, Hulshof CM, Cárdenas Varela LE, Healey JR (2018) Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica. *Scientific Reports* 8:285

Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC (2016) The global spectrum of plant form and function. *Nature* 529:167.

Escudero A, Valladares F (2016) Trait-based plant ecology: moving towards a unifying species coexistence theory. *Oecologia* 180:919-922

Fajardo A, Siefert A (2018) Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology* 99:1024-1030

Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ, Lichstein JW, Longo M, Matheny AM, Medvigy D, Muller-Landau HC, Powell TL, Serbin SP, Sato H, Shuman JK, Smith B, Trugman AT, Viskari T, Verbeeck H, Weng E, Xu C, Xu X, Zhang T, Moorcroft PR (2018)

Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, De Deyn GB, Johnson D, Klimešová J, Lukac M, McCormack ML, Meier IC, Pagès L, Poorter H, Prieto I, Wurzbürger N, Zadworny M, Bagniewska-Zadworna A, Blancaflor EB, Brunner I, Gessler A, Hobbie SE, Iversen CM, Mommer L, Picon-Cochard C, Postma JA, Rose L, Ryser P, Scherer-Lorenzen M, Soudzilovskaia NA, Sun T, Valverde-Barrantes OJ, Weigelt A, York LM, Stokes A (2020) Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*, doi:10.1111/nph.17072

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A (2004) Plant functional markers capture ecosystem properties during secondary succession *Ecology* 85:2630-2637

Goolsby EW, Bruggeman J, Ané C (2017) Rphylopars: fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution* 8:22-27

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148:185-206

Hofhansl F, Chacón-Madrigal E, Brännström Å, Dieckmann U, Franklin O (2021) Mechanisms driving plant functional trait variation in a tropical forest. *Ecology and Evolution*, doi: 10.1002/ece3.7256

Hogan JA, Hérault B, Bachelot B, Gorel A, Jounieaux M, Baraloto C (2018) Understanding the recruitment response of juvenile Neotropical trees to logging intensity using functional traits. *Ecological Applications* 28:1998-2010

Hogan JA, Valverde-Barrantes OJ, Ding Q, Xu H, Baraloto, C (2020) Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China. *Annals of Forest Science* 77:79

Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA (2011) Species-and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology* 99:954-963

Huang Q, Li Y, Zheng D, Zhang J, Wan L, Jiang Y, Zhao Y (1995) Study on Tropical Vegetation Series in Jianfengling, Hainan Island. In: Zeng Q, Zhou G, Yide L, Wu Z, Chen B (eds) *Researches on Tropical Forest Ecosystems in Jianfengling of China*. China Forestry Publishing House, Beijing, China, pp 5-25

Hulshof CM, Swenson NG (2010) Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* 24:217-223

Jin D, Cao X, Ma K (2013) Leaf functional traits vary with the adult height of plant species in forest communities. *Journal of Plant Ecology* 7:68-76

Johnson TF, Isaac NJB, Paviolo A, González-Suárez M (2021) Handling missing values in trait data. *Global Ecology and Biogeography* 30:51-62

Keddy P. (1992) A pragmatic approach to functional ecology. *Functional Ecology* 6:621-626

- Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT (2013) Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology* 27:1254-1261
- Kraft NJ, Metz MR, Condit RS, Chave J (2010) The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist* 188:1124-1136
- Kraft NJ, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580-582
- Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, Aiba M, Baraloto C, Caspersen J, Cornelissen JHC, Gourlet-Fleury S, Hanewinkel M, Herault B, Kattge J, Kurokawa H, Onoda Y, Peñuelas J, Poorter H, Uriarte M, Richardson S, Ruiz-Benito P, Sun IF, Ståhl G, Swenson NG, Thompson J, Westerlund B, Wirth C, Zavala MA, Zeng H, Zimmerman JK, Zimmermann NE, Westoby M. (2016) Plant functional traits have globally consistent effects on competition. *Nature* 529:204-207
- Laliberté E (2017) Below-ground frontiers in trait-based plant ecology. *New Phytologist* 213:1597-1603
- Laughlin DC (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* 102:186-193
- Laughlin DC, Gremer JR, Adler PB, Mitchell RM, Moore MM (2020) The net effect of functional traits on fitness. *Trends in Ecology & Evolution* 35:1037-1047
- Laughlin DC, Messier J (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* 30:487-496
- Lavorel S, Garnier É (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545-556
- Lepš J (1999) Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *Journal of Vegetation Science* 10:219-230
- Lepš J, de Bello F, Šmilauer P, Doležal J (2011) Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34:856-863
- Letcher SG, Lasky JR, Chazdon RL, Norden N, Wright SJ, Meave JA, Pérez-García EA, Muñoz R, Romero-Pérez E, Andrade AJJE (2015) Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites. *Journal of Ecology* 103:1276-1290
- Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Paz H, Pérez-García EA, Romero-Pérez IE, Tauro A, Bongers F (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* 94:1211-1216
- Lohbeck M, Poorter L, Paz H, Pla L, van Breugel M, Martínez-Ramos M, Bongers F. (2012) Functional diversity changes during tropical forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* 14:89-96

- McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207:505-518
- McCormack ML, Guo D, Iversen CM, Chen W, Eissenstat DM, Fernandez CW, Li L, Ma C, Ma, Z, Poorter H (2017) Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* 215:27-37
- Muscarella R, Uriarte M (2016) Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences* 283:20152434
- Muscarella R, Uriarte M, Aide TM, Erickson DL, Forero-Montaña J, Kress WJ, Swenson NG, Zimmerman JK (2016a) Functional convergence and phylogenetic divergence during secondary succession of subtropical wet forests in Puerto Rico. *Journal of Vegetation Science* 27:283-294
- Muscarella R, Uriarte M, Erickson DL, Swenson NG, Kress WJ, Zimmerman JK (2016b) Variation of tropical forest assembly processes across regional environmental gradients. *Perspectives in Plant Ecology, Evolution and Systematics* 23:52-62
- Odum EP (1969) Strategy of ecosystem development. *Science* 164:262-270
- Paine CET, Baraloto C, Chave J, Hérault B (2011) Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120:720-727
- Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 5:961-970
- Pillar VD, Blanco CC, Müller SC, Sosinski EE, Joner F, Duarte, LD (2013) Functional redundancy and stability in plant communities. *Journal of Vegetation Science* 24:963-974
- Poorter L, Castilho C, Schiatti J, Oliveira R, Costa F (2018a) Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist* 219:109-121
- Poorter L, Rozendaal DMA, Bongers F, de Almeida-Cortez JS, Almeyda Zambrano AM, Álvarez FS, Andrade JL, Villa LFA, Balvanera P, Becknell JM, Bentos TV, Bhaskar R, Boukili V, Brancalion PHS, Broadbent EN, César RG, Chave J, Chazdon RL, Colletta GD, Craven D, de Jong BHJ, Denslow JS, Dent DH, DeWalt SJ, García ED, Dupuy JM, Durán SM, Espírito Santo MM, Fandiño MC, Fernandez GW, Finegan B, Moser VG, Hall JS, Hernández-Stefanoni JL, Jakovac CC, Junqueira AB, Kennard D, Lebrija-Trejos E, Letcher SG, Lohbeck M, Lopez OR, Marín-Spiotta E, Martínez-Ramos M, Martins SV, Massoca PES, Meave JA, Mesquita R, Mora F, de Souza Moreno V, Müller SC, Muñoz R, Muscarella R, de Oliveira Neto SN, Nunes YRF, Ochoa-Gaona S, Paz H, Peña-Claros M, Piotto D, Ruíz J, Sanaphre-Villanueva L, Sanchez-Azofeifa A, Schwartz NB, Steininger MK, Thomas WW, Toledo M, Uriarte M, Utrera LP, van Breugel M, van der Sande MT, van der Wal H, Veloso MDM, Vester HFM, Vieira ICG, Villa PM, Williamson GB, Wright SJ, Zanini KJ, Zimmerman JK, Westoby M (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution* 3:928-934

Poorter L, van der Sande M, Arets E, Ascarrunz N, Enquist B, Finegan B, Licona J, Martinez-Ramos M, Mazzei L, Meave J, Muñoz R, Nyctch C, Oliveira A, Pérez-García E, Prado Júnior J, Rodríguez-Velazques J, Ruschel A, Negret B, Schiavini I, Peña-Claros M (2018b) Biodiversity and climate determine the functioning of Neotropical forests. *Global Ecology and Biogeography* 27:389-390

Poorter L, van der Sande MT, Arets EJ, Ascarrunz N, Enquist BJ, Finegan B, Licona JC, Martínez-Ramos M, Mazzei L, Meave JA (2017) Biodiversity and climate determine the functioning of Neotropical forests. *Global Ecology & Biogeography* 26:1423-1434

Powell TL, Koven CD, Johnson DJ, Faybishenko B, Fisher RA, Knox RG, McDowell NG, Condit R, Hubbell SP, Wright SJ, Chambers JQ, Kueppers LM (2018) Variation in hydroclimate sustains tropical forest biomass and promotes functional diversity. *New Phytologist* 219:932-946

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>

Reich PB (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275-301

Réjou-Méchain M, Tanguy A, Piponiot C, Chave J, Hérault B. (2017) biomass: an R package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution* 8:1163-1167

Rosenfield MF, Müller SC (2020) Plant traits rather than species richness explain ecological processes in subtropical forests. *Ecosystems* 23:52-66

Schindler DE, Armstrong JB, Reed TE (2015) The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13:257-263

Schrodte F, Kattge J, Shan H, Fazayeli F, Joswig J, Banerjee A, Reichstein M, Bönisch G, Díaz S, Dickie J (2015) BHPMF—a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. *Global Ecology and Biogeography* 24:1510-1521

Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB (2016) Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180:923-931

Siefert, A, Violle, C, Chalmandrier, L, Albert, C. H, Taudiere, A, Fajardo, A, Aarssen, L. W, Baraloto, C, Carlucci, M. B. & Cianciaruso, M. V. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18: 1406-1419

Slik JWF, Franklin J, Arroyo-Rodríguez V, Field R, Aguilar S, Aguirre N, Ahumada J, Aiba SI, Alves LF, A K, Avella A, Mora F, Aymard CGA, Báez S, Balvanera P, Bastian ML, Bastin JF, Bellingham PJ, van den Berg E, da Conceição Bispo P, Boeckx P, Boehning-Gaese K, Bongers F, Boyle B, Brambach F, Brearley FQ, Brown S, Chai SL, Chazdon RL, Chen S, Chhang P, Chuyong G, Ewango C, Coronado IM, Cristóbal-Azkarate J, Culmsee H, Damas K, Dattaraja HS, Davidar P, DeWalt SJ, Din H, Drake DR, Duque A, Durigan G, Eichhorn K, Eler ES, Enoki T, Ensslin A, Fandohan AB, Farwig N, Feeley KJ, Fischer M, Forshed O, Garcia QS, Garkoti SC, Gillespie TW, Gillet JF, Gonmadje C, Granzow-de la Cerda I, Griffith DM, Grogan J, Hakeem KR, Harris DJ, Harrison RD, Hector A, Hemp A, Homeier J, Hussain MS, Ibarra-Manríquez G, Hanum IF, Imai N, Jansen PA, Joly CA, Joseph S, Kartawinata K, Kearsley E, Kelly DL, Kessler

M, Killeen, TJ, Kooyman RM, Laumonier Y, Laurance SG, Laurance WF, Lawes MJ, Letcher SG, Lindsell J, Lovett J, Lozada J, Lu X, Lykke AM, Mahmud KB, Mahayani NPD, Mansor A, Marshall AR, Martin EH, Calderado Leal Matos D, Meave JA, Melo FPL, Mendoza ZHA, Metali F, et al. (2018) Phylogenetic classification of the world's tropical forests. *Proceedings of the National Academy of Sciences* 115:1837-1842

Soliveres S, Maestre FT, Bowker MA, Torices R, Quero JL, García-Gómez M, Cabrera O, Cea AP, Coaguila D, Eldridge DJ (2014) Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics* 16:164-173

Spasojevic MJ, Suding KN (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100:652-661

Spasojevic MJ, Turner BL, Myers JA (2016) When does intraspecific trait variation contribute to functional beta-diversity? *Journal of Ecology* 104:487-496

Swenson NG (2014) Phylogenetic imputation of plant functional trait databases. *Ecography* 37: 105-110

Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94:451-459

Swenson NG, Stegen JC, Davies SJ, Erickson DL, Forero-Montaña J, Hurlbert AH, Kress WJ, Thompson J, Uriarte M, Wright SJ (2012) Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology* 9:490-499

Turcotte MM, Levine JM (2016) Phenotypic Plasticity and Species Coexistence. *Trends in Ecology & Evolution* 31:803-813

Umaña MN, Mi X, Cao M, Enquist BJ, Hao Z, Howe R, Iida Y, Johnson D, Lin L, Liu X, Ma K, Sun IF, Thompson J, Uriarte M, Wang X, Wolf A, Yang J, Zimmerman JK, Swenson NG (2017) The role of functional uniqueness and spatial aggregation in explaining rarity in trees. *Global Ecology and Biogeography* 26:777-786

van Buuren S, Groothuis-Oudshoorn K (2010) MICE: Multivariate imputation by chained equations in R. *Journal of Statistical Software* 45:1-68

van der Sande M, Arets E, Peña-Claros M, Hoosbeek M, Cáceres-Siani Y, Van der Hout P, Poorter L (2018) Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. *Functional Ecology* 32:461-474

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27:244-252

Warren JM, Hanson PJ, Iversen CM, Kumar J, Walker AP, Wullschlegel SD (2015) Root structural and functional dynamics in terrestrial biosphere models—evaluation and recommendations. *New Phytologist* 205:59-78

Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181-183

- Wenhua L. (2004) Degradation and restoration of forest ecosystems in China. *Forest Ecology and Management* 201:33-41
- Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21:261-268
- Wright SJ, Kitajima K, Kraft NJ, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Díaz S. (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664-3674
- Wu Z (1995) An Introduction to the Tropical Forest Soils and Effect of Shifting Cultivation on Soils in Jianfengling. In: Zeng Q, Zhou G, Yide L, Wu Z, Chen B (eds) *Researches on Tropical Forest Ecosystems in Jianfengling of China*. China Forestry Publishing House, Beijing, China, pp 5-25
- Xu H, Detto M, Fang S, Li Y, Zang R, Liu S (2015a) Habitat hotspots of common and rare tropical species along climatic and edaphic gradients. *Journal of Ecology* 103:1325-1333.
- Xu H, Li Y, Liu S, Zang R, He F, Spence JR (2015b) Partial recovery of a tropical rain forest a half-century after clear-cut and selective logging. *Journal of Applied Ecology* 52:1044-1052
- Xu X, Trugman A (2021) Trait-Based Modeling of Terrestrial Ecosystems: Advances and Challenges Under Global Change. *Current Climate Change Reports* doi:10.1077/s406541-020-00168-6
- Yang J, Cao M, Swenson NG (2018) Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution* 33:326-336
- Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. <https://doi.org/10.5061/dryad.234>
- Zeng Q (1995) Survey of Water-Heat Condition and Vegetation Ecological Series in Jianfengling. In: Zeng Q, Zhou G, Yide L, Wu Z, Chen B (eds) *Researches on Tropical Forest Ecosystems in Jianfengling of China*. China Forestry Publishing House, Beijing, China, pp 5-25
- Zhou G (1995) Ecological Effects of Human Activities in Jianfenglin Forest Region, Hainan Island. In: Zeng Q, Zhou G, Yide L, Wu Z, Chen B (eds) *Researches on Tropical Forest Ecosystems in Jianfengling of China*. China Forestry Publishing House, Beijing, China, pp 38-48
- Zuo X, Yue X, Lv P, Yu Q, Chen M, Zhang J, Luo Y, Wang S, Zhang, J (2017) Contrasting effects of plant inter- and intraspecific variation on community trait responses to restoration of a sandy grassland ecosystem. *Ecology and Evolution* 7:1125-1134

Tables

Table 1: Trait flex Analysis of Variance (ANOVA) table for forest type as a factor in assemblage-weighted functional trait variance. Statistics for residual variance not shown (see Online Resource 2). These assemblage-weighted analyses use small plot tree community data and functional trait data for 72 species (i.e., only those for which trait data was directly measured along the 6.6 km transect in JFL). Fixed assemblage-weighted mean

values use all functional trait data from individuals sampled along the transect ($n = 423$), whereas specific assemblage-weighted means match functional trait data from plant individuals to plots with corresponding forest-type classification ($n = 198$ for primary forest and $n = 225$ for secondary forest). Intraspecific variability = fixed – specific. Abbreviations are as follows: df = degrees of freedom, SS = sum of squares, F = F-statistic, p = probability of obtaining the F-statistic. Probabilities are denoted as: $*p < .05$, $**p < .01$, $***p < .001$. Note that in this case, the mean squared error is equal to the sum of squares because there is 1 degree of freedom; therefore, mean squared errors are not shown. (See Online Resource 2)

Trait	Fixed				Specific				Intraspecific variability			
	df	SS	F	p	df	SS	F	p	df	SS	F	p
Leaf Area	1	20.00	0.04	0.84	1	4260.00	8.15	**	1	3696.90	47.42	***
SLA	1	3.46	1.50	0.22	1	61.50	19.10	***	1	94.12	112.14	***
Leaf Thickness	1	8.00E-05	0.19	0.67	1	0.02	28.28	***	1	0.02	89.12	***
Root Diameter	1	3.01E-03	0.29	0.59	1	0.04	3.15	0.08	1	0.07	18.42	***
SRL	1	81.30	0.83	0.36	1	4400.80	37.20	***	1	3285.60	88.93	***
RTD	1	8.99E-03	0.73	0.39	1	0.04	6.49	*	1	0.10	86.33	***
RBI	1	1.59E-02	4.92	*	1	5.59	156.76	***	1	5.15	275.00	***

Table 2: Trait flex Analysis of Variance (ANOVA) table for forest type in community-weighted functional trait variance. Statistics on residual variance are not shown. These ANOVAs were done using small plot tree community data and functional trait data for 582 species (i.e., the entire community for which we applied pGLM data imputation to). Fixed values use pGLM-imputed functional trait data for a matrix containing species means irrespective of forest type (i.e., all trait data collected along the 6.6 km transect), whereas specific values use pGLM-imputed functional traits data corresponding to either secondary or primary forest portions of the transect. Intraspecific variability = fixed – specific. Abbreviations are as follows: df = degrees of freedom, SS = sum of squares, F = F-statistic, p = probability of obtaining the F-statistic. Probabilities are denoted as: $*p < .05$, $**p < .01$, $***p < .001$. Note that in this case, the mean squared error is equal to the sum of squares because there is 1 degree of freedom; therefore, mean squared errors are not shown.

Trait	Fixed				Specific				Intraspecific variability			
	<i>df</i>	SS	<i>F</i>	<i>p</i>	<i>df</i>	SS	<i>F</i>	<i>p</i>	<i>df</i>	SS	<i>F</i>	<i>p</i>
Leaf Area	1	48.10	0.44	0.51	1	5548.40	56.97	***	1	4563.30	271.24	***
SLA	1	3.45E-4	5E-4	0.98	1	47.68	50.36	***	1	47.91	317.85	***
Leaf Thickness	1	6.76E-5	0.53	0.47	1	6.24E-3	38.69	***	1	5.02E-3	150.38	***
Root Diameter	1	9.01E-3	2.24	0.14	1	0.09	21.26	***	1	0.16	192.09	***
SRL	1	50.10	1.63	0.20	1	1515.60	51.59	***	1	2116.90	361.98	***
RTD	1	1.91E-3	1.80	0.18	1	0.03	15.42	***	1	0.04	132.44	***
RBI	1	5.68E-3	1.50	0.22	1	4.58	528.60	***	1	4.26	1480.70	***

Figures

Jianfengling Forest Reserve - Hainan Island, China

Figure 1

The study site: the Jianfengling Forest Reserve (JFL) of Hainan Island, China. Hainan Island is a small continental island off China's southeastern coast, shown in the red box of the inset map. The 47,200 ha JFL boundary is shown with red boundary. The 6.6 km transect of where functional traits of saplings were sampled is shown in black. The first half of the transect is in secondary forest with a history of logging, and the second half of the transect is in unlogged, primary forest. Small 1/16th-ha plots (Xu et al. 2015a, Xu et al. 2015b) in unlogged, primary and either clear-cut or logged secondary forest are shown as pink and green points, respectively. Logging and forest disturbance in the secondary plots has happened in the last 20-55 years. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever

on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Relative stem densities (% of stems ha⁻¹) for the 72 species in 164 1/16th-ha plots in Jianfengling, Hainan Island, China (Fig. 1, Xu et al. 2015b), for which trait data were sampled (Hogan et al. 2020). Fifty-two of those plots are in well-conserved, primary forest, while 112 are in secondary forest (i.e., previously logged or clear-cut). Relative stem densities of these 72 species sum to 44% of stems in primary forest plots, and 33% of stems in secondary forest plots. Colors of species names correspond to plant family in order from phylogenetically oldest (i.e., more basal) to youngest (i.e., more derived): Lauraceae, Magnoliaceae, Annonaceae, Moraceae, Fagaceae, Juglandaceae, Burseraceae, Anacardiaceae, Sapindaceae, Rutaceae, Pentaphylacaceae, Sapotaceae, Ebenaceae, Theaceae, Styracaceae.

Figure 3

Community weighted mean (CWM) trait values for leaf area (A), SLA (B) and leaf thickness (C) for 164 1/16th-ha plots in Jianfengling, Hainan, China. Points are mean CWM values (± 95% confidence intervals) for plots by forest type (52 in primary and 112 in secondary). Fixed CWMs (in black) use trait values irrespective of forest type, while specific CWMs (in gray) use trait data from individuals collected within each forest type. The left panel in each figure shows assemblage-weighted mean (AWM) values, which use only measured data from 72 species, while the

right panel shows PhyloPars pGLM-imputed CWM functional trait values using the entire community (582 species).

Figure 4

Community weighted mean (CWM) trait values for fine root system average diameter (A), specific root length (SRL, B), root tissue density (RTD, C), and root branching intensity (RBI, D) for 164 1/16th-ha plots in Jianfengling, Hainan, China. Points are mean CWM values ($\pm$ 95% confidence intervals) for plots by forest type (52 in primary and 112 in secondary). Fixed CWMs use trait values irrespective of forest type, while specific CWMs use trait data that accounts for ITV between forest types. The left panel in each figure shows assemblage-weighted mean (AWM) values, which use only measured data from 72 species, while the right panel shows PhyloPars pGLM-imputed CWM functional trait values using the entire community (582 species).

Figure 5

Decomposition of the total variability in root and leaf traits for the tree communities in 164 1/16th-ha small plots in Jianfengling, Hainan China. The blue portion of the bars corresponds to the percent of variance explained by species turnover, while the red part shows the intraspecific variability effect – or the percent of variance explained by ITV. Black bars denote total variation (i.e., the variation, or total sum of squares – SS, in specific weighted-mean averages). The space between the top part of the column and bar corresponds to ITV and species turnover covariation; if the bar is above the column, the covariation is positive, and if below, the covariation is negative. The values are standardized by the total variation in specific CWM averages. The figure follows Figure 3 in Lepš et al. (2011).

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