

**Low functional and phylogenetic turnover, but high taxonomic turnover of melastomes across a Costa Rican elevation gradient**

Journal:	<i>Journal Of Tropical Ecology</i>
Manuscript ID	Draft
Manuscript Type:	Short Communication
Date Submitted by the Author:	n/a
Complete List of Authors:	Kandlikar, Gaurav; University of California Los Angeles, Vaz, Marcel; University of California Los Angeles Kriebel, Ricardo; University of Wisconsin Madison, Department of Botany Vargas, German; University of Minnesota Twin Cities, Department of Ecology, Evolution and Behaviour; Universidad Nacional de Costa Rica, Escuela de Ciencias Biologicas Michelangeli, Fabian; New York Botanical Garden, Institute of Systematic Botany Cordero, Roberto; Universidad Nacional, Biological Sciences Avalos, Gerardo; School for Field Studies; Universidad de Costa Rica, Escuela de Biologia Almeda, Frank; California Academy of Sciences, Institute for Biodiversity Science and Sustainability Fetcher, Ned; Wilkes University, Biodiversity and Ecological Research Insitute Kraft, Nathan; University of California Los Angeles
Keywords:	beta diversity, functional traits, MONTANE FOREST, Melastomataceae, Miconia, SLA, tropical forest

SCHOLARONE™  
Manuscripts

**Title:** Low functional and phylogenetic turnover, but high taxonomic turnover of melastomes across a Costa Rican elevation gradient

**Running title:** Melastome Functional Trait Turnover

**Keywords:** beta diversity, functional traits, Melastomataceae, *Miconia*, montane forest, SLA, tropical forest.

**Authors:** Gaurav S. Kandlikar<sup>1\*</sup>, Marcel Vaz<sup>1</sup>, Ricardo Kreibel<sup>2</sup>, German Vargas<sup>3</sup>, Fabián A. Michelangeli<sup>4</sup>, Roberto Cordero<sup>3</sup>, Frank Almeda<sup>5</sup>, Gerardo Avalos<sup>6</sup>, Ned Fetcher<sup>7</sup>, Nathan J. B. Kraft<sup>1</sup>

<sup>1</sup> Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, California 90095

<sup>2</sup> Department of Botany, University of Wisconsin-Madison

<sup>3</sup> College of Biological Sciences, National University of Costa Rica

<sup>4</sup> Institute of Systematic Botany, The New York Botanical Garden

<sup>5</sup> Institute for Biodiversity Science and Sustainability, California Academy of Sciences

<sup>6</sup> School of Biology, University of Costa Rica

<sup>7</sup> Institute for Environmental Science and Sustainability, Wilkes University

\*gkandlikar@ucla.edu

**Abstract:** Turnover in community-wide plant functional traits across elevational gradients is well-documented. Specifically, environmentally favorable landscapes in lower elevations tend to be dominated by species with resource-acquisitive traits, while more resource-conservative taxa dominate the harsher environments of higher elevation communities. However, the extent to which individual clades exhibit similar patterns of functional turnover is unclear. Patterns of functional turnover along a Costa Rican elevational gradient were tested within the plant family Melastomataceae. Counter to expectations, it was found that many functional traits do not turnover across the gradient, despite substantial functional diversity among Costa Rican melastomes. Additionally, taxonomic beta diversity across the gradients is well correlated with the elevational dissimilarity between sites. Phylogenetic beta diversity was only correlated with elevation dissimilarity when measured with a metric that emphasizes turnover at the phylogeny tips. These results highlight how community wide trait-environment relationships may obscure idiosyncratic responses of individual clades to environmental gradients. These findings are relevant to understanding family-level responses to climate change along elevational gradients in highly diverse communities.

Biotic and abiotic environmental conditions shape the distribution of plant taxa across the globe (Kraft et al. 2014, Weiher & Keddy 1999, Westoby & Wright 2006). The influence of environmental variation on community structure is often reflected in the distribution of plant functional traits, which capture underlying variation in plant strategy (Cornwell & Ackerly 2009, Westoby et al. 2002). Communities found in harsher environmental conditions, such as low temperature or low resource availability, tend to be dominated by plants with resource-conservative functional strategies such as higher wood density and lower specific leaf area (SLA) (Poorter et al. 2009, Reich 2014). Such shifts have been documented across various abiotic gradients: for example, a recent global meta-analysis by Read et al. (2014) showed a negative correlation between mean annual temperature (MAT) and both leaf mass per area and area-based leaf nitrogen concentration.

In gradients that have been studied in detail, however, patterns of community-wide shifts in trait values may belie the functional responses of individual species or clades, which can exhibit idiosyncratic responses to the same gradient (Ackerly & Cornwell 2007). A key component for better understanding of functional turnover of communities along abiotic gradients lies in the role that individual clades play in shaping these patterns. There are several possible relationships between clade- and community-wide trait shifts along gradients (Westoby et al. 2002). First, turnover patterns within clades may mirror community-wide trait responses (e.g., Ackerly & Cornwell 2007). Second, clades may exhibit counter-gradient responses relative to the rest of the community, e.g., in contrasting responses of evergreen and deciduous species to shade (Lusk et al. 2008). Finally, members of a clade may have similar functional traits along a gradient despite shifts in community-wide means. Such patterns in trait

turnover may be driven by the degree of taxonomic and phylogenetic turnover of the clade across the gradient, along with any phylogenetic constraints on trait variation.

As patterns of plant community functional turnover across gradients have been well-documented (Cornwell & Ackerly 2009, Read et al. 2014), here we focus on better understanding the relationship within an important clade that spans a broad environmental gradient. We focus on the plant family Melastomataceae, which contains > 5000 species distributed from lowland rainforests to high-elevation páramos (Reginato et al. 2016). The turnover of melastome species along environmental gradients has been shown to correlate well with the taxonomic turnover of the tree communities along these gradients (Ruokolainen et al. 1997), but the patterns of functional turnover remain unknown. Here, we assess whether patterns of functional turnover within melastomes either track or run counter to established underlying patterns of community functional turnover across an elevation gradient in the tropics.

Following the standard protocols of Perez-Harguindeguy et al. (2013), we measured a suite of functional traits (SLA, leaf dry matter content (LDMC), leaf toughness, leaf N concentration, stem density) of melastomes growing at five sites along the 2500 m elevational transect of Volcán Barva in Costa Rica's Cordillera Central. This transect covers a ~13°C difference in mean annual temperature (MAT, Table 1) and substantial variation in soil chemistry and geology (Clark et al. 2015, Lieberman et al. 1996). We sampled herbaceous, epiphytic, and woody species in the environments where they were most likely to grow (e.g., herbs on forest edges; trees and epiphytes in forest interiors). We estimated mean traits for each species from two fully expanded, healthy leaves from up to three individuals of a species at each site. We measured seed dimensions at the species-level from herbarium material at the New York Botanical

Garden collections. To generate a phylogeny of the species found in our study transect, we built a matrix including six chloroplast markers and the nuclear ribosomal spacers ETS and ITS which have been broadly used in the family (see Goldenberg et al. 2016, Kriebel et al. 2015). A majority of the DNA sequences were downloaded from Genbank and were supplemented by targeted sequencing of some species present in our study.

We sampled 286 individuals from 101 taxa (97 species, 4 sub-species), a vast majority of which (76) were found at a single elevation. Species richness decreased monotonically with elevation, ranging from 45 species found at the lowland site to only six at the top of Volcán Barva (Table 1). We found remarkable trait variation within communities: e.g., at the 30 m elevation site, leaf area ranged from ~19 cm<sup>2</sup> to ~608 cm<sup>2</sup>. We used two approaches to test for different patterns of trait turnover with elevation. First, we performed simple linear regressions of site-specific species trait means against elevation. We found only weak shifts in mean functional trait values with elevation (Figure 1). In accordance with community-wide predictions, leaf toughness showed a positive, albeit weak correlation with elevation, whereas leaf area and SLA showed a negative correlation with elevation. None of the other measured traits was significantly correlated with elevation. These patterns remained consistent when we included only the woody taxa (SLA:  $R^2 = 0.08$ ,  $P < 0.01$ ; leaf area:  $R^2 = 0.10$ ,  $P < 0.01$ ; leaf toughness:  $R^2 = 0.23$ ,  $P < 0.01$ ), and were robust to a bootstrap approach that took a subsample of only six species from each community to account for the unequal species diversity across sites (proportion of bootstrapped regressions with significant  $R^2$  were 25% for SLA, 11% for LDMC, 70% for leaf area, 93% for leaf toughness, 3% for leaf nitrogen, <1% for stem density, and 6% for seed mass).

Second, to test if functional dissimilarity among melastomes in a given pair of sites is correlated to environmental dissimilarity between the sites, we performed Mantel tests between trait distance matrices and an elevational dissimilarity matrix. The trait distance matrices were computed as Euclidean distance of the trait values of the species growing at each site. Correlation between trait and elevational dissimilarity was significant only for leaf toughness (Mantel  $r = 0.88$ ,  $P < 0.01$ ). To test for aggregated patterns of functional turnover across all measured traits, we computed a single community distance matrix using all principal component axes constructed from all seven traits. Again, we performed a Mantel test between this composite distance matrix and the elevational dissimilarity matrix. We found no significant correlation between these matrices (Mantel  $r = 0.61$ ,  $P = 0.08$ ).

We also performed Mantel correlations between taxonomic and phylogenetic dissimilarity matrices and the elevational dissimilarity matrix to explore the patterns of species turnover that may drive functional shifts. We computed taxonomic beta diversity as the Jaccard dissimilarity index between each community pair, and used two metrics of phylogenetic beta diversity: UniFrac, which emphasizes turnover across the tips of the phylogeny, and Dpw, which emphasizes basal turnover (Swenson 2011). We found that taxonomic beta diversity was significantly correlated with differences in elevation (Mantel  $r = 0.86$ ,  $P < 0.01$ ). However, the phylogenetic basis for this compositional turnover was unclear: phylogenetic beta diversity was well correlated with elevational dissimilarity when calculated according to the UniFrac method (Mantel  $r = 0.74$ ,  $P = 0.03$ ), but not when calculated using Dpw (Mantel  $r = 0.14$ ,  $p = 0.40$ ).

Our result that melastomes tend to exhibit a similar range of functional traits across a 2500 m elevation gradient (Figure 1) contradicts the expectation that within a

clade, species growing in higher elevation communities would on average exhibit more resource-conservative trait syndromes than those found in less-stressful, lower elevation communities. Such community wide turnover is well-documented in elevational gradients globally (Read et al. 2014), though data are not available for the Volcán Barva region. This result leads us to suggest that there is no within-clade turnover in the melastomes despite community-wide turnover. It is possible that the low turnover of melastome functional traits in fact mirrors a low turnover of community-wide means along the Volcán Barva transect, but this is unlikely given the significant drop in MAT along the gradient. Low species turnover is not a likely explanation for low functional turnover, as a large majority of the taxa (76 out of 101) were restricted to just one site along the gradient. However, low functional turnover can be caused by the low turnover of the major clades within the melastomes (low Dpw).

Our results raise the question of why the taxonomic beta diversity of melastomes is strongly correlated with elevational turnover even when the species occurring at different sites exhibit similar ranges of functional traits. One explanation might be that the distribution of melastome species across the gradient is strongly limited by dispersal: e.g., the bird-dispersed berry fruits of most melastomes may be confined to the same altitudinal range as the disperser (Renner 1989). Moreover, the dispersers for most berry-fruited melastomes are small Passeriformes whose gut retention time for melastome seeds is usually ~20 min (Ribeiro et al. 2016), thus limiting their effective dispersal capability. It is also possible that the integrative functional traits that we measured obscure some key physiological differences between species that are the targets of abiotic filtering. For example, tolerance of environmental extremes (e.g., chilling or freezing temperatures) may be the driver of species ranges. Similarly, it is



possible that the pattern of functional and species turnover in adult plants may arise due to community assembly processes that act primarily at the seedling stage (Spasojevic et al. 2014).

While general trends in plant functional traits along environmental gradients are well studied (Read et al. 2014), the underlying drivers of these patterns are poorly understood (Violle et al. 2012). Our results highlight the potential for community-wide trait turnover patterns to obscure the responses of individual species or clades to environmental gradients. Our data suggest that melastome species display similar ranges of functional strategies across a 2500 m elevation gradient across which we expect community-wide trait means to shift. Our study also highlights the need for more community-wide and clade-based studies of plant function and physiology across altitudinal gradients in the tropics, where climate change is already impacting the composition of forest communities (Feeley et al. 2013). The melastomes, which display remarkable functional variation and occur throughout the tropics and across elevational gradients, are an ideal group in which to investigate the ecology and evolution of plant response to environmental pressures.

## ACKNOWLEDGMENTS

We would like to thank the staff of the Organization for Tropical Studies for logistic support, Juan Gabriel Huertas for field assistance, Mariel Cruz for measuring seed dimensions, Maria Gavrutenko for assistance with DNA sequencing, Johanna Hurtado Astaiza and David Clark for helpful advice, Claire Fortunel, Ian McFadden, and Lei Chen for comments that improved this manuscript. Funding for this research was provided by NSF grant OISE-CNIC-1444192 and the University of Maryland.

LITERATURE CITED

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.

CLARK, D. B., HURTADO, J., & SAATCHI, S. S. 2015. Tropical Rain Forest Structure, Tree Growth and Dynamics along a 2700-m Elevational Transect in Costa Rica. *PLoS ONE*:e0122905.

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.

FEELEY, K. J., HURTADO, J., SAATCHI, S., SILMAN, M. R., & CLARK, D. B. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology* 19:3472–3480.

GOLDENBERG, R., ALMEDA, F., SOSA, K., RIBEIRO, R. C. & MICHELANGELI, F. A. 2015. *Rupestrea*: A new Brazilian genus of Melastomataceae, with anomalous seeds and dry indehiscent fruits. *Systematic Botany* 40:561-571.

KRAFT, N. J. B., ADLER, P. B., GODOY, O., JAMES, E. C., FULLER, S., & LEVINE, J. M. 2014. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29:592–599.

KRIEBEL, R., MICHELANGELI, F.A., & KELLY, L.M. 2015 Discovery of unusual anatomical and continuous characters in the evolutionary history of *Conostegia* (Miconieae: Melastomataceae). *Molecular Phylogenetics and Evolution* 82:289-313.

- LIEBERMAN, D., LIEBERMAN, M., PERALTA, R., & HARTSHORN, G. S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84:137-152.
- LUSK, C.H., REICH, P. B., MONTGOMERY, R.A., ACKERLY, D.D., CAVENDER-BARES, J. 2008. Why are evergreen trees so contrary about shade? *Trends in Ecology and Evolution* 23:299-303.
- PEREZ-HARGUINDEGUY, N., DÍAZ, S., GARNIER, E., LAVOREL, S., POORTER, H., JAUREGUIBERRY, P., BRET-HARTE, M. S., CORNWELL, W. K., CRAINE, J. M., GURVICH, D. E., URCELAY, C., VENEKLAAS, E. J., REICH, P. B., POORTER, L., WRIGHT, I. J., RAY, P., ENRICO, L., PAUSAS, J. G., DE VOS, A. C., BUCHMANN, N., FUNES, G., QUETIER, F., HODGSON, J. G., THOMPSON, K., MORGAN, H. D., TER STEEGE, H., VAN DER HEIJDEN, M. G. A., SACK, L., BLONDER, B., POSCHLOD, P., VAIERETTI, M. V., CONTI, G., STAVER, A. C., AQUINO, S. & CORNELISSEN, J. H. C. 2013. New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167–234.
- POORTER H., NIINEMETS, U., POORTER, L., WRIGHT, I.J., & VILLAR, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182:565-588.
- READ, Q. D., MOORHEAD, L. C., SWENSON, N. G., BAILEY, J. K., & SANDERS, N. J. 2014. Convergent effects of elevation on functional leaf traits within and among species. *Functional Ecology* 28:37–45.

REGINATO, M., NEUBIG, K.M., MAJURE, L.C., MICHELANGELI, F.A. 2016. The first complete plastid genomes of Melastomataceae are highly structurally conserved. *PeerJ* 4:e2715.

REICH, P. B. 2014 The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275-301.

RENNER, S. S. 1989. A Survey of Reproductive Biology in Neotropical Melastomataceae and Memecylaceae. *Annals of the Missouri Botanical Garden* 76:496-518.

RENNER, S. S. 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic Journal of Botany* 13:519-540.

RIBEIRO, R. C., FIGUEIREDO, M. L. N., PICORELLI, A., OLIVEIRA, D. M .T. & SILVEIRA, F. A. O. 2016. Does seed coat structure modulate gut-passage effects on seed germination? Examples from Miconieae DC. (Melastomataceae). *Seed Science Research* 26:136-147.

RUOKOLAINEN, K., LINNA, A., & TUOMISTO, H. 1997. Use of Melastomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. *Journal of Tropical Ecology* 13:243-256.

SPASOJEVIC, M. J., YABLON, E. A., OBERLE, B., & MYERS, J. A. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* 5:129.

SWENSON, N. G. 2011. Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLoS ONE* 6:e21264.

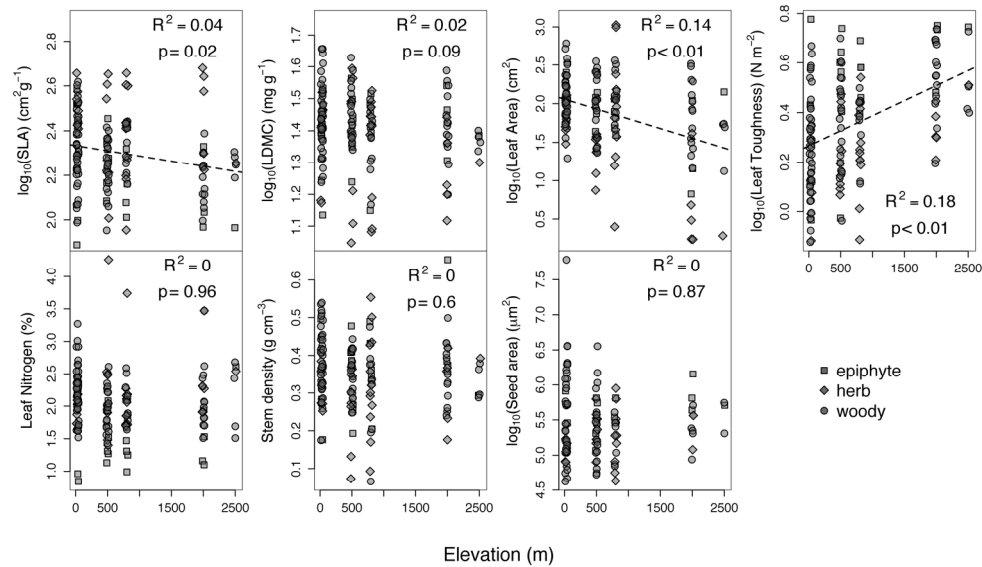
- 1  
2  
3  
4 VIOLLE, C., ENQUIST, B. J., MCGILL, B. J., JIANG, L., ALBERT, C. H., HULSHOF,  
5  
6 C., JUNG, V., & MESSIER, J. 2012. The return of the variance: intraspecific variability  
7  
8 in community ecology. *Trends in Ecology & Evolution* 27:244–252.  
9  
10  
11 WEIHER, E. & KEDDY, P. A. 1999. Ecological assembly rules: perspectives,  
12  
13 advances, retreats. Cambridge University Press, Cambridge.  
14  
15 WESTOBY, M., FALSTER, D. S., MOLES, A. T., VESK, P. A., & WRIGHT, I. J. 2002.  
16  
17 Plant ecological strategies: Some leading dimensions of variation between species.  
18  
19 *Annual Review in Ecology and Systematics* 33:125–159.  
20  
21 WESTOBY, M. & WRIGHT, I. J. 2006. Land-plant ecology on the basis of functional  
22  
23 traits. *Trends in Ecology and Evolution* 21:261-268.  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**Table 1:** Description of the five surveyed sites sampled along an elevation gradient in Cordillera Central, Costa Rica.

Site	Elevation (m)	Coordinates	Mean Annual Temperature (°C)*	Number of species sampled
La Selva Biological Station	30	10.431078° N -84.006085° W	24.6	45
Selva Tica	500	10.301476° N -84.034244° W	22.2	35
Virgen del Socorro	800	10.256408° N -84.169790° W	20.7	24
Refugio 2000	2000	10.174319° N -84.114425° W	14.5	20
Volcan Barva	2500	10.130454° N -84.125065° W	11.9	6

\* Interpolated from data reported in Clark et al. (2015).

**Figure 1.** Turnover of melastome functional traits along the elevational transect of Volcán Barva in Cordillera Central, Costa Rica. SLA = specific leaf area, and LDMC = leaf dry matter content. R<sup>2</sup> and P values from a linear regression are shown for each trait.



**Figure 1.** Turnover of melastome functional traits along the elevational transect of Volcán Barva in Cordillera Central, Costa Rica. SLA = specific leaf area, and LDMC = leaf dry matter content.  $R^2$  and  $P$  values from a linear regression are shown for each trait.

177x113mm (300 x 300 DPI)