

Intraspecific trait variation affects community distributions of alpine meadow plant communities

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**Advanced Independent Research
Summer 2010**

Abstract:

Differences between individuals are often not accounted for in studies using plant functional trait data. Variation due to biotic and abiotic conditions is common for many plant traits that are crucial for fitness and survival. However, functional trait methods usually do not account for differences that could be present between sites and between individuals. In order to see how much intraspecific variation impacts our understanding of community functioning I collected a full sample of functional traits (height, biomass and LMA) for all individuals within a community. I compared this true community LMA distribution to the abundance weighted species mean LMA distribution. The statistical moments from these two distributions did not match up, indicating that intraspecific trait variation was present in the sampled communities. While the differences between the methods was not statistically significant, including more sites would likely elucidate differences more clearly. Our understanding of functional traits has been limited without taking into account intraspecific trait variation. Further insight into how functional traits vary between and within species can help in the process of scaling from organisms to community and ecosystem processes.

Keywords: LMA, plant biomass, plant functional traits, intraspecific variation, community distributions

Introduction

Plant fitness and survival in a particular environment depends greatly on functional traits that influence reproduction and growth (Violle *et al.* 2007; Enquist *et al.* 2007). Functional traits are integral to different life history strategies. Plants can be described in terms of trait identity based on where specific traits fall on spectra between allocation for defense and longevity and allocation for high productivity (Wright *et al.* 2004; Chave *et al.* 2009). The trait identity of plants is crucial for relating organism functioning to ecosystem functioning, perhaps more so than species richness alone (Grime 1998).

For studies involving ecosystem functioning there has been a switch away from diversity as an indicator to plant functional data. Commonly functional traits are measured for a few individuals in a species and the mean value is applied to all individuals. However, this method ignores important trait differences between individuals. Recently, there has been a movement towards recognizing the importance of measuring the full range of traits present within communities. Quantification of community traits should provide a more comprehensive link between specific characteristics of individual organisms and entire ecosystem functioning. (Diaz *et al.* 2007; Luck *et al.* 2009; Suding *et al.* 2008).

While there have been many studies on trait variation between species there is a current lack of understanding in how trait variation within species relates to interspecific variation, and the implications this relationship has for ecosystem processes. Interspecific trait differences have been thought to impact ecosystem processes (Grime 1998), however it has been only relatively recently that other studies have pointed out that intraspecific variation is also likely to have a significant impact (Lecerf & Chauvet 2008). It is likely that in many cases plant traits vary

within species depending on the environment, level of competition and other factors. However, these differences are ignored when a mean trait value is used to describe an entire species.

Trait distributions are one way to capture a more complete picture of community level functional characteristics. Two methods have been used to develop community trait distributions. The first method employs a community species list and assigns a mean trait value for each species. Mean and variance values for community traits can then be calculated from this list of species and set trait values (Swenson & Enquist 2007). The second method assumes that a more accurate measure of connecting community traits to ecosystems requires a weighting of mean species trait values by the abundance of that particular species (Grime 1998). Both of these methods operate under the assumption that a mean value is sufficient to describe specific traits for an individual species. However if intraspecific variation is large, describing a species with a trait mean will be less informative than the variance observed for that trait. One way to capture both inter and intraspecific variation is to determine the distribution of specific traits by sampling every individual in a community. This method provides a snapshot of traits present in a community, and captures variation due to plant age and size as well as phenotypic differences between species.

Different characteristics of the community trait distribution such as mean, variance, skew and kurtosis (the first four moments that characterize a statistical distribution) can be compared between the two different methodologies used to determine trait distributions. I looked for differences between these distributions to see if the methods based on mean trait values are adequate descriptions of the actual sampled trait distribution. Alternatively, the underestimation of intraspecific trait variation could create important differences in the moments of these distributions compared to the true community distribution. Statistical moments of distributions

can also be informative about important factors driving plant traits (Norberg *et al.* 2001; Savage *et al.* 2007). Stressful abiotic conditions might decrease variance in a trait distribution while competitive biotic interactions could cause overdispersion of traits represented by negative kurtosis (lack of peakedness) (Cornwell & Ackerly 2009; Grime 2006). Therefore, distributions can be compared between communities to begin to address the different conditions that drive the shape of trait distributions.

This study aims to compare the trait distributions based on actual community trait values and those based on mean trait values. To accomplish this I completed a full census of plots for leaf mass per area (LMA), height and biomass. These traits in particular are central to describing plant growth, and so are essential for linking organism traits to ecosystem functioning (Violle *et al.* 2007; Enquist *et al.* 2007). We also measured community carbon flux measurements in order to make a direct connection between community trait composition and ecosystem processes.

This project helps to build a link between organisms and ecosystems by making a full account of community traits. While we expect intraspecific variation to have a large impact on community trait distributions, it would be extremely valuable to know if the less time intensive method (finding a mean trait value for a species from just a few individuals) is just as effective as finding trait values for every individual within a community. Also, trait distributions from communities experiencing different environmental conditions will help to explain what factors drive community composition. Trait distribution data can also give crucial information that can help predict community reactions to climate change depending on the range of trait values.

Methods

Study Sites:

Plots were chosen for this project based on the objective of capturing a range of species diversity, species composition and LMA values. The plots were located on an elevation gradient near Crested Butte, Colorado in the Rocky Mountains and represent a spectrum of environmental conditions (Table 1). At each site I sampled one plot (1.3m x 1.3m) with species compositions that were representative of the site as a whole.

Functional Traits:

In the field I measured the height of every individual plant in each plot and clipped the aboveground biomass. Samples were brought back to the lab so that dry mass of the plant could be weighed. Leaf area was calculated using a flatbed scanner and ImageJ image analysis software. After scanning, I dried the leaf samples in an oven at 65° C for at least 72 hours and measured the dry mass of each leaf. Leaf mass per area (LMA g/m^2) was then calculated by dividing leaf dry mass by leaf area. Methods for collection and processing for LMA follow Cornelissen *et al.* (2003).

The abundance-weighted species mean trait distribution was generated for each site. I used the species list from my plot collection but applied a mean LMA value for each species from a trait database developed in previous years. Each species LMA value represents the mean of at least five individuals. If sufficient data wasn't available for a species then means were determined by pooling data within a genus.

Carbon Flux:

Community carbon flux associated with each plot was measured using a closed tent system and an open-path infrared CO₂ gas analyzer (Li-Cor 7500 Lincoln, Nebraska). A fully

sealed cube of known volume was placed over the entire community within a plot (1.3 x 1.3m) for 90 seconds to accurately measure carbon flux around ambient CO₂ levels (protocol modified from Arnone and Obrist 2003). Rate of carbon uptake through photosynthesis was measured during the day (beginning at 9:00am) and rate of carbon emission through respiration was measured during the night (beginning at 9:00pm). Along with the community flux measurements soil respiration was measured using a Li-Cor 6400 (Lincoln, Nebraska) with a soil chamber head that was fitted to two established soil collars within each plot. These two procedures allowed us to differentiate between carbon flux associated with aboveground biomass and underground biomass and organisms. Net ecosystem exchange (NEE) was calculated using an exponential model to account for any leaks in the system (following Saleska *et al.* 1999).

Analysis:

In order to determine if community trait distributions based on mean values are less robust than the true trait distribution I analyzed the difference between four moments (mean, variance, skew and kurtosis). A linear regression was utilized to plot the moments from the community list method against the moments from the true community distribution method (mean vs. mean, variance vs. variance etc.). In this way I could test for a slope of 1.0 and an intercept of 0, which indicates that both methods give the same trait distribution. The actual community distribution moments were also analyzed between communities to begin to address the biotic and abiotic factors that influence trait distributions. I will use the combined LMA, height and biomass data in conjunction with our calculations of NEE for future analyses.

Results

Community distributions of LMA were extremely dependent on site conditions, where the high elevation sites (Painterboy Mine and Pfeiler) had the narrowest distributions. The lower elevation sites display much more overdispersion (Fig 1). The lowest elevation, hottest site (Almont) had a slight peak at a higher LMA value than the high elevation sites.

The effect of sites accounted for the majority of variance (61.12%) found between all of the individuals, when partitioning the variance from the effect of site, species and within species (Fig 2a). When comparing the variance from family, genus, species and within species, family had an extremely small effect but the partitioning was nearly equal for the other factors (Fig 2b). In both partitioning graphs the variance from within species was greater than the variance from between species (Fig 2a and b).

Comparisons of the statistical moments from the true LMA distributions and abundance weighted species mean LMA distributions showed a difference for all four moments, though not significantly so. For all of the moments the slope was not 1 and the intercept was not 0, however the confidence intervals were so large for the analyses that none of them were significantly different statistically.

Discussion

Plant functional trait data are an excellent means of relating specific aspects of individual plants to the entire community, and ultimately the entire ecosystem. By taking a complete census of all individuals in a community we are able to take a snapshot of the variation present within and between species. This is crucial because there is no static state for any species. Individuals will differ depending on age, fitness, competition etc. Therefore, it is crucial to know whether

these differences are substantial enough that a representative mean trait value for each species would not be sufficient to correctly describe a community distribution.

We found that distributions of LMA were different depending on the site. LMA means showed a clear elevational pattern with lowest values at high elevation and increased LMA down gradient. The middle elevational sites (CBT and Road) showed the most overdispersion of LMA suggesting that the plants there are less constrained by abiotic conditions (Cornwell & Ackerly 2009; Grime 2006).

With the environmental differences among elevations it makes sense that site factors would account for a large amount of the variance found in the sample. LMA is clearly affected by environmental conditions, and species show trait plasticity depending on local conditions. Therefore it also makes sense that a large amount of the variance was partitioned to within species differences. What is surprising though is that the intraspecific variance was greater than interspecific variance. Similar results were found in a tropical system looking at trait variation at different scales (Messier *et al.* 2010). This would lead us to think that trait values within species are different enough that a mean trait value would not be sufficient to describe the community across a wide variety of habitats.

The comparisons of statistical moments indicate that this might be the case, but the spread of values in the comparisons was too large to make a definitive answer. It is likely that with more sites included in the analysis we would be able to observe clearer differences. Despite the statistical insignificance in each case the moments generated from the two distributions were different enough that it is likely the species mean method does not correctly predict the true distribution. This would further indicate that intraspecific variation is present in the communities we sampled.

Intraspecific trait variation is extremely important in functional ecology and needs to be taken into account to a greater degree. This study suggests that using species trait means might not be sufficient to correctly estimate the characteristics of a true community trait distribution. However, site-specific mean trait values could be a way of maintaining accuracy without censusing an entire community because a large amount of variance in LMA values was due to environmental factors. The time and effort involved in finding a true community trait distribution is not feasible for most studies dealing with functional traits. Therefore, other methodologies need to be developed that mimic the true distribution that don't require as intensive of an approach.

Acknowledgements

I would like to thank all members of the Enquist lab group for their assistance with field collection and lab processing. My mentors, Dr. Brian Enquist and Christine Lamanna, gave indispensable guidance and assistance at all levels of this project. I would also like to thank Lindsey Sloat for her plant identification expertise and willingness to scan and measure hundreds of samples. Special thanks also go to Benjamin Blonder for his help with image and statistical analyses, as well as lab processing. This research was funded by the National Science Foundation research experience for undergraduates (REU) program.

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Tables and Figures:

Table 1. Abiotic descriptions of each site along the elevational gradient.

Site	Latitude	Longitude	Elevation (m)	% Soil Moisture	% Soil Carbon
Almont	38.655111	-106.86	2468	8.43	1.24
Crested Butte Land Trust	38.878014	-105.980883	2710	24.80	3.66
Road	38.897019	-106.979161	2815	17.21	3.24
Pfeiler	38.960781	-107.016686	3155	15.23	2.15
Painterboy Mine	38.969178	-107.011506	3380	17.60	2.08

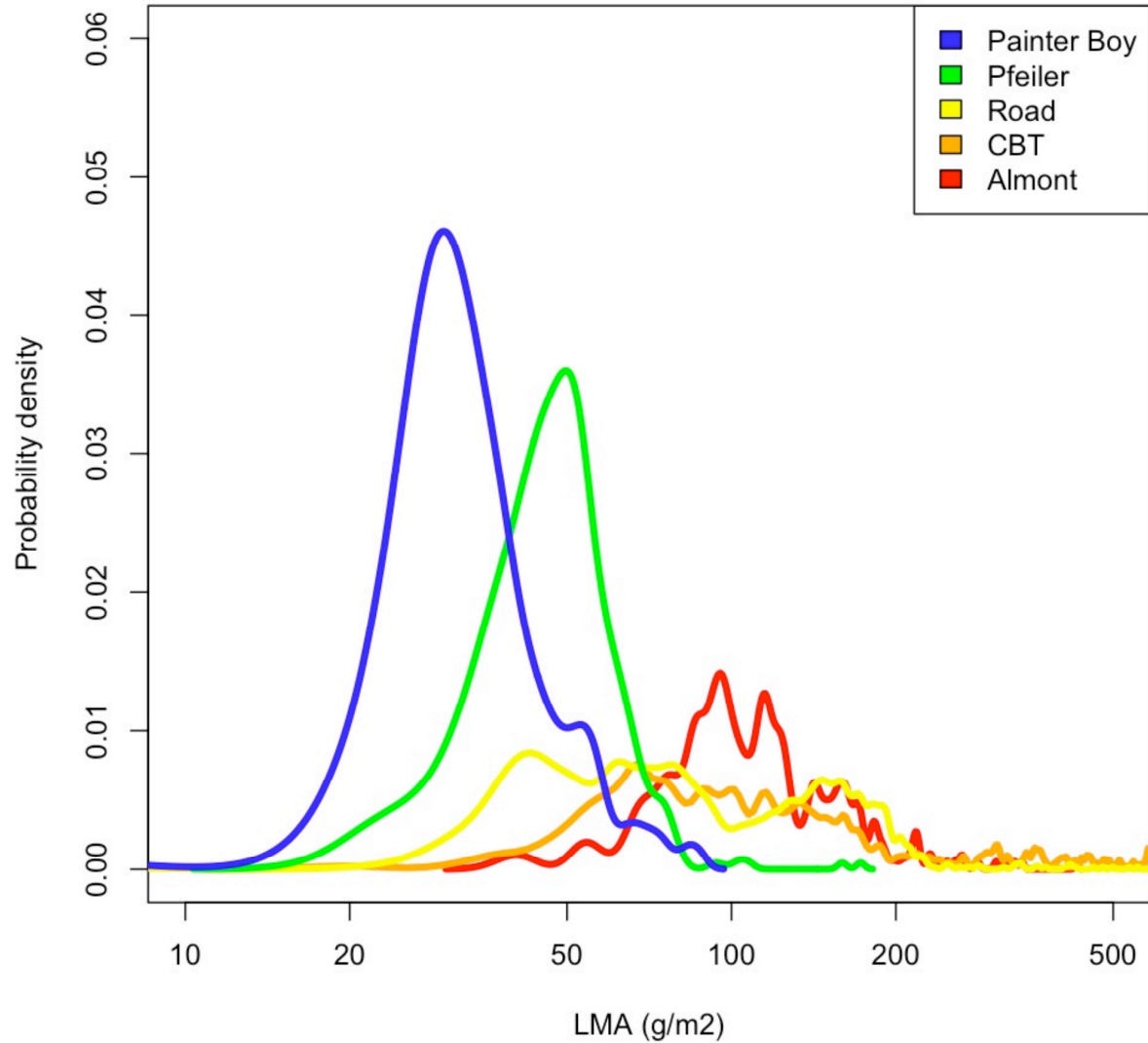


Figure 1. Probability density distributions of log LMA values for each site.

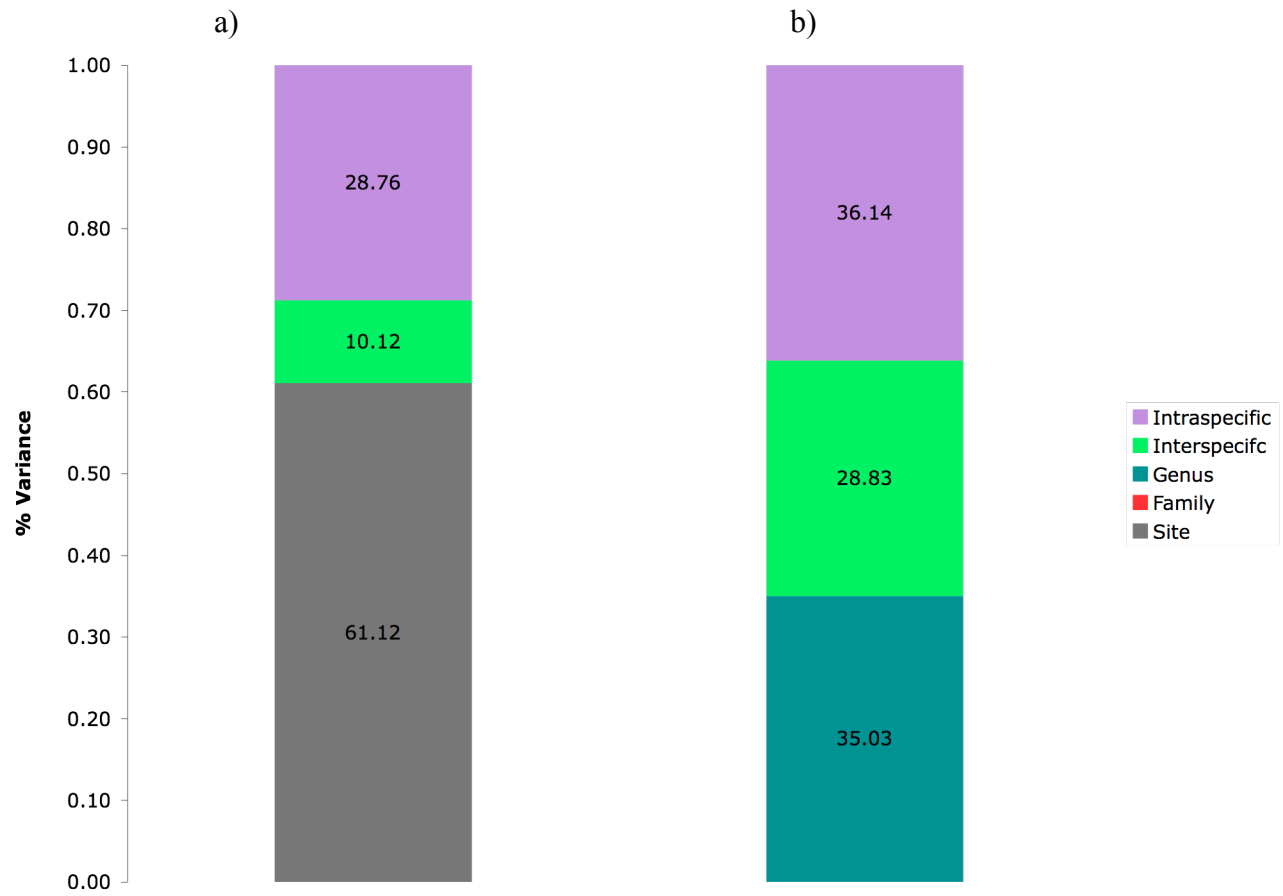
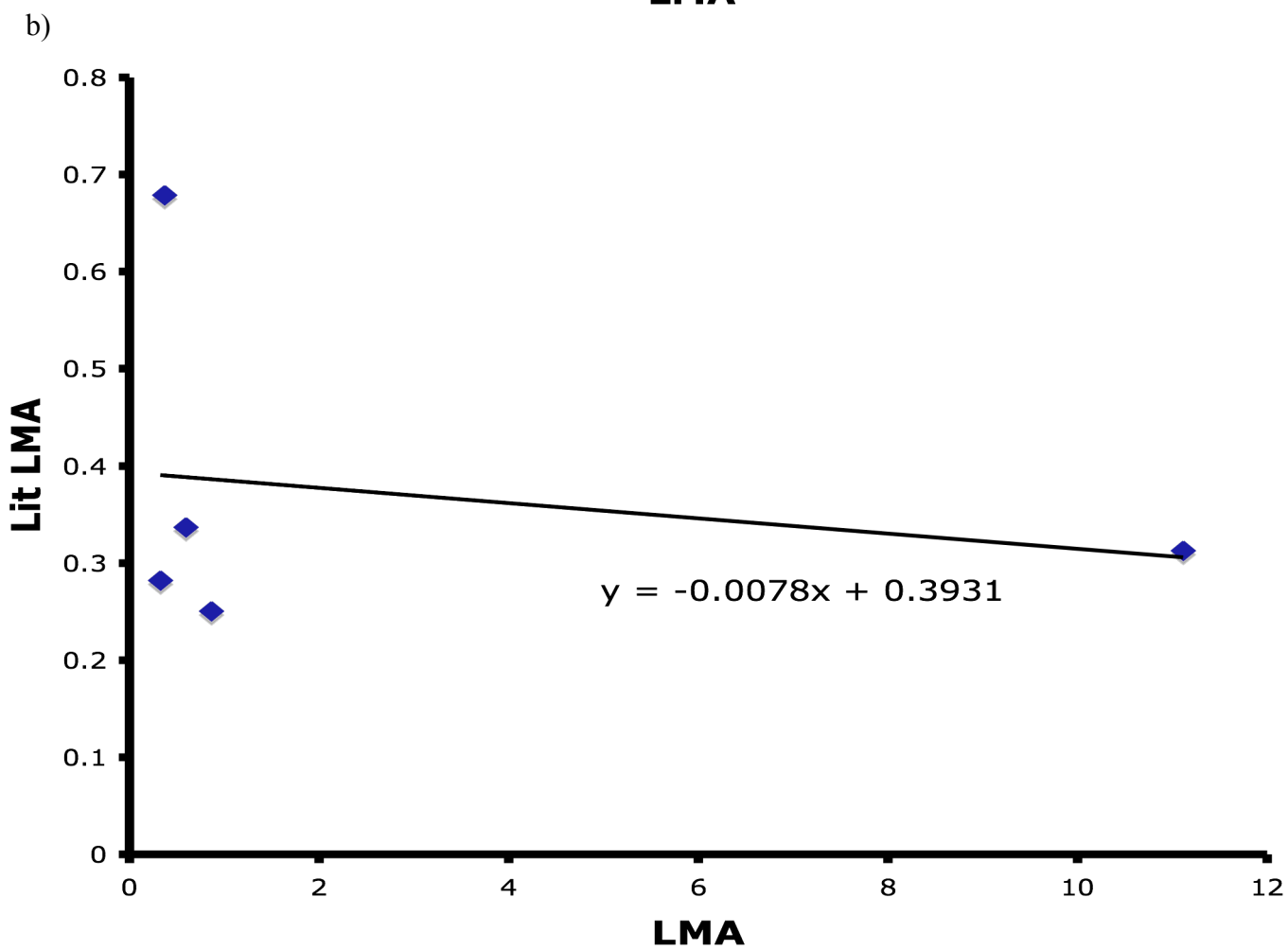
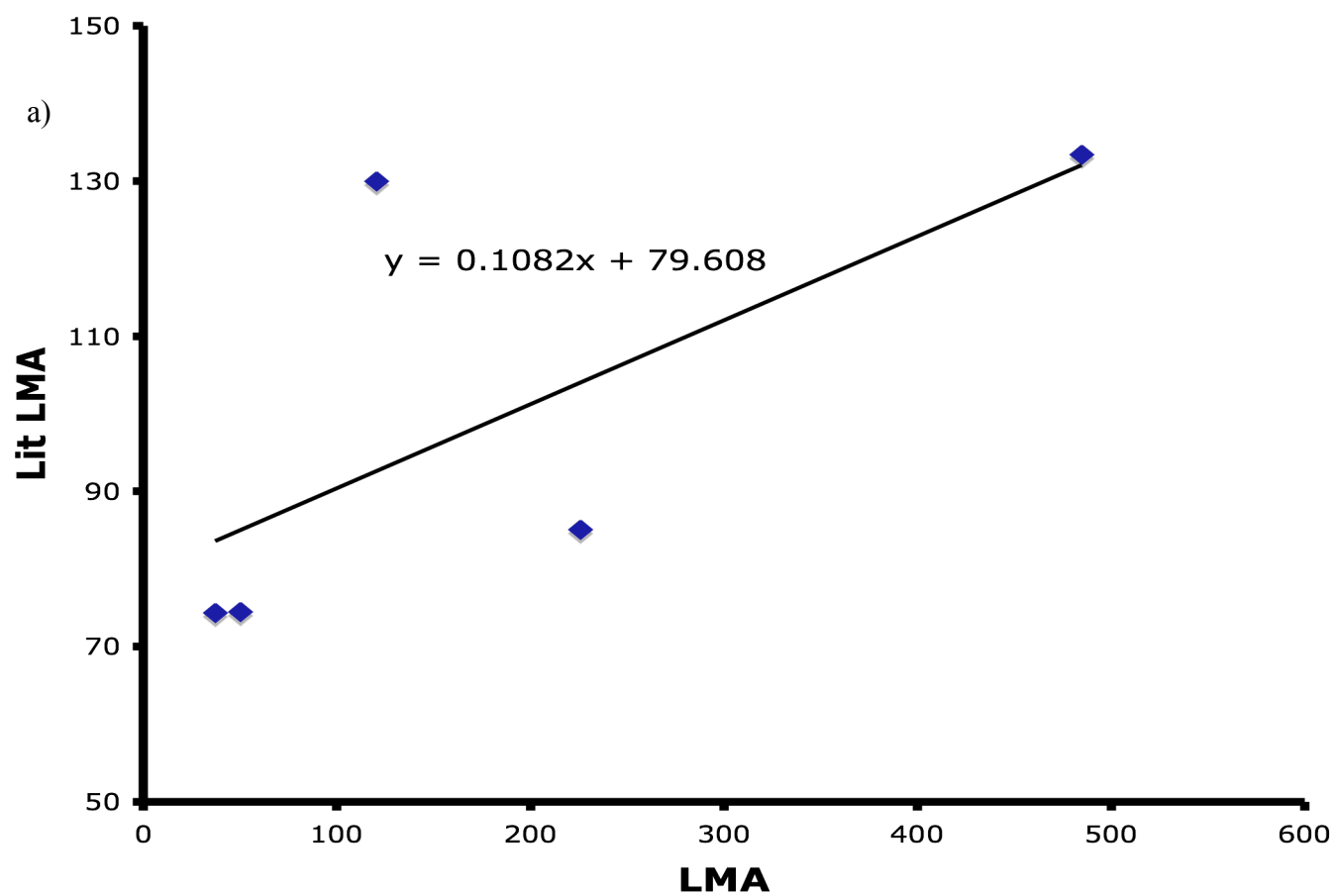


Figure 2. Variance partitioning of LMA for all individuals based on a) site, interspecific, and intraspecific variation and b) family, genus, interspecific, and intraspecific variation.



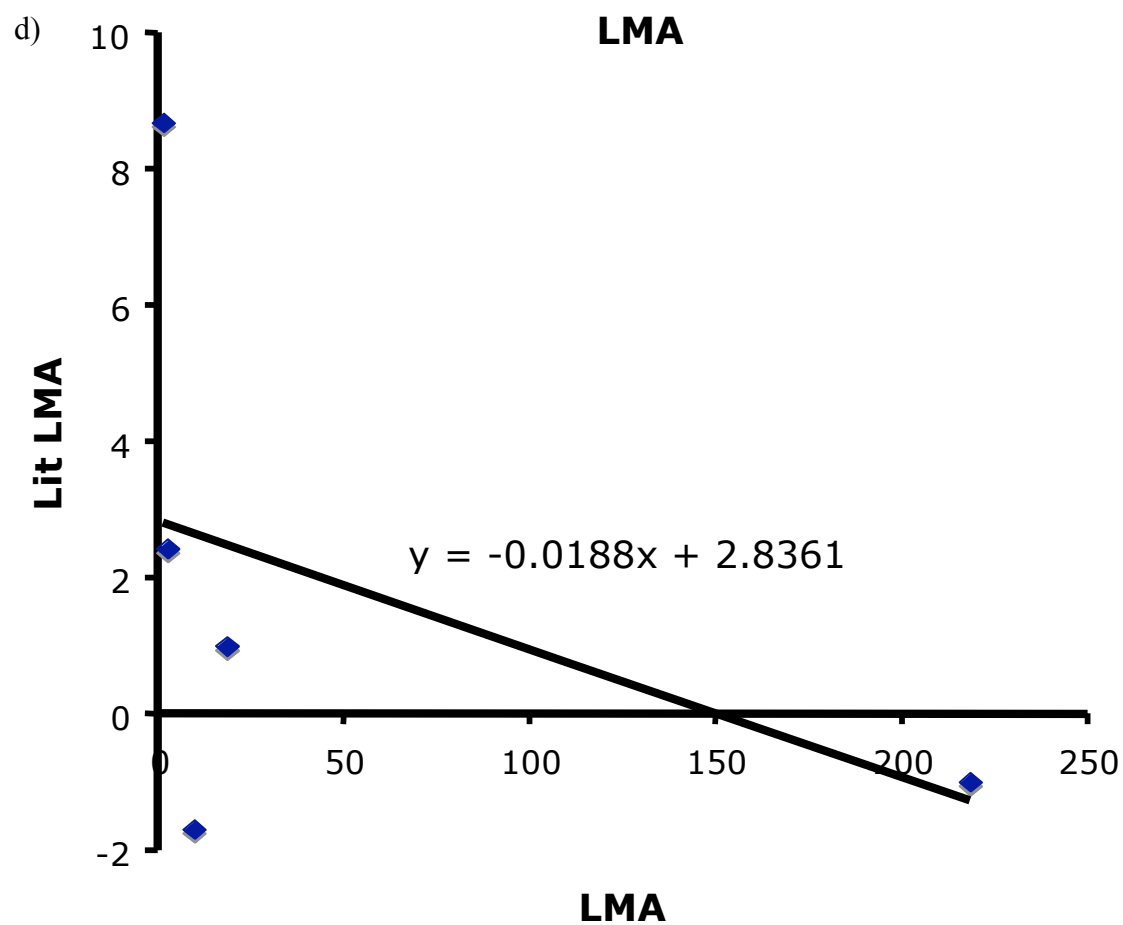
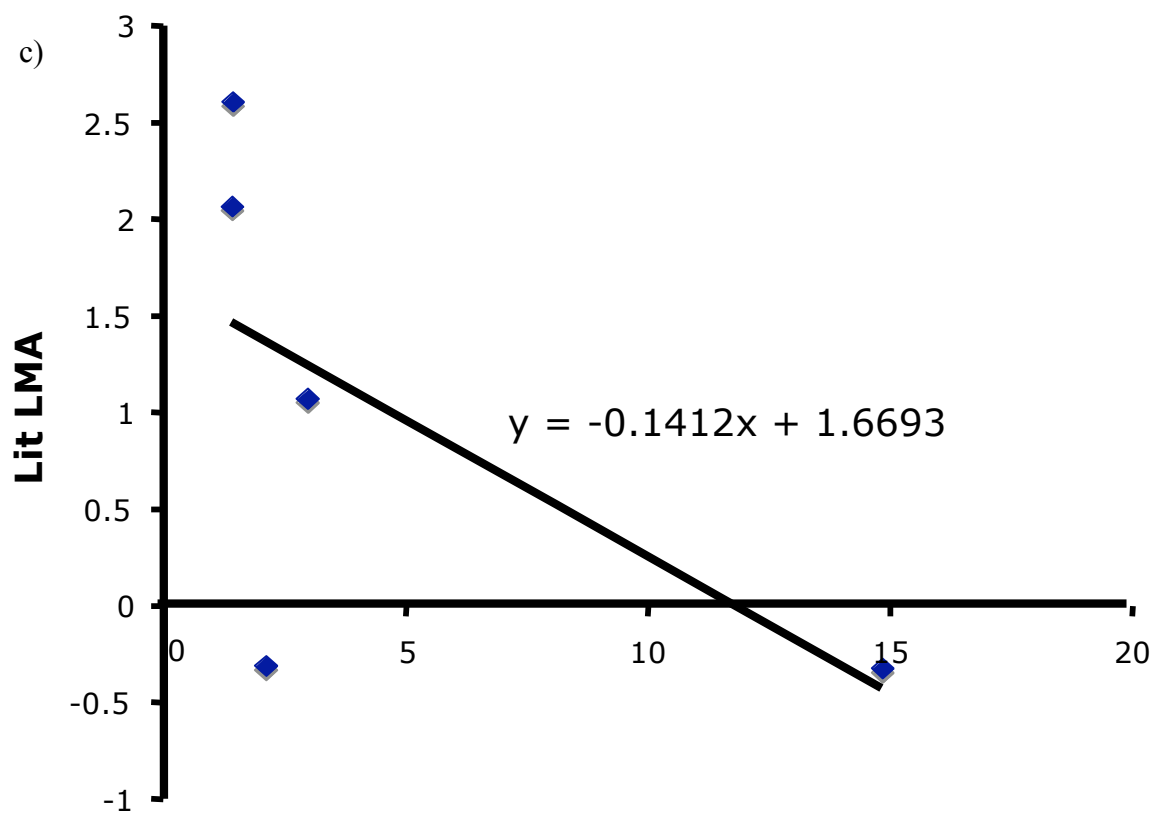


Figure 3. Each graph shows the statistical moments generated from the true community trait distribution (x axis) plotted against moment values generated from the abundance weighted species mean community trait distribution. This is done for the mean (a), coefficient of variation (b), skewness (c), and kurtosis (d).