

Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest

Catherine M. Hulshof^{1,*} and Nathan G. Swenson²

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA; and ²Center for Tropical Forest Science – Asia Program, Arnold Arboretum, Harvard University, Cambridge, MA 02138, USA

Summary

1. Patterns of species co-existence and species diversity in plant communities remain an important research area despite over a century of intensive scrutiny. To provide mechanistic insight into the rules governing plant species co-existence and diversity, plant community ecologists are increasingly quantifying functional trait values for the species found in a wide range of communities.

2. Despite the promise of a quantitative functional trait approach to plant community ecology, we suggest that, along with examining trait variation across species, an assessment of trait variation within species should also be a key component of a trait-based approach to community ecology. Variability within and between individuals and populations is likely widespread due to plastic responses to highly localized abiotic and biotic interactions.

3. In this study, we quantify leaf trait variation within and across ten co-existing tree species in a dry tropical forest in Costa Rica to ask: (i) whether the majority of trait variation is located between species, within species, within individuals or within the leaves themselves; (ii) whether trait values collected using standardized methods correlate with those collected using unstandardized methods; and (iii) to what extent can we differentiate plant species on the basis of their traits?

4. We find that the majority of variation in traits was often explained by between species differences; however, between leaflet trait variation was very high for compound-leaved species. We also show that many species are difficult to reliably differentiate on the basis of functional traits even when sampling many individuals.

5. We suggest an ideal sample size of at least 10, and ideally 20, individuals be used when calculating mean trait values for individual species for entire communities, though even at large sample sizes, it remains unclear if community level trait values will allow comparisons on a larger geographic scale or if species traits are generally similar across scales. It will thus be critical to account for intraspecific variation by comparing species mean trait values across space in multiple microclimatic environments within local communities and along environmental gradients. Further, quantifying trait variability due to plasticity and inheritance will provide a better understanding of the underlying patterns and drivers of trait variation as well as the application of functional traits in outlining mechanisms of species co-existence.

Key-words: community ecology, functional ecology, functional trait, plasticity, power analysis, species differentiation, tropical dry forest

Introduction

The co-existence of plant species is often thought to be constrained by the ability of individuals to function in different

abiotic and biotic environments. Thus, information pertaining to functional ecology of the species in communities is essential for testing mechanistic hypotheses regarding species co-existence (Weiher & Keddy 1995; McGill *et al.* 2006). In particular, community ecologists would benefit from quantitative information that describes the functional

*Correspondence author. E-mail: hulshof@email.arizona.edu

differences between individuals of different species and individuals of the same species. Increasingly, community ecologists have sought to generate functional trait information for all species in their study systems as means to reconcile hypotheses regarding species co-existence (Weiher & Keddy 1995; McGill *et al.* 2006).

The proposed functional trait-based community ecology has drawn considerable interest with an increasing number of trait-based studies of plant species co-existence appearing in the literature (Weiher, Clarke, & Keddy 1998; Ackerly & Cornwell 2007; Swenson & Enquist 2007; Swenson and Enquist in press; Swenson *et al.* 2007; Kraft, Valencia, & Ackerly 2008; Cornwell & Ackerly 2009; Swenson 2009). The power of this functional trait approach is twofold. First, plant functional ecologists have generated and refined a small list of plant traits that are robust indicators of plant ecological and life-history strategies (Westoby *et al.* 2002). Second, the traits of interest are easily measured allowing one to generate a distribution of species-level trait values even in extraordinarily species diverse communities (i.e. Kraft, Valencia, & Ackerly 2008).

Despite the above strengths of the functional trait-based approach to community ecology, there is one central criticism that is inevitable. As sessile organisms, plants are renowned for their plasticity both within species and individuals. Additionally, interspecific variation in leaf traits has been correlated with climatic variation, geology, altitude, latitude and niche breadth (Schimper 1903; Raunkjær 1934; Whittaker 1967; Givnish 1979; Wright *et al.* 2004; Ackerly & Cornwell 2007), while intraspecific variation has been correlated with microhabitat differences in topography, slope, soil moisture availability (e.g. Lambrecht & Dawson 2007), and insolation (e.g. Ackerly *et al.* 2002). Plant functional ecologists have sought to minimize the impact of intraspecific variation by formulating standardized protocols for plant functional trait measurement (Cornelissen *et al.* 2003) and by sampling multiple individuals. For example, in order to minimize the variability in leaf traits due to ontogeny, canopy position or shading, plant functional ecologists will generally only sample fully expanded, mature, and sun-exposed leaves (Cornelissen *et al.* 2003). This type of standardized trait collection protocol is generally feasible. Further, in global scale data sets the degree of intraspecific variation in plant functional trait values has been shown to be negligible compared with the global variability in species trait values (Diaz & Cabido 1997; Westoby 1998; Cornelissen *et al.* 2003; Garnier *et al.* 2004; Wright *et al.* 2004; Swenson & Enquist 2007). What is less clear is whether intraspecific variability in plant functional trait values is still negligible when one examines species in a more constrained geographic area where the range of interspecific trait values is likely much lower.

There is also a less well-established course of action for a plant ecologist interested in a functional trait study of their community when using standardized protocols is not easily accomplished (Kraft, Valencia, & Ackerly 2008; Swenson & Enquist 2008; Lake & Ostline 2009). For example, in tropical forests sun-exposed leaves can be exceedingly difficult to col-

lect due to the height of the vegetation or impossible to collect due to the fact that the vegetation only occurs in shaded habitats (Kraft, Valencia, & Ackerly 2008). The population density of many species in diverse tropical plant communities can be very low making it also difficult to achieve large sample sizes. Lastly, there is the considerable concern that the mean trait value for a species does not adequately represent the mean trait values for all populations or individuals of that species even if the trait values used to calculate the mean trait value for a species were collected using standardized protocols.

Ultimately, this leads to three questions that require answers. First, where does the majority of functional trait variation occur for locally co-existing species: between species, between individuals within the same species, within individuals or within plant organs (i.e. leaves)? Second, how well do trait values collected using standardized methods correlate with those collected using unstandardized methods (Kraft, Valencia, & Ackerly 2008; Swenson & Enquist 2008)? Third, how much power do we have to differentiate species on the basis of their functional traits when the sample size is low? Here we present a study that addresses the above three questions by quantifying leaf functional trait values within and across several tree species in the dry tropical forests of north-western Costa Rica.

Materials and methods

STUDY LOCATION AND SPECIES

This study was conducted in Bosque San Emilio of Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (10°48'53"N, 85°36'54"W). The study location is characterized as seasonal dry tropical forest (Holdridge *et al.* 1971) with a 6-month rainy season beginning mid-May and lasting through November, followed by a 6-month dry season during which much of the vegetation is fully to semi-deciduous. We selected the following 10 species for our study: Sapindaceae: *Allophylus occidentalis* (Sw.) Radlk., Burseraceae: *Bursera simaruba* (L.) Sarg., Capparaceae: *Capparis indica* (L.) Fawc. and Rendle, Rubiaceae: *Guettarda macrosperma* Donn. Sm., Celastraceae: *Hemiangium excelsum* (H.B.K.) A.C. Smith, Simaroubaceae: *Simarouba glauca* DC., Anacardiaceae: *Spondias mombin* L., Apocynaceae: *Stemmadenia obovata* (Hook & Arm.) Schum., Bignoniaceae: *Tabebuia ochracea* Standl., and Sterculiaceae: *Guazuma ulmifolia* (Lam.). Taxonomic nomenclature follows Janzen & Liesner (1980). The species *A. occidentalis*, *B. simaruba*, *S. glauca*, *S. mombin*, and *T. ochracea* have compound leaves and *C. indica*, *G. macrosperma*, *H. excelsum*, *S. obovata*, and *G. ulmifolia* have simple leaves. These species were chosen because they are among the most abundant species within this forest (Hubbell 1979). Specifically, all ten of these species are among the top 25% most abundant species in the San Emilio Forest Dynamics Plot (Hubbell 1979; Enquist *et al.* 1999; Swenson unpublished data).

LEAF TRAIT MEASUREMENT

During June 2008 we located ten individuals for each species in the study growing within Bosque San Emilio. The individuals selected were collected from locations distant from one another to reduce the

likelihood of collecting genetically similar individuals. From each individual we collected 10 fully-expanded, non-senescent leaves from multiple branches. Five of the leaves were fully exposed sun leaves collected from the upper canopy and five fully shaded leaves were collected from the lower canopy. All individuals within a species were collected on the same day within a 1-hour period and all leaves from all species were collected during a 4-day period. Immediately upon returning from the field, the fresh mass (M_w , g) for each leaf or leaflet was measured using an SP202 Ohaus® Scout Pro electronic balance (Ohaus Corporation, Pine Brook, New Jersey, USA). Leaf area (LA) was measured for each fresh leaf or leaflet using a CI-203 Portable Laser Area Meter (CID, Inc., Camas, Washington, USA). All leaves and leaflets were then placed in a drying oven for a minimum of 72 hours at 70°C and the final dry mass was recorded (M_D , g). Specific leaf area (SLA; $\text{cm}^2 \text{ g}^{-1}$) was calculated as: $\text{SLA} = A_w/M_D$; where A_w is the fresh leaf area (cm^2) and M_D is the final dry mass in grams. Leaf water content (LWC, $\text{g H}_2\text{O cm}^{-2}$) was calculated by subtracting leaf dry mass from leaf fresh mass and dividing by leaf fresh area.

STATISTICAL ANALYSES

The first goal of this study was to determine how variance in the four-leaf traits studied (LA, M_D , SLA, and LWC) is partitioned across and within species and individuals. To do this, we used a nested analysis of variance (ANOVA) and calculated how the variance in these traits was partitioned using the following nested levels: among species, among individual trees within a species, canopy position within individuals, and leaves within a canopy position. We performed this analysis for (a) all species, (b) simple-leaved species and (c) compound-leaved species. Next, we performed this analysis for all compound-leaved species with an additional nested level of leaflets within individual leaves. This subsequent procedure was carried out to allow for estimates of within leaf variation. Recent work by Kraft, Valencia, & Ackerly (2008) quantified leaf functional trait values on the 'minimum photosynthetic unit' (i.e. a leaflet) as a way to estimate the trait value for an entire leaf. Thus, this subsequent procedure was carried out to allow for estimates of within leaf variation and to test whether there is substantial variation among 'minimum photosynthetic units'. Lastly, all of the above analyses were repeated using only sun or shade leaves and excluding the canopy position level in the nested ANOVA. This procedure was performed to simulate a researcher that standardized their trait collection to only include sun or shade leaves, but not both.

The second goal of this study was to determine the degree to which shade leaf functional trait values correlate with sun-exposed leaf functional trait values collected from the same individual. To do this, we performed reduced major axis (RMA) regression of the sun-exposed leaf trait values onto the shade leaf trait values. We recorded the coefficient of determination and the confidence intervals of both the slope and intercept. The null expectation was that the intercept of the regression would not deviate significantly from zero and the slope would not significantly deviate from one. The RMA analyses were performed using the R package 'smatr' (R Development Core Team (2005); R Foundation for Statistical Computing, Vienna, Austria).

The third goal of this study was to determine whether we could differentiate the locally common species used in this study on the basis of their functional trait values and, if so, how many individuals must we sample to differentiate these species. To do this we performed a series of power analyses. First, we performed power analyses for one-way ANOVAs using sample sizes ranging from two to ten and using the

observed within and between group variances. These analyses reported the power to detect a significant difference ($\alpha = 0.05$) in trait values between at least two of the 10 species in our study at different sample sizes. Second, we performed a two-sample *t*-test power analysis between all possible species pairs using the observed trait variances and means within each species. This analysis generated a power curve that reports the power to detect a significant difference ($\alpha = 0.05$) between two species at sample sizes ranging from 0–50. The power analyses were performed using (a) all leaves, (b) only sun leaves and (c) only shade leaves collected from individuals.

Results

VARIANCE PARTITIONING

The first goal of this study was to determine how variance in the four-leaf traits studied (LA, M_D , SLA, and LWC) is partitioned across and within species and individuals. The nested ANOVA quantifies the variance in the four-leaf traits studied attributed to the levels: among species, among individual trees within a species, canopy position within individuals, and leaves within a canopy position for simple-leaved species (Table 1), for compound-leaved species (Table 1) and for all species (Table 2). All three analyses follow a general trend with variation between species being greatest, followed by between individuals and lastly, between leaves within individuals.

The nested ANOVA that includes the additional level of variation among leaflets for compound-leaved species, however, did not follow this trend (Table 3). Specifically, for all traits studied, variation among leaves was lowest for both high and low canopy positions, but within individual compound leaves variation was found to be higher among leaflets.

SHADE VS. SUN LEAVES

The second goal of this study was to determine the degree to which shade leaf functional trait values correlate with sun-

Table 1. Partitioned variance for each of the various levels of the nested analysis of variance for four functional traits measured on simple and compound-leaved species at high (sun) and low (shade) canopy positions

	Levels	Leaf Area	Dry Mass	SLA	LWC
Compound High	Species	0.46	0.47	0.4	0.46
	Individuals	0.31	0.38	0.28	0.34
	Leaves	0.23	0.16	0.32	0.20
Compound Low	Species	0.51	0.45	0.45	0.36
	Individuals	0.26	0.16	0.38	0.26
	Leaves	0.23	0.39	0.17	0.38
Simple High	Species	0.64	0.38	0.63	0.20
	Individuals	0.20	0.38	0.22	0.40
	Leaves	0.16	0.24	0.15	0.40
Simple Low	Species	0.61	0.34	0.60	0.17
	Individuals	0.21	0.38	0.28	0.39
	Leaves	0.19	0.28	0.12	0.44

Each field represents the proportion of variance in each level for each functional trait measured.

Table 2. Partitioned variance for each of the various levels of the nested analysis of variance for four functional traits for all leaves collected at high (sun) and low (shade) canopy positions, excluding the leaf type (i.e. simple or compound-leaved)

	Levels	Leaf area	Dry mass	SLA	LWC
All high	Species	0.59	0.55	0.49	0.38
	Individuals	0.24	0.32	0.26	0.35
	Leaves	0.17	0.13	0.25	0.27
All low	Species	0.65	0.55	0.51	0.32
	Individuals	0.19	0.13	0.34	0.29
	Leaves	0.16	0.32	0.15	0.39

Each field represents the proportion of variance in each level for each functional trait measured.

Table 3. Partitioned variance for each of the various levels of the nested analysis of variance for four functional traits for compound-leaved species at high (sun) and low (shade) canopy positions, with an additional leaflet level included in the analyses

	Levels	Leaf area	Dry mass	SLA	LWC
Compound leaflet high	Species	0.38	0.39	0.17	0.40
	Individuals	0.21	0.26	0.07	0.29
	Leaves	0.06	0.11	0.08	0.10
	Leaflet	0.36	0.25	0.68	0.20
Compound leaflet low	Species	0.50	0.24	0.59	0.15
	Individuals	0.18	0.07	0.18	0.09
	Leaves	0.10	0.06	0.12	0.04
	Leaflet	0.22	0.63	0.12	0.72

Each field represents the proportion of variance in each level for each functional trait measured.

exposed leaf functional trait values collected from the same individual. The RMA results are reported in Table 4. When regressing the sun leaf trait data onto the shade leaf data, all four trait-specific regressions had slopes significantly different from one and LA and LWC regressions had intercepts significantly different from one. The R^2 values ranged from 0.60 to 0.27 (Table 4).

DIFFERENTIATING SPECIES ON THE BASIS OF TRAIT VALUES

The third goal of this study was to determine whether we could differentiate the common species used in this study on

Table 4. Results from reduced major axis (Model II) regression of sun-exposed leaf trait values onto shade leaf trait values

	Intercept	Slope	R^2
Leaf area	-17.75* (-10.38–23.88)	1.08* (1.14–1.02)	0.68
Dry mass	-0.02 (0.10–0.11)	1.14* (1.22–1.05)	0.50
SLA	9.54 (16.25–6.22)	0.83* (0.91–0.74)	0.52
LWC	0.001* (0.0015–0.0003)	0.81* (0.85–0.74)	0.27

The asterisk for the intercept indicates that values were significantly different from zero. The asterisk for the slope indicates that values were significantly different from one. The 95% confidence intervals are given in parentheses (CI_{High} – CI_{Low}).

the basis of their functional trait values and, if so, how many individuals must we sample to differentiate these species. The ANOVA power analyses found that, for all traits, the statistical power to detect a significant difference between at least one species pair in our study was 99–100% even when sample sizes were below $n = 4$ (results not shown). This result was not surprising given the large range in trait values amongst some of the species in this study particularly for traits such as LA.

The two sample t -test power analyses were designed to quantify the power to differentiate the mean trait values between two species at different sample sizes. Due to the large number of pair-wise comparisons, we will only report three comparisons that represent the breadth of the results. The first example in Fig. 1 is given to demonstrate the power curves for comparisons between two species with very different mean trait values, *C. indica* and *T. ochracea*. In this case, for all traits except for LWC, the power to detect a significant difference in trait means is near one, even at very low sample sizes.

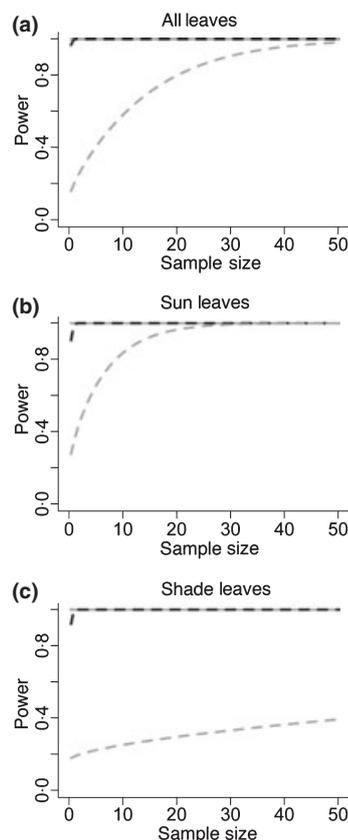


Fig. 1. Two sample t -test power curves for the species pair of *Capparis indica* and *T. ochracea*. In panel a, sun and shade leaves were used to calculate the individual and species means and variances. In panel b, only sun leaves were used to calculate the individual and species means and variances. In panel c, only shade leaves were used to calculate the individual and species means and variances. The solid black line represents LA. The solid grey line represents M_D . The dashed black line represents SLA. The dashed grey line represents LWC.

The second two cases in Figs 2 and 3 are given to display the power curves for species pairs with very similar trait values. In Fig. 2, two simple-leaved species, *C. indica* and *G. ulmifolia*, are used for the analysis. In Fig. 3, two compound-leaved species, *T. ochracea* and *B. simarouba*, are used. In both cases, the power analyses show that, for LA and M_D , a sample size of 10 or greater generally achieved 80% power (Figs 2 and 3). The LWC and SLA results suggest that a sample size of 20 or greater is generally needed to achieve 80% power (Figs 2 and 3). All of the trait mean and standard deviation data used to generate the power curves reported and not reported are available in Table S1 in Supporting information.

Discussion

Recently, plant community ecologists have become increasingly interested in incorporating functional trait data into their research in order to more rigorously test mechanistic hypotheses regarding species co-existence and diversity (Mcgill *et al.* 2006). Two dominant paradigms include the

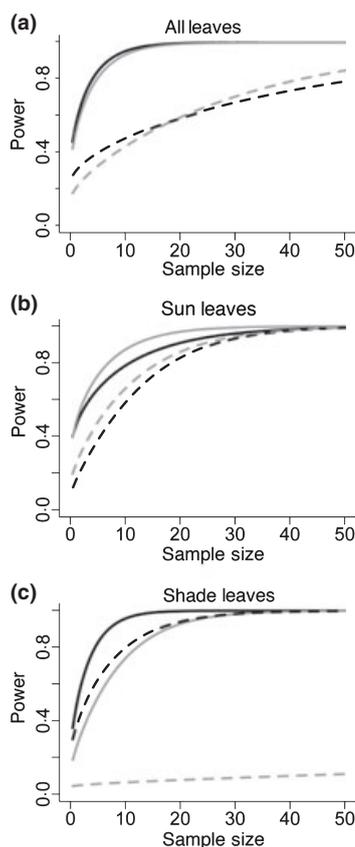


Fig. 2. Two sample *t*-test power curves for the species pair of *Capparis indica* and *Guazuma ulmifolia*. In panel a, sun and shade leaves were used to calculate the individual and species means and variances. In panel b, only sun leaves were used to calculate the individual and species means and variances. In panel c, only shade leaves were used to calculate the individual and species means and variances. The solid black line represents LA. The solid grey line represents M_D . The dashed black line represents SLA. The dashed grey line represents LWC.

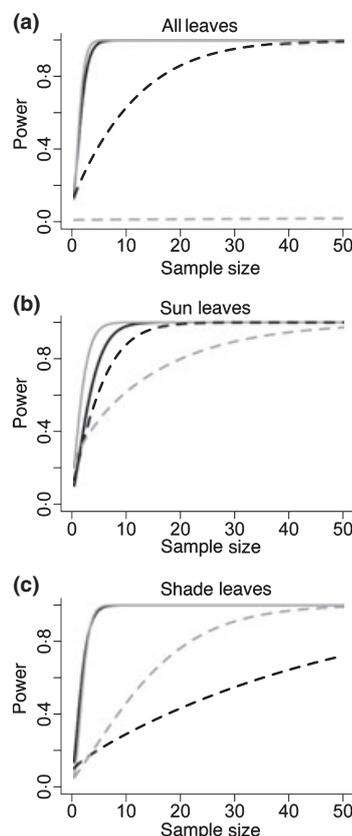


Fig. 3. Two sample *t*-test power curves for the species pair of *T. ochracea* and *Bursera simarouba*. In panel a, sun and shade leaves were used to calculate the individual and species means and variances. In panel b, only sun leaves were used to calculate the individual and species means and variances. In panel c, only shade leaves were used to calculate the individual and species means and variances. The solid black line represents LA. The solid grey line represents M_D . The dashed black line represents SLA. The dashed grey line represents LWC.

distinct and shared resource preference models (Wisheu 1998) and the neutral theory (Hubbell 2001) of species co-existence. The majority of the research to date has utilized species-specific mean trait values and less focus has been placed on the variation in trait values within species. In this study, we quantified leaf trait variation within and across ten co-existing tree species in a dry tropical forest in northwestern Costa Rica. The first major question we asked was: Is the majority of trait variation located between species, within species, within individuals or within the leaves themselves?

VARIANCE PARTITIONING

In addressing the first question we found that simple-leaved species followed a general trend across all leaf traits sampled with variation between species being greatest, followed by between individuals and lastly, between leaves of separate individuals. Similarly, compound-leaved species followed this trend when individual leaflet trait values were not considered. When including leaflet trait values for compound-leaved species, variation was found to be highest between species and

between leaflets. The above findings suggest the importance of leaflet level trait variation and suggest that quantifying leaf functional traits on these 'minimum photosynthetic units' (sensu Kraft, Valencia, & Ackerly 2008) may not be a reliable method for determining whole-leaf trait values. Thus, for compound-leaved species it will be necessary to quantify whole leaf trait values using multiple or all leaflets. The finding that, at least for the 10 species in this study, the majority of the trait variation was among species and not within species suggests that species may be able to be differentiated on the basis of their trait values.

ESTIMATING SUN LEAF TRAIT VALUES WITH SHADE LEAF TRAIT VALUES

The second major question we asked in this study was: How well do trait values collected using standardized methods correlate with those collected using unstandardized methods? To answer this question we regressed sun leaf data onto shade leaf data (Table 4). In all cases the slopes of the regressions were significantly different from one suggesting that shade and sun leaves do indeed have different trait values. The finding that sun and shade leaves have different trait values is not particularly surprising. What is perhaps more surprising is the finding that the R^2 -values never exceed 0.60. We argue that these values are quite low if one is attempting to estimate the trait value of sun leaves from shade leaves (e.g. Kraft, Valencia, & Ackerly 2008). A similar, but more prevalent, issue includes the exclusive use of sun leaves (Cornelissen *et al.* 2003) to describe species' mean trait values. While it is evident that intracanalopy plasticity is often driven by variability in levels of irradiance and plays an important role in whole plant function (Rozendaal, Hurtado, & Poorter 2006; Sack *et al.* 2006), few studies incorporate trait collections from all canopy positions to account for this degree of plasticity in trait values. In particular, because plant ecologists are interested in utilizing functional traits to gauge whole-plant performance and ecological strategies, a valid question is whether it is more appropriate to quantify trait values from all canopy positions rather than just the sun-exposed leaves (Lake & Ostling 2009)? Ultimately, we suggest that similar RMA regressions of sun-exposed leaf trait values onto shade leaf trait values in other forests and communities should be performed to test if the predicted correlation between sun and shade leaves holds true across multiple communities (but see Sack *et al.* 2006; Rozendaal, Hurtado, & Poorter 2006).

SPECIES DIFFERENTIATION ON THE BASIS OF FUNCTIONAL TRAITS

The third question we asked in this study was: how much power do we have to differentiate plant species on the basis of their traits when the number of individuals sampled is small? We have presented a series of power analyses between three different species pairs to show the breadth of the power curves we generated when doing all pair-wise species comparisons. Unsurprisingly, in some cases, the two species are so different

in their trait means that they can be differentiated at very low sample sizes (Fig. 1). More interesting were the power curves generated when comparing species pairs that had very similar mean trait values (Figs 2 and 3). In these cases, we found that a sample size of greater than 10, and often greater than 20, was needed to achieve a statistical power of 80%. For the functional trait LWC, there were such high levels of variance in the data that extremely high sample sizes would be needed to differentiate similar species and maybe even dissimilar species. Ultimately, the power analysis results suggest that if plant community ecologists want to reliably distinguish the species in their systems on the basis of leaf functional traits, sample sizes of 10 or greater are likely needed. In species rich communities this sample size may need to be even larger, unfortunately making the challenge of generating functional trait data sets for tropical communities ever more challenging.

Finally, if we are to fully adopt a functional trait approach to studying species co-existence and community ecology, multiple, orthogonal trait axes may be necessary to differentiate species across local and broad geographic ranges on the basis of functional traits. Even at large sample sizes, it remains unclear if community level trait values will allow comparisons on a larger geographic scale, or if species traits are generally similar across scales. It will thus be important to compare species mean trait values across space in multiple microclimatic environments within the same community and throughout the entire species range. This will determine whether or not species have similar values across their range or if the interplay between plasticity and local adaptation is an important driver of community level trait values. Finally, further quantifying trait variability due to plasticity and inheritance across multiple scales will allow for a better understanding of the underlying patterns and drivers of trait variation as well as the application of functional traits in outlining mechanisms of species co-existence.

Acknowledgements

The authors thank Jason Pither for stimulating our interest in functional trait plasticity and for his statistical advice and James Stegen for insightful comments on an early version of the manuscript. We also thank Jim Dalling, Jeff Lake and an anonymous reviewer for their suggestions and comments. CMH is supported by a National Science Foundation Graduate Research Fellowship. NGS is supported by a National Science Foundation Postdoctoral Fellowship in Bioinformatics. We would like to extend our sincerest appreciation to Roger Blanco, Maria Marta Chavarría, Felipe Chavarría, Roberto Espinoza, Adrian Guadamuz, Winnie Hallwachs, Daniel Janzen and Alejandro Masis for their logistical and technical support, encouragement and expertise.

References

- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135–145.
- Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K. & Starmer, K.P. (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia*, **130**, 449–457.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden,

- M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.
- Diaz, S. & Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science*, **8**, 463–474.
- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. (1999) Allometric scaling of production and life history variation in vascular plants. *Nature*, **401**, 907–911.
- Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Givnish, T.J. (1979) On the adaptive significance of leaf form. *Topics in Plant Population Biology* (eds O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven), pp. 375–407. Columbia University Press, New York.
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. Jr (1971) *Forest Environments in Tropical Life Zones: A Pilot Study*. Pergamon, San Francisco.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Hubbell, S.P. (2001) *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Janzen, D.H. & Liesner, R. (1980) Annotated check-list of plants of lowland Guanacaste province, Costa Rica, exclusive of grasses and non-vascular cryptogams. *Brenesia*, **18**, 15–90.
- Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an amazonian forest. *Science*, **322**, 580–582.
- Lake, J.K. & Ostling, A. (2009) Comment on 'Functional traits and niche-based community assembly in an Amazonian forest'. *Science*, **324**, 1015.
- Lambrecht, S.C. & Dawson, T.E. (2007) Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia*, **151**, 574–583.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–184, Elsevier, 178–185.
- R Development Core Team (2005) *R: A Language and Environment For Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>, accessed 3/7/2009.
- Raunkier, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.
- Rozendaal, D.M.A., Hurtado, V.H. & Poorter, L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, **20**, 207–216.
- Sack, L., Melcher, P.J., Liu, W.H., Middleton, E. & Pardee, T. (2006) How strong is intracanalopy leaf plasticity in temperate deciduous trees? *American Journal of Botany*, **93**, 829–839.
- Schimper, A.F.W. (1903) *Plant-Geography Upon a Physiological Basis*. Clarendon Press: Oxford.
- Swenson, N.G. (2009) Herbaceous monocot form and function along a tropical rain forest light gradient: a reversal of dicot strategy. *Journal of Tropical Ecology*, **25**, 103–106.
- Swenson, N.G. & Enquist, B.J. (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, N.G. & Enquist, B.J. (2008) The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *American Journal of Botany*, **95**, 516–519.
- Swenson, N.G. & Enquist, B.J. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, in press.
- Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.
- Weiher, E., Clarke, G.D.P. & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, **81**, 309–322.
- Weiher, E. & Keddy, P.A. (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**, 159–164.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Reviews*, **49**, 207–264.
- Wisheu, I.C. (1998) How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos*, **83**, 246–258.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Received 28 March 2009; accepted 16 June 2009

Handling Editor: Jim Dalling

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. The mean and standard deviation in parentheses of trait values for the 10 species.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.