

THE ROLE OF PLANT TRAIT VARIATION IN COMMUNITY ASSEMBLY AND
PLANT DIVERSITY AT LOCAL TO CONTINENTAL SCALES

by

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DEDICATION

This work is dedicated to my parents, Chuck and Maria Teresa Hulshof, my sisters Gloria and Jessica Hulshof, y mis abuelos Hilario y Gloria De la Peña.

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ABSTRACT

The trait based approach has been proposed as a way to reconcile community ecology. Despite recent advances in trait based ecology, such as the development of global trait databases and standardized methodology for trait collections, it remains unclear to what degree traits vary across individuals, species, and communities. In addition, the drivers of trait variation may shed light on the underlying processes that maintain species diversity and community assembly at local to continental scales yet these have been poorly studied. In this study, I examine both the magnitude of trait variation as well as the patterns of trait variation at local to continental scales in order to understand the drivers of diversity patterns across environmental gradients.

First, I quantified the magnitude of trait variation at local scales in a dry tropical forest and determined that intraspecific variation is not negligible and can be quite large for compound-leaved species. However, I showed that the sample sizes necessary for quantifying trait variation are tractable and should encourage the adoption of trait variation in trait based ecology. Second, I tested whether climatic variables are predominantly responsible for observed trait variation across dry tropical forests in the Americas. I showed that climatic variability, specifically variability in precipitation, explained a large degree of observed trait variation across dry tropical forests and may provide a unique approach for classifying dry tropical forests based on their inherent degree of climatic seasonality. Third, I quantified patterns of trait variation at continental scales across elevational gradients at high to low latitudes. I showed that climatic variables largely drive patterns of trait variation at high latitudes while biotic factors

largely drive patterns of trait variation at low, tropical latitudes. This finding has implications for understanding large-scale patterns of species diversity across elevational and latitudinal gradients. Finally, I apply trait variation to life history theory by quantifying variation in two life history traits (growth and reproduction) in a tropical tree species using a legacy dataset. I showed that variation in these two life history traits is due to both resource availability and allometric related effects on both traits. In sum, this study advances our understanding of the magnitude and underlying drivers of trait variation at local to continental scales.

INTRODUCTION

A Review of the Literature and an Explanation of the Problem

Understanding what drives patterns of species diversity across environmental gradients remains an important research area despite over a century of intensive scrutiny (von Humboldt 1849; Kraft *et al.* 2011). Research during the early phases of ecology adopted a species-centric approach in which the numbers and types of species were compared within and between different habitats and ecosystems and along environmental gradients (von Humboldt 1849; Shreve 1915; Whittaker and Niering 1964). While these early observations outlined that species diversity increases towards tropical latitudes (see Connell 1978; Rosenzweig 1995), an understanding of the biological mechanism responsible for this pattern remains elusive (Pianka 1966; Rhode 1992; Gaston 2000; Wright 2002). Further, the traditional species-centric approach of quantifying species diversity and distribution along environmental gradients has provided limited generalizations and has poor predictive ability between different habitats and ecosystems (Keddy 1990; Keddy 1992). It is this challenge that fueled debate whether community ecology can produce general laws at all (Brown 1995; Lawton 1999; Simberloff 2004).

In response, the trait based approach has been proposed as a way to reconcile long-standing hypotheses within ecology (Lavorel and Garnier 2002; McGill *et al.* 2006), particularly with respect to understanding the nature and underlying mechanisms that give rise to diversity gradients. A functional trait is any morphological, physiological, or phenological trait that impacts an organism's growth, reproduction, or survival and, ultimately, fitness (McGill *et al.* 2006; Violle *et al.* 2007). Further, key functional axes

have been identified as having important roles for ecological variation between species (Westoby 1998) In particular, community ecologists have been able to predict community composition and ecosystem functioning from quantitative information that describes the functional differences between individuals of different species as well as between individuals of the same species (Lavorel and Garnier 2002). Increasingly, community ecologists have sought to generate functional trait information for all species in their study systems as a means to test how both biotic and abiotic factors influence diversity patterns across space (Weiher and Keddy 1995; Diaz and Cabido 1997; Weiher et al. 1999; McGill *et al.* 2006).

The power of this functional trait approach is threefold. 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, and Ackerly 2008). Third, the functional approach links population, community, and ecosystem processes to the key traits that influence organismal performance (e.g., growth, metabolism, reproduction; McGill et al. 2006). As a result, many studies have compared the similarity among species' functional traits in order to determine the mechanisms underlying community assembly. Specifically, trait based community assembly theory suggests that trait variation among co-occurring species is shaped by two main processes: abiotic filtering, important in stressful environments and promoting trait similarity, and competition, more important in productive environments and promoting

trait dissimilarity (Diamond 1975; Keddy 1992; Weiher and Keddy 1995; Weiher et al. 1998). Indeed, many studies have quantified mean trait values for all species within a community and have shown that community-wide trait similarity and dissimilarity generally supports the abiotic and/or biotic filtering of communities across different ecosystems (e.g. Kraft, Valencia, and Ackerly 2008, Swenson and Enquist 2009; Cornwell and Ackerly 2009).

Despite the above strengths of the functional trait based approach to community ecology, there are several inevitable criticisms. As sessile organisms, plants are renowned for their plasticity both within species and individuals. Thus, the emphasis of mean trait values has limited the ability of the trait based approach to reconcile long-standing hypotheses regarding the diversity and coexistence of plant communities. For example, intraspecific variation is minimized in standardized protocols for plant functional trait measurement by sampling only healthy, mature, sun leaves (Cornelissen *et al.* 2003). 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, and Ackerly 2008; Swenson and Enquist 2008; Lake and Ostling 2009). In tropical forests, for example, sun leaves can be exceedingly difficult to collect due to the height of the canopy or impossible to collect due to the fact that the species only occurs in shaded understory habitat. In addition, the extrapolation of trait values collected from individuals in one geographical location to those located in another fails to capture intraspecific variation due to phenotypic or genetic variation and, thus, the

mean trait value of a species may not adequately represent the mean trait value for all populations or individuals.

The first objective of this dissertation was to quantify the magnitude of trait variation both between and within species and determine a minimum sample size necessary for calculating a trait mean and variance value for individual species. This study was among the first studies to highlight the magnitude and importance of intraspecific variation in trait based ecology. Specifically, this study revealed that intraspecific variation is not negligible and that sampling 5-10 leaves are necessary for generating trait mean and variance values (Hulshof and Swenson 2010). This study has helped to generate much interest in intraspecific variation. Since this publication, a burgeoning number of studies now highlight the magnitude and importance of intraspecific trait variation, and, as a result, intraspecific variation has now moved to the fore-front of functional ecology (see Bolnick *et al.* 2012; Violle *et al.* 2012). What's most important about this paradigm shift in trait based research is that quantifying trait variation within and across species and communities provides a critical link between trait based approaches and evolutionary and niche-based perspectives (Violle and Jiang 2009).

The interest in quantifying intraspecific variation is continuing to dominate trait based studies; as evidence of this the majority of studies to date continue to highlight the magnitude of intraspecific variation. A common recipe for trait based studies is to quantify patterns of trait similarity and dissimilarity both with and without measures of intraspecific variance in order to determine the effect that intraspecific variance has on community wide patterns (e.g. Albert *et al.* 2011; de Bello *et al.*

2011). While the quantification of intraspecific variation is important for advancing the trait based approach in community ecology, the emphasis on characterizing the sheer magnitude of variation must eventually give way to the application of trait variation for addressing long-standing questions in ecology (Violle *et al.* 2012) such as what underlies patterns of species diversity within and among communities as well as the development of theoretical applications (e.g. Shipley *et al.* 2006a; Enquist *et al.* 2007).

The second objective of this dissertation was to provide a preliminary application of trait variation for determining underlying drivers of diversity patterns across communities. To do this, I quantified trait variation across tropical dry forest communities in both Mexico and Costa Rica—two areas where large portions of tropical dry forests remain intact despite intense anthropogenic disturbance to surrounding areas. Due to the long history of anthropogenic disturbance in these and other areas, tropical dry forests are likely the most endangered ecosystem (Janzen 1988). As a result, there is a high priority for understanding what determines the assembly and structure of different types of dry forests, not just from a conservation management perspective, but also for understanding how these fragmented forests may be impacted by future climate and land-use changes (Murphy and Lugo 1986; Burquez and Martinez-Yrizar 2010; Laurance *et al.* 2011). Thus, in order to explore the underlying drivers of plant diversity across dry forests, I was able to quantify trait variation for different dry forest sites across a gradient of climatic conditions. I tested whether functional trait diversity can be explained by climatic variables, including seasonality precipitation, a characteristic of dry tropical

forests that distinguishes this ecosystem from other tropical forest types. Indeed, I showed that climatic variability, and specifically precipitation seasonality, was a key driver of functional trait variation across different types of dry forests (Hulshof *et al. In Press*). This study is among the first to link trait variation across multiple forests with abiotic factors and supports the application of trait variation for understanding what drives the assembly and structure of plant communities across broad spatial gradients. In addition, this study shows that dry tropical forest ecosystems can indeed be distinguished based on differences in climatic variability. In sum, this study is an example of how trait variation can be applied to understanding what drives the structure and assembly of plant communities.

To extend the above approach of applying trait variation to addressing patterns of assembly and diversity, the third objective of this dissertation was to quantify patterns of trait variation between and within three mountain gradients across latitude. This study critically examined how the distribution of trait variation changes across broad geographical scale and tests two key hypotheses of regarding species diversity patterns—the abiotic and biotic filtering (or limiting similarity) hypotheses. Explorations of assembly and diversity patterns using a trait based approach have previously been limited either by (i) the mean approach in which species trait means are compared or mean values are extrapolated based on global trait values (e.g. Kraft, Valencia, and Ackerly 2008; Swenson and Enquist 2008; Swenson et al. 2012) or by (ii) sampling only one or a few communities across a local or regional environmental gradient (e.g. Cornwell and

Ackerly 2009). Thus, the approach taken here specifically applied intraspecific trait variation to assembly and diversity patterns across both elevation and latitude.

This study is among the first of its kind to apply intraspecific trait variation for understanding diversity patterns. In so doing, this study revealed that both biotic and abiotic forces have likely been important in the evolution of plant function and diversity on contrasting ends of elevational and latitudinal gradients (Hulshof *et al.* 2012). Further, this study provides one of the most systematic and standardized trait sampling at broad spatial scales to dates. This allows an unprecedented understanding of how trait variation changes across key environmental gradients. In addition, this study proposes a unique trait variation ratio between intraspecific and interspecific variation which provides a parallel to previous niche literature. Whereas a species' niche is often difficult to characterize, this study showed that the use of traits to characterize species niches' (e.g. Violle and Jiang 2009) makes it possible to test hypotheses relating how niche breadth (i.e. intraspecific variation) should change relative to the total niche space (i.e. interspecific variation) across environmental gradients.

Finally, the above studies adopted a community-wide approach for understanding patterns of plant function and provide limited discussion of population level dynamics. Thus, the final objective of this dissertation was to assess the effects of trait variation for a single tropical tree population. Specifically, I determined the effects of allometry and resource availability for two key life history traits, growth and reproduction. In general, The principle of allocation states that resources devoted to growth, maintenance, and reproduction are constrained by the rate of acquisition of limiting resources from the

environment (Cody 1966, Levins 1968). For example, variation in two traits, such as growth and reproduction, is linked and the allocation of resources is a zero sum whereby allocation to one function should come at the cost of allocation to other functions. Trait tradeoffs are common in nature, however, an understanding of what drives tradeoff patterns in nature is unclear (Roff and Fairbairn 2006; Shipley et al. 2006b). Further, the generality of tradeoffs is questionable as correlations between traits may be positive, flat, or negative depending on the study system and species. For example, a key assumption underlying the tradeoff between growth and reproduction is that reproduction is costly and reduces resources available for growth (Roff 1992). However, negative correlations between the two life history traits is not always apparent and can even be positive (e.g. Fox and Stevens 1991; Knops et al. 2007; Koenig et al. 2009). In addition, variation in functional traits including growth and reproduction may be driven by other factors including confounding environmental factors (Knops et al. 2007). Together, these findings call into question whether the trade-off between growth and reproduction is actually an important driver of the observed variation in growth and reproduction in natural populations. To understand trait variation between growth and reproduction, this study used a 10-year legacy dataset to determine the effects of allometry (i.e. plant size) and resource availability (precipitation) for a population of *Bursera simaruba* trees in a dry tropical forest in northwestern Costa Rica. By decoupling the relationship between growth and reproduction, this study showed that variation in these two life history traits arises due to both variation in plant size and interannual precipitation. In the context of

trait based ecology, this study highlights the importance and possible underlying drivers of trait correlations in nature.

In sum, the objective of this dissertation was to quantify the magnitude of trait variation both between and within species and use trait variation as a way to reconcile hypotheses regarding species diversity patterns and species co-existence. The approach I used encompasses multiple spatial scales. Each spatial scale emphasizes key processes which largely influence species diversity. For example, I sampled plant traits within a single dry tropical forest in order to characterize the magnitude of trait variation at local scales. Next, I tested whether trait variation across dry tropical forests in the Americas could be explained by existing hypotheses that relate climatic variability to trait variation. I also used trait variation between and within three mountain gradients across latitude to test several long-standing hypotheses in ecology, namely, limiting similarity and abiotic filtering. Finally, I use a single population of a tropical tree species to determine how trait variation is influenced by allometry and resource availability. Together, the research within this dissertation advances our understanding of the underlying drivers of trait variation and supports the use of trait variation for reconciling outstanding questions in ecology.

An Explanation of the Dissertation Format

In this dissertation, I present the results of a broad study at several different spatial scales in order to understand the degree and drivers of plant trait variation.

First, in Appendix A “*Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest*”, I detailed the magnitude of plant trait variation both within and between species in a dry tropical forest in northwestern Costa Rica. In Appendix B “*Plant functional trait variation in tropical dry forests: A review and synthesis*”, I detailed the role of trait variation within and between multiple dry tropical forests across the Americas. In addition, I provide an empirical test of the role of climatic variables on trait variation for dry tropical forests varying in seasonality. In Appendix C “*Intraspecific and interspecific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude*”, I expanded the analysis of trait variation to broad biogeographical scales and quantified the degree and patterns of intra- and interspecific trait variation across latitude and across three mountain ranges in tropical, desert, and Mediterranean biomes. Using patterns of trait variation for one key leaf trait, specific leaf area, I tested for evidence of abiotic and biotic drivers of assembly and diversity patterns. Lastly, in Appendix D “*Interannual variability of growth and reproduction in *Bursera simaruba*: The role of allometry and resource variability*”, I apply the concept of trait variation to a single population of a tropical tree species in a dry tropical forest. I test how two life history traits (growth and reproduction) vary in response to climatic and allometric factors.

Together, these chapters represent a critical assessment of the varying effects of trait variation at local, regional, and continental scales. Quantifying trait variation is an important and necessary next step for understanding patterns of assembly and diversity across a broad range of spatial scales.

PRESENT STUDY

I present the methods, data, analyses, and conclusions of this study in the four appended manuscripts. Below, I briefly summarize the main conclusions from each of these studies.

First, in Appendix A “*Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest*” I detailed the magnitude of plant trait variation both within and between species in a dry tropical forest in northwestern Costa Rica. Previous trait based studies generally ignored intraspecific trait variation assuming that it was negligible compared to interspecific variation; however, the study presented here was among one of the first studies to highlight that intraspecific variation can in fact be comparable in magnitude to interspecific variation. In addition, this study highlighted the high degree of trait variation in compound-leaves species as well as the lack of power for predicting shade trait values based on sun-collected leaves. This local-scale study provided important implications for trait sampling and the general emphasis of intraspecific trait variation in functional ecology has ensued.

Second, in Appendix B “*Plant functional trait variation in tropical dry forests: A review and synthesis*” I detailed the role of trait variation within and between multiple dry tropical forests across the Americas. Here, I tested whether functional diversity can be used to understand compositional, structural, and functional differences within and between dry tropical forests. I showed that functional diversity of a key leaf trait, specific leaf area, increases with increasing climatic variability. Distinguishing dry tropical forests has been a challenge and this study provides a unique approach for classifying dry

tropical forests based on the degree of seasonality which ultimately effects plant form and function. This has important implications for understanding the differences between dry tropical forests and the assembly mechanisms responsible in forests of increasing seasonality.

Third, in Appendix C “*Intraspecific and interspecific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude*” I expanded the analysis of trait variation to broad biogeographical scales and quantified the degree and patterns of intra- and interspecific trait variation across latitude and across three mountain ranges in tropical, desert, and Mediterranean biomes. This is among the few studies to quantify intraspecific trait variation in situ at large spatial scales. The patterns of trait variation for one key leaf trait, specific leaf area, support the notion that biotic drivers underlie observed assembly and diversity patterns in low latitude tropical forests whereas abiotic drivers are more important for assembly and diversity patterns in high latitude temperate forests. In addition, I used intraspecific variation to show how trait breadth and total trait space in communities vary across broad environmental gradients. This study will likely inspire future work to apply intraspecific variation for understanding how trait space and trait distributions vary over small to large spatial scales.

Lastly, in Appendix D “*Interannual variability of growth and reproduction in *Bursera simaruba*: The role of allometry and resource variability*”, I apply the concept of trait variation to a single population of a tropical tree species in a dry tropical forest. I test how two life history traits (growth and reproduction) vary in response to climatic and

allometric factors and showed that observed trait variation within this population of tropical trees was both a result of resources and size-related effects. By using a legacy dataset, I was able to show that allometric effects must be accounted for when exploring tradeoffs between life history traits.

In sum, this dissertation provides an assessment of the varying effects of trait variation for local populations as well as for entire plant communities at local, regional, and continental scales. Yet, several key challenges remain for trait based research. First, the research here, as well as that of other trait based studies, emphasizes variation in one to a few plant traits. For example, here, emphasis has been placed on a variation for a single leaf trait—specific leaf area. Although specific leaf area is a principle axis of variation in ecological strategies (Westoby 1998) and is known to be tightly correlated to other functional traits including relative growth rate, photosynthetic rate, leaf longevity, among others (Reich et al. 1997), few mechanistic relationships have been developed to explain variation in plant traits (see Blonder et al. 2010). Thus, whether physical or evolutionary constraints underlie functional trait variation should be further explored. Similarly, various mechanisms have been proposed to understand individual trait-trait correlations (Poorter and De Jong 1999; Niklas et al. 2009), yet these are largely based on empirical observations of traits in nature and an understanding of the physical or evolutionary constraints to trait variation is limited.

Secondly, despite the use of the trait based approach for testing patterns of community assembly, it has been difficult to link observed trait patterns to mechanisms of species coexistence. For example, advances in the development of statistical methods

to compare trait distributions within and between communities have increased our understanding of how traits are distributed among species (e.g. Ackerly & Cornwell 2007). On the one hand, the distribution of traits within and between communities reflects cumulative effects of stabilizing niche differences, relative fitness differences, long-term evolutionary processes, as mediated by the environment and species interactions during assembly (HilleRisLambers et al. 2012). On the other hand, patterns of different assembly drivers are not always opposing; both abiotic filtering and competitive exclusion can lead to trait clustering (Mayfield and Levine 2010). Similarly, trait distributions that do not differ from random expectations are difficult to interpret as these could reflect a combination or cancelling out of environmental filters, relative fitness differences, or stabilizing niche differences (Mayfield et al. 2005; HilleRisLambers et al. 2012). Thus, quantifying trait-environment relationships, linking specific coexistence mechanisms to trait differences, and testing whether trait differences truly reflect stabilizing niche differences will provide a more direct link between community assembly and coexistence theory.

Lastly, there is an urgent need to understand and predict how global climatic changes are altering, and will continue to alter, the structure and function of ecosystems worldwide. Yet current approaches are limited by the absence of robust trait based vegetation models. Instead, dynamic global vegetation models heavily rely on plant functional types—a group of species with presumed similar roles in ecosystem functions (Lavorel et al. 1997). This approach has several drawbacks including the mismatch between using discrete plant functional types to calculate continuously varying fluxes (of

H₂O and CO₂, for example) (see Van Bodegom et al. 2012). However, in order for a trait based approach to be applied in global climatic models, trait-environment relationships must be reliably quantified and integrated into a predictive framework which can successfully link trait tradeoffs and plant strategies to current and future environmental conditions.

Quantifying trait variation is an important and necessary next step for understanding patterns of assembly and diversity across a broad range of spatial scales. By highlighting intraspecific trait variation, this dissertation begins to bridge the divide between trait based ecology, global modeling, and coexistence theory. Yet several key challenges emerge from this dissertation that will likely shape the future of trait based ecology. First, a mechanistic understanding of trait variation is needed to explain trait tradeoffs as well as trait-environment responses. Second, trait based ecology should be incorporated into global vegetation models for a more accurate predictive framework of how ecosystem level function will vary with ongoing global climatic changes. Finally, trait based ecology should be more strongly tied to coexistence theory by linking specific coexistence mechanisms to trait variation. In sum, trait variation provides the raw material for natural selection and thus provides a direct link between ecological and evolutionary theory. The structure of intraspecific variability in actual communities can reveal the signature of past community assembly processes and will ultimately advance a predictive framework in community ecology (Violle et al. 2012).

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APPENDIX A:
VARIATION IN LEAF FUNCTIONAL TRAIT VALUES WITHIN AND ACROSS
INDIVIDUALS AND SPECIES: AN EXAMPLE FROM A COSTA RICAN DRY
FOREST

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

Running Title: Variation in functional trait values

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Abstract

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. 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.

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? 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. 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.

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 and Keddy 1995; McGill *et al.* 2006). In particular, community ecologists would benefit from quantitative information that describes the functional 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 and 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, and Keddy 1998; Ackerly and Cornwell 2007; Swenson and Enquist 2007; Swenson and Enquist in press; Swenson *et al.* 2007; Kraft, Valencia, and Ackerly 2008; Cornwell and 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, and 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; Raunkiær 1934; Whittaker 1967; Givnish 1979; Wright *et al.* 2004; Ackerly and Cornwell 2007), while intraspecific variation has been correlated with microhabitat differences in topography, slope, soil moisture availability (e.g. Lambrecht and 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 and Cabido 1997; Westoby 1998; Cornelissen *et al.* 2003; Garnier *et al.* 2004; Wright *et al.* 2004; Swenson and 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, and Ackerly 2008; Swenson and Enquist 2008; Lake and Ostline 2009). For example, in tropical forests sun-exposed leaves can be exceedingly difficult to collect 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, and 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, and Ackerly 2008; Swenson and 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 northwestern Costa Rica.

Methods

Study locations 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 and Arm.) Schum., Bignoniaceae: *Tabebuia ochracea* Standl., and Sterculiaceae: *Guazuma ulmifolia* (Lam.). Taxonomic nomenclature follows Janzen and Liesner (1980). The species *A. occidentalis*,

B. simaruba, *S. glauca*, *S. mombin*, and *T. ochraceae* 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 (MW, 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 (MD, g). Specific leaf area (SLA; cm² g⁻¹) was calculated as: $SLA = A_w * MD$; where A_w is the fresh leaf area (cm²) and MD is the final

dry mass in grams. Leaf water content (LWC, g H₂O 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 fourleaf traits studied (LA, MD, 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, and 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, MD, 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 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 R² 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 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.

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 MD, 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 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, and 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, and 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 intracanopy plasticity is often driven by variability in levels of irradiance and plays an important role in whole plant function (Rozendaal, Hurtado, and 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 and 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 and 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 pairwise 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.

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Tables Appendix A

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

	Levels	Leaf Area	Dry Mass	SLA	Succulence
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

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

	Levels	Leaf Area	Dry Mass	SLA	Succulence
All High	Species	0.590	0.551	0.494	0.377
	Individuals	0.239	0.319	0.256	0.352
	Leaves	0.172	0.130	0.250	0.271
All Low	Species	0.653	0.551	0.514	0.315
	Individuals	0.187	0.133	0.341	0.293
	Leaves	0.161	0.316	0.145	0.392

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

	Levels	Leaf Area	Dry Mass	SLA	Succulence
Compound Leaflet High	Species	0.375	0.386	0.168	0.400
	Individuals	0.207	0.257	0.068	0.294
	Leaves	0.057	0.108	0.081	0.103
	Leaflet	0.362	0.250	0.683	0.203
Compound Leaflet Low	Species	0.498	0.241	0.588	0.150
	Individuals	0.181	0.068	0.178	0.088
	Leaves	0.104	0.063	0.115	0.041
	Leaflet	0.217	0.629	0.119	0.721

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

	Intercept	Slope	R²
Leaf Area	-17.751*	1.08*	0.68
Dry Mass	-0.023	1.14*	0.50
SLA	9.542	0.83*	0.52
Succulence	0.001*	0.81*	0.27

Figures Appendix A

Figure 1. Two sample t-test power curves for the species pair of *C. indica* and *T. ochroma*. 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 MD. The dashed black line represents SLA. The dashed grey line represents LWC.

Figure 2. Two sample t-test power curves for the species pair of *C. indica* and *G. 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 MD. The dashed black line represents SLA. The dashed grey line represents LWC.

Figure 3. Two sample t-test power curves for the species pair of *T. ochroma* and *B. simaruba*. 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 MD. The dashed black line represents SLA. The dashed grey line represents LWC.

Figures
Figure 1:

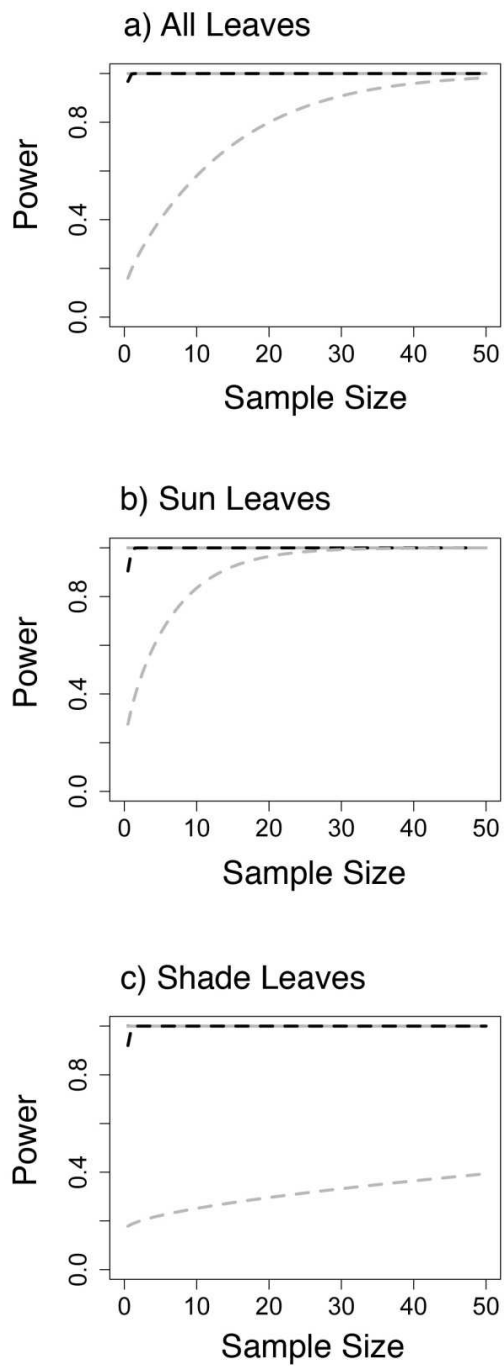


Figure 2:

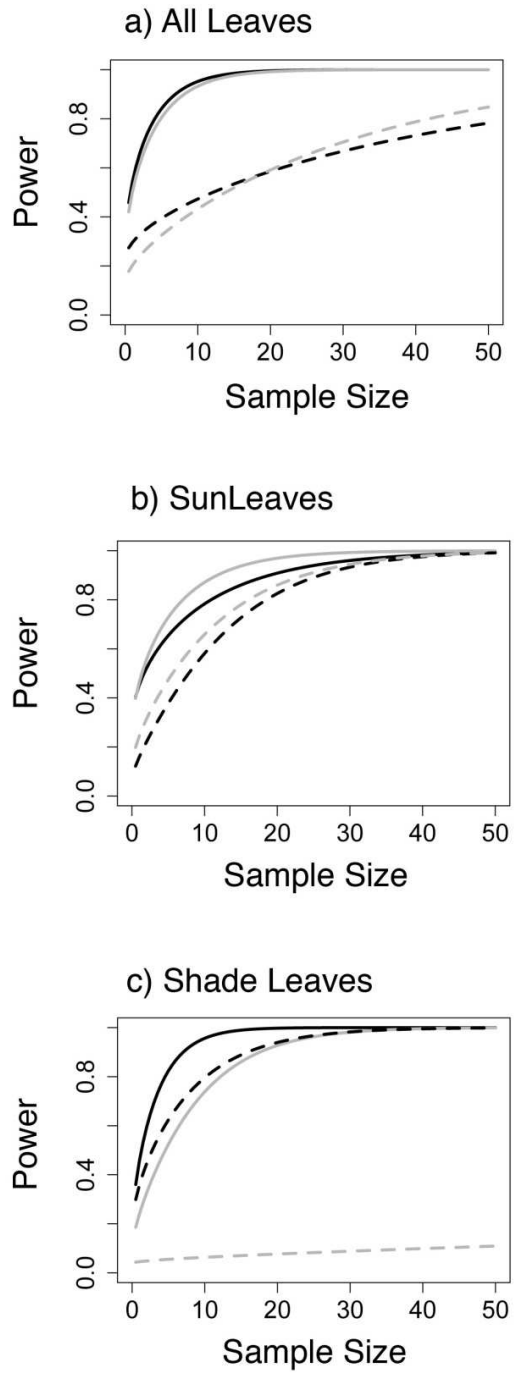
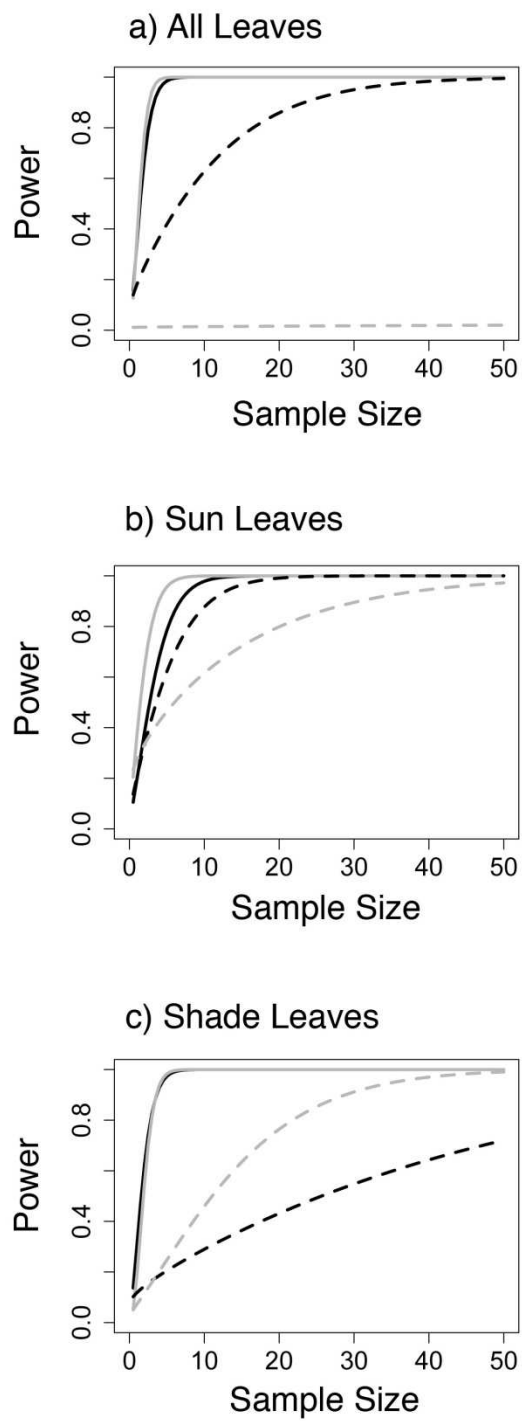


Figure 3:



Supplementary Material Appendix A

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

	LA			M_D			SLA			LWC		
	All Leaves	Sun Leaves	Shade Leaves	All Leaves	Sun Leaves	Shade Leaves	All Leaves	Sun Leaves	Shade Leaves	All Leaves	Sun Leaves	Shade Leaves
<i>A. occidentalis</i>	151.05 (58.10)	152.59 (79.53)	149.52 (55.08)	0.44 (0.08)	0.47 (0.17)	0.41 (0.09)	349.09 (92.31)	321.34 (74.04)	376.84 (149.86)	0.008 (0.002)	0.008 (0.002)	0.008 (0.002)
<i>B. simaruba</i>	401.09 (82.64)	383.15 (98.01)	419.02 (100.77)	1.54 (0.43)	1.55 (0.48)	1.53 (0.48)	271.50 (52.21)	256.34 (50.20)	286.66 (55.29)	0.009 (0.001)	0.009 (0.001)	0.009 (0.001)
<i>C. indica</i>	27.64 (4.37)	28.82 (3.77)	26.46 (7.55)	0.21 (0.03)	0.23 (0.04)	0.19 (0.07)	136.65 (10.90)	130.79 (17.57)	142.50 (20.18)	0.010 (0.001)	0.010 (0.001)	0.010 (0.002)
<i>G. macrosperma</i>	63.23 (10.49)	63.84 (12.58)	62.62 (13.07)	0.23 (0.08)	0.26 (0.12)	0.19 (0.06)	308.42 (67.97)	269.01 (60.62)	347.82 (92.65)	0.010 (0.001)	0.011 (0.001)	0.010 (0.001)
<i>G. ulmifolia</i>	38.97 (13.18)	36.47 (13.64)	41.47 (16.50)	0.28 (0.08)	0.310 (0.12)	0.26 (0.10)	143.60 (28.11)	121.15 (16.50)	166.06 (44.94)	0.010 (0.002)	0.011 (0.002)	0.010 (0.002)
<i>H. excelsum</i>	36.38 (5.97)	36.45 (7.33)	36.32 (7.08)	0.15 (0.03)	0.16 (0.04)	0.14 (0.04)	253.33 (19.60)	246.10 (26.51)	260.56 (33.96)	0.010 (0.001)	0.010 (0.001)	0.009 (0.001)
<i>S. glauca</i>	327.31 (45.82)	318.24 (70.18)	336.39 (38.57)	2.29 (0.50)	2.19 (0.67)	2.40 (0.83)	155.80 (10.85)	150.34 (18.60)	161.25 (23.54)	0.009 (0.002)	0.010 (0.002)	0.009 (0.003)
<i>S. mombin</i>	600.65	660.04	541.25	3.87	4.34	3.41	167.53	170.45	164.61	0.014	0.014	0.014

	(155.31)	(242.51)	(145.72)	(1.32)	(2.31)	(0.91)	(39.87)	(64.38)	(28.10)	(0.002)	(0.002)	(0.002)
<i>S. obovata</i>	137.62	141.61	129.96	0.36	0.40	0.31	397.34	369.37	429.43	0.011	0.012	0.011
	(23.57)	(28.36)	(25.70)	(0.08)	(0.11)	(0.09)	(47.54)	(52.47)	(63.69)	(0.001)	(0.001)	(0.001)
<i>T. ochroma</i>	529.35	495.66	563.03	2.25	2.38	2.12	243.27	216.19	270.36	0.009	0.010	0.009
	(72.04)	(93.97)	(85.68)	(0.35)	(0.61)	(0.31)	(42.22)	(44.07)	(46.37)	(0.001)	(0.001)	(0.001)

APPENDIX B:
PLANT FUNCTIONAL TRAIT VARIATION IN TROPICAL DRY FORESTS: A
REVIEW AND SYNTHESIS

Plant functional trait variation in tropical dry forests: A review and synthesis

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Book Chapter

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Abstract

Functional traits can describe the ecological strategy and evolutionary history of a species and provide insight into patterns of plant form and function, community assembly, and ecosystem functioning. Although patterns of plant trait variation are well studied in temperate and tropical wet forests, our understanding of plant functioning in tropical dry forests is comparatively limited. Here, we overview three key plant functional traits important in seasonally dry tropical environments in the Neotropics. We describe the underlying sources of trait variation at local to broad spatial scales. Specifically, we detail the effects of local topography and disturbance on plant trait variation within tropical dry forests as well as the effects of broad geographical gradients. Based on the literature we hypothesize that, compared to more wet and aseasonal tropical forests, tropical dry forests should have higher functional diversity as a result of plant adaptations to seasonal drought. We test whether functional diversity can be used to understand compositional, structural, and functional differences within and between dry forests. To do this we use a global trait and plant inventory database in addition to our own data to compare functional diversity of dry forests to other tropical systems throughout the Americas and quantify how functional diversity is related to climatic factors (e.g. temperature, precipitation, seasonality). In support of our hypothesis, we show that functional diversity of a single key functional trait (specific leaf area) increases with increasing precipitation seasonality. Finally, we discuss the potential effects of climate change on plant and ecosystem function as well as outline key areas of research

where trait based approaches will advance our understanding of the ecology and functioning of tropical dry forest ecosystems.

Important Functional Traits in TDFs

Plant functional traits are an integrative measure of plant fitness in different environments and strongly impact ecosystem processes such as primary productivity, decomposition, and nutrient cycling (Diaz et al. 2004). Across environmental gradients, shifts in functional traits at the whole-plant level are consistent with a trade-off between rapid biomass production and efficient nutrient conservation (Reich et al. 1997). Species in resource-rich environments tend to be fast growing, have rapid rates of resource acquisition and tissue turnover, while species in resource-poor environments tend to have a resource conservation strategy with slow rates of growth, tissue turnover, and high longevity (Westoby et al. 2002). The diversity and spacing (or dispersion) of plant functional traits along environmental gradients also provides insight into community assembly and species coexistence mechanisms (Weiher and Keddy 1995). Despite the explosion of trait based studies in ecology, most studies emphasize trait patterns in temperate, Mediterranean, or tropical moist forest ecosystems. Surprisingly, there have been relatively few studies addressing patterns of functional trait diversity in tropical dry forests or other extensive water-limited ecosystems (Chaturvedi et al. 2011). Thus, our understanding of the underlying drivers of plant trait variation and community assembly in tropical dry forests is unclear.

Tropical dry forests (TDFs) are characterized by pronounced seasonality in precipitation, with several months of prolonged drought, 80% of annual precipitation

occurring during a four to six month rainy season, and high interannual rainfall variability (Mooney et al. 1995; Pennington et al. 2009; Maass and Burgos 2011). The marked temporal availability of soil water selects for adaptive traits associated with the avoidance, resistance, or tolerance of water stress (Olivares and Medina 1992). Unsurprisingly, adaptations to strong seasonal drought and limited water supply, high solar irradiance, and high evaporative demand largely determine the physiological activity, growth, reproduction, and survival of dry forest plant species (Borchert 1994). A review of previous functional trait studies within TDFs and an overview of important traits in dry forests has recently been described (e.g. Chaturvedi et al. 2011). Here, we highlight three important functional traits related to water stress. Specifically, leaf phenology (i.e. deciduous, semi-deciduous, evergreen, etc.), wood specific gravity (i.e. wood density), and specific leaf area (SLA) are strongly linked to soil water availability and whole-plant water status in tropical dry forest trees.

Variation in Deciduousness

One striking aspect of TDFs is the range of species variation in deciduousness (Sobrado 1991). For example, dry tropical forests usually consist of both evergreen and deciduous species. The degree of deciduousness and patterns of leaf renewal and senescence in dry forest trees are thought to be strongly linked to the extent and intensity of seasonal drought (Borchert 1994) as well as to spatial heterogeneity in soil water availability (Janzen 1986; Powers et al. 2009 but see also Aide 1992). A rich area of research is whether plants with different leaf phenologies (i.e. degrees of deciduousness

or leaf habit) also possess different suites of functional traits (Eamus 1999; Powers and Tiffin 2010). For example, in TDFs, broad-leaved deciduous trees were reported to have higher nitrogen content, SLA, and rates of photosynthesis compared to broad-leaved evergreen trees (Sobrado 1991; Prior et al. 2003; Ishida et al. 2006; Kushwaha et al. 2011; Pringle et al. 2011). In contrast, recent studies found that interspecific variation in leaf phenology is insufficient to predict leaf function and physiology within TDFs (Brodribb and Holbrook 2004; Powers and Tiffin 2010) and highlight the diversity of functional strategies within phenological categories (see Giraldo and Holbrook 2011). In addition, leaf deciduousness can vary within species depending on local microhabitat conditions (Elliott et al. 2006) such as differences in temperature, soil water availability, and rooting depth (Singh and Kushwaha 2006). Since previous studies often categorize a species' deciduousness based on literature reviews or local expert knowledge it is difficult to determine how variable deciduousness actually is within species. An individual approach in which both trait data and phenological observations are recorded from the same individuals over time would further elucidate the interaction between leaf phenology and functional strategies (e.g. Kushwaha et al. 2011).

Wood Density

An example of how plant functional traits can elucidate key ecological and physiological strategies is the linkage between plant distribution, leaf phenology, and wood density. Wood density is an important factor for determining carbon stocks (Chave et al. 2009) and resource turnover and is thus a critical functional trait for linking species-

level physiology to ecosystem level function. Wood density is strongly related to soil water availability (Borchert 1994), with a larger proportion of denser woods in drier soils (Borchert 1994) and is known to respond to gradients of soil fertility and climate (Swenson and Enquist 2007). For example, in TDFs of Costa Rica and western Mexico, dry upland forest sites are primarily comprised of deciduous hardwood trees and water-storing softwood trees (hardwoods such as *Lysiloma microphyllum*, *Tabebuia* spp., and *Guaiaacum coulteri*; softwoods like *Cochlospermum vitifolium*, *Bursera* spp., and several species of columnar cacti) while evergreen and semi-deciduous, hard- and softwood trees (hardwoods such as *Enterolobium cyclocarpum*, *Brosimum alicastrum*, and *Hymenaea courbaril*; softwood like *Ceiba pentandra*, *Bursera instabilis*, and *Cedrela* spp.) are confined to moist lowland forests (Janzen 1986; Borchert 1994). Thus, tree water status, wood density, and phenology depend on both functional adaptations to drought in addition to local environmental variables (Borchert 1994). In the context of TDFs, wood density is particularly informative because it represents a fundamental trade-off between growth, mechanical support, hydraulic conductivity, and water storage capacity (Niklas 1995). Denser wood is thought to convey stronger mechanical stability (Niklas 1995), higher resistance to xylem embolism and cavitation (Hacke et al. 2001), slower stem radial growth, longer lifespan, and lower rates of mortality (Enquist et al. 1999). As a result, high density wood may allow heavy-wooded plant species in TDFs to continue growing when lighter-wooded species, particularly those that lack water storage tissues, are forced to shut down water transport during drought (Chave et al. 2009). Indeed, wood density emerges from vascular properties such as diameter and frequency of xylem

conduits; wood density increases with decreasing conduit diameter and frequency and increasing fiber density (Russo et al. 2010). Some studies suggest that diameter growth rate may be more strongly related to xylem traits (i.e., lumen area and vessel density) rather than wood density (Russo et al. 2010) and xylem conductivity is known to critically determine plant water balance (Gleason et al. 2012).

Differences in plant functional traits and trade-offs between different trait axes is thought to cause functional divergence and niche separation of tree species along gradients of light and water availability (Poorter 2005; Sterck et al. 2011). A better understanding of spatial and temporal variation in functional traits including wood density and wood hydraulic properties will further clarify the role of trade-offs in plant physiological functioning and species distributions in TDFs.

Specific Leaf Area

Specific leaf area, defined as the light capturing surface area per unit of dry biomass, reflects a trade-off between resource capture and conservation (Poorter 2009), and has been shown to correlate with net photosynthetic capacity, leaf longevity, relative growth rate, wood density, and competitive ability (Reich et al. 1997). SLA is thought to vary with leaf phenology, with deciduous species having higher SLA and evergreen species having lower SLA values, representing a trade-off between short leaf life span with high resource acquisition and long leaf life span with slow resource acquisition (Reich et al. 1997). As mentioned, although the correlation between SLA and leaf phenology has been shown for a collection of evergreen and deciduous tropical species

(e.g. Sobrado 1991; Ishida et al. 2006; Pringle et al. 2011) the generality of this relationship is still unclear (see Williams-Linera 2000; Brodribb and Holbrook 2004; Powers and Tiffin 2010). SLA has also been shown to shift across large-scale latitudinal gradients (Reich et al. 1997). Specifically, SLA was found to be higher in TDFs compared to wetter tropical forests (Gotsch et al. 2010). In addition, leaf traits such as leaf mass per area (i.e., the inverse of SLA) were found to have lower variation in dry forests in response to light compared to wetter forests which suggests that light-related variation is not as important for dry forest plant species as in wet forests and the low soil water availability likely constrains the magnitude of leaf trait variation (Markesteijn et al. 2011). However, a comparison of SLA values between contrasting ecosystems across the world, including tropical dry and rain forests, showed that dry forest ecosystems have some of the largest variation in SLA (Villar and Merino 2001). Differences in SLA are likely important for the coexistence of species in TDFs, because a larger variation in SLA within a community might allow different species to partition resources across the highly variable environment of TDFs both in time (i.e., rainfall seasonality) and space (i.e., variation in topography and soil water content). The magnitude and patterns of trait variation in TDFs compared to other ecosystems is an interesting area of research for understanding the assembly of dry forest communities as well as for understanding species distributions within and between TDFs, and across dry-wet forest transitions.

The functional composition and phenology of TDFs has direct consequences for ecosystem functioning particularly for seasonal variation in primary productivity and biogeochemistry (Giraldo and Holbrook 2011; Jaramillo et al. 2011), and energy, water, and carbon cycles (Sanches et al. 2008; Maass and Burgos 2011). Although studies on NPP and biogeochemistry in TDFs are still very scarce (Jaramillo et al. 2011), ecosystem functioning can be related to several key functional traits (Murphy and Lugo 1986). For example, it has been reported that TDF species generally have higher leaf nitrogen content, SLA, and light-saturated photosynthetic rates, and lower leaf lifespan and N:P compared to desert, tropical evergreen, temperate evergreen, and tundra biomes (Chaturvedi et al. 2011). These characteristics have direct consequences for the timing and nutrient composition of leaf-fall (Martinez-Yrizar et al. 1999; Xuluc-Tolosa et al. 2003), rates of decomposition (Harmon et al. 1995; Sundarapandian and Swamy 1999; Powers et al. 2009) as well as carbon and nutrient cycling (Jaramillo et al. 2011). Specifically, leaf nitrogen concentration or lignin:N ratio are among the best predictors of decomposition rates (Cornwell et al. 2008), yet due to dry conditions, decomposition is drastically reduced during the dry season compared to wetter forests (Powers et al. 2009). Further, water availability regulates nutrient dynamics in litter and soil in TDFs (Jaramillo et al. 2011; Anaya et al. 2012).

Perhaps because water plays such a dominant role in the regulation of structure and the dynamics of TDFs, very little attention has been given to the interaction between soil nutrients and plant functional traits within TDFs (Murphy and Lugo 1986; Jaramillo et al. 2011). Leguminous species are particularly dominant in TDFs (Gentry 1995;

Pennington et al. 2009) and are critical in determining levels and rates of N-fixation within communities. However, detailed studies relating the contribution of fixed N to ecosystems is surprisingly rare, although, given the seasonality, water availability regimes may affect nutrient acquisition more strongly in species without root symbionts than those with N-fixing bacteria or mycorrhizae. Among the few studies that relate the amount of fixed N in tropical forests, the majority has taken place in humid regions with a few recent studies in TDFs (Freitas et al. 2010). There is thus a large knowledge gap relating the effects of leguminous, nitrogen-fixing plant species on ecosystem nitrogen dynamics.

Trait Variation and Environmental Gradients

Environmental gradients within TDFs

The degree of deciduousness and other plant adaptations to seasonal drought varies both within TDFs as a result of topography, forest structure, and land-use history (Janzen 1986; Powers et al. 2009) as well as between TDFs due to differences in annual rainfall, temperature, and solar radiation regimes. In addition, on a landscape scale geological substrate may decouple the expected relationship between rainfall and deciduousness (Bohlman 2010). Tropical dry forests are characterized by high environmental complexity (Mooney et al. 1995) and, as a result, the inherent variability of dry forest ecosystems allows only coarse generalizations regarding the ecological characteristics and classifications of dry forests (Murphy and Lugo 1986; Burquez and Martinez-Yrizar 2010). Topography within seasonal dry forests is a major driver of insolation and hydrologic processes (Martinez-Yrizar et al. 2000) and results in patchy

availability of soil nutrients (Roy and Singh 1994) and water availability (Oliveira-Filho et al. 1998; Daws et al. 2002; Segura et al. 2003). For example, gravity-driven runoff causes a larger moisture accumulation in lower topographic positions (Daws et al. 2002; Markesteijn et al. 2010). Temporal variation is also another obvious source of variation in water availability; during the wet season most water is found in the top soil layers while during the dry season more water is available in deep soil layers (Markesteijn et al. 2010).

Within TDFs, variation in forest structure, species diversity, and distributions reflect differences in soil water availability (Borchert 1994; Oliveira-Filho et al. 1998; Balvanera et al. 2010; Enquist and Enquist 2011). Due to increased resource partitioning within TDFs as a result of the spatio-temporal heterogeneity of soil water availability, functional shifts in water use and acquisition should be apparent across gradients of soil moisture (Poorter 2005; Sterck et al. 2011). While this has been shown for wood density, phenology, and other key plant traits for TDF species in northwestern Costa Rica (Borchert 1994; Gotsch et al. 2010) and Bolivia (Markesteijn et al. 2010; Sterck et al. 2011), this remains an interesting area of research for understanding the maintenance of species diversity and functional diversity within TDFs. Specific leaf area, for example, plays an important role in the assembly of plant communities (Weiher and Keddy 1995). Within other forests, SLA has been shown to play a large role in the assembly of species across gradients of light and water availability (Poorter 2009). Though temporal and spatial variation in water availability drive habitat associations and niche partitioning within tropical forests (see Segura et al. 2003; Balvanera et al. 2010), whether variation

in plant functional traits such as SLA reflect shifts in plant distributions both within and between TDFs is unknown, yet would provide a possible way to distinguish TDFs.

Another primary source of environmental variation within TDFs is land-use and anthropogenic disturbance. TDFs are widely cited as the most fragmented and endangered tropical forest type (e.g. Janzen 1988; Gentry 1995). The variation in land-use history, time since last disturbance, frequency of disturbance, size of disturbance, among other key factors (Chazdon et al. 2007) strongly influences the functional variation and assembly of resulting plant communities in TDFs (Lebrija-Trejos et al. 2011). Understanding how plant and ecosystem-level functioning change over time could enhance the ability to predict and manage succesional forests in order to recover key ecosystem services or functions long before they recover, if any, floristic similarity to previous conditions (Alvarez-Yépez et al. 2008). On a fundamental level, secondary succession is community assembly in action (Lebrija-Trejos et al. 2011). Studies relating plant functional diversity along succesional trajectories within TDFs argue that abiotic processes restrict initial colonization stages while competitive interactions constrain later succesional stages (Lebrija-Trejos et al. 2011). The majority of succesional studies to date, however, use chronosequences or a series of sites of different ages (e.g. Kennard et al. 2002; Lebrija-Trejos et al. 2011). These studies are based on the assumption that environmental conditions, site history, and seed availability are similar across sites and over time (Chazdon et al. 2007) which rarely reflects true site conditions. Thus, long-term studies are needed to monitor the functional properties and assembly of specific sites over time in TDFs (e.g. Chazdon et al. 2007; Enquist and Enquist 2011). In sum, more

research is needed to quantify the spatio-temporal variation in functional composition and ecosystem processes in TDFs over large spatial and temporal scales (Maass and Burgos 2011; Anaya et al. 2012).

Geographical Gradients: A trait based Approach for Comparing TDFs

A primary research goal within tropical dry forest studies is to identify the current extent and the degree of fragmentation of TDFs (Sanchez-Azofeifa et al. 2005). However, as previously mentioned, the inherent variability of dry forest ecosystems allows only coarse generalizations regarding the ecological characteristics and classifications of dry forests (Murphy and Lugo 1986; Burquez and Martinez-Yrizar 2010). Attempts to characterize differences among TDFs by the degree of deciduousness and to explain them by variation in amount and seasonality of annual rainfall have been challenging (Murphy and Lugo 1986; Burquez and Martinez-Yrizar 2010). A functional trait based approach offers insight into the functional differences between and within TDFs across large geographical gradients. At local scales, previous studies have been successful in linking coordinated changes in plant functional traits that affect primary productivity and nutrient cycling to seasonality, such as hydraulic conductivity and wood density and changes in mean annual precipitation over space (e.g. Poorter 2009; Gotsch et al. 2010; Sterck et al. 2011) and time (e.g. Rentería and Jaramillo 2011). To test whether functional diversity can indeed describe functional differences between and within TDFs across large geographical gradients, here we compare functional diversity of one key leaf trait (SLA) between Neotropical forests to climatic factors. First, we

compare the magnitude of functional diversity in TDFs to other tropical forest ecosystems and, secondly, we relate functional diversity to climatic variables across broad spatial scales.

There are two contrasting hypotheses for how climate and seasonality should influence functional diversity in TDFs. On the one hand, increased seasonality and decreased precipitation are strong environmental filters for drought-adaptive traits (Poorter 2005) and should thus limit trait variation at the community level. Specifically, the extended periods of drought that are characteristic of dry forests (usually from 6 to 8 months) can be thought of as a selective filter, allowing only those species with traits that confer drought avoidance, resistance, or tolerance to coexist in these water-limited ecosystems. As a result, we expect functional diversity to decrease in drier, more seasonal environments. On the other hand, if seasonality results in an increase in temporal and spatial variation in soil moisture then we might expect an increase in functional diversity in more seasonal forests. Indeed, TDFs are characterized by highly heterogeneous habitats both in space and time. The differing abilities of plant species to tolerate drought leads to niche differentiation; for example, within forests species sort out along slope gradients of water availability (Balvanera et al. 2010). Thus, spatio-temporal heterogeneity within TDFs can allow for increased functional diversity despite a shorter growing season compared to wetter tropical forests.

To test these hypotheses, we paired plant inventory and trait collections across multiple tropical forest sites throughout the Americas. We obtained inventory and trait data from a total of 26 plots ranging from tropical dry to wet forests throughout Mexico

and Costa Rica. We used the online database SALVIAS (www.salvias.net) to download plot and trait data from B. Enquist; we also used plot and trait data from Gómez-Sapiens (2001) and Hulshof et al. (2012). Based on the latitude and longitude coordinates of each plot, we extracted mean annual temperature, temperature seasonality (coefficient of variation of mean monthly temperatures), total annual precipitation, precipitation seasonality (coefficient of variation of monthly precipitation totals), in addition to 15 other bioclimatic variables at a 2.5 min resolution from WorldClim (Hijmans et al. 2005). To quantify functional diversity, we calculated functional dispersion of specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) for each plot using the FD package in R (<http://cran.r-project.org/web/packages/FD/>). Functional dispersion is the mean distance in multidimensional trait space of individual species, weighted by relative abundances, to the centroid of all species within a community (Laliberté and Legendre 2010). Among the many metrics of functional diversity, we chose dispersion because it describes the distribution of individuals in trait space, can be used for single and multiple traits, is not strongly influenced by outliers, is independent of species richness, and incorporates species' abundances (Laliberté and Legendre 2010). We calculated functional dispersion for SLA because it represents a fundamental trade-off axis between resource capture and conservation (Poorter 2009). SLA was also widely sampled for the majority of species in each plot in our database, eliminating the need to extrapolate species mean trait values (i.e. assigning a species mean trait value collected in one site to individuals of that species found in another site) which underestimates the total amount of variation between

species and sites. In general, one to five leaves were collected from a minimum of three individuals of each species across all plots.

To understand how functional traits vary with climate, we performed a forward stepwise multiple regression model of functional dispersion of SLA against all 19 bioclimatic parameters provided by WorldClim (see Hijmans et al. 2005 and worldclim.org/bioclim). A standard least squares regression was then performed between functional dispersion of SLA and the parameters that minimized the Akaike's Information Criteria score (AIC) in the stepwise model. All statistical analyses were conducted in R (R Development Core Team 2011).

Of the 19 bioclimatic parameters provided by WorldClim, the parameters that minimized the AIC score in the stepwise model included precipitation seasonality, precipitation of the wettest month, and precipitation of the warmest quarter (Table 8.1). The standard least squares regression of functional dispersion against precipitation seasonality had the lowest AIC score (Table 8.2). Specifically, functional dispersion was positively correlated with precipitation seasonality (Figure 8.1). Interestingly, the plots located in the northern distribution of TDFs at 28 oN (San Javier TDF, and La Colorada, Mexico TDF/Thornscrub transition; Gómez-Sapiens 2001) were among the sites with the highest precipitation seasonality and the highest levels of functional diversity (Figure 8.1). In addition, the dry forest sites with similar functional dispersion as wetter forests tend to be characterized by evergreen and semi-deciduous species, typical of the “bosque húmedo” or wetter microhabitats commonly found within the tropical dry forest life zone. Finally, species richness was not correlated to precipitation seasonality (Figure 8.2)

which highlights the challenges of using a species-centric approach for distinguishing TDFs based on patterns of species richness and composition. Together, these findings support the hypothesis that functional diversity increases with increasing rainfall seasonality due to plant adaptations to seasonal drought. Further analyses that include other functional traits (e.g. wood density, hydraulic traits, seed mass) will help to determine whether TDFs can be distinguished based on the amount and seasonality of annual rainfall. Using a single functional trait, SLA, we show here that it may be possible to use a functional trait based approach to distinguish and classify TDFs based on climatic factors, primarily, precipitation seasonality.

Conclusions

In summary, TDFs are characterized by strong spatio-temporal variation in environmental factors which directly impacts plant and ecosystem-level function. We briefly outlined how three key plant functional traits vary in response to environmental variability including local topographical and land-use gradients and broad-scale geographical gradients within and between TDFs. Trait based ecological research within TDFs will advance our understanding of how these fragmented ecosystems interact with and differ from other tropical ecosystems. We identify key research priorities where a trait based approach could be easily implemented to quantify adaptive plant strategies and ecosystem functioning within TDFs.

Many regions that encompass TDFs are predicted to experience more frequent/extended periods of drought, warming temperatures, and decreased mean precipitation (Meir and Pennington 2011). Thus, a major research priority is to

understand the effect of climatic changes on dry forest plant communities. Although the effects of climatic change on biodiversity, structure and functioning of TDFs is discussed in detail elsewhere (Meir and Pennington 2011), a trait based approach can provide additional insight into plant responses to changing environmental conditions (Enquist and Enquist 2011). Phenological shifts in response to changing climates have been widely documented in temperate regions; yet the complex interactions between plant phenology (both leaf and reproduction phenologies), pollination, dispersal, herbivory, and changing climate are relatively underexplored in TDFs (Sanchez-Azofeifa et al. 2005). Although TDFs are considered drought-resistant (Meir and Pennington 2011), the decoupling of pollinators, dispersers, herbivores and plant reproduction could have large effects on plant population dynamics of many species (Janzen 1967; Bawa and Dayanandan 1998; Elzinga et al. 2007). This is particularly true for TDFs as dry season plant reproduction coincides with increased pollinator and disperser activity (Janzen 1967).

The importance of connectivity between dry and wet forests is another rich area of research. Research relating dry forest ecology and conservation often refer to TDFs as distinct ecosystems even though the exchange of organisms and genetic material between dry and wetter ecosystems is an important source of genetic diversity (Bawa and Dayanandan 1998). In addition, nearby rain forests and mesic microhabitats within TDFs are essential sources of refugia for dry forest species, permitting the migration out of the dry forest during the dry season (Janzen 1987; Hanson 2011). Research linking functional diversity within and between species across tropical landscapes that include TDFs will broaden our understanding of the diverse interactions between tropical dry and wet forest

ecosystems as well as the biotic and abiotic drivers of plant trait variation and community assembly.

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Tables Appendix B

Table 1. Summary statistics of forward stepwise model showing the parameters used in the standardized least squares regression of functional dispersion of SLA functional dispersion against the bioclimatic variables ($r^2 = 0.25$, $P = 0.0039$, $F_{3,46} = 5.11$, $AICc = 8.79$, $BIC = 16.99$). Bioclimatic codes from Hijmans *et al.* (2005).

Bioclimatic Code	Parameter	Estimate	Sum of Squares	F-value	P-value
	Intercept	-0.655	0	0	1.000
Annual mean temperature	BIO_1	0	0.027	0.433	0.514
Mean diurnal range	BIO_2	0	0.001	0.010	0.922
Isothermality	BIO_3	0	0.001	0.021	0.885
Temperature seasonality	BIO_4	0	0.009	0.150	0.700
Max temperature of warmest month	BIO_5	0	0.018	0.288	0.594
Min temperature of coldest month	BIO_6	0	0.025	0.408	0.526
Temperature annual range	BIO_7	0	0.000	0.007	0.934
Mean temperature of wettest quarter	BIO_8	0	0.030	0.496	0.485
Mean temperature of driest quarter	BIO_9	0	0.011	0.184	0.670
Mean temperature of warmest quarter	BIO_10	0	0.027	0.444	0.509
Mean temperature of coldest quarter	BIO_11	0	0.026	0.418	0.521
Annual precipitation	BIO_12	0	0.000	0.004	0.953
Precipitation of wettest month	BIO_13	0.002	0.575	9.519	0.003
Precipitation of driest month	BIO_14	0	0.006	0.097	0.757
Precipitation seasonality	BIO_15	0.011	0.792	13.100	0.001
Precipitation of wettest quarter	BIO_16	0	0.015	0.249	0.620
Precipitation of driest quarter	BIO_17	0	0.000	0.000	0.985
Precipitation of warmest quarter	BIO_18	0.000	0.216	3.579	0.065
Precipitation of coldest quarter	BIO_19	0	0.006	0.098	0.755

Table 2. Standardized linear regression summary statistics for each regression model of SLA functional dispersion against the bioclimatic variables which minimized the model AICc score. BIO13 = Precipitation of wettest month; BIO15 = Precipitation seasonality; BIO18 = Precipitation of warmest quarter.

Parameter	AICc	r^2	P	F-value
BIO15	20.00	0.3862	0.0007	15.1
BIO15 + BIO13 +BIO18	24.32	0.5543	0.0004	9.12
BIO15+BIO13	24.67	0.5251	0.0002	12.72

Figures Appendix B

Figure 1: Functional dispersion (FDis) of specific leaf area (SLA: $\text{cm}^2 \text{g}^{-1}$) for each plot as a function of precipitation seasonality (coefficient of variation of monthly precipitation; $r^2 = 0.39$, $P = 0.0007$, $F_{1,24} = 15.1$).

Figure 2: Species richness within each plot as a function of precipitation seasonality; $r^2 = 0.0013$, $P = 0.86$, $F_{1,24} = 0.032$).

Figure 1:

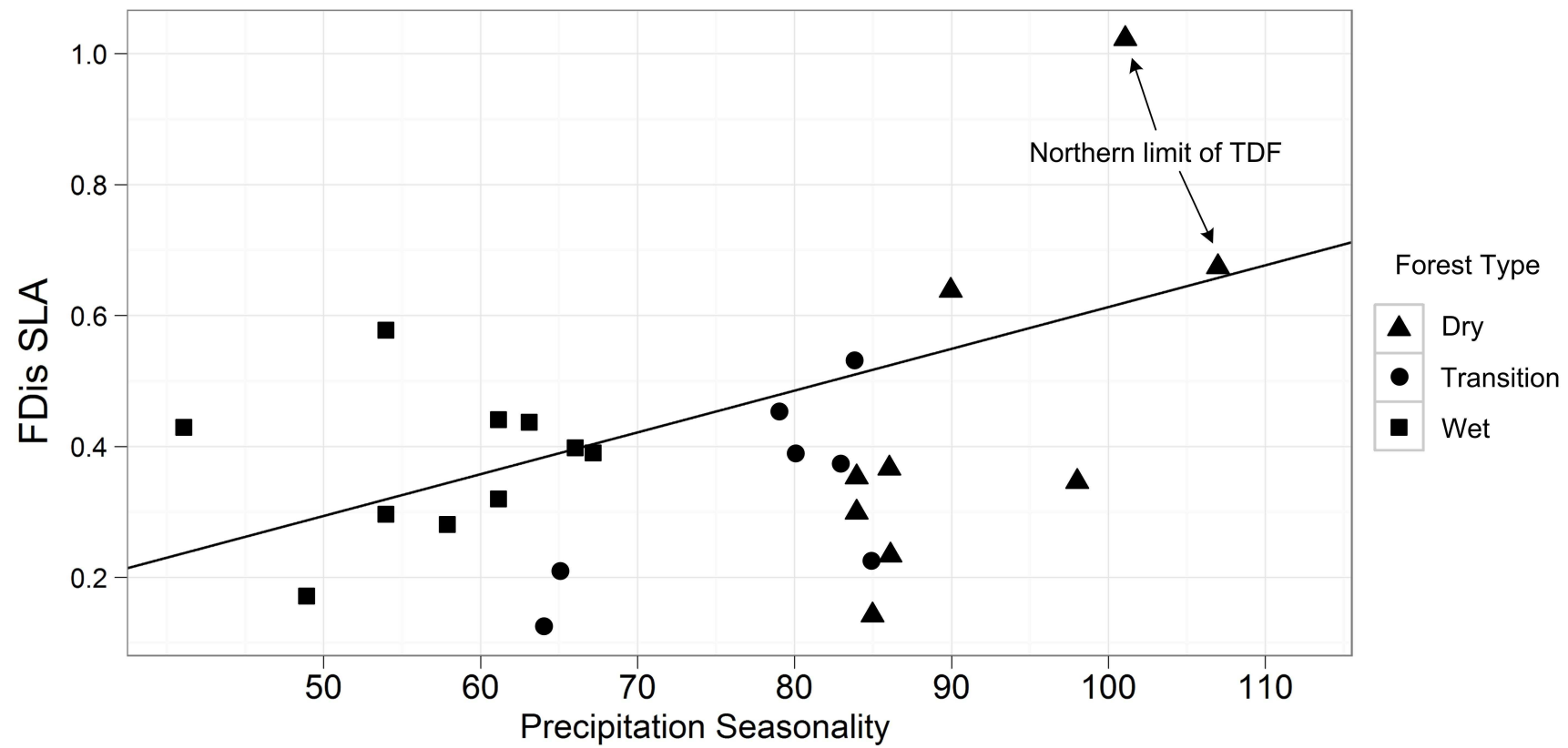
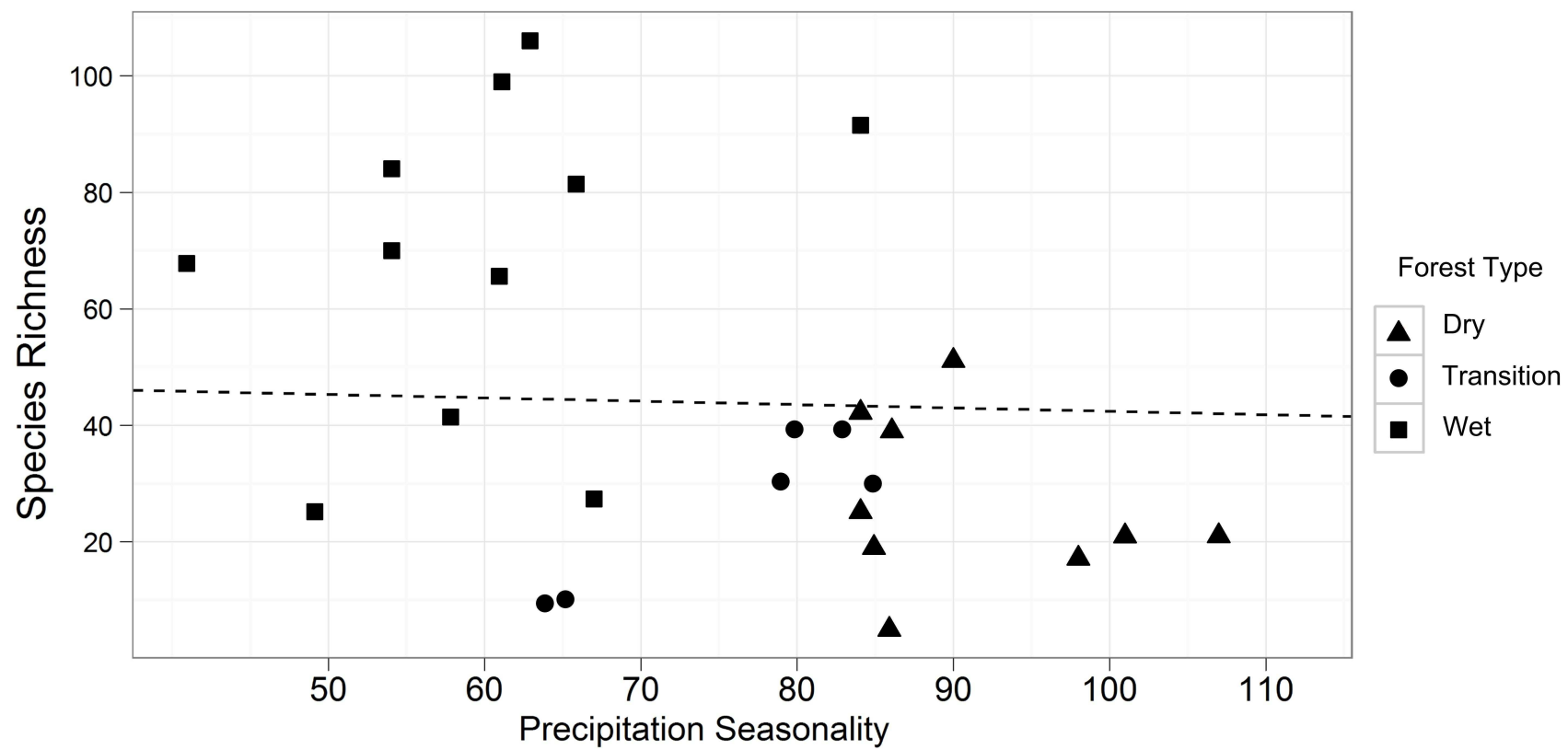


Figure 2:



APPENDIX C:
INTRASPECIFIC AND INTERSPECIFIC VARIATION IN SPECIFIC LEAF AREA
REVEAL THE IMPORTANCE OF ABIOTIC AND BIOTIC DRIVERS OF SPECIES
DIVERSITY ACROSS ELEVATION AND LATITUDE

Intraspecific and interspecific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude

Running Title: Trait variation across elevation and latitude

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Abstract

Using a functional trait based approach we ask: are patterns of intra- and interspecific functional trait variation consistent with greater abiotic filtering on community assembly at high latitudes and elevations, and greater biotic filtering at low latitudes and elevations? To answer this question we measured plant species abundance and a key functional trait associated with competition for resources and environmental tolerance (specific leaf area) along elevational gradients in low-latitude tropical (Costa Rica), mid-latitude desert (Arizona), and high latitude Mediterranean (southern Oregon) biomes. We explored patterns of abiotic and biotic filtering by comparing observed patterns of community weighted means and variances along elevational and latitudinal gradients to those expected under random assembly. In addition, we relate trait variability to niches and explore how total niche space and breadth vary across broad spatial gradients by quantifying the ratio of intra- to interspecific variation.

Both the community-wide mean and variance of SLA decreased with increasing latitude consistent with greater abiotic filtering at higher latitudes. Further, low elevation communities had higher trait variation than expected by chance, consistent with greater biotic filtering at lower elevations. Finally, in the tropics and across latitude the ratio of intra- to interspecific variation was negatively correlated to species richness, which further suggests that competitive interactions influence plant assembly at low latitudes. Intra- and interspecific patterns of SLA variation appeared broadly consistent with the idea that the relative strength of biotic and abiotic drivers on community assembly changes along elevational and latitudinal gradients; evidence for biotic drivers appeared

more prominent at low latitudes and elevations and evidence for abiotic drivers appeared more prominent at high latitudes and elevations.

Introduction

Understanding how local processes influence diversity patterns across environmental gradients has been central to the study of plant community ecology (von Humboldt 1849; Kraft et al. 2011). Studies across latitudinal (e.g. Willig et al. 2003; Schemske et al. 2009; Stegen et al. 2009) and elevational gradients (e.g. Körner 2007; Bryant et al. 2008; McCain and Grytnes 2010) have highlighted both biotic and abiotic mechanisms to explain diversity patterns across these gradients (Dobzhansky 1950; Pianka 1966; MacArthur 1972; Schemske et al. 2009). However, connecting local ecological processes to broad latitudinal and elevational gradients has been challenging. For example, elevational gradients differ from latitudinal gradients in several key ways including smaller species pools and land area, and increased isolation (Lomolino 2001). Further, while many of the potential processes invoked to explain latitudinal diversity patterns covary along latitudinal gradients (i.e. area, history, climate) they generally do not covary across elevational gradients (Körner 2007).

Recently, trait based approaches have been used to understand how multiple mechanisms influence community assembly across environmental gradients (McGill et al. 2006; Weiher et al. 2011) including elevational (Kluge and Kessler 2011; Spasojevic and Suding 2012; Hoiss et al. 2012) and latitudinal gradients (Swenson and Enquist 2007; Kooyman et al. 2011; Swenson and Weiser 2010; Swenson et al. 2012). These studies

often focus on two assembly mechanisms thought to influence diversity patterns along environmental gradients: environmental filtering which can increase species trait similarity through abiotic constraints (Weiher and Keddy 1995) and competitive interactions (i.e. niche partitioning, limiting similarity) that prevent coexisting species from being too similar (MacArthur and Levins 1967; Chesson 2000). However, these two hypotheses have been difficult to reconcile in species rich communities in environments that seem to be severe (i.e. the Sonoran desert; Whittaker and Niering 1964; Huston 1979). Thus, making generalizations about how abiotic filtering should influence communities across latitude or elevation has been challenging (Swenson and Enquist 2007). Furthermore, while evidence for greater competitive interactions at lower elevations is more strongly supported (Callaway 1998; Wang et al. 2008; Spasojevic and Suding 2012), the idea of greater competitive interactions at low latitudes is equivocal at best (Vázquez and Stevens 2004; Ricklefs 2009; but see Schemske 2009; Schemske et al. 2009). Thus, it has been difficult to link the mechanisms that underlie diversity patterns across both elevational and latitudinal gradients (Swenson and Enquist 2007).

One prominent, and seemingly simplistic, hypothesis relating assembly across broad gradients is that abiotic factors should limit diversity at high latitudes and elevations while biotic factors should underlie diversity patterns at low latitudes and elevations (Pianka 1966). In order to link abiotic and biotic mechanisms to diversity patterns across elevation and latitude, we can begin by assuming that trait variability reflects variation in resource use within a population and, thus, reflects niche space and breadth (Roughgarden 1972; Violle and Jiang 2009; Violle et al. 2012). Recent insights

from trait based ecology, building on classical niche theory, have outlined the use of intra- and interspecific trait variation for understanding diversity patterns across local to broad spatial scales (Jung et al. 2010; Violle et al. 2012). First, abiotic factors are known to shape the diversity of traits within a community; specifically, a change in the mean and variance of trait values across an environmental gradient (either higher or lower mean and/or variance values depending on the trait and environmental gradient considered) can indicate whether abiotic filtering is occurring (Weiher and Keddy 1995). In addition, over evolutionary time scales, stronger stabilizing selection in increasingly harsh environments should further filter or reduce the total amount of phenotypic variation within a community (Fischer 1960; Violle et al. 2012). Second, biotic interactions can also shape the diversity of traits within a community. For example, on the one hand, competitive exclusion will eliminate extreme phenotypes so that intra- and interspecific trait variance is reduced (Grime 1973). On the other hand, if competition imposes limiting similarity with resource partitioning, the diversity of traits will depend on the ratio between species' niche breadth (e.g. intraspecific variation) and total niche space (e.g. interspecific variation; MacArthur and Levins 1967; MacArthur and Wilson 1967). Thus, for limiting similarity and resource partitioning to occur in a community: (i) the interspecific packing of traits along a niche or trait axis will tend to be uniformly distributed (e.g. Roughgarden 1972; Brown 1975) and (ii) either the ratio of intra- to interspecific variation should decrease with increasing species richness (MacArthur and Wilson 1967; Violle et al. 2012) and/or (iii) the total niche space (phenotypic diversity of the entire community) must increase (Tilman et al. 1997).

Here, we focus on how patterns of one ecologically important trait, specific leaf area (SLA), change along three elevational gradients located in tropical (Costa Rica), desert (Arizona), and Mediterranean (southern Oregon) biomes. By quantifying the distribution of intra- and interspecific trait variation in local communities across broad elevational and latitudinal gradients we address two long-standing questions in plant community ecology. Specifically, we ask: (1) are assembly mechanisms similar across elevational and latitudinal gradients, and (2) are patterns of trait variation consistent with greater abiotic filtering on community assembly at high latitudes and elevations, and greater biotic pressures on assembly at low latitudes and elevations?

To answer these questions we use three trait based metrics. First, we determine whether shifts in community trait mean and variance across latitude are similar to those across elevation. Second, we compare the similarity of community trait values relative to random trait similarity which can further describe the nature of assembly patterns (MacArthur and Levins 1967; Pacala and Tilman 1994; Weiher and Keddy 1995; Grime 2006) where high functional similarity is thought to be a signature of abiotic filtering and low functional similarity is a signature of limiting similarity (Weiher and Keddy 1995). Third, we describe the relationship between intra- and interspecific variation and species richness. The ratio of intra- to interspecific variation expresses the rate at which niche breadth (i.e. intraspecific trait variation) changes relative to total niche space (i.e. interspecific variation) and can thus be used to determine how total niche space and niche breadth change with increasing species richness across diversity gradients.

Methods

Study sites

We conducted our study in three locations that span a 30-degree latitudinal gradient and an average elevational range of 2000 meters above sea level (Table 1). Area de Conservación Guanacaste (ACG) in northwestern Costa Rica is characterized by a six-month dry season in low elevation (0-300 m above sea level) dry tropical forests with a mean annual temperature of 25°C. However, the length of the dry season decreases and mean annual precipitation increases with elevation; mean annual precipitation in a rain forest site at 700 m above sea level is approximately 3500 mm in comparison with 1500 mm in a lowland dry tropical forest site at 300 m in elevation. The Santa Catalina Mountains in southern Arizona are characterized by summer and winter monsoons which together can bring about 330 mm of precipitation annually to lower elevations and 750 mm at the highest elevations (Whittaker and Niering 1964). Finally, the Siskiyou Mountains in southern Oregon (part of the California Floristic Province) are characterized by Mediterranean-type climate with warm, dry summers (mean max. July temperature; 27°C) and cool, wet winters (mean min. January temperature: 2°C); mean annual precipitation ranges from 1400 to 5000 mm with less than 15% occurring during May through September (Daly et al. 2002).

Floristic surveys and plant trait collection

Plant abundance (number of woody individuals) was measured in 20 x 50 m (0.1 hectare) plots arrayed across the three elevational gradients in which all stem diameters greater than 2.5 cm at breast height were measured and species identified. Only woody

trees and shrubs were included as woody plants consistently dominate the total abundance and biomass in each sampled community relative to non-woody species. A total of 25 plots were surveyed in Costa Rica, 22 plots in Arizona, and 12 plots were surveyed in Oregon. In Costa Rica, the plots spanned an elevational range of 9 - 1111 m; 740 - 2502 m in Arizona; and 438-1255 m in Oregon. The location of plots were determined using a stratified sampling regime (Gauch 1982). Using vegetation maps for each site (Oregon: Whittaker 1960; Arizona: Whittaker and Niering 1964; Costa Rica: Holdridge et al. 1971), at least one plot was included in each plant zone across elevation. Locations that had evidence of recent disturbance (e.g. fire, logging) were avoided. Where habitats were more heterogeneous, additional plots per habitat type were included (Gauch 1982). In topographically complex habitats, for example, plots were placed in various slope directions and inclinations in order to represent the continuum of soil moisture availability within a particular habitat type (Whittaker 1960; Whittaker and Niering 1964). This was particularly true in the lowland dry tropical forests of Costa Rica where plant communities differ in deciduousness ranging from about 20% evergreen hillsides to almost completely evergreen lowlands (Janzen 1986; Powers et al. 2009). After surveying the obvious extreme habitats (e.g. ridge, valley, slope), plots were continually added until the number of new species encountered with increasing area neared zero.

For all woody species within each plot we measured specific leaf area (SLA), a key functional trait associated with competition for resources and environmental tolerance (Poorter et al. 2009). Specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) is defined as the light

capturing surface area per unit of dry biomass and correlates with differences in life history strategies (e.g. net photosynthetic capacity, leaf longevity, relative growth rate, and competitive ability; Reich et al. 1997). For example, SLA is known to reflect a tradeoff in plant resource-use strategy from rapid biomass production (high SLA) to efficient nutrient conservation (low SLA; Wright et al. 2004). Further, variation in SLA is tightly coupled with variation in resource gradients such as light and productivity (Grime 1998). For the collection of plant traits, five mature, healthy, sun leaves were collected from five different individuals for each species within a plot (Cornelissen et al. 2003). Once leaves were collected, the fresh area of each leaf was measured within a few hours of collection. Fresh leaf area (cm²) was measured using a Canon CanoScan LiDE 110 portable electronic scanner (Canon, U.S.A., Inc.) and leaf area was calculated using the ImageJ imaging software (Abramoff et al. 2004). All leaves were then placed in a drying oven for a minimum of 72 hours at 70°C until a constant mass was reached, and the final dry mass was recorded.

If there were not sufficient individuals within the plot to meet the minimum criteria of five individuals, then leaves were collected from nearby individuals located outside of, but never more than 500 m away from a plot. Rare species with less than five sampled individuals were not included in the analyses but did not total more than 8% of the total relative abundance in any plot. All individuals in Arizona were sampled during March and April 2010; in Oregon during early May 2010; and in Costa Rica in mid-May through June 2010. These times correspond with the early growing season in each location.

Statistical Analyses

To explore patterns of abiotic filtering across elevation and latitude, we first compared how community-wide trait means and variances change with elevation and latitude. To do this, the abundance-weighted plot mean and variance (community weighted mean and variance, CWM and CWV, respectively; Violle et al. 2007) of SLA values were calculated for each plot k as:

$$\text{CWM}_k = \sum a_{ik} t_{ik} \quad (1)$$

$$\text{CWV}_k = \sum a_{ik} (t_{ik} - \text{CWM}_k)^2 \quad (2)$$

where a_{ik} is the relative abundance of species i in plot k , and t_{ik} is the trait mean of species i in plot k . To explore whether the observed trait patterns differ from random, a null modeling approach is necessary (Gotelli and Graves 1996). A null model compares whether the observed variation in community weighted mean or variance across elevation is greater than or less than expected given the observed species richness. To create a null community, trait data for each sampling region (i.e. Costa Rica, Arizona, or Oregon) were pooled into a regional trait community. For each plot, we calculated the null trait mean and variance value and the 95% confidence interval (CI) based on 999 iterations by shuffling the species-by-plot trait values and thus, conserving species richness and abundance within each plot (Gotelli and Graves 1996). This approach avoids averaging the mean and variance of species' SLA values across all plots, which ultimately reduces the observed trait variation both between and within species. Shuffling trait values, as

opposed to species' abundances, can also indicate which assembly processes, including abiotic filtering and limiting similarity, structure communities.

First, to understand how plant function varies with elevation and whether abiotic filtering drives assembly at high elevations and latitudes, we performed simple linear regressions of community mean and variance of SLA against elevation for each community. Second, to determine whether the observed trait values were clustered or over-dispersed compared to random assemblages (and thus the influence of abiotic or biotic drivers), we compared the observed community trait means and variances to random communities. Finally, we explored the central ideas of limiting similarity and niche packing by comparing how the ratio of intra- and interspecific trait variation changed with increasing species richness. For each plot, we calculated the ratio of intraspecific to interspecific variation. Plot interspecific variation was calculated as the variance of all species' mean trait values (i.e. the variance of species' means). Plot intraspecific variation was calculated as the mean of all species' intraspecific variances for each trait (i.e. the mean of species' variances). We also included a null model to resample trait variation with increasing sample size (i.e. increasing species richness) without replacement using the sample package in R. For example, for a sample size of 45 species, we randomly drew 45 values of trait mean and 45 values of intraspecific trait variance. We then calculated the null interspecific variation as the variance of 45 mean values and the null intraspecific variation as the mean of 45 variance values and calculated the ratio between intra- and interspecific variance. This was done for each of 999 iterations for each increase in sample size. Finally, we compared the observed and

randomized slopes and intercept coefficients from linear regressions between variance (intraspecific, interspecific, and intra:inter) and species richness using the `smatr` package (Warton et al. 2012) in R.

Although variance is often correlated with mean values (Taylor 1961), this ratio is informative for three reasons. First, intraspecific variance includes standardized measurements from a set number of leaves and individuals (five) from each species found within each plot and is thus measured systematically across all plots. Second, calculating the average of intraspecific variances in each plot partially accounts for differences in species richness between plots. Third, by including a resampling model, we can compare the observed patterns of trait variation to those expected under random sampling of trait variation. We used this ratio to explore the biological patterns of variance with increasing species richness (Violle et al. 2012). We regressed intraspecific variation, interspecific variation and the ratio of intra- to interspecific variation against species richness. If abiotic and biotic drivers are truly asymmetric across environmental gradients, then a decrease in the ratio of variation with increasing species richness should be evident at low latitudes, suggesting greater limiting similarity in tropical latitudes. All statistical analyses were conducted in R (version 2.15.1; R Development Core Team 2012).

Results

There were a total of 275 woody plant species in our plots in Costa Rica; 65 in Arizona; and 18 in Oregon. Species richness decreased with latitude and was not correlated to elevation in Costa Rica ($r^2 = 0.089$, $P = 0.14$); decreased with increasing

elevation in Arizona ($r^2 = 0.71$, $P < 0.001$); and was not correlated to elevation in Oregon ($r^2 = 0.16$, $P = 0.20$; Fig. S1 in Supporting Information). With increasing latitude, both community mean and variance of SLA decreased (Fig. 1d and 1h) and the ratio of intra- to interspecific variation decreased (Fig. 2d) with increasing species richness.

Decomposing this ratio into individual components, both intra- and interspecific variation increased with increasing species richness at different rates (i.e. slopes; Fig. 2h).

At the lowest latitude (Costa Rica) community mean (Fig. 1a) and variance (Fig. 1e) of SLA were not correlated to elevation. Compared to a random model of assembly, SLA was more variable than expected at low elevations (Fig. 1e) and the ratio of intra- to interspecific variation was negatively correlated to species richness ($r^2 = 0.27$, $P = 0.0083$; Fig. 2a) even though the individual components of this ratio were not correlated to species richness (Fig. 2e). At the mid-latitude site (Arizona) community mean ($r^2 = 0.60$, $P < 0.0001$; Fig. 1b) and variance ($r^2 = 0.26$, $P = 0.016$; Fig. 1f) of SLA decreased with increasing elevation. In comparison with a random model of assembly, community mean SLA was also greater than expected in the low elevation communities and less than expected in high elevation communities (open data points; Fig 1b). Similarly, community variance SLA was more variable than expected at low elevations (Fig. 1f) compared to a random model of assembly. The ratio of intra- to interspecific variation of SLA was not significantly correlated to species richness (Fig. 2b) even though the individual components of this ratio were both positively correlated to species richness (Fig. 2f). Finally, at the highest latitude site (Oregon), community mean and variance of SLA were not correlated to elevation (Figs. 1c and 1g). Relative to a null model of assembly,

community mean and variance of SLA in the Oregon plots were more variable than expected at low elevations (open data points; Fig. 1c and 1g), but neither the ratio of intra- to interspecific variation of SLA nor the individual components were significantly correlated to species richness (Figs. 2c and 2g). Interestingly, the randomized values of intraspecific variation, interspecific variation, and the trait variation ratio did not increase with increasing species richness (not shown). For each regression analysis between SLA variance and species richness, the observed communities significantly differed in slope from the randomized communities and generally did not differ in intercept (not shown).

Discussion

The origins of diversity gradients continue to remain a central area of focus and debate (Wiens 2011; Stegen et al. 2012). Few studies, however, have examined whether traits vary in similar ways across gradients of latitude and elevation. Here, we show that at higher latitudes, but not necessarily high elevations, the variance in SLA decreased, consistent with increased abiotic filtering (Weiher and Keddy 1995) at higher latitudes. Further, lower elevation plots across sites tended to have greater variance in SLA than expected by chance consistent with limiting similarity (MacArthur and Levins 1967; Chesson 2000). In addition, we found that both intra- and interspecific variation increased with species diversity but at different rates so that the total ratio between intra- and interspecific variation decreased with increasing species richness. This suggests that the total trait space indeed increases towards tropical latitudes; however, because intraspecific variation increases at a slower rate, species are more ‘tightly packed’ in

tropical systems. Together, these community-level findings are consistent with the often cited but rarely tested assumption that variation in diversity across broad scale gradients is constrained by available niche space (see Willig et al. 2003; Wiens 2011) but that biotic pressure at lower elevations and latitudes increases the total niche volume and thus phenotypic diversity. These results are consistent with previous findings that both biotic and abiotic forces have likely been important in the evolution of plant function and diversity on contrasting ends of elevational and latitudinal gradients (Shepherd 1998; Stevens et al. 2006; Swenson et al. 2012). We discuss these results in light of both the strengths and current challenges of a trait based approach for understanding diversity patterns across broad environmental gradients.

Patterns of trait variation across elevation and latitude

Across latitude, community mean and variance of SLA decreased with increasing latitude. These patterns are similar to global trends (Reich et al. 1997; Wright et al. 2005). Specifically, SLA has been shown to shift across productivity gradients (Reich et al. 1997; Grime 2006), and increases in mean annual precipitation and temperature are thought to be the two best predictors of mean SLA across broad geographical gradients (Swenson et al. 2012). Although this study uses a single functional trait, the patterns shown here mirror those found for other plant traits including wood density, maximum height, and seed mass (Swenson and Enquist 2007; Swenson and Weiser 2010; Swenson et al. 2012), consistent with the idea that whole-plant level function responds in concert to gradients of elevation and latitude.

Across elevation in Costa Rica, community mean and variance of SLA were not correlated with elevation (Figs. 1a and 1e). This pattern suggests that either abiotic filtering is a weak driver of trait values across elevation in Costa Rica, the abiotic differences between lowland dry forests and higher elevation communities are reduced during the rainy season (Gotsch et al. 2010), abiotic filtering of SLA is not relevant at this site or spatial scale (see Swenson et al. 2006), or the high habitat heterogeneity characteristic of dry tropical forests obscured our ability to detect patterns in the context of broader environmental gradients (Baraloto and Coutron 2010). For example, the high heterogeneity found in Costa Rica may be related to topographical differences or historical disturbance regimes (i.e. land-use, timber extractions, fire; Powers et al. 2009), and each can affect the structure and composition of forest communities. Although areas that had obvious evidence of disturbance were avoided, the long-term legacies of past disturbance events (see Foster et al. 2003) could potentially obscure our ability to detect non-random assembly patterns at larger spatial scales. That the community means were similar to random assemblages in Costa Rica may further indicate the opposing effects of both abiotic and biotic filtering at local scales (Swenson et al. 2006) due to either long-term successional processes or the effects of local topographical differences.

In Arizona, the decrease of mean trait values with elevation mirrors the known decrease in SLA with increasing latitude (Reich et al. 1997). This latitudinal trend is thought to be primarily due to the increasing dominance of gymnosperms at high latitudes (McCarthy et al. 2007). Similarly, the increasing dominance of gymnosperms at high elevations in Arizona likely underlies the observed shift in trait mean.

Gymnosperms are known to have relatively low values of SLA (Royer et al. 2010) as well as low plasticity compared to angiosperms (Bond 1989). Thus, whether the range of SLA variation is a consistent proxy of functional strategies for gymnosperms and angiosperms requires further exploration.

Similarly, although this study offers the first standardized quantification of how trait variation differs across elevation and latitude, sampling a single functional life form (i.e. woody species) likely underestimates the total observed variation in SLA. Thus, a critical next step for trait based ecology will be to determine whether functional strategies of non-woody species respond similarly across environmental gradients compared to woody species. On the one hand, non-woody species can evade harsh abiotic conditions by being non-persist so that patterns of trait variation across environmental gradients may not reflect patterns of abiotic filtering as seen in woody species. On the other hand, competition between non-woody and woody species may be critical for assembly (see House et al. 2003) particularly during the seedling stage. An emerging research question is thus how patterns of trait variation differ between coexisting life forms and how trait differences may confer competitive and/or fitness differences.

Finally, in Oregon, a gradient dominated by gymnosperms, the lack of clear correspondence between trait mean and variation with elevation may be due to either the stabilizing maritime influence on climate across the Siskiyou Mountains (Whittaker 1960) or that the use of SLA as a proxy for functional strategies is not consistent between gymnosperms and angiosperms. We can thus infer that, first, the processes that influence assembly across elevation are not the same between the three mountain gradients

sampled. This is intuitive since elevational gradients reflect the combined effect of regional peculiarities and general altitude phenomena (Körner 2007), and the three mountain gradients sampled here differ in climate, seasonality, topography, age, isolation, among other factors that affect biodiversity along elevational gradients (see Körner 2007). Thus, it would be highly desirable to systematically sample many replicate elevational gradients across a wide spectrum of climatic zones. Although patterns of variation in SLA across environmental gradients provide reasonable support for assembly mechanisms, the use of SLA as a proxy for functional strategies may break down when making comparisons between distinct clades, or even life forms within the same clade. Thus, experimental or simulation approaches may better link differences in SLA to plant function, and ultimately, fitness across environmental gradients.

Despite climatic and topographical differences between elevational gradients, low elevation communities across all sites had higher trait variance than expected by chance. This finding points to the role of competitive interactions that prevent coexisting species from being too functionally similar. Yet recent debate challenges whether trait variation can be used to infer the relative importance of abiotic versus biotic filters (HilleRisLambers et al. 2012) since competitive exclusion, like abiotic filtering, can also lead to low trait variation within and between species. Although clear relationships between environmental gradients and traits provide reasonable support that an abiotic filter is important for assembly (HilleRisLambers et al. 2012), experimental approaches that explicitly link abiotic and biotic factors to the distribution of trait values within

communities will further shed light on trait-assembly patterns across environmental gradients.

Trait variation and species richness

In order to determine the relationship between trait variation and species richness we quantified the ratio between intra- and interspecific variation. By doing so we were able to test a specific prediction of limiting similarity, namely that the amount of intraspecific variation (niche-breadth) compared with interspecific variation (total niche space) does indeed vary with community species richness. The limiting similarity hypothesis predicts that (i) niche breadth, or intraspecific variation in resource use, should decrease with increased richness (MacArthur and Wilson 1967) and/or (ii) that the total amount of niche space should increase with species richness (Tilman et al. 1997; Weiher et al. 1998). An open question for niche-based ecological theory is whether the amount of intraspecific variation compared with interspecific variation actually varies with species richness as predicted by niche theory (Violle et al. 2012).

Consistent with niche theory, we showed that the ratio of intra- to interspecific variation does decrease with increasing species richness across latitude and elevation. Decomposing the individual components of this ratio, we showed that interspecific variation of SLA increased with species richness at a faster rate compared to intraspecific variation. This finding, while consistent with limiting similarity in tropical forest communities (e.g. Pianka 1966), may also suggest that other processes, such as developmental constraints, can limit intraspecific trait expression. Despite the use of

functional traits to define species' niches, there is still a large gap in our understanding of how traits relate to fitness as well as to the evolutionary mechanisms that drive niche separation (Sterck et al. 2011).

Conclusions

We provide an investigation into the predominant patterns of trait variation across elevational gradients using mountains at three widely separated latitudes in the New World. This study combines measures of both intra- and interspecific trait variation observed within each forest plot across multiple elevational gradients. Although intraspecific trait variation is thought to promote species diversity and improve detection of abiotic filtering and limiting similarity (Jung et al. 2010), and, as such, has appeared at the forefront of trait based ecology (see Bolnick et al. 2011; Violle et al. 2012), there is a limited understanding of how both intra- and interspecific variation change over latitudinal and elevational gradients. We demonstrate that patterns of intra- and interspecific trait variation at broad scales are consistent with the idea that local abiotic and biotic interactions influence diversity patterns across environmental gradients. While our findings support the use of a trait based approach for understanding broad scale diversity gradients (see Roughgarden 1972; Violle and Jiang 2009; Violle et al. 2012), several key challenges remain for linking local ecological processes to broad environmental gradients.

First, our analyses include three elevational gradients that differ in a number of ways including regional climate. Future studies are needed to compare elevational

gradients with similar climatic regimes (such as in the moist tropics) in order to disentangle the effects of potentially confounding abiotic and biotic factors (Körner 2007; Malhi et al. 2010). Further, by only measuring SLA of woody species, our conclusions are limited to a single axis of plant variation in ecological strategies for one life form and we cannot infer how reproductive, regenerative (Grime 2006) or whole-plant strategies differ across broad spatial scales, life forms or even different taxa. In addition, testing for abiotic and biotic filters using a trait based approach should be expanded to include experimental and demographic analyses (HilleRisLambers et al. 2012) to more strongly link traits to plant fitness. Finally, in order for intraspecific trait variation to be integrated into functional ecology, there is still a need to determine the magnitude and patterns of intraspecific variation within and across ecosystems. In summary, quantifying patterns of community assembly and trait variation across diverse environmental gradients will advance our understanding of the mechanisms that give rise to large-scale biogeographic gradients.

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Tables Appendix C

Table 1. Site characteristics including latitude (Lat), longitude (Lon), elevational range (in meters above sea level), major vegetation zones, and relevant previous studies along each elevational gradient.

Site	Lat / Lon	Elevation	Major vegetation zones	Previous studies
Area de Conservación Guanacaste, Costa Rica	10°51' N 85°37' W	0 – 1500 m	Lowland dry tropical forest; transitional moist forest, rain forest, cloud forest	Lowlands: Janzen 1986; Powers <i>et al.</i> 2009
Santa Catalina Mountains, Arizona	32°26' N 110° 47' W	740 – 2790 m	Sonoran desert scrub; oak woodlands; coniferous forest; subalpine forest	Shreve 1915; Whittaker and Niering 1964
Siskiyou Mountains, Oregon	41°49' N 123°40' W	0 – 2100 m	Coniferous forest; montane forest; alpine and subalpine forests	Whittaker 1960; Damschen <i>et al.</i> 2010; Harrison <i>et al.</i> 2011

Figures Appendix C

Figure 1: Community weighted mean (CWM) and variance (CWV) of specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) against elevation (in meters) for Costa Rica (CR), Arizona (AZ), and Oregon (OR) and across latitude. Solid black lines indicate a significant ($p < 0.05$) relationship; dashed black lines indicate a non-significant relationship. Each data point represents a single community (plot). Solid data points indicate communities that are not statistically distinguishable from random communities; open data points indicate communities that are distinguishable from random communities. For latitudinal comparisons, sites separated by letters are statistically distinguishable in a one-way ANOVA. For each site, the lower elevation communities tend to have increased trait 'diversity' or variance than expected by chance.

Figure 2: Intraspecific variation (red lines), interspecific variation (blue lines), and the ratio of intraspecific to interspecific variance (Intra:Inter Variance) of specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) as a function of species richness for elevational gradients in Costa Rica, Arizona, and Oregon and across latitude. Each data point represents a single community (plot). Solid lines indicate a significant ($p < 0.05$) relationship; dashed lines indicate a non-significant relationship.

Figure 1:

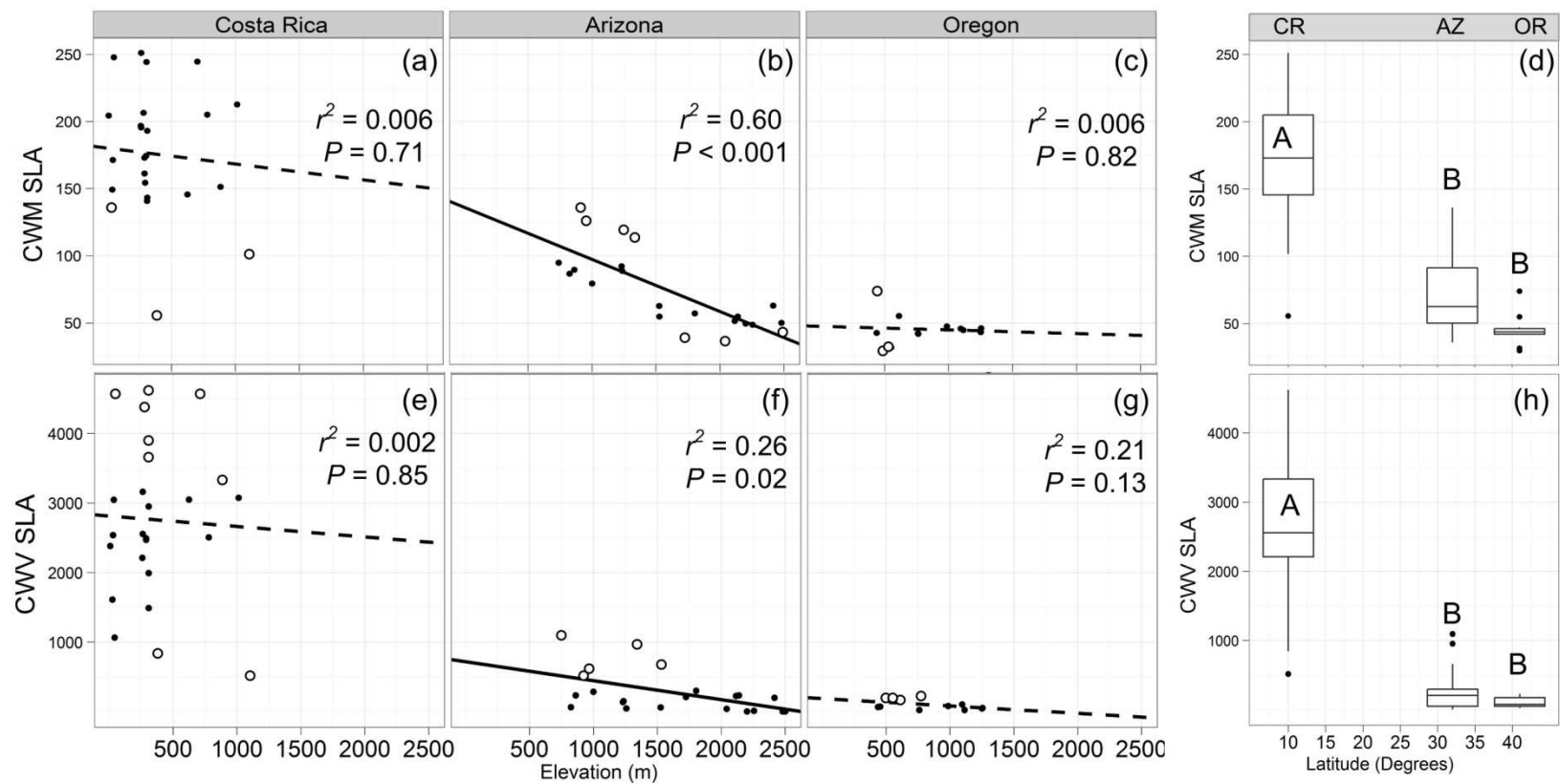
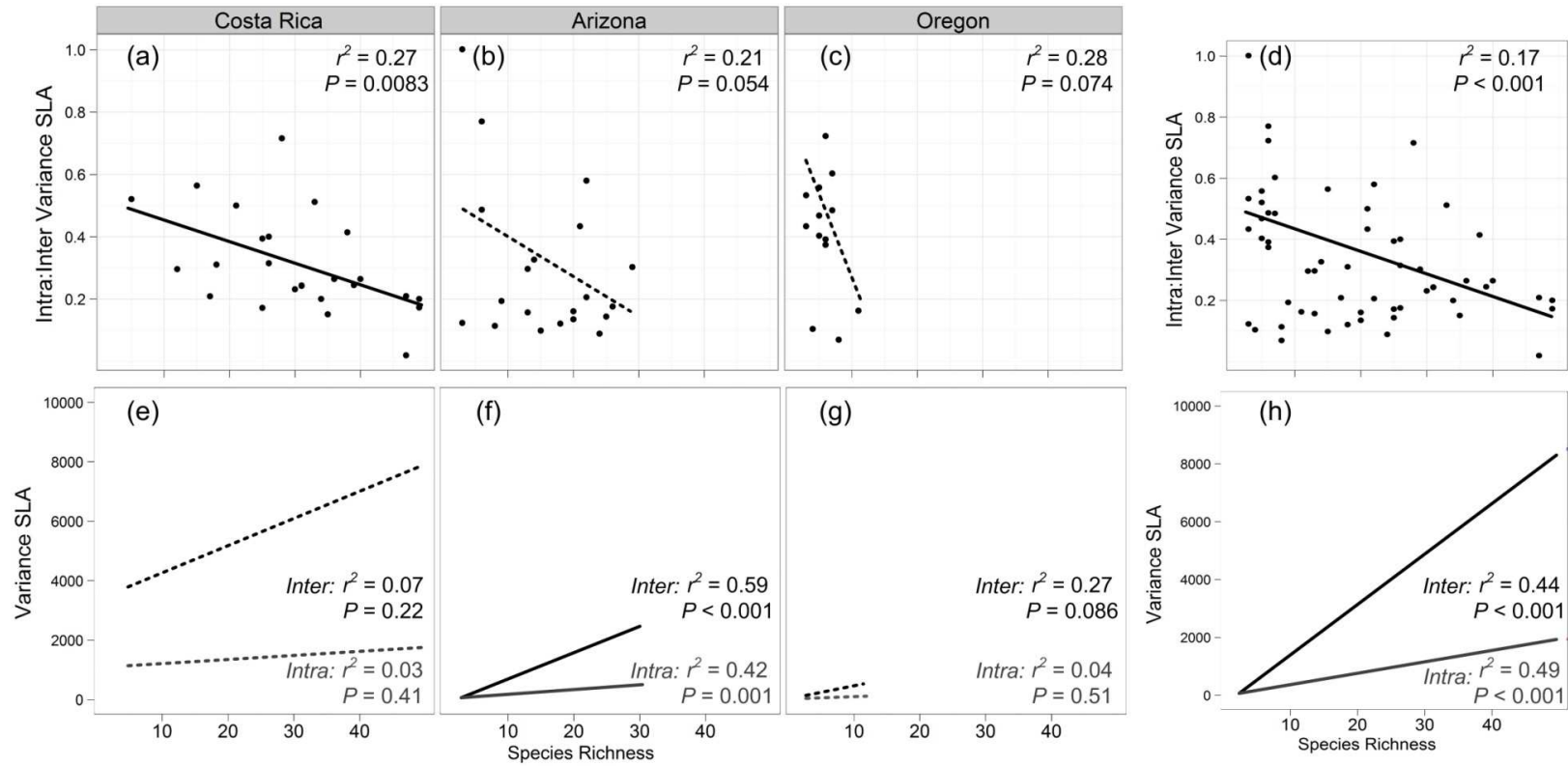
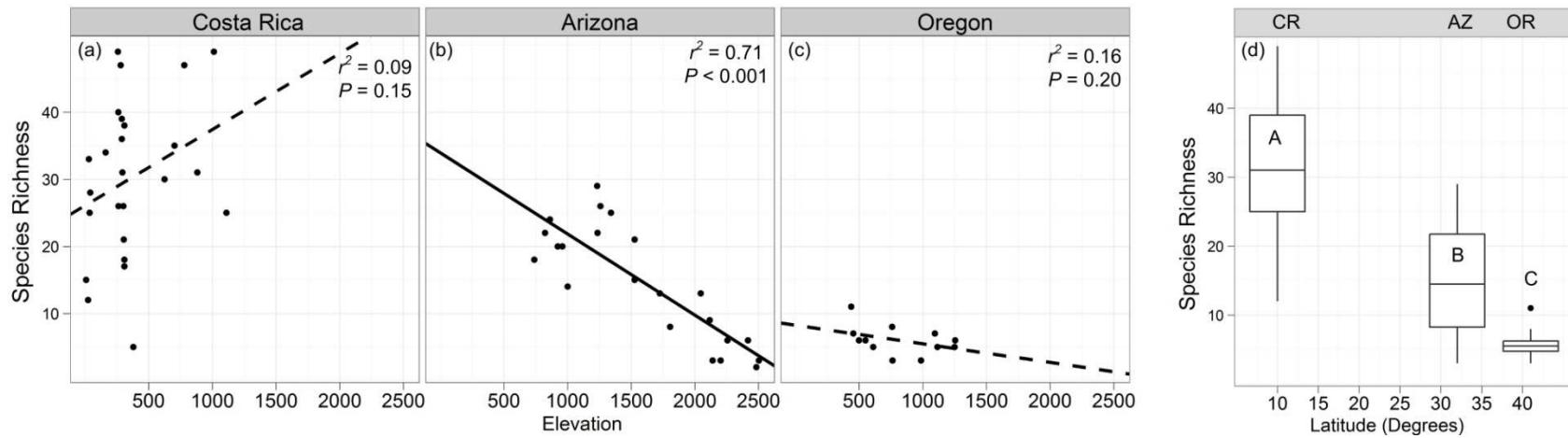


Figure 2:



Supplementary Material Appendix C

Figure S1. Species richness as a function of elevation in (a) Costa Rica (CR), (b) Arizona (AZ), and (c) Oregon (OR) and (d) as a function of latitude. Solid black lines indicate a significant ($p < 0.05$) relationship; dashed black lines indicate a non-significant relationship. Each data point represents a single community (plot). For latitudinal comparisons, sites separated by separate letters are statistically distinguishable in a one-way ANOVA.



APPENDIX D:
INTERANNUAL VARIABILITY OF GROWTH AND REPRODUCTION IN
BURSERA SIMARUBA: THE ROLE OF ALLOMETRY AND RESOURCE
VARIABILITY

Interannual variability of growth and reproduction in *Bursera simaruba*: The role of allometry and resource variability

Running Title: Growth Reproduction Tradeoff

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Interannual variability of growth and reproduction in *Bursera simaruba*: The role of allometry and resource variability. *Ecology*.

Abstract

Plants are expected to differentially allocate resources to reproduction, growth and survival in order to maximize overall fitness. Life history theory predicts that the allocation of resources to reproduction should occur at the expense of vegetative growth. Although it is known that both organism size and resource availability can influence life history traits, few studies have addressed how size-dependencies of growth and reproduction and variation in resource supply jointly affect the coupling between growth and reproduction. In order to understand the relationship between growth and reproduction in the context of resource variability, we utilize a long-term observational dataset consisting of 670 individual trees over a 10-year period within a local population of *Bursera simaruba* (L.) Sarg. We: (i) quantify the functional form and variability in the growth reproduction relationship at the population and individual-tree level and (ii) develop a theoretical framework to understand the allometric dependence of growth and reproduction. Our findings suggest that the differential responses of allometric growth and reproduction to resource availability both between years and between microsites underlie the apparent relationship between growth and reproduction. Finally, we offer an alternative approach for quantifying the relationship between growth and reproduction that accounts for variation in allometries.

Introduction

The Principle of Allocation states that resources devoted to growth, maintenance, and reproduction are constrained by the rate of acquisition of limiting resources from the environment (Cody 1966; Levins 1968). That is, variation in growth and reproduction are linked and the allocation of resources is zero-sum whereby allocation to one function should come at the cost of allocation to other functions. A key assumption underlying this tradeoff hypothesis is that reproduction is costly and reduces resources available for growth (Roff 1992). However, the central prediction linking reproduction and vegetative growth has received mixed empirical support (e.g. Fox and Stevens 1991; Knops *et al.* 2007; Koenig *et al.* 2009). Further, positive correlations are known between many life history traits (see Stearns 1977; van Noordwijk and de Jong 1986) suggesting that a general negative relationship between growth and reproduction remains questionable. Studies have also argued that variation in growth and reproduction may be more strongly driven by other factors including: (i) photosynthetic reproductive structures; (ii) increased resource uptake during reproduction (i.e. the compensation hypothesis; Tuomi *et al.* 1983); (iii) excess resources above some threshold are used for sexual reproduction without added costs to somatic growth (i.e. the threshold hypothesis; Tuomi *et al.* 1983); (iv) inability of the methods used to accurately detect reproductive costs (Bazzaz *et al.* 2000); and (v) confounding environmental factors that underlie the negative correlation between life history traits (Knops *et al.* 2007). Together, these findings may call into question whether the tradeoff between growth and reproduction is actually an important driver of the observed variation in growth and reproduction in natural populations.

Deconstructing the factors that differentially affect growth and reproduction is central to discovering the mechanistic underpinnings of the relationship between growth and reproduction. Empirical evidence and theoretical arguments show that reproductive investment and other life history traits are moderated by the environment (e.g. Grime 1979), and some empirical studies have demonstrated the effects of growing conditions on patterns of resource production and allocation (Bazzaz and Reekie 1985; Harper and Ogden 1970). For example, in perennial species, both reproductive allocation (the proportion of aboveground biomass in reproductive structures) and community-wide fruit production have been shown to decrease in response to resource limitation (Chiariello and Gulmon 1991; Wright *et al.* 1999, respectively). Environmental conditions can also influence the cost of reproduction, independent of growth. For example, reproductive costs have been observed to vary spatially as a result of differing soil, water availability, growing season length and altitude (Obeso 2002). Furthermore, theoretical work has suggested that both environmental and genetic factors can result in a non-existent or weak correlation between growth and reproduction (Reznick *et al.* 2000).

There are two methodological and practical issues that limit our understanding of the factors that influence the growth-reproduction relationship. First, while variation in growth and reproduction are often linked to variation in abiotic conditions, it is unclear how reproduction and growth are both influenced by resource supply. Our lack of knowledge is particularly acute in long-lived trees due, in part, to the impracticality of experimental manipulations. Second, body size is a primary factor underlying variability in life history strategies (Calder 1984; Niklas 1994). Indeed, it is crucial to take into

account allometric effects when assessing the impact of environmental factors on life history (Samson and Werk 1986); yet studies detailing the size-dependency of life history traits in woody perennials are relatively few (Hubbell 1980; Peters *et al.* 1988; Acosta *et al.* 1993; Wheelwright and Logan 2004).

Here, we use a long-term intraspecific study of over 600 individual trees to assess the primary factors influencing variation in tree growth and reproduction. We test the Principle of Allocation in a natural population of the tropical tree species *Bursera simaruba* (L.) Sarg., by examining ten years of reproduction and growth. In order to parse the various factors that can influence variation in growth and reproduction, we derive a theoretical framework that allows the allometries of growth and reproduction to vary independently from each other. Our model allows us to assess the relative importance of opposing factors controlling variation in plant growth and reproduction. We empirically test the analytical link between the growth and reproduction allometries and the growth–reproduction relationship itself and assess the role of annual variation in a key resource, water (i.e. precipitation). After accounting for size-dependent growth and reproduction, we further provide an alternative method for quantifying the true nature of the relationship between growth and reproduction.

Methods

Site description

The 15-hectare San Emilio Long Term Forest Dynamics Plot (SE-LFDP) is located in Sector Santa Rosa of Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10° 45' N, 85° 40' W). The larger area encompassing the SE-LFDP is a mosaic of old growth (>200 years) and younger, secondary forests (>80 years) that have regenerated from abandoned banana plantations, pastures and selective logging (Janzen 1988). The area is characterized as seasonally dry tropical forest (Holdridge *et al.* 1971) with the dry season beginning in late December and lasting until early May. Annual rainfall ranges from 900-2600 mm with an average of 1500 mm, though annual variation in precipitation is known to be quite high (Hartshorn 1983). During the dry season much of the vegetation, including *Bursera simaruba*, is drought-deciduous.

Natural history and other characteristics of Bursera simaruba

This study focused on a population of the tropical tree species, *Bursera simaruba*, in the SE-LFDP. *Bursera simaruba* is a tropical, dioecious, perennial, canopy tree and is characterized by a single cylindrical stem. Staminate and pistillate individuals, referred to as male and female onward for simplicity, flower at the end of the dry season and flowers retain color and turgor for a single day (Greenberg *et al.* 1995). Within three weeks of pollination by moths, bees and flies, the newly formed fruit expands to full size and will remain on the tree for up to 12 months before they are dispersed (Stevens 1983). The major dispersers of *B. simaruba* are primate species and more than forty species of

frugivorous and insectivorous birds (Scott and Martin 1984). Fruits ripen asynchronously within a tree throughout the rainy season and ripening can extend up until the time of the following years' flowering. Fruits that are not dispersed are dropped *en masse* by the female at the time of new fruit production (Stevens 1983). The fruit consists of an aril, a capsule, and seeds. The mean dry mass of the fruit is ~0.20 g, with the capsule comprising approximately 50% of the total mean dry mass of the fruit (Greenberg *et al.* 1995). Individual female trees appear to have some control on reproductive allocation. For example, Dunphy and Hamrick (2007) found that seed abortion was common and suggested that it was related to the amount of outcrossing.

Data collection

We utilized a unique long-term demographic record for *Bursera simaruba* collected by George C. Stevens (see Stevens 1987). Each January, during 1976-1986, the circumference at breast height was measured in 1 cm increments for approximately 500 male and 170 female *B. simaruba* individuals within the 15-ha SE-LFDP. Diameter at breast height (DBH; circumference / π) ranged from approximately 2 – 60 cm. Similarly, each January, for each female tree, the total number of fruits was counted from the ground by eye (Stevens 1987). The accuracy of fruit counts was checked by comparing fruit counts made on the ground to counts made by an observer in the tree crown (Stevens 1987). In this previous study, five trees were selected for experimental manipulation. We excluded these five female trees for the present analyses. Across years, the percent of

total population tree biomass in fruit varied considerably – ranging from 1.6 – 17%, with an average of 5.7% (see below).

To assess the linkage between climate, growth, and reproduction, we used annual rainfall for the years 1979-1986 from the Meteorological Station in Sector Santa Rosa of Área de Conservación Guanacaste (ACG 2007). The station is located a few kilometers from the SE-LFDP. Rainfall records for the years 1976-1978 were not available; thus, rainfall for these years was taken from Hagnauer (1993) for Cañas, Guanacaste, Costa Rica, approximately 60 km southeast of Sector Santa Rosa. Mean annual rainfalls at Cañas and Sector Santa Rosa for 1979 – 1986 were similar ($r^2 = 0.75$, $p < 0.01$). This decade-long study provides an extensive growth and reproduction dataset that encompasses one La Niña (1975) and three El Niño events (1976-1977 and 1983), according to the United States Department of Commerce National Oceanic and Atmospheric Administration (2002).

We utilize the Stevens dataset to quantify: (i) the functional relationship between above-ground tree biomass, annual reproduction, and annual growth rate and (ii) the variability in the annual growth – reproduction relationship. Using a theoretical framework to derive the allometric dependence of growth and reproduction, we then (iii) quantify how the growth – reproduction relationship and the size dependencies of growth and reproduction respond to variability in annual precipitation.

Data analyses

Above ground biomass (AGB , kg) was estimated for each individual (n), for each year (t), according to the following equation for tropical dry forest trees (Chave *et al.* 2005):

$$AGB_{t,n} = \rho \cdot \exp(-0.667 + 1.784 \cdot \ln(D_t) + 0.207 \cdot \ln(D_t)^2 - 0.0281 \cdot \ln(D_t)^3) \quad (1)$$

where D_t is the stem diameter of the tree (DBH in cm) in a given year and ρ is the mean wood density of the plant species ($\text{g} \cdot \text{cm}^{-3}$). For *B. simaruba*, $\rho = 0.307 \text{ g} \cdot \text{cm}^{-3}$ (Williamson 1984). Here, we assume that wood density is constant across all trees and all years. On a population level, the total increment in AGB , or total growth ($TotG_t$, kg), for all individuals for a given year t , can then be expressed by:

$$TotG_t = \sum_{n=1}^{n=x} G_{n,t} = \sum_{n=1}^{n=x} (AGB_{n,t+1} - AGB_{n,t}) \quad (2)$$

where x is the total number of individuals. Here, $G_{n,t}$ can be defined as an individual-level variable to describe the growth of an individual in one year. Similarly, the population total reproductive biomass ($TotRB_t$, kg) was estimated by:

$$TotRB_t = \sum_{n=1}^{n=x} RB_{n,t} = \sum_{n=1}^{n=x} (N_{F_{n,t}} \cdot M_{Fruit}) \quad (3)$$

where, $N_{F_{n,t}}$ is the total number of fruit produced by an individual at time t and M_{Fruit} is the average mass of an individual fruit. Likewise, $RB_{n,t}$ can be defined as an individual-level variable to describe the reproductive production in one year. While the magnitude of variation in fruit mass for *B. simaruba* was not measured in this study, the variation in length and width of whole fruits was small for *B. simaruba* populations in tropical dry forests of Mexico (Greenberg *et al.* 1995). Further, variation in fruit mass is small compared to the large variation in fruit number between trees and between years. Thus,

assuming a constant fruit mass is reasonable. Finally, total biomass production ($TotB_t$, kg) for all individuals in a given year can be represented by:

$$TotB_t = TotG_t + TotRB_t \quad (4)$$

For each year, we quantified (i) $TotRB_t$ and $TotG_t$ and (ii) the percent of total biomass production, $TotB_t$, represented by $TotRB_t$ and $TotG_t$, and evaluated each as a function of precipitation (Appendix A). This provides a population-wide summary of the influence of annual precipitation on total growth and the fractions of total growth due to somatic and reproductive biomass. Community-wide fruit production in tropical trees has been shown to respond to extreme drought events (e.g. Wright *et al.* 1999), and we wanted to test if population level growth and reproduction of *B. simaruba* were affected by annual precipitation.

The use of population level measures provides an aggregate measure across individuals and summarizes the influence of annual precipitation on growth patterns. However, these measures average out the variation in growth and allocation among individual trees. This is particularly important when assessing direct environmental effects on phenotypic traits and reproductive fitness. Further, the absolute size of the pool from which resources are allocated to reproductive and somatic growth may vary with tree size, as well as natural variation in the environment (Chapin *et al.* 1987). In order to characterize the relationship between growth and reproduction across individuals that differ in size as well as to fully understand phenotypic variation, it is necessary to examine proportional changes in biomass on an individual tree level (Enquist *et al.* 1999;

Kerkhoff and Enquist 2009). Thus, for all male and female individuals, Relative Growth Rate (*RGR*) and Reproductive Allocation (*RA*) were quantified as:

$$RGR_{n,t} = \frac{(AGB_{n,t+1} - AGB_{n,t})}{AGB_{n,t}} \quad (5)$$

$$RA_{n,t} = \frac{(N_{n,Ft} \bullet M_{Fruit})}{AGB_{n,t}} \quad (6)$$

Both *RGR* and *RA* represent the change in somatic biomass and the production of reproductive biomass, respectively, over one year relative to the standing somatic biomass at the start of the year. Interpretations of *RA* assume that reproductive parts make no energetic contribution to their own production (Thompson and Stewart 1981), an important tenet of Cody's "Principle of Allocation" (Cody 1966). As with many plant species, this is likely violated in *B. simaruba* as fruit are likely to be photosynthetic; the developing fruit is bright green with a darker green layer underneath the cuticle. Equation 6 can be modified to account for reproductive tissue contribution to reproduction as:

$$RA_{n,t} = \frac{(N_{n,Ft})[(M_{Fruit}) - (\mathcal{G})]}{AGB_{n,t}} \quad (7)$$

Here \mathcal{G} is the mass of the fruit that originated from photosynthetic contributions from the reproductive tissue. The value of \mathcal{G} is unknown for *B. simaruba*. However, it is reasonable to assume that $\mathcal{G} < M_{Fruit}$ and that \mathcal{G} does not appreciably vary between individuals, years, or with AGB_t . Thus, using Eq. 6 to calculate *RA* in *B. simaruba*, is a reasonable comparative measure.

Next, we derive the functional relationship between RA and RGR . In doing so, we show that an assessment of the drivers behind variation in growth and reproduction must first assess the role of allometry because plant growth and seed/fruit production are directly related to plant size (Niklas 1994; Niklas and Enquist 2003; Moles *et al.* 2004; Enquist *et al.* 2007; Weiner *et al.* 2009). We begin by allowing rates of allometric growth and reproduction to vary independently from each other. The simplest model of plant net growth rate ($\text{kg} \cdot \text{time}^{-1}$) is related to plant size (M) as a power function:

$$\frac{dM}{dt} = c_1 M^a = G_t \quad (8)$$

The total plant fruit production ($\text{kg} \cdot \text{time}^{-1}$) can also be expressed as a power function of plant size:

$$\frac{dRB}{dt} = c_2 M^b = RB_t \quad (9)$$

Here, on log-log axes, c_1 and c_2 are the intercepts and a and b are the exponents of the mass-dependence of plant net growth rate and total plant fruit production (see Appendix B). Note, Eqns. 8 and 9 are annual rates that describe net plant growth rate ($\text{kg} \cdot \text{year}^{-1}$) and total plant fruit production ($\text{kg} \cdot \text{year}^{-1}$), respectively. We can use Eqns. 8 and 9 to define c_1 and c_2 on an individual tree level where $c_1 = (dM/dt) / M^a$ and $c_2 = (dRB/dt) / M^b$. In this case, c_1 and c_2 can then be defined as allometrically normalized measures of the relationships between growth and reproduction across years. Thus, comparing values of c_1 and c_2 across individuals within and between years provides a quantitative measure of growth and reproduction that is standardized for allometric effects. Further, Eqn. 8

implicitly includes Reproductive Allocation. To explicitly include reproduction in the growth equation we can define RA as the quotient of fruit production (RB_t) and plant mass such that:

$$RA = \frac{c_2 M^b}{M} = c_2 M^{b-1} \quad (10)$$

where RA has the units of $\text{kg kg}^{-1} \text{ yr}^{-1}$. Second, the relative growth rate of a plant can be defined by the growth rate divided by the mass such that:

$$RGR = \frac{dM/dt}{M} = \frac{c_1 M^a}{M} = c_1 M^{a-1} \quad (11)$$

One can relate RA to RGR by noting that:

$$M = \left(\frac{1}{c_1} RGR \right)^{1/(a-1)} \quad (12)$$

so that substituting Eqn. 12 into Eqn. 10 provides the functional relationship between reproductive allocation and relative growth rate where:

$$RA = \left(\frac{c_2}{c_1^{(b-1)/(a-1)}} \right) RGR^{(b-1)/(a-1)} \quad (13)$$

Equation 13 shows that a plot of RA and RGR is governed by the allometric dependency of growth and reproduction. Specifically, the functional relationship between growth and reproduction is determined by the relative magnitudes of a and b as well as c_1 and c_2 .

Our model makes three critical predictions when assessing the primary drivers of variation in growth and reproduction. First, a plot of RA and RGR does not necessarily imply a tradeoff in the classic sense but instead represents a function that is dependent upon the magnitude of the allometric exponents that govern growth and reproduction.

The functional relationship between RA and RGR can be positive, negative, or even flat depending on the relative magnitudes of a and b . If the allometric normalizations c_1 and c_2 are approximately independent of plant size, then a negative relationship is predicted to be observed if either b or a , but not both, are greater than 1. If both a and b are less than 1 but greater than zero, or if a and b are both greater than 1, then the slope between RA and RGR should be positive. Further, if a and b are equal to each other, the slope should take on a value of one. In sum, variation in the relationship between growth and reproduction critically depends on variability in the allometry of growth and reproduction.

Second, our framework shows that assessing relationships between growth and reproduction are best reflected in the residual variation in Eqns. 8 and 9. In the case where variation in growth and reproduction are governed primarily by a tradeoff, and do not respond strongly to resource availability, a positive allometric residual for fruit production (a tree that is producing more fruit than expected for its size) will be followed by a negative residual for vegetative production (that same tree will produce less biomass than expected for its size). In other words, c_1 and c_2 will be inversely related. However, the above critically assumes that c_1 and c_2 are governed by internal resource allocation and are a constant across resource levels – either across space, reflecting differences in microsites, or across time, reflecting differences in resource supply.

A third prediction from Eqn. 13 comes from relaxing the assumption that c_1 and c_2 are independent of resource supply across time or across microsites. If both of these allometric variables are strongly influenced by microsite variation or differences across years (i.e. if both reproduction and/or growth are resource limited; see Chiariello and

Gulmon 1991; Wright *et al.* 1999) then a plot of c_1 and c_2 will *not* show a negative relationship. Instead, there are two possible outcomes. If microsites strongly differ in resources, and growth and reproduction are strongly tied to external resource levels, then individuals in high resource sites will, for their size, grow and reproduce to a greater degree than individuals in poor resource sites. As a result, the relationship between c_1 and c_2 will be positive. If such a relationship were observed, we could infer that microsite resource variation is a stronger constraint shaping variation in growth and reproduction than individuals trading off growth and reproduction. Finally, if the relationship between c_1 and c_2 is flat, we can infer that the tradeoff and microsite resource variation have about the same effect on growth and reproduction.

To quantify the allometries of RGR and RA and the RA – RGR relationship (Table 1), ordinary least squares-bisector (OLSB) regression analyses were performed between log-log transformed female and male G and AGB (Fig. 1A and Appendix C), female RB and AGB (Fig 1B and Appendix D), and female RA and RGR (Fig. 2A and Appendix E). Because it is not clear which variable is the dependent variable, RMA and OLSB measures are preferable (see Warton *et al.* 2006, Isobe *et al.* 1990). Also, because the log-log linear regression models can produce low r^2 values, RMA regression can lead to highly unstable slope estimates (O’Conner *et al.* 2007). The OLSB method has been shown to be less biased than ordinary least squares regression and more stable than RMA regression when there is a large degree of scatter in the data (Isobe *et al.* 1990). For completeness, the OLSB results are compared to results from ordinary least squares and

RMA regression (see Appendix C-5). Finally, annual slopes from the *RA–RGR* regressions were evaluated as a linear function of precipitation for each year (Fig. 2B).

For each year, we also quantified the allometric variables a , b , c_1 and c_2 as the slopes and intercepts of the OLSB regressions relating log-transformed G and RB , respectively, to log-transformed AGB (Appendix B). We then regressed a as a function of b and c_1 as a function of c_2 , as well as a , b , c_1 and c_2 as functions of precipitation in linear model regressions (Fig. 3). Lastly, we calculated c_1 and c_2 for each individual using coefficients a , b and Eqns. 8, 9, and plotted c_1 against c_2 between years to account for variation in inter-annual precipitation (Fig. 3F). We also plotted c_1 and c_2 within years to account for variation in microsite resource availability (Fig. 3G). All analyses were performed using R (R Development Core Team 2011), including the SMATR and slope.s packages (by A.P. Allen and Isobe *et al.* 1990, available at <http://www.salvias.net/~brian/slopes.s>).

Results

Population-level Analyses

For *B. simaruba* females, population growth and reproduction responded differently to precipitation. While the total population woody growth did not change significantly (Appendix A; $r^2 = 0.31$, $p = 0.1$), the total population reproductive biomass was greater in years with greater rainfall (Appendix A; $r^2 = 0.44$, $p = 0.03$). Further, the percent of population woody growth decreased while percent of population reproductive biomass

increased with increasing precipitation (Appendix A; $r^2 = 0.51$, $p = 0.02$). The percent of population allocation to reproduction varied from 2% in dry years to 20% in wet years.

Individual-level Analyses: Relative Growth Rate, Reproductive Allocation and Size

For both *B. simaruba* females and males, growth of an individual in one year (G ; in kg of woody biomass produced) significantly increased with above ground biomass (Fig. 1A and Appendix C) and female reproductive biomass (RB ; in kg of fruit produced) significantly increased with above ground biomass (Fig. 1B and Appendix D). In sum, a (the scaling exponent between growth and mass) was found to be positive and less than one, and b (the scaling exponent between reproductive biomass and mass) was found to be positive and greater than one (Table 1). According to Eqn. 13, the observed values of a and b are then predicted to yield a negative relationship between RA and RGR . Indeed, for seven of the ten years of the study, RA did significantly decrease with increases in RGR (Fig. 2A and Appendix E) supporting a central prediction of the model. Assessing variation in the RA – RGR regression slopes across years reveals that they do not vary with precipitation (Fig. 2B; $r^2 = 0.14$, $p = 0.15$).

RA, RGR and Allometry

There was no response to precipitation for the scaling exponent of reproduction, b (Fig. 3B; $r^2 = 0.02$, $p = 0.66$), or the allometrically normalized reproduction rate, c_2 (Fig. 3D; $r^2 = 0.08$, $p = 0.39$). Similarly, there was no response to precipitation for the scaling exponent of growth, a , (Fig. 3A; $r^2 = 0.10$, $p = 0.45$) or the allometrically normalized

growth rate, c_1 (Fig. 3C; $r^2 = 0$, $p = 0.97$). Further, the allometric slopes of growth and reproduction were independent of each other as plotting a versus b revealed no significant relationship between these two scaling exponents (Fig. 3E; $r^2 = 0.05$, $p = 0.54$). Finally, between years, c_1 was not significantly correlated with c_2 (Fig. 3G; $r^2 = 0.38$, $p = 0.08$). This finding is consistent with our prediction that microsite variation is as important as the tradeoff between growth and reproduction. Interestingly, within years, c_1 was not significantly correlated with c_2 (Fig. 3F) except for one strong El Niño year (1983) during which c_1 was positively correlated with c_2 (solid line; $r^2 = 0.20$, $p < 0.001$) indicating that in dry years, resource differences govern growth and reproduction to a greater extent than does a tradeoff between growth and reproduction.

Discussion

The first focus of our study was to determine the relationship between growth and reproduction in this population of *B. simaruba*. We show that at the population level growth and reproduction are influenced by precipitation in opposing ways. Population level growth decreases and population level reproduction increases with increasing precipitation. Thus, it appears that when resources are scarce individuals preferentially invest in somatic growth and when resources are abundant (during high precipitation years) investment in reproductive biomass increases at the cost of somatic growth. Selection, for example, may adjust reproductive effort to anticipate conditions favorable for future seedling establishment (Wright *et al.* 1999). The abundance of resources may thus invoke higher investment in reproduction as more seeds are likely to survive

following germination during a high resource year. However, this hypothesis critically assumes that the resource pool is finite, equivalent across microenvironments and does not change with tree size – important components for understanding phenotypic variation in growth and reproduction (Kerkhoff and Enquist 2009).

While the use of population level measures summarizes the influence of annual precipitation on growth patterns, these measures can average out much of the variation in growth and allocation among individual trees. This is particularly true when the absolute size of the pool from which resources are allocated to reproductive and somatic growth varies between sites, between years and with tree size. Thus we examined proportional changes in biomass on an individual tree level in order to characterize the relationship between growth and reproduction across individuals that differ in size as well as in variable resource environments. First, across individuals, we found evidence for a negative relationship between growth (*RGR*) and reproduction (*RA*) for seven of the ten years of the study. Again, this is consistent with individuals investing in reproductive biomass at the cost of somatic growth. Yet three of the ten years of the study show no significant relationship between *RA* and *RGR*. We hypothesized that extreme conditions (i.e. El Niño/La Niña events) could potentially cause a decoupling between growth and reproduction; however, two of the three years had a precipitation level just below the ten-year average and one of the three years was just above the ten-year average annual precipitation. Also, tree size and location could influence the availability of microsite resource levels so that even during drought years individuals with access to deep or easily accessible water (i.e. a large individual with deep roots or an individual in a valley) could

still grow and reproduce at a higher rate than a similar sized individual in a drier microenvironment. Thus, we suspected that there were further influences on growth and reproduction that neither our population nor individual level analyses captured.

In order to explore the ultimate cause for variation in growth and reproduction we then turned to the scaling exponents, a and b , and their effects on the $RA-RGR$ relationship. Although plant size may explain many plant allocation patterns (Niklas 1994) and is an important determinant of absolute and proportional reproductive allocation, relatively few studies have assessed the effect of size-dependency of reproduction (Hubbell 1980; Wheelwright and Logan 2004; Weiner *et al.* 2009). Coupling our model and empirical results suggests that the relationship between RA and RGR is not due to a tradeoff per se, but instead emerges from allometric relationships that govern both growth and reproduction. In particular, the difference between size-dependencies of growth and reproduction within females is primarily responsible for the negative correlation between RA and RGR . In accordance with our model (Eqn. 13), a negative relationship between RGR and RA will emerge if either a or b (allometric growth and reproduction; respectively), but not both, are less than 1 and both are positive. Indeed, our results show that b is greater than 1.0 while a is less than 1 and both greater than zero (Table 1). This suggests that the fraction of total production allocated to growth and reproduction changes with tree size. Thus, even though RGR and RA are mass corrected, the $RA-RGR$ relationship does not evaluate the nature of the tradeoff since growth and reproduction are not isometric with tree size.

It is often argued that evidence of tradeoffs derived from phenotypic correlations

among individuals in nature can be ambiguous and that such correlations may be caused by variation in the environment rather than being primarily generated by tradeoffs (Fox and Stevens 1991, Knops *et al.* 2007). The issue is not if a tradeoff between growth and reproduction exists or not. Allocation is ultimately a zero-sum game; allocation of the total net energy production of an organism to any one function must, by definition, come at the expense to other functions. Instead, the issue is if observed variation in growth and reproduction is governed more by variation in other factors (e.g. spatial and temporal variation in resource availability) that can mask tradeoffs.

To evaluate the relative influence of a growth-reproduction tradeoff, the size dependence of growth and reproduction must first be accounted for. It is not enough, however, to simply normalize growth and reproduction by size because the size dependence of both variables is not isometric. To factor out the influence of size one must instead normalize growth and reproduction by their estimated allometries. Size-corrected growth and reproduction can subsequently be related to each other, and the observed relationship can be compared to predictions based on the relative influence of the growth-reproduction tradeoff. That is: comparing c_1 and c_2 , the allometrically normalized measures of growth and reproduction, respectively, will reveal the influence of the growth-reproduction tradeoff in comparison to the influence of resource availability on growth and reproduction. This is the only approach we are aware of that can use observational data to appropriately assess tradeoffs in growth and reproduction.

Recall that if growth and reproduction are governed primarily by a tradeoff rather than resource availability, then c_1 and c_2 will be inversely related. On the other hand, if

microsites strongly differ in resources, and growth and reproduction are strongly tied to external resource levels, then individuals in high resource sites will, for their size, grow *and* reproduce to a greater degree than individuals in poor resource sites. As a result, the relationship between c_1 and c_2 will be positive. If such a relationship was observed, we could infer that microsite resource variation is a much stronger constraint shaping variation in growth and reproduction than individuals trading off growth and reproduction. Finally, if the relationship between c_1 and c_2 is flat, we can infer that the tradeoff and microsite resource variation have similar effects on growth and reproduction. The finding that within years, c_1 was not significantly correlated with c_2 except for in one strong El Niño year (1983), during which c_1 was positively correlated with c_2 (solid line in Fig. 3F), might suggest that average levels of precipitation are sufficient to cancel out differences in microsite conditions. However, the positive correlation between c_1 and c_2 during the extreme drought in 1983 suggests when resources are scarce, microsite differences may be intensified whereby only those individuals with access to deep soil water can both effectively grow and reproduce. Further, the finding that between years c_1 was not significantly correlated with c_2 supports the hypothesis that variation in growth and reproduction across females is governed by spatial variation in resource supply and a resource allocation tradeoff. Though more statistical power may reveal a directional relationship between c_1 and c_2 , this relationship would presumably be quite weak as there is no evidence to suggest increasing statistical power would substantially change our ultimate conclusions. To further explore the effects of microsite differences and between year variability in resources, future efforts could be made to investigate whether

individuals of the same size located in contrasting microhabitats differ in allocation to growth and reproduction (e.g. Pitelka *et al.* 1980; Young 1984; Denslow *et al.* 1990; Sugiyama and Bazzaz 1998). Manipulating resource availability between years and between sites in an experimental design could help tease apart the interactive effects of microsite and interannual variability of resource availability on growth and reproduction (see Obeso 2002).

We propose that our theoretical derivation for the allometric size-dependency of growth and reproduction is appropriate for understanding the primary origin of the *RA-RGR* relationship. Thus, a positive or negative relationship between *RA* and *RGR* does not necessarily signify that reproduction slows or improves plant growth rate and is not necessarily a measure of a tradeoff. This is due to the fact that the functional relationship between *RA* and *RGR* is influenced by the allometries of growth rate and reproduction. A plot of *RA* as a function of *RGR* can most usefully be used to assess a tradeoff between vegetative and reproductive production if there is no variation in size or resource availability among individuals. However, a plot of *RA* versus *RGR* is often used to look for a tradeoff between vegetative and reproductive growth without holding tree size and resource availability constant (Calder 1984; Samson and Werk 1986; Bonser and Aarssen 2008). We recommend that future experimental studies eliminate variation in tree size and resource supply and that these experiments be coupled with observational studies that take an allometric approach similar to that developed here.

In this study, we quantified the relationship between two important life history traits – growth and reproduction. We asked how this relationship varies across time and

how it is influenced by underlying allometries and resource supply. Our results support and underscore the findings of several recent papers (see Knops *et al.* 2007). Specifically, a negative correlation between growth and reproduction is not a strong test of the processes that underlie variation in growth and reproduction. In particular, in *B. simaruba*, after controlling for allometric growth and reproduction, both growth and reproduction reveal three important patterns. First, we show that growth and reproduction are not isometric and thus do not scale similarly with size. Second, the relationship between RA and RGR is ultimately governed by the underlying allometries of growth and reproduction. Third, observed variation in growth and reproduction is consistent with resource variation and tradeoff mechanisms each playing important roles in the observed patterns. To better understand the processes governing individual growth and reproduction, we suggest that more emphasis be placed on studying the dual effects of size and variation in resource supply across microsites, particularly within long-lived trees.

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Tables Appendix D

Table 1: Results from calculating c_1 , c_2 , a and b using Eqns. 8 – 11 and the *RA–RGR* regressions. The standard error is given in parentheses. Fields with *NA* indicate growth data for calculations of c_1 and a were unavailable after the January 1986 census. Note – on log axes, c_1 and c_2 are the allometric normalizations and are the mass-normalized geometric mean responses of growth and reproduction, respectively, of the population and a and b are the slopes of the mass-dependence of plant net growth rate and total plant fruit production (see Appendix B). The slope of the *RA–RGR* regression is also noted for each year.

Year	Precip (mm)	c_1	c_2	a	b	Slope
1976	986	-0.56 (0.12)	-4.96 (0.27)	0.68 (0.05)	2.11 (0.12)	-2.17 (0.33)
1977	948	-0.48 (0.10)	-5.42 (0.43)	0.69 (0.04)	1.80 (0.18)	1.65 (0.27)
1978	1366	-0.40 (0.10)	-4.73(0.38)	0.72 (0.05)	1.78 (0.16)	-1.29 (0.19)
1979	1979	-0.34 (0.07)	-6.20 (0.39)	0.60 (0.04)	2.23 (0.17)	-1.61 (0.19)
1980	1708	-0.42 (0.07)	-4.63 (0.26)	0.64 (0.03)	1.78 (0.11)	-1.31 (0.24)
1981	2240	-0.73 (0.04)	-5.38 (0.23)	0.75 (0.03)	1.88 (0.10)	-2.24 (0.29)
1982	1821	-0.44 (0.06)	-4.55 (0.21)	0.59 (0.04)	1.74 (0.09)	-1.47 (0.15)
1983	915	-0.51 (0.07)	-4.88 (0.23)	0.70 (0.03)	1.66 (0.10)	-1.12 (0.13)
1984	1721	-0.35 (0.06)	-5.37 (0.25)	0.62 (0.03)	1.68 (0.11)	-1.38 (0.11)
1985	1431	-0.60 (0.07)	-4.16 (0.20)	0.70 (0.04)	1.54 (0.09)	-1.60 (0.20)
1986	1306	<i>NA</i>	-4.80 (0.25)	<i>NA</i>	1.86 (0.11)	<i>NA</i>

Figures Appendix D

Figure 1: OLS-Bisector regressions of \log_{10} - \log_{10} transformed **(A)** G (woody biomass increment; kg) and **(B)** RB (reproductive biomass; kg) against AGB (above ground biomass; kg) for females during 1976 –1986. Each line represents a single regression of G or RB onto AGB for all individuals in a given year for each of ten years. Individual trees for males (open triangles) and females (closed circles) are shown in **(A)** and females in **(B)** for one year – 1976. Note: The data points line up in **(A)** due to the rounding of circumference. Circumference was measured in 1 cm increments so that all G values for a 1 cm increase fall along a single line across AGB values. Each ‘line’ of data points is due to a discrete amount of increase (e.g. 1, 2 or 3 cm, etc.) on the log scale.

Figure 2: **(A)** OLS-Bisector regressions of \log_{10} - \log_{10} transformed RA (reproductive allocation) and RGR (relative growth rate) for female individuals, showing the expected negative relationship between RA and RGR for 7 of the 10 years of the study. Dashed lines represent years with no statistical significance between RA and RGR ; solid lines represent years with a significant relationship between RA and RGR . **(B)** Scatterplot of the RA – RGR regressions against annual precipitation for 1976-1986 for all years ($r^2 = 0.14$, $p = 0.15$).

Figure 3: Scatterplots of **(A)** a on precipitation for all years ($r^2 = 0.10$, $p = 0.45$) **(B)** b on precipitation for all years ($r^2 = 0.02$, $p = 0.66$), **(C)** c_1 on precipitation for all years ($r^2 = 0$, $p = 0.97$), **(D)** c_2 on precipitation for all years ($r^2 = 0.08$, $p = 0.39$), **(E)** a against b for all years ($r^2 = 0.18$, $p = 0.22$) and **(F)** c_1 against c_2 between years ($r^2 = 0.07$, $p = 0.46$), and **(G)** c_1 against c_2 within years. Dashed lines represent years with no statistical significance between c_1 and c_2 ; solid lines represent years with a significant relationship. Here, on log axes, c_1 and c_2 are the allometric normalizations and are the mass-normalized geometric mean responses of growth and reproduction, respectively, of the population and a and b are the regression slopes of the mass-dependence of plant net growth rate and total plant fruit production.

Figures

Figure 1:

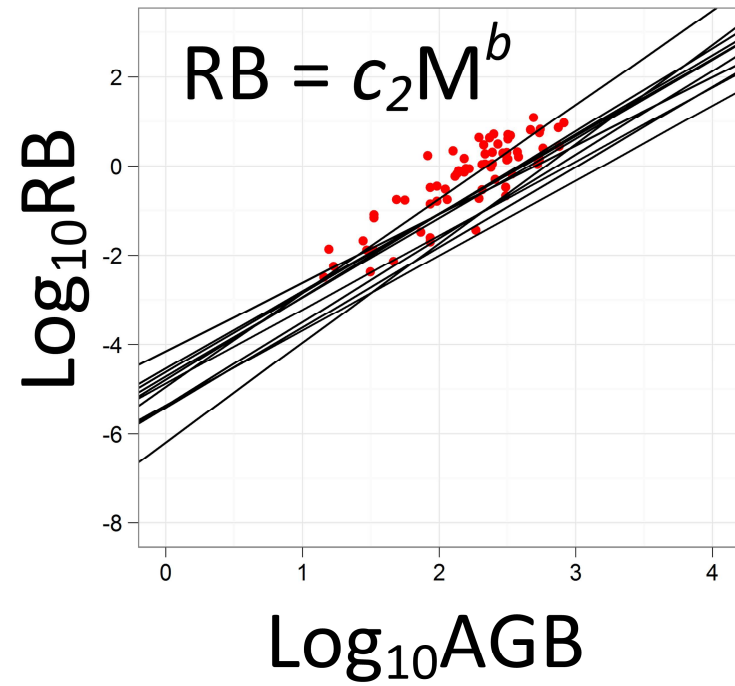
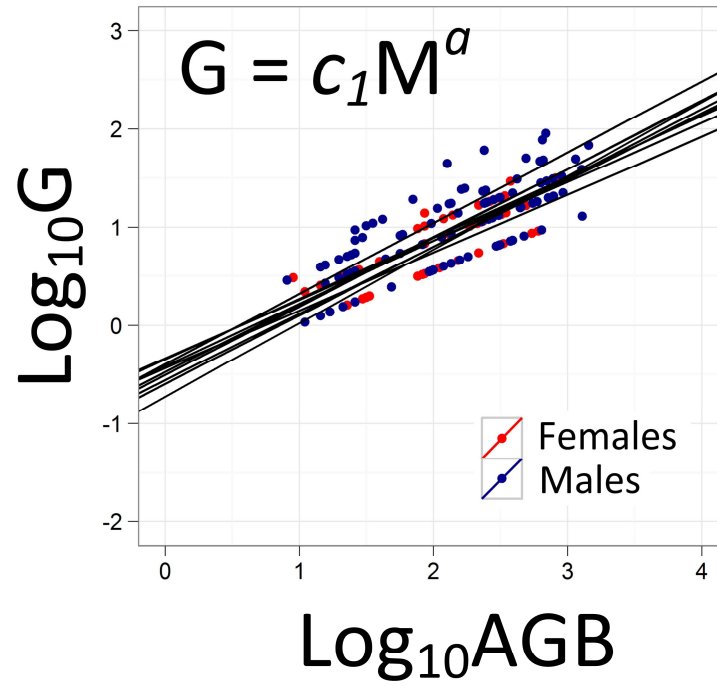


Figure 2:

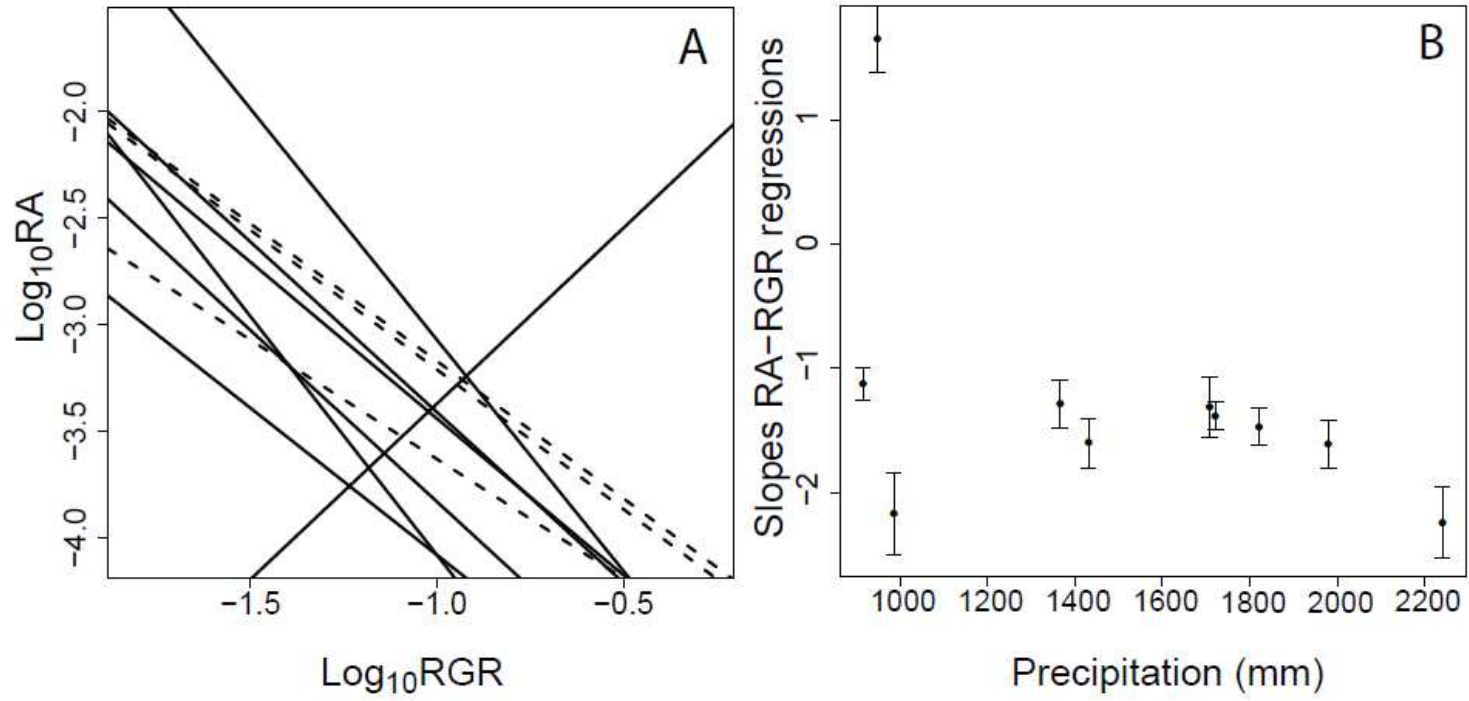
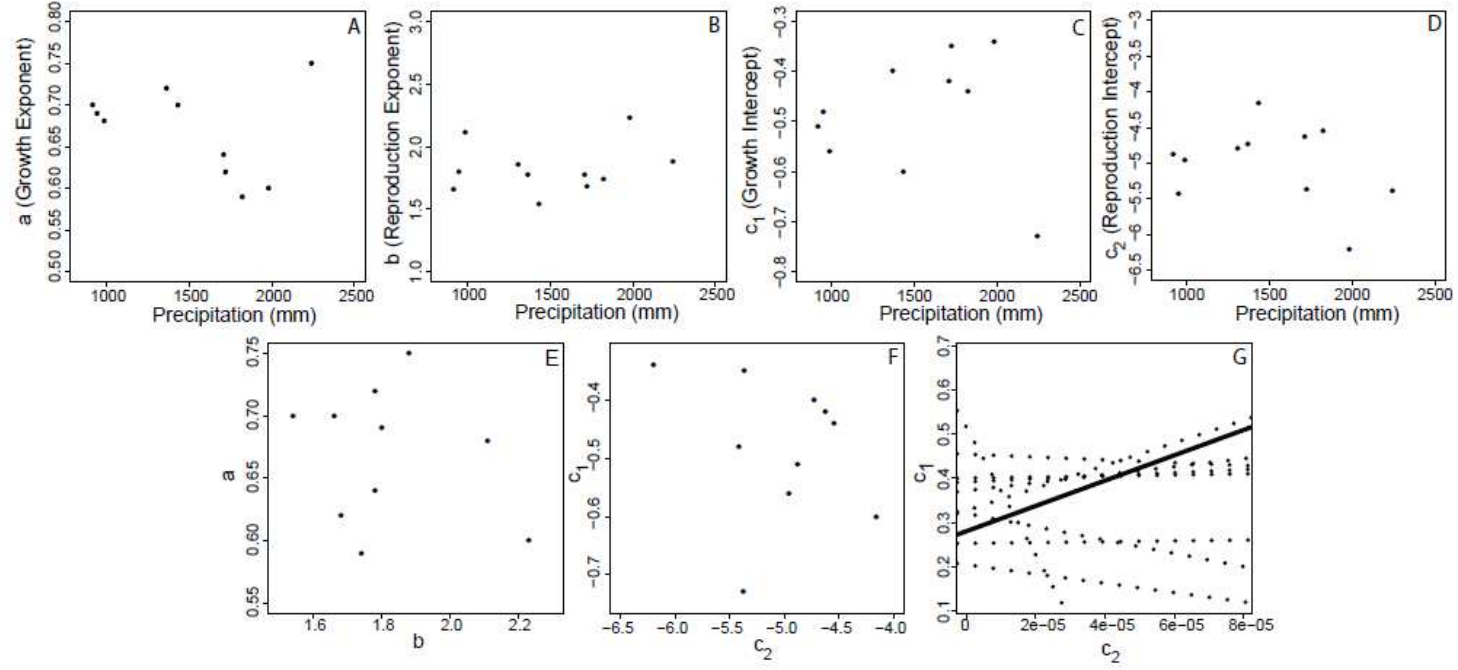


Figure 3:



Supplementary Material Appendix D

Table S1: Tabular results for female and male growth as a function of mass from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions.

Table S2: Tabular results for female reproductive biomass as a function of mass from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions.

Table S3: Tabular results for female reproductive allocation as a function of relative growth rate from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions

Figure S1: Simple linear regressions of total population woody growth, reproductive biomass, and percent population woody growth and reproductive biomass as functions of precipitation for each year.

Figure S2: Conceptual figure describing the calculation of a , b , c_1 and c_2 .

Table S1: Tabular results for female and male growth as a function of mass from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions.

	Year	Precip (mm)	R ²	p-val	Intercept			Slope		
					OLS	OLSB	RMA	OLS	OLSB	RMA
FEMALES	1976	986	0.78	<0.001	-0.25 (0.12)	-0.56 (0.12)	-0.55 (0.12)	0.53 (0.06)	0.68 (0.05)	0.67 (0.06)
	1977	948	0.66	<0.001	0.05 (0.10)	-0.48 (0.10)	-0.43 (0.10)	0.44 (0.05)	0.69 (0.04)	0.66 (0.04)
	1978	1366	0.73	<0.001	0.004 (0.10)	-0.40 (0.10)	-0.38 (0.11)	0.51 (0.05)	0.72 (0.05)	0.70 (0.05)
	1979	1979	0.73	<0.001	-0.01 (0.08)	-0.34 (0.07)	-0.32 (0.08)	0.43 (0.04)	0.60 (0.04)	0.58 (0.04)
	1980	1708	0.80	<0.001	-0.17 (0.07)	-0.42 (0.07)	-0.41 (0.07)	0.51 (0.04)	0.64 (0.03)	0.64 (0.03)
	1981	2240	0.91	<0.001	-0.62 (0.05)	-0.73 (0.04)	-0.73 (0.04)	0.68 (0.03)	0.75 (0.03)	0.74 (0.03)
	1982	1821	0.82	<0.001	-0.24 (0.06)	-0.44 (0.06)	-0.43 (0.06)	0.48 (0.03)	0.59 (0.04)	0.59 (0.04)
	1983	915	0.76	<0.001	-0.19 (0.08)	-0.51 (0.07)	-0.49 (0.07)	0.53 (0.04)	0.70 (0.03)	0.69 (0.04)
	1984	1721	0.74	<0.001	-0.04 (0.07)	-0.35 (0.06)	-0.33 (0.06)	0.45 (0.04)	0.62 (0.03)	0.61 (0.03)
	1985	1431	0.79	<0.001	-0.31 (0.08)	-0.60 (0.07)	-0.59 (0.07)	0.54 (0.04)	0.70 (0.04)	0.69 (0.04)
MALES	1976	986	0.78	<0.001	-0.19 (0.09)	-0.54 (0.09)	-0.53 (0.09)	0.56 (0.04)	0.73 (0.04)	0.72 (0.04)
	1977	948	0.82	<0.001	-0.12 (0.08)	-0.39 (0.08)	-0.38 (0.08)	0.57 (0.04)	0.70 (0.03)	0.70 (0.03)
	1978	1366	0.89	<0.001	-0.21 (0.05)	-0.36 (0.05)	-0.36 (0.05)	0.63 (0.03)	0.72 (0.03)	0.71 (0.03)
	1979	1979	0.90	<0.001	-0.34 (0.04)	-0.45 (0.03)	-0.45 (0.03)	0.64 (0.02)	0.71 (0.02)	0.71 (0.02)
	1980	1708	0.90	<0.001	-0.39 (0.03)	-0.49 (0.03)	-0.49 (0.03)	0.62 (0.02)	0.69 (0.02)	0.69 (0.02)
	1981	2240	0.92	<0.001	-0.47 (0.03)	-0.55 (0.03)	-0.55 (0.03)	0.62 (0.02)	0.68 (0.02)	0.68 (0.02)
	1982	1821	0.93	<0.001	-0.43 (0.03)	-0.50 (0.02)	-0.50 (0.02)	0.61 (0.02)	0.66 (0.02)	0.66 (0.02)
	1983	915	0.92	<0.001	-0.38 (0.02)	-0.46 (0.02)	-0.45 (0.02)	0.64 (0.02)	0.70 (0.01)	0.69 (0.01)
	1984	1721	0.90	<0.001	-0.41 (0.03)	-0.51 (0.03)	-0.51 (0.03)	0.66 (0.02)	0.73 (0.02)	0.73 (0.02)
	1985	1431	0.92	<0.001	-0.45 (0.02)	-0.53 (0.02)	-0.53 (0.02)	0.63 (0.02)	0.69 (0.02)	0.69 (0.02)

Note: Results from log-log transformed ordinary least squares (OLS; Y/X), ordinary least squares bisector (OLSB) and reduced major axis (RMA; type II) regressions. The standard deviations are given in parentheses. All years are statistically significant ($p < 0.05$).

Table S2: Tabular results for female reproductive biomass as a function of mass from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions.

Year	Precip (mm)	R ²	p-val	Intercept			Slope		
				OLS	OLSB	RMA	OLS	OLSB	RMA
1976	986	0.86	<0.001	-4.33 (0.26)	-4.96 (0.27)	-4.99 (0.28)	1.83 (0.11)	2.11 (0.12)	2.13 (0.12)
1977	948	0.50	<0.001	-3.68 (0.48)	-5.42 (0.43)	-5.96 (0.44)	1.01 (0.20)	1.80 (0.18)	2.04 (0.18)
1978	1366	0.67	<0.001	-3.53 (0.35)	-4.73 (0.38)	-4.90 (0.42)	1.23 (0.15)	1.78 (0.16)	1.85 (0.17)
1979	1979	0.72	<0.001	-4.88 (0.42)	-6.20 (0.39)	-6.39 (0.42)	1.65 (0.18)	2.23 (0.17)	2.31 (0.18)
1980	1708	0.77	<0.001	-3.79 (0.26)	-4.63 (0.26)	-4.70 (0.27)	1.39 (0.12)	1.78 (0.11)	1.81 (0.12)
1981	2240	0.82	<0.001	-4.70 (0.23)	-5.38 (0.23)	-5.42 (0.24)	1.56 (0.10)	1.88 (0.10)	1.90 (0.10)
1982	1821	0.84	<0.001	-4.00 (0.19)	-4.55 (0.21)	-4.58 (0.21)	1.47 (0.09)	1.74 (0.09)	1.75 (0.09)
1983	915	0.67	<0.001	-3.78 (0.27)	-4.88 (0.23)	-5.02 (0.26)	1.16 (0.12)	1.66 (0.10)	1.72 (0.11)
1984	1721	0.72	<0.001	-4.39 (0.28)	-5.37 (0.25)	-5.47 (0.26)	1.24 (0.13)	1.68 (0.11)	1.73 (0.12)
1985	1431	0.70	<0.001	-3.21 (0.25)	-4.12 (0.20)	-4.24 (0.21)	1.11 (0.12)	1.54 (0.09)	1.58 (0.09)
1986	1306	0.78	<0.001	-3.99 (0.28)	-4.80 (0.25)	-4.87 (0.25)	1.47 (0.13)	1.86 (0.11)	1.90 (0.11)

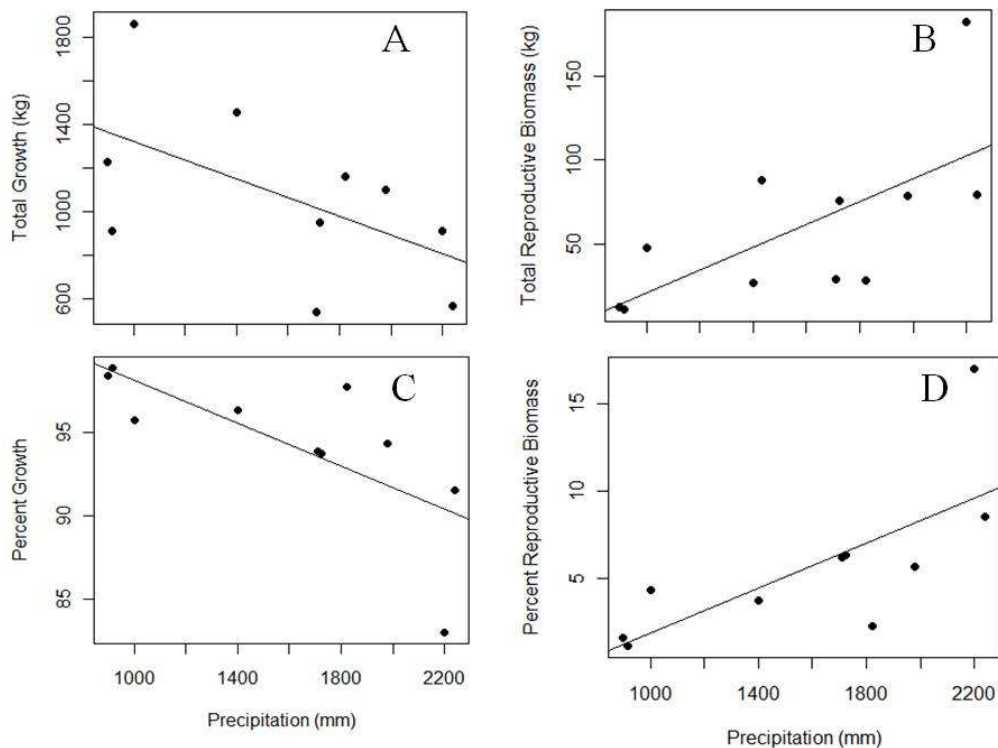
Note: Results from log-log transformed ordinary least squares (OLS; Y/X), ordinary least squares bisector (OLSB) and reduced major axis (RMA; type II) regressions. The standard deviations are given in parentheses.

Table S3: Tabular results for female reproductive allocation as a function of relative growth rate from log-log transformed ordinary least squares, ordinary least squares bisector and reduced major axis regressions

Year	Precip (mm)	R ²	p-val	Intercept			Slope		
				OLS	OLSB	RMA	OLS	OLSB	RMA
1976	986	0.46	0.003	-4.03 (0.49)	-5.24 (0.48)	-5.82 (0.46)	-1.22 (0.34)	-2.17 (0.33)	-2.64 (0.33)
1977	948	0.26	0.04	-2.89 (0.29)	-1.72 (0.31)	-0.69 (0.36)	0.66 (0.25)	1.65 (0.27)	2.52 (0.31)
1978*	1366	0.16	0.21	-3.41 (0.26)	-4.46 (0.26)	-5.37 (0.38)	-0.34 (0.21)	-1.29 (0.19)	-2.11 (0.31)
1979	1979	0.41	0.002	-4.41 (0.28)	-5.44 (0.26)	-5.85 (0.30)	-0.79 (0.21)	-1.61 (0.19)	-1.93 (0.21)
1980*	1708	0.17	0.17	-3.41 (0.34)	-4.52 (0.32)	-5.43 (0.30)	-0.36 (0.26)	-1.31 (0.24)	-2.10 (0.23)
1981	2240	0.52	<0.001	-5.20 (0.2)	-6.32 (0.35)	-6.75 (0.31)	-1.34 (0.33)	-2.24 (0.29)	-2.58 (0.25)
1982	1821	0.39	0.002	-3.89 (0.24)	-4.91 (0.21)	-5.26 (0.24)	-0.67 (0.18)	-1.47 (0.15)	-1.74 (0.18)
1983*	915	0.11	0.38	-3.64 (0.23)	-4.75 (0.17)	-5.40 (0.24)	-0.18 (0.19)	-1.12 (0.13)	-1.67 (0.17)
1984	1721	0.36	0.003	-4.55 (0.18)	-5.46 (0.14)	-5.76 (0.20)	-0.59 (0.15)	-1.38 (0.11)	-1.63 (0.15)
1985	1431	0.43	<0.001	-4.03 (0.24)	-5.01 (0.28)	-5.37 (0.37)	-0.80 (0.17)	-1.60 (0.20)	-1.89 (0.28)

Note: Results from log-log transformed ordinary least squares (OLS; Y/X), ordinary least squares bisector (OLSB) and reduced major axis (RMA; type II) regressions. The standard deviations are given in parentheses. The asterisk (*) next to the sampling year indicates statistical non-significance ($p > 0.05$).

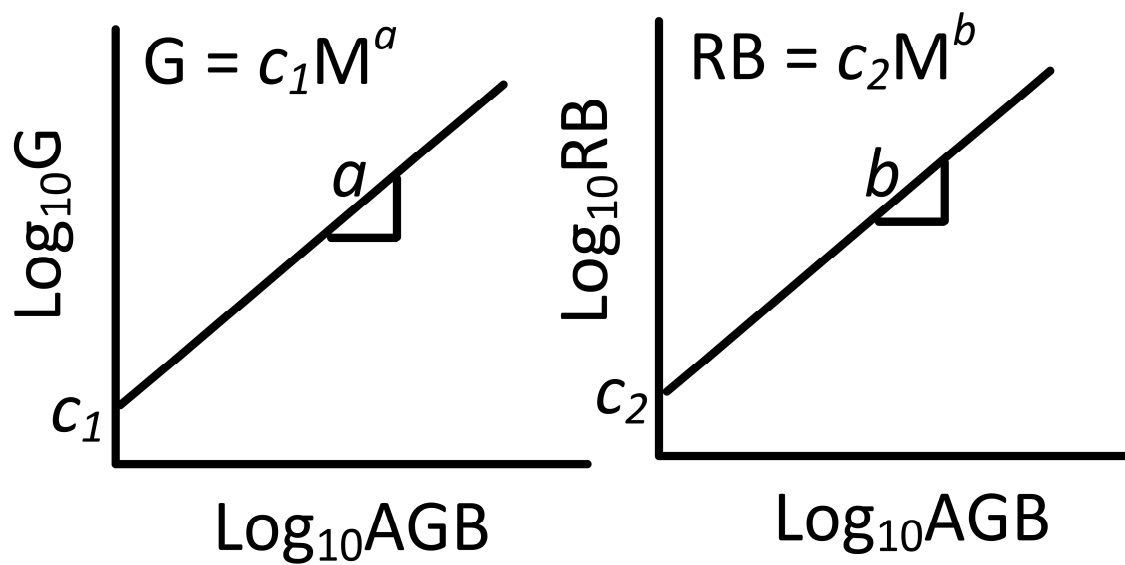
Figure S1:



Simple linear regressions of total population woody growth, reproductive biomass, and percent population woody growth and reproductive biomass as functions of precipitation for each year.

Simple linear regression of (A) total population woody growth ($r^2 = 0.31$, $p = 0.10$), (B) total population reproductive biomass ($r^2 = 0.44$, $p = 0.026$), (C) percent population woody growth ($r^2 = 0.51$, $p = 0.02$) and (D) percent population reproductive biomass ($r^2 = 0.51$, $p = 0.02$) as functions of precipitation for each year of the study.

Figure S2:



Conceptual figure describing the calculation of a , b , c_1 and c_2 .