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DISSERTATION / DOCTORAL THESIS

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„The relationship between the mean and variation of functional traits and the geographical range size of tropical trees“

verfasst von / submitted by

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Synopsis of Publications and Manuscripts

Chapter 1

Chacón-Madrigal, E, Wanek, W, Hietz, P & Dullinger. S. Range size in neotropical trees is weakly related to traits indicating a conservative resource strategy. *Perspectives in Plant Ecology, Evolution and Systematics*, 32:30-37, https://doi.org/10.1016/j.ppees.2018.01.003

Contributions

All the authors conceptualized and designed the study. I obtained the funds for fieldwork and laboratory analysis and made all the field and laboratory work. Stefan Dullinger and I designed the statistical analyses. I conducted the analysis and created the tables and figures. I wrote the manuscript with contributions of all other authors.

Chapter 2

Chacón-Madrigal, E, Wanek, W, Hietz, P & Dullinger. S. Is local trait variation related to total range size of tropical trees? PLoS ONE, 13(3): e0193268. https://doi.org/10.1371/journal.pone.0193268

Contributions

All the authors designed the study. I obtained the funds for fieldwork and laboratory analysis and made all the field and laboratory work. Stefan Dullinger and I designed the statistical analyses. I analyzed the data and created the tables and figures I wrote the manuscript with contributions of all other authors.

Chapter 3

Chacón-Madrigal, E, Alvarado, A., Wanek, W, Hietz, P, Hofhansl, F, & Dullinger. S (in preparation). What property of the species functional traits defines better the realized niche breadth of tropical trees: the central position or the variation?

Contributions

Stefan Dullinger and I designed the study. Stefan and I obtained the funds for the study. Alfredo Alvarado and I compiled the data. Stefan Dullinger and I designed the statistical analyses. I analyzed the data and created the tables and figures. I wrote the first draft of the manuscript and Stefan Dullinger made substantial contributions and modifications. Additional contributions were made by the other authors.

Introduction

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world"

Charles Darwin, 1859, On the origin of species by means of natural selection

I was surprised when I realized that the question that often came to my mind was also Charles Darwin's question. I have called it the first of Darwin's questions because it is the first one that he described in his famous book "On the origin of species by means of natural selection". However, after reading many papers, now, I am no longer surprised at all because I realized that the question is still commonly asked and by no means definitely answered in the scientific literature (Brown et al., 1996; Gaston & Spicer, 2001; Slatyer et al., 2013; Grossenbacher et al., 2015). As Charles Darwin knew, the comprehension of "these relations are of the highest importance" (Darwin, 1859). The striking differences in the range size of species have significant implications for their vulnerability to extinction, with those having narrow range size also more vulnerable (Purvis et al., 2000; Harris & Pimm, 2008; Pimm et al., 2014). In the Anthropocene, where humans have triggered a massive decline of many species' populations and sixth mass extinction may be impending (Barnosky et al., 2011), such differences in vulnerability are of obvious importance to the conservation of biological diversity.

However, if we want to avoid species extinctions, it is not sufficient to know which are narrowly and which are widely distributed. We need to answer Darwin's question because also the causes that allow the species to expand their ranges may be linked to their probability of extinction (Saupe et al., 2015). Unfortunately, these causes are still understood partly at best. In fact, many factors can affect the expansion of geographical ranges (Brown et al., 1996). Species may, for example, be limited by extrinsic factors, either, because they evolved in isolated places (geographical constraints) (Whittaker & Fernández-Palacios, 2007) or are evolutionary young (time constraints) (Grossenbacher et al., 2015). Moreover, characteristics of the species such as dispersal mecanisms (Thompson et al., 1999), mating systems (Grossenbacher et al., 2015) or the tradeoffs between resource allocation to fecundity or survivorship, or to growth versus survivorship (Sexton et al., 2009; Adler et al., 2014), as well as adaptations to specific habitats or biotic interactions can lead to maladaptation at the range limits (Gilbert et al., 2017), dispersal limitation (Hargreaves et al., 2014), low competive ability (Svenning et al., 2014) or slow growth rate of the population (Sexton et al., 2009), which all could affect the rate and magnitude of range expansion and hence, eventually, range size.

Among the hypotheses to explain differences in range sizes, those referring to the ecological niche and its breadth have partiuclar support (Peterson, 1999; Thompson et al., 1999; Slatyer et al., 2013). The ecological niche is defined as the multidimensional space which describes the requirements that a species has for growing and reproducing successfully enough to maintain positive population growth rates (Hutchinson, 1957). Species with broader niches commonly have wider ranges (Boulangeat et al., 2012; Slatyer et al., 2013). Functional traits, which are those with some adaptive value, may lead to differences in niche breadth via two mechanisms. . First, particular trait values may confer species higher competitive ability (Kunstler et al., 2016) or tolerance to a broader range of environmental variation (Stahl et al., 2014). For instance, in plants, species with small leaves are found in high and low rainfall regions, but species with large leaves are rare in regions with low rainfall (Wright et al., 2017). Second, differences in intraspecific trait variation, whether driven by genetic diversity or by phenotypic plasticity, should allow species to tolerate broader environmental conditions (Bradshaw, 1965; Sexton et al., 2017), that is, to have broader environmental niches. The possible contribution of these two properties of the species trait value distribution, mean and variance, to species' range sizes has hardly been directly compared so far.

Tropical tree species display significant variation in range size (Feeley & Silman, 2009). Although tropical tree species in the same genus tend to have similar range size, there is also considerable variation among species belonging to the same clades (Dexter & Chave, 2016). Besides, tropical trees have considerable variation in functional traits (Hulshof & Swenson, 2010; Messier et al., 2010; Mitchell et al., 2017), which makes them a useful group to understand relationships between inter- and intraspecific trait variation and the species range size or niche breadth. Tropical trees species also face a fast habitat loss, and they are directly affected by land-use change (da Silva & Tabarelli, 2000), which also calls for a better understanding of functional traits-range size relationships in this group of organisms. In my doctoral thesis work, I did fieldwork and collected data in a region of tropical rainforest in southern of Costa Rica aiming to explore the relations between range size and trait means as well as trait dispersion in a group of tropical trees with contrasting range size selected within a phylogenetic context. Besides, I explored these relations using a data compilation of functional traits for trees distributed across all the tropics of America.

Chapter 1: Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees.

In chapter 1, I explored whether traits commonly linked to a conservative resource-use strategy are associated with small range sizes. Trait values such as high wood density, high leaf thickness, high leaf dryer matter content, as well as low leaf nitrogen content, leaf phosphorus

content, leaf potassium content and specific leaf area, have been associated with plants following a conservative resource-use strategy. I sampled 345 trees from 35 species in 14 genera and measured the traits just mentioned. For each species, I estimated the range size as the extent of occurrence using known localities of occurrence and correlated it with trait data scaled within-genus. I also correlated the range size with ordination axes of a principal component analysis of the traits. I found that only wood specific gravity and leaf nitrogen content predicted the species range size. Species with low wood specific gravity and higher leaf nitrogen content had higher range sizes. The means of none of the other six traits were correlated with range size. Results were similar for a model using the principal components of the multivariate trait space, which explained 36% of the variation in species' extent of occurrence. Again, the traits most strongly associated with the selected components were wood specific gravity and leaf nitrogen content. Although high wood specific gravity and low leaf nitrogen content can be interpreted as indicators of conservative resource-use, we could hence not detect strong relationships between the respective trait syndrome and range size in our sample of species. Biological traits may thus be involved in determining the range size of the species analyzed, but other factors apparently modify the effect.

Chapter 2: Is local trait variation related to total range size of tropical trees?

In chapter 2, I analyzed whether intraspecific variation in functional traits realized on a regional scale (southern Costa Rica) is a possible predictor of total species' range size. Using the same dataset of tropical trees and functional traits as in Chapter 1, I formed 17 congeneric pairs of one narrow endemic and one widespread species. I tested whether there are significant differences in the locally expressed variation of individual traits or in the multidimensional trait variance between the species in congeneric pairs and whether species' range size could hence be predicted from local trait variability. However, in none of the traits I could find any significant differences in intra-specific variation between widely distributed and small range species.. I discussed the possible reasons why the local or even the overall species trait variation might not be related to the range size. I also discussed the direction of causality in the range size-intraspecific trait variation relationship. I hypothesized that that higher trait variability of widespread species may result from successive local adaptations during range expansion and may hence often be an effect rather than the cause of larger ranges.

Chapter 3: Is realized niche breadth of neotropical trees more closely related to trait means or to trait variation?

In the third chapter, I tried to compare the relative contributions of species' mean trait values and intra-specific trait variabilities to the breadth of realized niches. For doing so, I compiled information of three functional traits, wood density, leaf nitrogen content and specific

leaf area for as many tree species of tropical America as possible. For species with five or more documented values for at least one of these traits, I estimated the climatic niche breadth (realized niche) using six uncorrelated climatic variables from WorldClim from places where the species have been documented according to the Global Biodiversity Information Facility. I used both ordinary least-squares regressions and phylogenetically corrected regression models to test how much variation of the niche breadth could be explained by species' trait means or species' trait variation, respectively. In general, both traits means and trait variability explained only a low to moderate fraction of the variance in niche breadth (2 to 22%). Similar to the results found on a regional scale (Chapter 1), the results of this analysis suggest that a 'ruderal' strategy, evidenced by a low wood density and high values of specific leaf area and leaf nitrogen content, fosters broader niches. However, in univariate models relationships of niche breadth with trait variation was much stronger in case of leaf nitrogen content and specific leaf area, and approximately equally strong in case of wood density. Results were consistent between models with and without phylogenetic correction. Taken together, my findings corroborate that in neotropical tree species the niche breadth is influenced by both mean trait values and trait variation. Among these parameters, trait variability is apparently more closely related to niche breadth than mean trait states.

Concluding Discussion

The species' range size is the result of a complex and intriguing interaction of extrinsic and biological factors. In the case of tropical tree species, I found that the mean value of biological traits of the species can affect the extent of the realized niche and probably how much of the potential range is filled. This effects seem mediated by trait values that allow species fast growth rates and thus probably high colonization ability or great persistence. Tree species with low wood density and high leaf nitrogen content can achieve large range sizes (Chapter 1) or large niche breadth (Chapter 3). Although, it is widely conceived that species' trait variability is related to the species niche breadth and consequently to the range size, I found that regional trait variability it is not related to the range size (Chapter 2). However, if trait variability is measured across entire species ranges, it is positively related to the species niche breadth (Chapter 3). I hence tentatively conclude that high trait variability is a consequence rather than a cause of large realized niche.

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Abstract

The range size of a species is a key property of its geographical distribution. The vast variation of the species geographical range size is puzzling and partly understood, at best. The ecological niche, meaning the multidimensional space of the requirements that an individual or species has for growing and reproducing successfully, has a significant role within hypotheses to explain this variation. In general, broader niches are assumed to beget larger ranges. Niche breadth, in turn, is determined by the functional traits that species acquire throughout their evolutionary history via two mechanisms. First, particular trait values may confer species higher competitive ability or tolerance of a broader range of environmental conditions. Second, it is often assumed that species with higher intra-specific trait variation should tolerate more variable environmental conditions.

I investigated two hypotheses about how functional traits can affect the range size of a group of tropical trees. First, I explored the relationship between range size and the mean values of functional traits in a group of 35 tropical trees. I therefore used data sampled in regional populations of the study species in southern Costa Rica. I found that species with high wood specific gravity and low leaf nitrogen content tend to have smaller ranges, a result which suggests that conservative resource use constrain range expansion. However, those relations were weak, and additional factors hence apparently modify the trait effect. I also explored if the regional variation in functional traits could explain the differences in range size. However, I could not find any significant differences in intra-specific trait variation between widely distributed and small range species. I conclude that higher trait variability reported from widespread species may result from successive local adaptations during range expansion and may hence often be an effect rather than the cause of more extensive ranges.

Finally, I compiled data of three different traits for a larger number of trees ranging across the neotropics to directly compare the correlations between climatic niche breadth and trait means or trait variability, respctively. The results corroborated that in neotropical tree species the mean trait values can affect the realized niche breadth. As with the regional data, species with a conservative resource use strategy tend to have narrower niches. However, I also found that trait variability is apparently more closely related to realized niche breadth than trait means.

My general conclusion is that species' range size is the result of a complex and intriguing interaction of factors.In tropical tree species, the mean value of biological traits can affect the extent of the realized niche and probably how much of the potential range is filled. This effects seem mediated by trait values that allow species fast growth rates and thus probably high colonization ability. Species' trait variability is related to the species niche

breadth, but only if this variability is measured across entire species ranges. I hence tentatively conclude that high trait variability is a consequence rather than a cause of large realized niche.

Zusammenfassung

Arealgröße ist eine zentrale Eigenschaft der Biogeographie von Tier- und Pflanzenarten. Warum manche Arten weit verbreitet sind, während andere, oft nahe verwandte Arten nur kleine Gebiete besiedeln ist eine Frage, die die Ökologie seit langem beschäftigt, aber bis heute nicht vollständig beantwortet ist. Unter den verschiedenen Faktoren, die in diesem Zusammenhang diskutiert worden sind, spielt auch die Breite der ökologischen Nische eine wichtige Rolle. Es wird im Allgemeinen davon ausgegangen, dass Arten die mit unterschiedlichen Umweltbedingungen zurecht kommen, auch größere geographische Areale besiedeln können, d.h. dass größere Areale mit breiteren ökologischen Nischen positiv korreliert sind.

Die Nischenbreite wird neben anderen Faktoren durch die funktionellen Eigenschaften bestimmt, welche Arten im Laufe ihrer Evolutionsgeschichte erwerben. Interspezifische Unterschiede bezüglich funktioneller Eigenschaften können aus zwei Gründen zu Untschieden in der Nischenbreite führen: Erstens könnten bestimmte funktionelle Eigenschaften die Konkurrenzkraft von Arten oder ihre Umwelt-Tolernaz erhöhen; und zweitens könnte eine höhere intraspezifische Variabilität funktioneller Eigenschaften den Arten Anpassung an mehr unterschiedliche Lebensräume ermöglichen.

In meiner Doktorarbeit untersuchte ich zwei Hypothesen bezüglich der Effekte funktioneller Eigenschaften auf Nischenbreiten und Arealgrößen von neotropischen Baumarten. Meine erste Studie beschäftigte sich mit dem Zusammenhang zwischen Arealgröße und den Mittelwerten funktioneller Eigenschaften in einer Gruppe von 35 tropischen Bäume, die gemeinsam im südlichen Costa Rica vorkommen. Ich sammelte Daten zu diesen Eigenschaften von regionalen Populationen dieser Arten und verglich sie mit der ihrer gesamten Arealgröße. Ich fand negative Auswirkungen von hoher Holzdichte und geringem Blattstickstoffgehalt auf die Arealgröße. Meine Schlussfolgerung war, dass ein konservativer, sparsamer Umgang mit Ressourcen die Arealgröße einschränkt. Die Korrelation ist allerdings nur schwach ausgeprägt, ein konservativer Umgang mit Ressourcen kann daher nur einer von mehreren Faktoren sein, die die Arealgröße dieser Arten beeinflussen.

Innerhalb derselben Gruppe von Baumarten und mit den selben von mir erhobenen Daten untersuchte ich, ob die intraspezifische Varianz derselben funktionellen Eigenschaften die Unterschiede in der Größe ihrer Areale erklären könnten. Ich konnte für keine funktionelle Eigenschaft signifikante Unterschiede bezüglich intraspezifischer Variation zwischen Arten mit kleinen oder großen geographischen Arealen finden. Meine Schlussfolerung war, das die höhere Variabilität, von der bei weit verbreiteten Arten berichtet wurde, aus sukzessive lokalen

Anpassungen während der Arealgeschichte resultiert und daher eher ein Effekt als eine Ursache großer Areale darstellt.

In meiner dritten und letzten Studie benutzte ich Daten zu drei funktionellen Eigenschaften einer größeren Anzahl von neotropischen Baumarten, um den Zusammenhänge von Mittelwerten und Varianzen der Eigenschaften und den Nischenbreiten der Bäume direkt miteinander zu vergleichen. Die Daten für diese Analyse wurden aus verschiedenen Datenbanken kompiliert. Die Ergebnisse zeigen, dass die Mittelwerte funktioneller Eigenschaften die realisierte Nischenbreite neotropischer Bäume beeinflussen können. In Übereinstimmung mit den Ergebnissen der ersten Studie waren Arten mit konservativer Ressourcen-Ökonomie diejeinigen, die eine geringere Nischenbreite aufweisen. Allerdings zeigten diese aus dem gesamten Areal der Arten stammenden Daten auch, dass intraspezifische Variabilität der Eigenschaften anscheinend enger mit der Nischenbreite korreliert ist, als die Eigenschaftsmittelwerte.

Mein Resüme ist, dass Nischenbreite und Arealgröße neotropischer Bäume offensichtlich das Resultat einer komplexen Interaktion von Faktoren sind, in der die funktionellen Eigenschaften der Arten ein gewisse Rolle spielen, aber offensichtlich nicht allein ausschlaggebend sind. Bestimmte Ausprägungen funktioneller Eigenschaften können offensichtlich die Ausweitung der realisierten Nische und damit die Größe von Arealen beeinflussen, vermutlich weil sie höhere Wachstumsraten erlauben und damit auch die Kolonisierung neuer Standorte erleichtern .Die intra-spezifische Variabilität der Eigenschaften einer Art ist mit ihrer Nischenbreite korreliert, allerdings nur wenn diese Variabilität übertr ihr gesamtes Verbreitungsgebiet erhoben wird. Dieses Ergebnis suggeriert, dass eine hohe intra-spezifische Variabilität von funktionellen Eigenschaften eher eine Konsequenz als eine Ursache weiter Verbreitung und breiter ökologischer Nischen ist.

Chapter 1: Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees

Abstract

Biological traits may co-determine differences in geographical range sizes among closely related species. In plants, trait values linked to a conservative resource-use strategy have been hypothesised to be associated with small range sizes. However, the empirical support is mixed and limited to extra-tropical species so far. Here, we analyse the relationship between range size and eight functional traits linked to the plant economics spectrum in congeneric pairs of neotropical tree species of Costa Rica with contrasting range sizes. In the lowland tropical rainforests of southern Costa Rica, we sampled 345 trees from 35 species in 14 genera and measured leaf thickness, leaf dry matter content, specific leaf area, wood specific gravity (WSG), leaf nitrogen (N), leaf phosphorus, leaf potassium and leaf N:P ratio. For each species, we estimated range size as the extent of occurrence using known localities of occurrence. We correlated range sizes with trait data scaled within-genus and with the principal components of the multivariate trait space. WSG was higher and leaf N was lower in species with small range sizes in univariate regression models, although these traits were only weakly related to range size. None of the other six traits was correlated with range size. Results were similar for a model using the principal components of the multivariate trait space, which explained 36% of the variation in species' extent of occurrence. Again, the traits most strongly associated with the selected components were WSG and leaf N. Although high WSG and low leaf N can be interpreted as indicators of conservative resource-use, we could not detect strong relationships between the respective trait syndrome and range size in our sample of species. Traits related to conservative resource use may hence be involved in determining the range size of the species analysed, but other factors are apparently more important.

Keywords: conservative resource-use strategy, Costa Rica, leaf nitrogen content, range size, tropical rainforest, wood specific gravity

1.1 Introduction

“Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?” (Darwin, 1859).

Why some species are rare and have limited distributions while their close relatives are abundant and widespread is a question that has intrigued many naturalists through time (Wallace, 1876; Brown et al., 1996). Indeed, pronounced variation in geographical range sizes among closely related species is a frequent phenomenon (Brown et al., 1996). Evolutionary age (Brown et al., 1996; Grossenbacher et al., 2015), speciation in isolated places like oceanic islands or mountain peaks (Whittaker and Fernández-Palacios, 2007) as well as specialisation to rare habitat types (Morueta-Holme et al., 2013) are factors relevant for explaining these differences. However, relatively few species become widespread at any time over the course of their existence even if no (evident) geographical barriers to their distribution exist (e.g. Witkowski and Lamont, 1997; Walck et al., 2001; Murray and Lepschi, 2004). In addition to evolutionary age and geographical constraints, other factors hence likely affect the range expansion and, eventually, range size, such as maladaptation at the range limits (Gilbert et al., 2017), dispersal limitation (Hargreaves et al., 2014), interspecific competition (Svenning et al., 2014) and the growth rate of the population (Sexton et al., 2009). All these factors are mediated by intrinsic biological traits linked to the dispersal ability (e.g. number and size of propagules), the mating system (e.g. selfers vs. outcrossers, Grossenbacher et al., 2015) or the tradeoffs between resource allocation for fecundity or survivorship, or for growth or survivorship (Sexton et al., 2009; Adler et al., 2014).

Biological traits of plants have been structured along two functional dimensions. The first one of these dimensions is related to a continuum between colonisation and exploitation strategies and associated with traits such as maximum adult height and diaspore size (Diaz et al., 2016). Differences in these traits are highly relevant for range expansion, and thus likely for range size, as they control the spatial redistribution of seeds and hence possible migration speed (e.g. Schurr et al., 2007, Dullinger et al., 2012). However, traits of the dispersal syndrome are often strongly conserved within phylogenies (Jordano, 1995; Lord et al., 1995; see also Supplementary Material, Table A1, Appendix A1 and Fig. A1). While these traits may hence contribute importantly to range size variation across the tree of life, they are less likely candidates for explaining the often vast range size differences among closely related species.

The second dimension is related to a continuum between acquisitive and conservative strategies (Diaz et al., 2016), also known as the plant economics spectrum (Reich 2014). The plant economics spectrum has been shown to be associated with individual growth and carbon assimilation rates (Reich et al., 1998; Chave et al., 2009) and is expressed by traits of leaves

(Wright et al., 2004), roots (Roumet et al., 2016) and wood (Chave et al., 2009). Differences in these traits, several of which are phylogenetically labile (e.g. Kraft & Ackerly, 2010, Siefert et al., 2015), translate into variation in population growth rates and their elasticity to vital rates like individual growth, fecundity and survival. In particular, species 'on the slow side' of the leaf and wood economics spectra also tend to have slow life history traits and slow population growth rates (Adler et al., 2014; Reich, 2014). Population growth rate, in turn, is theoretically correlated to the pace by which species can spread in geographical space (e.g. Hastings et al., 2005). Moreover, 'slow' species are often well adapted to stressful environments but are competitively inferior under more benign conditions and higher resource availability (Grime, 2001). As species have to establish in resident communities during range expansion, traits that increase competitiveness should also increase expansion rates. Indeed, such a link has been repeatedly demonstrated in invasion biology (Hamilton et al., 2005; van Kleunen et al., 2010).

Taken together, there is hence reason to assume that, on average, species with slow life history traits and conservative resource use strategies should have smaller (native) ranges than their 'fast living' counterparts (Morin and Chuine, 2006). Typical features of such conservative strategists are low height, slow growth, high wood density, a high leaf dry matter content and/or long leaf lifespan, and a low resource acquisition capacity as indicated by a low maximum photosynthetic rate which is, in turn, related to low specific leaf area and low leaf nutrient content (Reich et al., 1998; Reich et al., 2003; Chave et al., 2009). Nevertheless, the empirical evidence for a link between these traits and small range sizes is mixed. While some studies could demonstrate the expected correlation (Snyder et al., 1994; Walck et al., 1999; Gorman et al., 2014), others could not (Witkowski and Lamont, 1997; Lavergne et al., 2003; Lavergne et al., 2004). However, comparative studies have so far been limited to certain life forms and biomes, especially to herbs and shrubs of temperate or subtropical regions (Snyder et al., 1994; Walck et al., 1999, 2001; Lavergne et al., 2004). By contrast, we still know little about the potential role of biological traits for limiting the range size of trees in the tropics. This lack of studies is surprising as the tropics harbor many endemic species (Myers, 1988; Stevens, 1989; Morueta-Holme et al., 2013) and knowledge of functional traits of tropical trees has increased in recent years (e.g. Chave et al., 2006; Poorter et al., 2008; Reich, 2014; Díaz et al. 2016, Garnier et al, 2016).

As a contribution to filling this gap, we here present a comparative analysis of functional trait differences between 35 tropical tree species, growing sympatrically in a tropical rainforest region in southern Costa Rica. The species are grouped into 14 genera, with each genus containing at least one species locally endemic (southern Costa Rica and western Panama) and one species with a wider geographic distribution. We measured leaf thickness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), wood specific gravity (WSG), and leaf nitrogen (N),

phosphorus (P) and potassium (K) concentrations, all traits related to the leaf or wood economics spectra (Wright et al., 2005; Chave et al., 2009; Reich, 2014, Díaz et. al., 2016). We hypothesised that trait values associated with faster resource acquisition will be positively correlated to range size and that narrow range species will have trait profiles suggesting a conservative resource-use strategy. With respect to our hypothesis, we hence expected that narrow-range species have higher WSG, LT and LDMC and lower SLA, leaf nutrients (leaf N, P, K) and higher foliar N:P than widespread species.

1.2 Methods

1.2.1 Study site

The study was conducted in the surroundings of four field stations in the Peninsula de Osa and Golfo Dulce area of southern Costa Rica (8°16'-8°55' N, 83° 4'-83°47 W, Fig. 1). The region has an average annual temperature of 27°C in the lowlands (Fig. A2 of Supplementary Material). Annual precipitation sums to between 2800 and 5400 mm (Hijmans et al., 2005). There is rainfall throughout the year, but ~90% falls between April and December. The dry season between January and March is much shorter than the five or six dry months common throughout most of the pacific lowlands of Central America (Fig. A2 of Supplementary Material).

The Pacific slope in the southern part of Costa Rica and western Panama is characterised by high species richness and a relatively high level of endemism (Benavides, 2008, but see discussion in Cornejo et al., 2012). In the region there are more than 2700 vascular plant species (Huber et al., 2008), more than 150 of which are endemic, some of them only known from few sites (Benavides, 2008). With almost 750 species of trees (Quesada et al., 1997) the area is recognised for its high tree diversity in the Americas (Williams et al., 1996).

Floristic affinities are strongest with South American lowland rainforests, especially the north-west of South America (Cornejo et al., 2012). The origin of endemic species has not been studied so far. The region has a long, complex and dynamic history of geological events from the Late Cretaceous until the Pleistocene which makes it difficult to disentangle the causes of speciation and endemism (Bagley and Johnson, 2014). Its result was a patchy landscape with mountains deeply incised by river valleys, hills, terraces, plains and swamps (Malzer and Fiebig, 2008; Scheucher et al., 2008; Bagley and Johnson, 2014). The local climate differs from the surroundings because the Talamanca Cordillera towards the North, with mountains as high as 3820 m, creates a vortex effect that increases precipitation and decreases rainfall seasonality (Coen, 1983). High precipitation and low rainfall seasonality in the region may have attenuated the climatic fluctuations of the Late Pleistocene (Leigh et al., 2014) and thus probably enhanced chances of in-situ survival for species of the regional flora (Morueta-Holme et al., 2013).

Mountains and slopes in the region are dominated by Ultisols formed from marine basalts, highly weathered and poor in phosphorus. Plains and valleys are dominated by Inceptisols formed from alluvial deposits from the Quaternary, the soils being richer in phosphorus than Ultisols (Alvarado and Mata, 2015).

1.2.2 Field work

We selected 35 tree species belonging to 14 genera (Table 1 and Table A1 of Supplementary Material). For each genus, we selected between two and four species. Within each genus, one or two species had a limited distribution, either restricted to the central and southern Pacific slope of Costa Rica, or, in some cases, reaching western Panama or the Caribbean slope in Costa Rica, while one or two species had a wider geographical range (Table 1). The selection of endemic species was limited to tree genera that have sympatric species with different range sizes in the area. For reasons of feasibility, our selection focused on endemic species with known populations in 20 1-ha plots (Wanek et al., unpublished data) (Table 1). Among possible widespread congeners, we selected those that were found growing in the immediate neighbourhood of the selected endemics (see below).

The field work was conducted during the rainy season 2015 (March to October). We tried to collect samples from at least ten individuals per species. Some of the species were too rare, however, to accomplish a full sample (Table 1). Eighty-five individuals were collected at known localities in permanent plots (Wanek et al., unpublished data) and 260 by chance on the way to these plots. For all collected trees, we took geographical coordinates by means of a GPS device (Garmin 60 CSX, mean RSE: 6 m). After having sampled an individual of an endemic species we tried to locate an individual of its widespread congener as close to it as possible (average ± standard deviation of the minimum distance between congeneric tree individuals: 0.35 ± 0.86 km). Within species, vice versa, we tried to collect data from individuals as spatially separate as possible to avoid sampling siblings (average ± standard deviation of the minimum distance between conspecific tree individuals: 1.45 ± 1.34 km). Average minimum distances between conspecific trees did not differ significantly between widespread and endemic species (Table A2 of Supplementary Material).

Our sampling design intended to keep differences in environmental conditions between sites of widespread and endemic species as low as possible. To test whether this ‘standardization’ had been successful, at least with respect to climatic conditions, we extracted data on six bioclimatic variables for each tree’s sampling site from WorldClim (Hijmans *et al.*, 2005): annual mean temperature, mean diurnal range of temperature, isothermality (ratio of day-to-night temperature oscillation to summer-to-winter oscillation), mean annual precipitation, precipitation seasonality and precipitation of warmest quarter. Using a linear mixed-effect model

with genus as random factor, we then compared these climatic descriptors between endemic and widespread species. The results corroborate that climatic conditions did not differ among the sampling sites of endemic and widespread species (see Table A3 in Supplementary Material).

For all collected trees, we measured eight functional traits: leaf thickness, specific leaf area, leaf dry matter content, wood specific gravity, and leaf macronutrient content: leaf nitrogen, phosphorus, and potassium; as well as leaf N:P ratio. LT, SLA, and LDMC were measured on five leaves per individual. Macronutrient contents (leaf N, P, K) were determined from a pooled sample of these five leaves and the leaf N:P ratio calculated from these contents. WSG was measured from a wood core per tree individual. Details on measurement methods are provided in the section: Field methods and trait measurements in the Supplementary Material (Appendix A2 of Supplementary Material).

1.2.3 Geographical range size

We defined a species' geographical range size as the extent of occurrence (EOO) (Gaston and Fuller, 2009). For each species, we collected geographical coordinates of occurrences from different sources through the Global Information Biodiversity Facility (GBIF) (Appendix B), and own field records. We removed the following types of occurrence data: a) uncertain occurrences i.e. those separated widely in space from other occurrence points and with locality descriptions that suggest that species were planted in parks or gardens, b) duplicated occurrences inside of the same 1 x 1 km cell in a raster map and c) occurrences without detailed information about locality. We constructed a polygon based on an α-hull around the localities of occurrences (Burgman and Fox, 2003) using the R package "alphahull" (Pateiro-Lopez and Rodriguez-Casal, 2010). For each species, the α-hull was constructed using 8 as α value, i.e. we aimed to obtain the smallest possible polygon with all internal angles greater than 0 which includes all occurrence points of the respective species. The EOO was then calculated from the intersection of the α-hull and the continental contour map (projected by a Lambert Equal Area Projection).

1.2.4 Statistical analysis

For each individual, we calculated the average of LT, SLA, and LDMC from the five leaves sampled. To correct for phylogenetic relatedness, we scaled the individual tree values of each trait by subtracting the mean of the genus and dividing by the standard deviation of the genus. This removed differences in mean trait values among genera from the data. Put in another way, we standardised for phylogeny to focus on the question whether the extent of range size difference between closely related species is related to how distinct they are in terms of functional traits (and not to phylogenetically determined trait differences among the genera in

the sample). The means of the thus scaled trait values per species were then related (as predictor variables) to the species' extent of occurrence by means of generalised linear models (GLM). Traits that were significant in univariate models were used to construct a multiple regression model to explain EOO.

Because multicollinearity could obscure the effects of variables, we tested if the principal components built from the eight functional traits could explain the EOO. We performed a principal component analysis (PCA) using the trait values scaled within-genus for each individual and extracted the centroid scores for each species. We tested if the species centroid scores in each one of the first five principal components explained EOO using a stepwise regression to select the best model or models according to Akaike's Information Criterion.

We ran GLMs assuming a Gaussian distribution of the response variable (EOO) log-transformed as evaluated by qq-plots of model residuals. Statistical significance of regression terms was assessed by likelihood ratio tests. For the multivariate model, we evaluated the goodness of model fit by calculating an adjusted D^2-value that accounts for the number of degrees of freedom spent for the predictor variables (Guisan and Zimmermann, 2000). All analyses were run in R 3.3.1 (R Development Core Team, 2016).

1.3 Results

We analysed 345 individual trees belonging to 35 species (Table 1). Mean trait values of species ranged from 38.0 to 1645 cm^2 for LA, from 0.16 to 0.61 mm for LT, from 66.4 to 236 $cm^2 \cdot g^{-1}$ for SLA, from 195 to 472 $mg \cdot g^{-1}$ for LDMC, from 0.25 to 0.85 for WSG, from 1.17 to 3.07 % for leaf N, from 0.04 to 0.24 % for leaf P, from 0.26 to 1.70 % for leaf K, and from 10.6 to 33.3 for foliar N:P (Tables A4, A5 of Supplementary Material).

The EOO of our study species varied between $5.37 \cdot 10^1$ to $2.38 \cdot 10^4$ km^2 for the narrow range species within each genus, and from $2.80 \cdot 10^4$ to $1.34 \cdot 10^7$ km^2 for the wide range species within each genus (Table 1). EOO sizes of narrow and wide range species within a genus differed by a minimum of $2.7 \cdot 10^4$ km^2 in the genus *Unonopsis*, while the ratio between the maximum and minimum EOO range was between 15 in the genus *Chrysochlamys* and $2.18 \cdot 10^5$ in the genus *Faramea* (Table 1).

Among the single-trait models, only WSG and leaf N were significantly related to EOO, WSG being negatively related ($p = 0.016$, $r^2 = 0.16$) and leaf N positively related to EOO ($p = 0.029$, $r^2 = 0.13$; Table 2, Fig. 2). Therefore, species with lower WSG and higher leaf N tended to have wider range sizes (Fig. 2). A multivariate model with both traits together explained 17% of the variance in EOO ($D^2 = 0.17$), however only WSG remained as a significant term ($\beta \pm SE = -0.793 \pm 0.413$, $Chi^2 = 15.46$, $p = 0.009$). Leaf N was not significant in the multivariate model (β

± SE = 0.695 ±0.442, Chi ^{2} = 5.62, p = 0.116) and was negatively correlated with WSG (*r* = -0.34. p = 0.04; Fig. A3 of Supplementary Material).

Similar results were obtained when the analysis was done with principal components. Trait values of 345 tree individuals (35 species) after standardizing within genus followed the leaf economics spectrum, with the first principal component being negatively related to LDMC and positively to SLA, leaf N, P and K (Fig A3 and Table A6 of Supplementary Material). The third component of the PCA, which was strongly related to WSG (Table A6 of Supplementary Material), explained 23 % (D ^{2} = 0.23) of the variation in EOO (Table 3). When all the PC-axes were tested in a stepwise model using the AIC, the lowest AIC was obtained in a model including the axes 2, 3 and 5. Altogether, this model explained 36 % of the variation in EOO (D ^{2} = 0.36). However, only PC-axes 3 and 5 had coefficient estimates significantly different from 0 (Table 3, Fig. 3). These two axes were strongly related to WSG and leaf N, respectively (Table A6 of Supplementary Material).

1.4 Discussion

Our results suggest that range size differences between closely related neotropical tree species can partly be explained by differences in traits related to the plant economics spectrum. As expected, narrow range species tended to have higher wood specific gravity and lower leaf N contents than their widespread congeners. However, we did not find any support for our hypotheses in the other six traits studied. Relationships between range size and biological traits related to the plant economics spectrum hence do exist in the sampled set of species but appear rather weak overall.

In our data, the hypothesised relationship is most clearly corroborated by the resource allocation trade-off conceptualised as the wood economics spectrum. Wood specific gravity has been shown to be negatively related to relative growth rate and positively to survival in tropical trees (Poorter et al., 2008; Greenwood et al., 2017). Tropical trees with high WSG hence generally follow a conservative strategy, prefer less competitive and more stressful environments such as dry, shaded or nutrient-poor habitats (Augspurger, 1984; Poorter and Markesteijn, 2008; Heineman et al., 2016) and are, presumably, characterized by slow life cycles and population growth rates (Adler et al., 2014). Moreover, WSG is phylogenetically conserved among tropical tree species (Chave et al., 2006) which makes differences in this trait a particularly sensitive indicator of adaptation to different levels of stress or competition. The fact that WSG significantly differed among endemic and widespread species hence strongly suggests that adaptation to competitive environments is likely fostering range expansion in tropical trees. By contrast, high WSG may have fostered survival in glacial refugia but hampered

subsequent spread afterwards. Indeed, some endemic species in our dataset are likely glacial relicts (Morueta-Holme et al., 2013).

Leaf nitrogen content is related directly to photosynthetic capacity of the leaf (Evans, 1989) and the rate of carbon assimilation (Reich et al., 1998, 2003; Wright et al., 2004). The direct relation with photosynthesis makes leaf N one of the strongest indicators of plant economic strategies. Since endemic and widespread congeners were growing close together, the low leaf N of endemics is likely not due to low soil N availability but rather controlled by some other inherent differences in N demand or allocation. Low leaf N comes with higher LT and LDMC and lower SLA (Fig. A3 of Supplementary Material), pointing to greater investment in structural leaf support, thickening of cell walls, higher lignification and other traits that enhance the durability of tissue, better defend against herbivores and increase the leaf lifespan (Wright et al., 2002). This extra carbon investment dilutes leaf N, causing lower leaf N contents on a mass basis (Reich et al., 1998); and all of these investments are commonly associated with conservative resource use of plants in stressful environments (Grime, 2001). The lower leaf N in our endemic species can hence also be interpreted as an indicator of conservative resource use (Diaz et al., 2016) and is hence in line with our hypothesis.

Phosphorus is considered the most limiting nutrient in the tropical lowlands (Vitousek, 1984) and a strong association between the availability of soil P and the distribution patterns of tropical tree species has already been documented (Condit et al., 2013; Dalling et al., 2016; Zalamea et al., 2016). In particular, species unable to translate high P supply into high growth rates may be disadvantaged by competition under more favourable soil conditions (Zalamea et al., 2016). Such restrictions are typical for conservative resource use strategists (Grime, 2001) and may hence impose constraints on range expansion. Nevertheless, in our data, foliar P was not a predictor of range size. It may, however, be that P was limiting for most species in our sample because of the generally low soil P availability in the tropics (Alvarez-Clare and Mack, 2011) and that leaf P is hence only loosely related to species´ resource use strategies. An unequivocal answer to the question whether narrow range species have lower leaf P will hence have to standardise for P supply in the soil.

Several other functional traits commonly related to a conservative resource-use strategy were also not related to range size in our study. They were, however, correlated with WSG and/or leaf N (e.g. SLA was positively correlated with leaf N, LT negatively with leaf N, and LDMC was positively correlated with WSG, Fig. A3 of Supplementary Material). We hence do not exclude the possibility that these traits are part of a syndrome characterising species with narrow range size. However, the possible relationship of such a conservative resource use

syndrome and range size is apparently not strong enough to be detectable with the given sample of 14 congeneric species pairs.

As a caveat, we emphasize that our sampling strategy involves estimates of mean trait values that are likely more precise for the entire population of the endemic than of the widespread species. Indeed, most of the widespread species occupy a considerable latitudinal gradient with varied climatic and edaphic conditions, and predominant trait values in the study area might hence deviate from trait means across their entire range (Reich et al., 2003). However, we do not see any reason to expect that traits of widespread species in our study area are generally biased towards values indicating either a more or a less conservative resource use strategy as compared to their total-range means. As a corollary, geographical restriction of sampling may have decreased our ability to find generic differences among endemic and widespread species, but it has unlikely biased our results towards either masking or exaggerating existing differences.

1.4.1 Conclusions

Taken together, our results indicate that the functional trade-offs involved in adaptation to stressful and low-resource vs. benign and high-resource environments have contributed to the restricted range size of endemic tree species in tropical wet forests to a certain extent. However, the impact of these adaptations on current range size differences among closely related tree species is weak to moderate, at best, and apparently modified by other factors of comparable or stronger influence. Nevertheless, these moderate correlations have ramifications for conservation biology. Endemic species are of major concern since restricted range size and small populations make species particularly prone to extinction (Harnik et al., 2012). The fact that the endemic tropical tree species studied here are characterized by a trend towards conservative resource use strategies lets these species appear even more vulnerable because the slow growth rates, low fecundity and low colonization abilities associated with such conservative resource use (van Kleunen et al., 2010, Adler et al., 2014; Visser et al., 2016) likely also decrease their ability to cope with changing environmental conditions.

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1.8 Tables

Table 1. The species sampled, the number of individuals sampled per species (N), and its global extent of occurrence. Shades indicate the species with small range sizes within each genus.

Family	Species name	Range size class	N	Extent of Occurrence
Annonaceae	Guatteria amplifolia Triana & Planch.	widespread	10	1.02 • 106
Annonaceae	Guatteria chiriquiensis R. E. Fr.	endemics	9	8.60 • 103
Annonaceae	Guatteria pudica N.Zamora & Maas	endemics	16	6.87 • 102
Annonaceae	Guatteria rostrata Erkens & Maas	widespread	10	6.45 • 104
Annonaceae	Unonopsis osae Maas & Westra	endemics	10	7.54 • 102
Annonaceae	Unonopsis theobromifolia N. Zamora & Poveda	widespread	10	2.81 • 104
Araliaceae	Dendropanax arboreus (L.) Decne. & Planch.	widespread	10	7.69 • 106
Araliaceae	Dendropanax ravenii M. J. Cannon & Cannon	endemics	10	1.96 • 103
Boraginaceae	Cordia cymosa (Donn. Sm.) Standl.	widespread	8	3.66 • 105
Boraginaceae	Cordia liesneri J. S. Mill.	endemics	9	4.07 • 103
Burseraceae	Protium panamense (Rose) I. M. Johnst.	widespread	8	1.98 • 105
Burseraceae	Protium pecuniosum D. C. Daly	endemics	10	1.48 • 103
Clusiaceae	Chrysochlamys glauca (Oerst. ex Planch. & Triana) Hemsl.	widespread	10	3.79 • 105
Clusiaceae	Chrysochlamys skutchii Hammel	endemics	9	2.38 • 104
Clusiaceae	Garcinia aguilari Hammel	endemics	10	9.43 • 101
Clusiaceae	Garcinia magnifolia (Pittier) Hammel	widespread	10	1.64 • 105
Euphorbiaceae	Sapium allenii Huft	endemics	11	8.89 • 102
Euphorbiaceae	Sapium glandulosum (L.) Morong	widespread	10	1.35 • 107
Fabaceae	Inga skutchii Standl.	endemics	10	7.79 • 103
Fabaceae	Inga spectabilis (Vahl) Willd	widespread	9	2.51 • 106
Lauraceae	Ocotea mollifolia Mez & Pittier	widespread	10	1.14 • 105
Lauraceae	Ocotea rivularis Standl. & L. O. Williams	endemics	9	6.68 • 102
Melastomataceae	Miconia dissitinervia Kriebel, Almeda & A. Estrada	endemics	11	3.75 • 103
Melastomataceae	Miconia donaeana Naudin	widespread	10	1.22 • 106
Melastomataceae	Miconia osaensis Aguilar, Kriebel & Almeda	endemics	10	9.61 • 101
Melastomataceae	Miconia trinervia (Sw.) D. Don ex Loudon	widespread	10	5.89 • 106
Primulaceae	Ardisia compressa Kunth	widespread	9	1.44 • 106
Primulaceae	Ardisia dunlapiana P. H. Allen	endemics	10	1.44 • 103
Rubiaceae	Faramea occidentalis (L.) A. Rich.	widespread	11	1.18 • 107
Rubiaceae	Faramea permagnifolia Dwyer ex C. M. Taylor	endemics	12	5.38 • 101
Sapotaceae	Pouteria lecythidicarpa P. E. Sánchez & Poveda	endemics	10	1.33 • 104
Sapotaceae	Pouteria subrotata Cronquist	widespread	8	1.72 • 106
Sapotaceae	Pouteria torta (Mart.) Radlk.	widespread	10	1.08 • 107
Sapotaceae	Pouteria triplarifolia C. K. Allen ex T. D. Pennington	endemics	6	2.41 • 103

Table 2. Coefficients estimated ± 1 standard error (β), and the associated test statistics (Chi2) of the likelihood ratio tests, together with their p-values, for the generalised linear models relating the extent of occurrence to one of the following functional traits in 35 tropical tree species of Costa Rica: wood specific gravity (WSG), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content (LDMC), leaf nitrogen content (N), leaf phosphorus content (P), leaf potassium content (K), and leaf N:P ratio.

Functional Trait	β	Std. Error	Chi2	p (>Chi2)
WSG	-1.013	0.397	15.46	0.011*
SLA	0.635	0.390	6.99	0.10
LT	-0.538	0.376	5.47	0.15
LDMC	0.117	0.428	0.21	0.78
N	0.982	0.433	12.69	0.029*
P	0.378	0.511	1.52	0.46
K	-0.151	0.703	0.13	0.83
N:P	0.276	0.549	0.41	0.61

Table 3. Coefficients estimated ± 1 standard error (β), and the associated test statistics (Chi2) of the likelihood ratio tests, together with their p-values, for generalised linear models relating the principal components calculated from eight functional traits (wood specific gravity, WSG; specific leaf area, SLA; leaf thickness, LT; leaf dry matter content, LDMC; leaf nitrogen content, N; leaf phosphorus content, P; leaf potassium content, K; and leaf N:P ratio, NP) to the extent of occurrence of 35 neotropical tree species of Costa Rica. Models a) Univariate models; b) a multivariate model with relevant axes selected by stepwise regression using the Akaike Information Criterion. For each PC-axis the traits that explain most variation are given in parentheses, with the sign showing the direction of the trait-axis correlation.

Factor	Estimate	Std. Error	Chi2	p (>Chi2)
Univariate models with PCA made with within-genus scaled trait values				
PC 1 (P, -LDMC, N)	0.328	0.252	4.584	0.193
PC 2 (-LT, NP, SLA)	0.370	0.327	3.518	0.257
PC 3 (-WSG)	-1.396	0.415	23.982	0.001**
PC 4 (-K, LDMC, -NP)	0.405	0.583	1.359	0.487
PC 5 (N,-K, LT)	0.758	0.612	4.180	0.215
Multivariate model with PCA made with within-genus scaled trait values				
PC 2 (-LT, NP, SLA)	0.50	0.264	3.456	0.166
PC 3 (-WSG)	-1.62	0.386	25.085	<0.001***
PC 5 (N, -K, LT)	1.246	0.503	10.8	0.019*

1.9 Figures

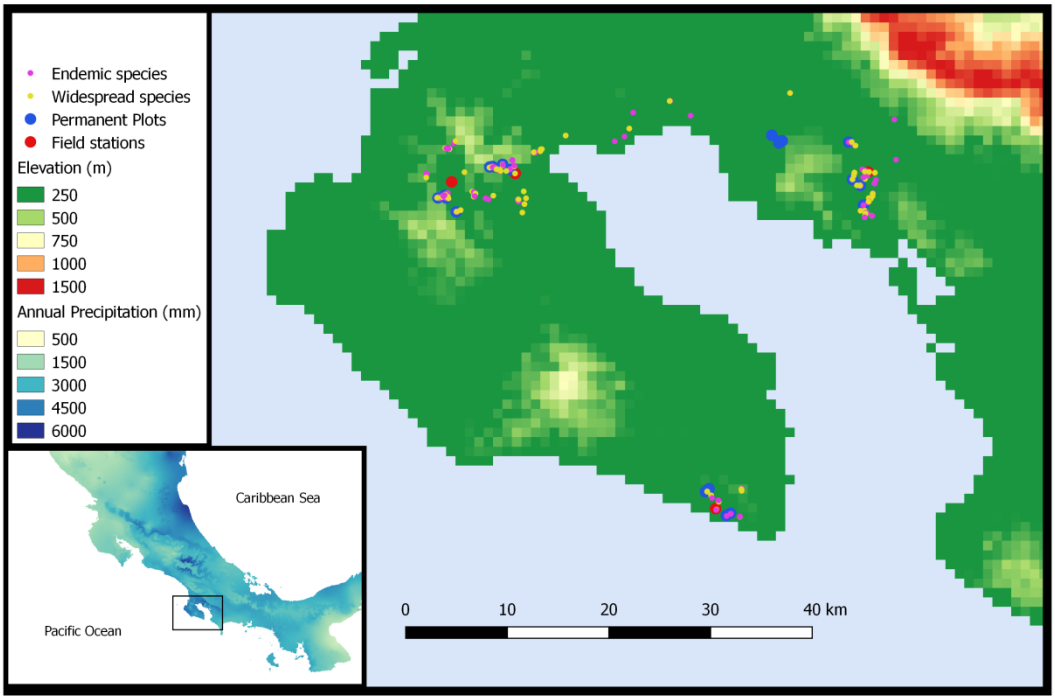

Figure 1. Study area and sites where trees were sampled. The map in the box represents the distribution of mean annual rainfall according to Worldclim (Hijmans et al., 2005).

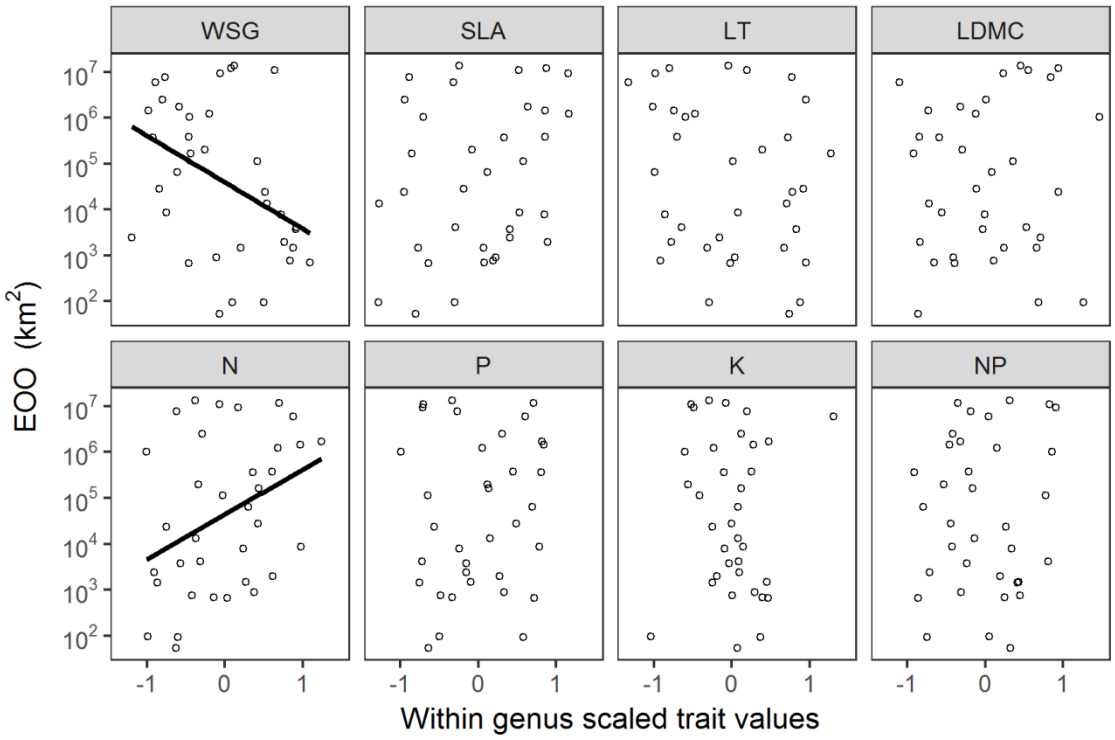

Figure 2. The relationship between the log10-transformed extent of occurrence (EOO) and the following functional traits studied in 35 tropical tree species of Costa Rica: wood specific gravity (WSG), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content (LDMC), leaf nitrogen (N), phosphorus (P), potassium (K), and leaf N:P ratio (NP). The solid line represents the fit of the model when the estimated regression coefficients were statistically different from zero ($p<0.05$). Values on the trait axes are centred to 0 and scaled to unit variance (within each genus), and therefore without units.

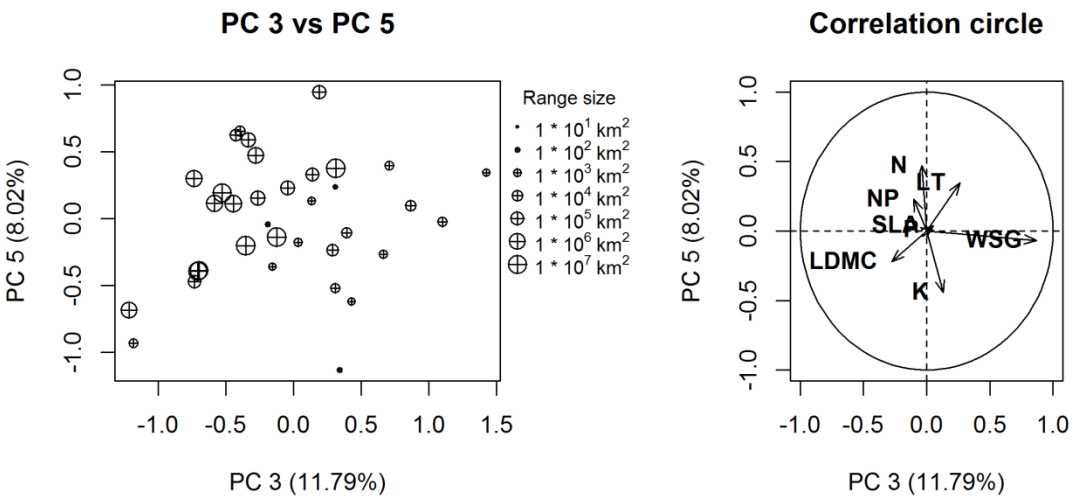

Figure 3. Species scores and correlation plot of the third and fifth component of the principal component (PC) analysis calculated with eight functional traits (wood specific gravity, WSG; specific leaf area, SLA; leaf thickness, LT; leaf dry matter content, LDMC; leaf nitrogen content, N; leaf phosphorus content, P; leaf potassium content, K; and leaf N:P ratio, NP) of 35 tropical tree species of Costa Rica. The two components were significant predictors ($p<0.05$) of the species' range size in a multivariate model.

Chapter 2: Is local trait variation related to total range size of tropical trees?

Abstract

The reasons why the range size of closely related species often varies significantly have intrigued scientists for many years. Among other hypotheses, species with high trait variation were suggested to occupy more diverse environments, have more continuity in their distributions, and consequently have larger range sizes. Here, using 34 tree species of lowlands tropical rainforest in southern Costa Rica, we explored whether inherent trait variability expressed at the local scale in functional traits is related to the species' total geographical range size. We formed 17 congeneric pairs of one narrow endemic and one widespread species, sampled 335 individuals and measured eight functional traits: leaf area, leaf thickness, leaf dry matter content, specific leaf area, leaf nitrogen content, leaf phosphorus content, leaf nitrogen to phosphorus ratio, and wood specific gravity. We tested whether there are significant differences in the locally expressed variation of individual traits or in multidimensional trait variance between the species in congeneric pairs and whether species' range size could hence be predicted from local trait variability. However, we could not find such differences between widely distributed and narrow range species. We discuss the possible reasons for these findings including the fact that higher trait variability of widespread species may result from successive local adaptations during range expansion and may hence often be an effect rather than the cause of larger ranges.

2.1 Introduction

Even closely related species often vary in range size by orders of magnitude (Brown et al., 1996). The reasons of this variation have intrigued scientists for many years (Wallace, 1867; Brown et al., 1996). Nevertheless, why some species are narrowly distributed endemics, while other related species have spread widely is still a puzzling question with probably complex causation (Lavergne et al., 2004; Gaston & Fuller, 2009; Holt, 2009; Slatyer et al., 2013). Species can, for example, occupy a narrow range because they have not had the chance to disperse after a range collapse following e.g. climatic changes (Svenning & Skov, 2004), are evolutionary young (Brown et al., 1996), limited to isolated places like oceanic islands or mountain peaks (Whittaker & Fernández-Palacios, 2007), or adapted to rare habitat types (Morueta-Holme et al., 2013). However, many species are range-restricted even without (evident) geographic barriers limiting their distributions (Witkowski & Lamont, 1997; Walck et al., 2001; Murray & Lepschi, 2004), suggesting that factors other than dispersion are involved in shaping their ranges.

Biological traits determine the ecological niches of species and hence control the composition of ecological communities along environmental gradients (Kraft & Ackerly, 2010; Messier et al., 2010; Meng et al., 2017). Indeed, trait variation across geographical ranges of a species often co-varies with components of the physical environment such as soil and climate, likely reflecting environmental filtering of particular trait values (Lasky et al., 2013; McKown et al., 2014). As a corollary, high intra-specific variation in relevant functional traits, whether due to genetic diversity or phenotypic plasticity, should be associated with broad environmental tolerance and / or the ability to exploit a greater variety of resources. These attributes should, in turn, allow species to occupy more diverse environments and thus, eventually, larger ranges (Bradshaw, 1965; Gaston & Fuller, 2009; Boulangeat et al., 2012; Slatyer et al., 2013). However, intra-specific trait variation is often geographically structured (Leimu & Fischer, 2008; Albert et al., 2011; Read et al., 2014), among other things as a result of the adaptation of individual populations to the new environments they face with range expansion (Reich et al., 1996; Siefert et al., 2015; Turcotte & Levine, 2016). It is thus unclear whether trait variability is actually a determinant or merely a consequence of range size (Slatyer et al., 2013). In other words, endemic species may be endemic because they have lower trait variability than their widespread relatives, or they may have lower trait variability because they are endemic. This question cannot be resolved by comparing trait variation of narrow and wide range species across their entire respective ranges. However, if geographical area is fixed, the range of environmental variation is similar between the species to be compared. In addition, if we focus

on regional population only in such a comparison, continued gene flow is more likely to restrict the effects of local adaptation on intra-specific trait variability for the species to be compared (Sexton & Dickman, 2016). In such a case, higher trait variability in widespread species would hence actually indicate that this variability is a driver rather than a consequence of range size differences.

Here, we compare intra-population variability in functional traits among congeneric pairs of endemic and widespread tree species that co-occur in a restricted region of southern Costa Rica. Tropical tree species offer an appropriate system for studying these questions because they show significant variation in range sizes (Feeley & Silman, 2009) as well as pronounced inter- and intraspecific variation in functional traits (Messier et al., 2010). Nevertheless, the relationship between range size and trait variation has rarely been considered in this group of species (Mitchell et al., 2017a). We explore the variability in leaf area, leaf thickness, leaf dry matter content, specific leaf area, leaf nitrogen content, leaf phosphorus content, leaf nitrogen-to-phosphorus ratio and wood specific gravity. These traits have been shown to be strongly related to the economic spectrum of plants (Wright et al., 2004; Chave et al., 2009), some of them have also been used as predictors of tolerance to abiotic and biotic stressors such as drought, nutrient-poor soils, shade, fire and competition, and vary across environmental gradients (Koerselman & Meuleman, 1996; Güsewell, 2004; Preston et al., 2006; Markesteijn et al., 2011; Peppe et al., 2011; Kunstler et al., 2015; Uriarte et al., 2016; O'Brien et al., 2017). Following the rationale outlined above, we expect that widespread species will be more variable in individual functional traits and in multivariable trait space than narrow range species. We use congeneric pairs of wide- and narrow-range species in our comparison to exclude confounding phylogenetic constraints on functional trait variability (Coelho de Souza et al., 2016).

2.2 Materials and Methods

2.2.1 Study site

We worked on the Peninsula de Osa and Golfo Dulce area of southern Costa Rica, in the surroundings of four field stations (8°16'-8°55' N, 83° 4'-83°47 W, Fig 1). Rainfall in the region is between 2800 and 5400 mm/year (Hijmans et al., 2005) and mean annual temperature is c. 27°C in the lowlands. There is a short dry season between January and March with occasional rains. On average, 90 % of the rain falls between April and December (Fig 1).

High diversity and high levels of endemism characterise the region where more than 2700 vascular plant species have been recorded (Huber et al., 2008) of which approx. 150 are endemics (Benavides, 2008). The area is particularly recognised for its high richness of trees and palms, with ca. 750 species of trees and 47 species of palms (Quesada et al., 1997).

Floristic affinities are strongest with South American lowland rainforests, especially the northwest of South America (Cornejo et al., 2012).

A complex geological history has formed the region since the Late Cretaceous resulting in a landscape with mountains deeply incised by river valleys, hills, terraces, plains and swamps (Bagley & Johnson, 2014). The causes of speciation and endemism in the region are difficult to disentangle (Bagley & Johnson, 2014). Compared with the surroundings, the region has a distinct climate because the Talamanca Cordillera towards the North, with mountains as high as 3820 m, creates a vortex effect that increases precipitation and decreases rainfall seasonality (Coen, 1983). The wetter conditions may have attenuated the climatic fluctuations of the Late Pleistocene (Leigh et al., 2014) and thus probably enhanced chances of in-situ survival for species of the regional flora (Morueta-Holme et al., 2013). Among soils, Ultisols highly weathered and poor in phosphorus are predominant. Alluvial deposits from the Quaternary created the plains and valleys which are dominated by Inceptisols richer in phosphorus (Alvarado & Mata, 2015).

2.2.2 Species studied

We selected 34 tree species from 14 genera (three genera with each two endemics and two widespread species, and 11 genera with each one endemic and one widespread species) and grouped them into 17 pairs of congeneric species, randomly selecting the pairs in the three genera with four species (Table 1). We note, however, that all analyses were repeated using all possible pairs in the three genera with four species. Results were qualitatively identical. Each congeneric pair comprises one narrowly endemic species either restricted to the central and southern Pacific slope of Costa Rica, or, in some cases, reaching western Panama or the Caribbean slope in Costa Rica, and one species distributed more widely. The selection of endemic species was limited to tree genera that include regionally sympatric species with larger range sizes. For reasons of feasibility, our selection focused on species documented from known localities (Wanek *et al.*, unpublished), in particular in case of the rarer endemic species (Table 1). Among possible widespread congeners, we selected those found growing in the neighbourhood of our sample of endemics (see below).

2.2.3 Field work

We collected samples during the rainy season 2015 (March to October). Sample collection was allowed under INV-ACOSA-018-14 permission granted by SINAC (Sistema Nacional de Áreas de Conservación, Costa Rica). We tried to sample at least ten individuals per species. Some of the species were too rare, however, to accomplish a full sample (Table 1). We collected 82 individuals previously located in permanent plots (Wanek *et al.*, unpublished data) and 253 trees outside of these plots. After sampling a tree of an endemic species, we tried to

locate an individual of its widespread congener as close to it as possible, usually within a radius of 1000 m. We tried to avoid ontogenetic effects on trait variation by selecting only mature individuals (classified as such based on their diameter at breast height). A subsequent test confirmed that this sampling strategy had largely removed effects of tree size on trait values (S1 Fig). For each species, we sought individuals as spatially separated as possible to avoid sampling siblings. All sampled trees were growing within a 35 km radius.

We collected five fully expanded, mature leaves with no signs of damage and one wood core from each tree (S2 File). For each leaf of each tree, we measured or calculated four functional traits: leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), and specific leaf area (SLA) according to standard protocols (Pérez-Harguindeguy et al., 2013). For each tree, we additionally measured wood specific gravity (WSG) on a collected wood core. Details on measurement methods are provided in the supplementary material (S2 File). On a pooled leaf sample per individual, we further measured leaf nitrogen content (N) and leaf phosphorus content (P) and calculated the leaf N:P ratios. Leaf N was measured by dry combustion using an autoanalyzer Rapid Exceed (Elementar, Langenselbold, Germany), and leaf P by acid digestion and inductively coupled plasma-optical emission spectroscopy (ICP-OES) using a spectrometer Optima 8300 (Perkin Elmer, Waltham, US) at the laboratory of the Agronomic Research Center (Centro de Investigaciones Agronómicas) of the University of Costa Rica.

2.2.4 Environmental variation

To ease interpretation of possible differences in trait variation among congeneric species we also sampled a number of environmental covariates. For each tree, we measured the slope of the growing site (using a clinometer) and estimated crown exposure to light using an index from 0 to 5 (Bechtold, 2003). Moreover, we took geographical coordinates using a GPS device (Garmin 60 CSX, mean RSE: 6 m). Based on these coordinates, we extracted the values from six not too closely correlated (Spearman's correlation coefficient < 0.7) bioclimatic variables from Worldclim (resolution ~1 km) (S3 Table) (Hijmans et al., 2005). These variables were: annual mean temperature, mean diurnal temperature range, isothermality, (ratio of day-to-night temperature oscillation to summer-to-winter oscillation), annual precipitation, precipitation seasonality and precipitation of warmest quarter. We performed a PCA with those bioclimatic variables after normalization by means of z-scores. The scores of the first ordination axis, which explained the 86 % of the variation was then used to characterize the mesoclimatic environment of each sampled tree individual. To obtain positive values for all trees, we added the absolute of the overall minimum value to all the PCA scores. From these values, we calculated the coefficient of variation of the climatic environment for each species. We also calculated the coefficient of variation for the slope of growing sites and the crown exposure to light.

2.2.5 Functional variation and dispersion

Similar to the sampled environmental variables, we calculated the coefficient of variation (CV) for each trait, separately for each species. Because the species differed in sample size, we corrected the CV for unequal sample size assuming a normal distribution for each trait within the species (Sokal & Rohlf, 1995). A subsequent test confirmed that this correction had successfully removed possible bias from uneven sample sizes (S4 Table). To account for the variability of species in multidimensional trait space, we computed the functional dispersion of each species using the index proposed by Laliberté & Legendre (Laliberté & Legendre, 2010). This index is the average of the Euclidean distance between each individual and the centroid of all individuals per species in an ordination space. To calculate the index, first, the traits were scaled using standard scores and then subject to a principal component analysis to guarantee orthogonality. For the principal component analysis, we removed the LDMC and leaf N:P because these variables were calculated from other variables included in the PCA. We chose the first five principal components, which accounted for the 93% of the variance (S5 Table). We selected five components because this was the maximum the algorithm could use without a reduction of dimensionality (Laliberté et al., 2014). Finally, we calculated the functional dispersion index using the package "FD" in R (Laliberté et al., 2014).

2.2.6 Geographical range size

We defined a species' geographical range size as the extent of occurrence (EOO) *sensu* Gaston & Fuller (Gaston & Fuller, 2009). For each species, we collected geographic coordinates of occurrences from different sources through the Global Biodiversity Information Facility (GBIF) (S6 File) and own field records during the collection of samples. We removed or checked the following kind of occurrences: a) uncertain occurrences, i.e. those separated from the nearest other record at least twice the mean distance between all records and with locality descriptions that suggest that species were planted in parks or gardens, b) duplicated occurrences inside of the same 1x1 km cell in a raster map, and c) occurrences without detailed information about locality. We constructed a polygon based on an α-hull around the occurrence localities (Burgman & Fox, 2003) using the R package "alphahull" (Pateiro-López & Rodríguez-Casal, 2010). For each species, we constructed the α-hull using 8 as α value because it was the smallest value to obtain polygons with all internal angles greater than 0 that included all the occurrence points of the respective species. The EOO was then calculated from the intersection of the α-hull and the continental contour map (projected by a Lambert Equal Area Projection).

2.2.7 Statistical analysis

For a more detailed description of trait variability, we decomposed the variance of each functional trait across three scales: genera, species, trees. We used the method described by

Messier et al. (Messier et al., 2010) which fits a generalised linear model to the hierarchically nested variances (across scales). The trait values were normalized using log transformations. For the model and variance decomposition, we used the R-packages "nlme" (Pinheiro et al., 2016) and "ape" (Paradis et al., 2004).

We used two alternative analytical approaches to compare the intraspecific variation of traits between endemic and widespread species. First, the CV of each trait was compared between widespread and endemic species by testing whether the differences among congeneric species pairs significantly differ from zero, on average. We, therefore, used a linear mixed effects model with this difference as response and the intercept as the only term on the right-hand side of the model equation. To account for the phylogenetic structure in the data, we additionally estimated a random intercept for each genus in the mixed model. We used the same model structure to compare the CV of the environmental variables (crown exposure to light, slope of the growing sites and climate) between congeneric species with contrasting range size to consider that effect in the interpretation of the results. Moreover, we tested the correlation between the magnitude of trait values and environmental variables by means of linear mixed effects models with a random effect for species identity. Finally, we also tested whether similarity of trait values among individuals depends on geographical distances between them using Mantel tests, separately for each trait and species.

In a second analysis, we tested whether the CV of individual traits could successfully predict the species' range size. We, therefore, used a linear mixed effects model with the log-transformed extent of occurrence as the response, the CV as the predictor and the genus as a random factor. Finally, we applied both approaches to the multivariate trait space, i.e. we (1) compared functional dispersion indices between the 17 pairs of endemic and widespread species and tested whether the average difference among congeneric species pairs significantly differed from zero; and (2), we tested whether the functional dispersion could predict the log-transformed range size. We used likelihood ratio tests to assess the statistical significance of regressions terms.

To back-up our results, we additionally ran an analysis that included variation of environmental variables at the tree level directly. We, therefore, first, regressed trait values of individual trees against each environmental variable (climate, crown light exposure, slope inclination), separately for each trait, species and environmental variable. Environmental variables predicting trait values in these uni-variable regression models (p-value < 0.1) were combined in one linear model per species and trait (S7 Fig). We then retained those environmental variables with a p-value < 0.05 in these (potential) multiple regression models. From these final models, we extracted the residuals and added the original trait mean to each

residual to preserve the original measurement scale. The resulting values were used in subsequent analyses. They represent the individuals' variability in the respective trait that could not be explained by the measured dimensions of the physical environment, and in cases where species traits were uncorrelated to any environmental variable, the original trait values were retained. With these new values, we estimated, again, the CV for each trait and the functional dispersion index across all the traits and compared these metrics between widespread and endemic species using the same procedures as described above.We ran all analyses in R 3.3.1 (R Development Core Team, 2016).

2.3 Results

The range size of our study species ranged from $5.37 \cdot 10^1$ to $2.38 \cdot 10^4$ km^2 for endemic species and from $2.80 \cdot 10^4$ to $1.34 \cdot 10^7$ km^2 for widespread species (Table 1, S8 File). The smallest difference between species in a congeneric pair (endemic-widespread) was $2.7 \cdot 10^4$ km^2 between the two species in the genus *Unonopsis* (Table 1), while the ratio between the maximum and minimum range size was between 7.5, in one of the pairs in the genus *Guatteria,* and $2.18 \cdot 10^5$ in the genus *Faramea* (Table 1, S8 File).

We sampled 335 individual trees of the selected 34 species (Table 1). Among the species analysed, functional traits varied with respect to the magnitude of CV and in how the variance was partitioned among levels of biological organization (Fig 2, S9 Table). For traits such as WSG and LDMC, CVs were low (averages ± 1 standard deviation (SD): 0.09 ± 0.05 and 0.09 ± 0.04, respectively (S10 Fig) and most variance was explained by differences between genera (61.8 % and 57.1 % respectively, Fig 2). For other traits like LA and SLA, CVs were much higher (averages ± 1 SD: 0.28 ± 0.11 and 0.16 ± 0.07 respectively, S10 Fig) and most of the variance was explained by differences between species (49.4 % and 64.4 %, respectively, Fig 2). The part of total trait variance explained by variation within trees ranged from c. 9.31 % for LA to about 45% in NP (Fig 2).

The CVs of the three environmental variables did not differ between congeneric species with contrasting range size (S11 Fig). Concerning the magnitude of trait values, the climatic environment had an effect on LT and WSG. LDMC and LT increased, and SLA decreased with crown light exposure. Slope inclination was not related to the value of any trait (S12 Table). Mantel tests demonstrate that there is limited correlation between similarity of trait values and geographical distance among species (32 significant correlations out of 272, S13 Fig). Local (genetic) adaptation of trait values hence seems to play a relatively minor role within the regional populations of both widespread and endemic species.

The CV of none of the traits could significantly explain species' range sizes (Fig 3). Similarly, endemic and widespread congeners did hardly differ in trait CVs, even if variation in WSG was marginally significantly higher, and variation in leaf N marginally significantly lower in widespread species (Fig 4, S14 Fig). The functional dispersion index, as a multivariate metric, could neither explain species' range sizes (Fig 5) nor was it different between endemic and widespread species (Fig 5, S15 Fig).

The alternative analysis using environmental variables as covariates provided qualitatively identical results. The CV of the functional traits was not different between endemic and widespread species (S16 Fig). Overall, there was no single trait for which trait variability was significantly larger in the widespread species. The functional dispersion neither explained the EOO (S17 Fig) nor did it differ between the two groups (S17 Fig).

2.4 Discussion

Trait variability among individuals of the same species makes an important contribution to community-level trait variation in general (Siefert et al., 2015). Although our results demonstrate that for the traits considered interspecific and intergeneric trait differences predominate, the scale of intra-specific variability (10 – 45%) is similar to the global average of 25% found in the recent meta-analysis (Siefert et al., 2015). For tree species in the tropical forest of Panama, near to our own study area, this intra-specific trait variation has been demonstrated to compensate for species turnover among local plots of similar environments reducing trait differences among these plots to a low level (Messier et al., 2010). Taken together, these results indicate that the local environment exerts a filter on the traits of individuals, at least in neotropical forests of Central America. As a corollary, species with larger intra-specific trait variability should indeed be able to occur at more diverse environments and thus, eventually, occupy larger ranges across the neotropical forest biome as environmental variation tends to increase with spatial scale (Sexton & Dickman, 2016). Nevertheless, our results did not provide support for a relationship between the local intra-specific trait variation and range size in the sampled tree genera. Trait variability, measured separately for individual traits or as a combined metric across several traits, does not predict range sizes of the 34 tree species considered nor does it differ substantially among the 17 pairs of widespread and endemic congeners. Several reasons may be responsible for these findings.

First, species may differ in how an individual trait responds to the same ecological gradient. If trait-environment relationships vary among species, e.g. if the same difference in wood specific gravity results in a different decrease of drought-induced mortality (O'Brien et al., 2017), different levels of trait variation are necessary for the two species to cope with the same variation in environmental conditions. Vice versa, the same level of trait variability allows for

coping with different levels of environmental heterogeneity, i.e. it results in distinct niche breadth and hence, potentially, also range size. Indeed, differences in the slope of trait-environment correlations among species have repeatedly been reported (Sides et al., 2014) and may result from processes of general phenotype integration (Pigliucci, 2003). Moreover, the effect of trait variability on niche breadth may not be independent of the trait mean, i.e. the same amount of variability may convey higher environmental tolerance under lower or higher average trait values. For instance, species with high xylem hydraulic vulnerability are found in high and low rainfall regions, but species with low vulnerability are rare in regions with high rainfall (Choat et al., 2012); similar patterns can be described with leaf size, with small leaves found in high and low rainfall regions, but species with large leaves being rare in regions with low rainfall (Wright et al., 2017). Finally, several environmental variables often simultaneously affect many, partly interdependent traits (Sides et al., 2014; Wright et al., 2017). These interactions may result in compensation effects, with species maintaining high fitness levels along an environmental gradient despite little variation in a particular trait but variation in other traits (Valladares et al., 2007).

Second, maximum or average trait values of species may be more important for geographical success than trait variability, as has been shown for some groups of trees with respect to e.g. maximum height, WSG and N (Morin & Lechowicz, 2011; Gorman et al., 2014). The importance of absolute trait values may result, for example, from the competitive superiority they provide (Kunstler et al., 2015). From the traits analyzed here, leaf nitrogen content is, for example, linked directly to photosynthetic rate (Evans, 1989), which in turn is related to growth and demographic processes of survival and recruitment (Werf et al., 1993), and hence also to competitive ability (Grime, 2001; Kunstler et al., 2015). If the competitive ability is more important in determining species' rate of geographical expansion and eventual range size (Wisz et al., 2013; Svenning et al., 2014) than environmental tolerance, then absolute values of these traits may be more closely linked to range sizes than trait variation, and selection may generally disfavour variability of these traits in successful species. More generally, the idea of a causal link between biogeographical success and intra-specific trait variation may overlook the possible negative effects of inherently high trait variability (Valladares et al., 2007; Sexton et al., 2014). Indeed, too large variation can be maladaptive, especially on a local scale where correlated environmental conditions exert selective pressures on populations towards phenotypic stability (Valladares et al., 2007). The balance between negative and positive effects of trait variability may depend on the harshness of environmental conditions, i.e. the strength of environmental filtering in a species preferred habitat (Cadotte et al., 2013; Mitchell et al., 2017b). In line with this idea, our data actually indicate that species with higher WSG, i.e. those likely adapted to drought (O'Brien et al., 2017), had proportionally lower variation in this trait than species with

low WSG (S18 Fig). We moreover emphasize that further evaluations of the correlation between trait variability and range size should include aspects of evolutionary history and clade age (Grossenbacher et al., 2015), and account for differential evolutionary constraints on the variability of individual traits. Here, we tried to minimize confounding effects of evolutionary history by focusing on congeneric species pairs. However, even the individual species in these pairs may substantially differ in evolutionary age and these differences may have had an important impact on current range sizes. Unfortunately, detailed phylogenies are currently available for only three of the studied genera (*Dendropanax*, *Guatteria* and *Protium*) (Erkens et al., 2007; Li & Wen, 2013; Fine et al., 2014). From the coarse information deducible from these phylogenies, effects of evolutionary age on range size differences are not apparent (S19 Table), but additional data for other genera, and with a higher temporal resolution, may change these conclusions.

Third, documented intra-specific trait variation across the entire geographical distribution of a species, including that of traits analyzed here (Reich et al., 1996; Soolanayakanahally et al., 2015; Zadworny et al., 2016) may actually be a result of range expansion rather than a prerequisite. Indeed, our data do not provide any support for the idea that inherent trait variability begets large range sizes (Slatyer et al., 2013). However, they do not, exclude that large range sizes beget high trait variability at the whole-range scale.

Fourth, range size is of course not exclusively controlled by the traits studied here. For example, traits related to the reproduction, dispersal and migration of species, such as preferred dispersal vector, seed size, or mating system, are likely important for range expansion (Guo et al., 2000; Lester et al., 2007; Grossenbacher et al., 2015). The information available for the species studied here is not sufficient for a quantitative analysis of these effects. However, the available literature data do not suggest that seed traits or predominant dispersers differ saliently between congeneric widespread and endemic species pairs, nor did we find any evidence for their impact on range sizes in our data (S20 Table). In fact, within-genus variation is often low for these two traits (Jordano, 1995; Lord et al., 1995). As a corollary, while these traits certainly affect biogeography (Guo et al., 2000; Lester et al., 2007), they are unlikely to have a major effect on range differences among closely related species

Finally, we emphasize that our results do not strictly falsify intra-specific variability as a driver of range size (Sexton et al., 2017). In particular, our regional-scale

study may not have captured the full extent of inherent heritable trait variability, particularly in widespread species. However, as the sampling sites did vary in environmental conditions at least to a certain extent, our data suggest that the observed level of environmental variation did not trigger the display of larger trait variability in species with larger ranges. This finding suggests that these species are not per se more flexible when confronted with varying environments.

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2.7 Figures

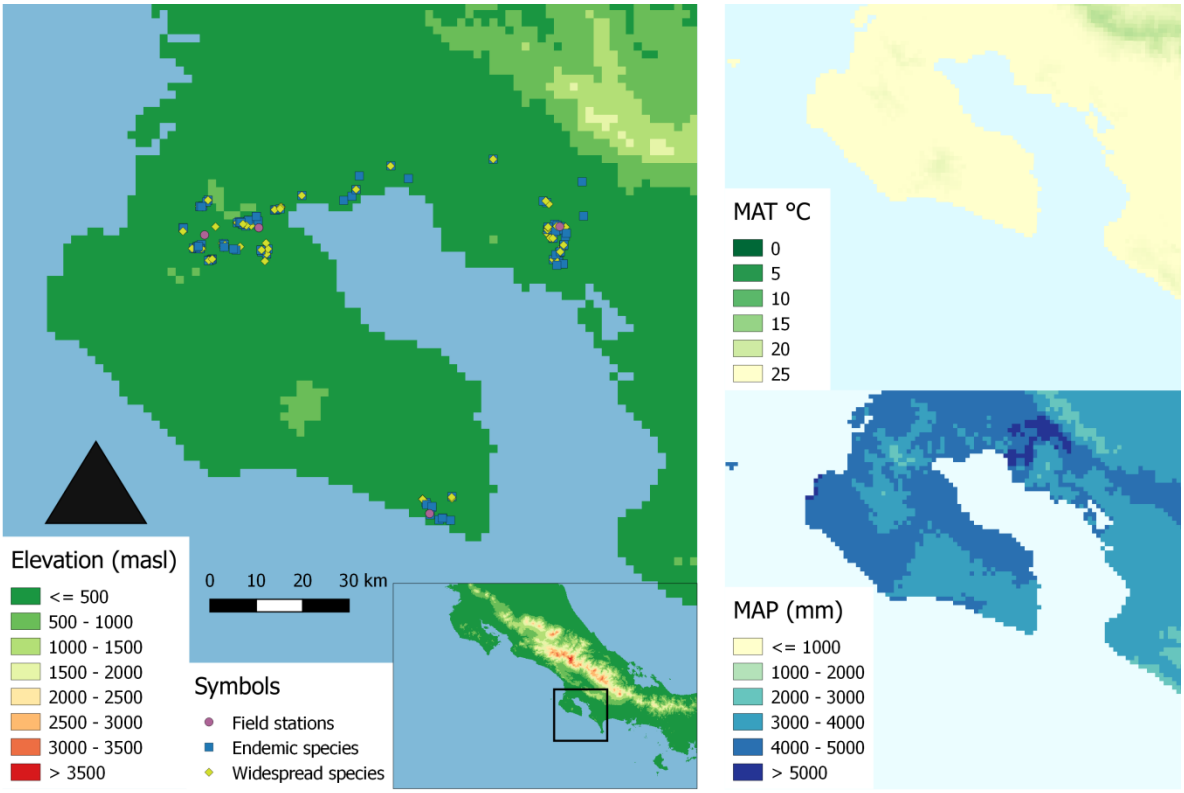


Fig 1. Study area and sampling sites of endemic and widespread species in southeastern Costa Rica (Peninsula de Osa and Golfo Dulce). MAT: mean annual temperature, MAP: annual precipitation sum, both according to Hijmans et al. (2005) (Hijmans et al., 2005).

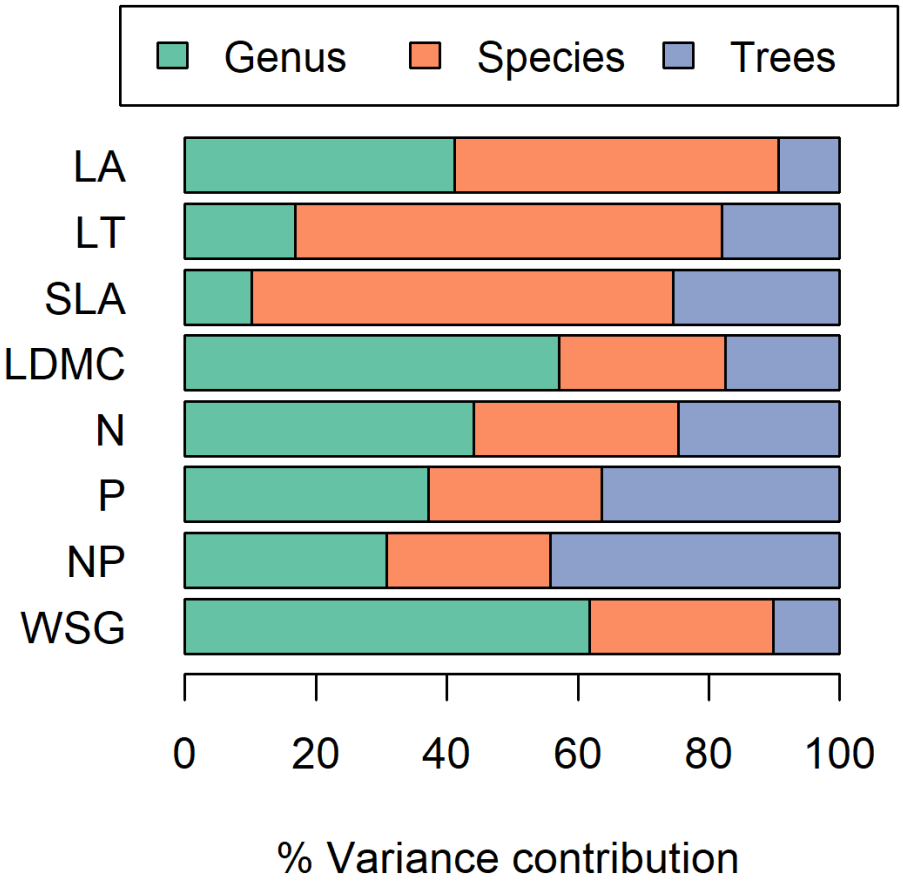


Fig 2. Partitioning of the nested variance in eight functional traits measured in 34 tropical tree species. Leaf area (LA), leaf thickness (LT), specific leaf area (SLA) and leaf dry matter content (LDMC), wood specific gravity (WSG), leaf nitrogen content (N) and leaf phosphorus content (P), and N:P ratio (NP).

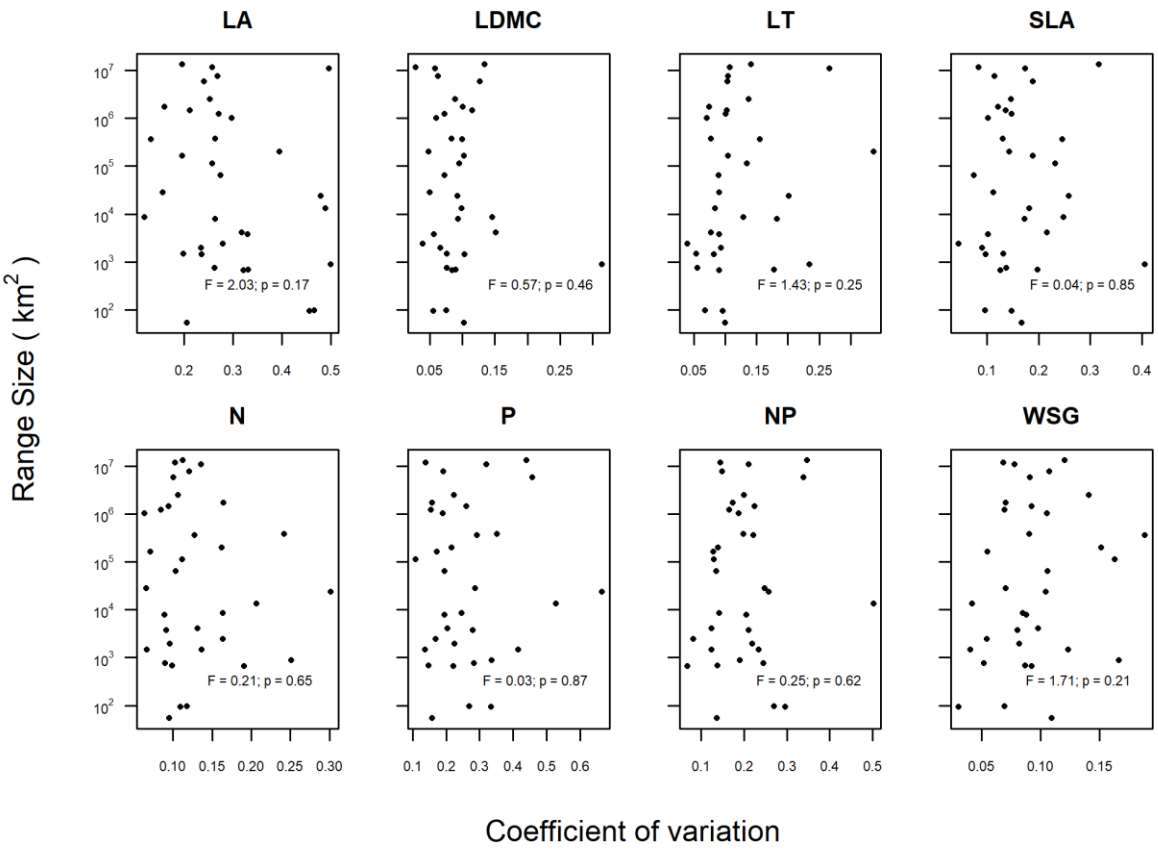


Fig 3. Coefficients of variation (CV) in eight functional traits printed against range size of 34 tropical tree species. Functional traits: leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N), leaf phosphorus content (P), N:P ratio (NP) and wood specific gravity (WSG). The test represents the F-value and the correspondent p-value of a generalised linear mixed effects model testing the dependence of range size on CV and using genus as a random factor. All F-tests used 1 and 19 numerator and denominator degrees of freedom, respectively.

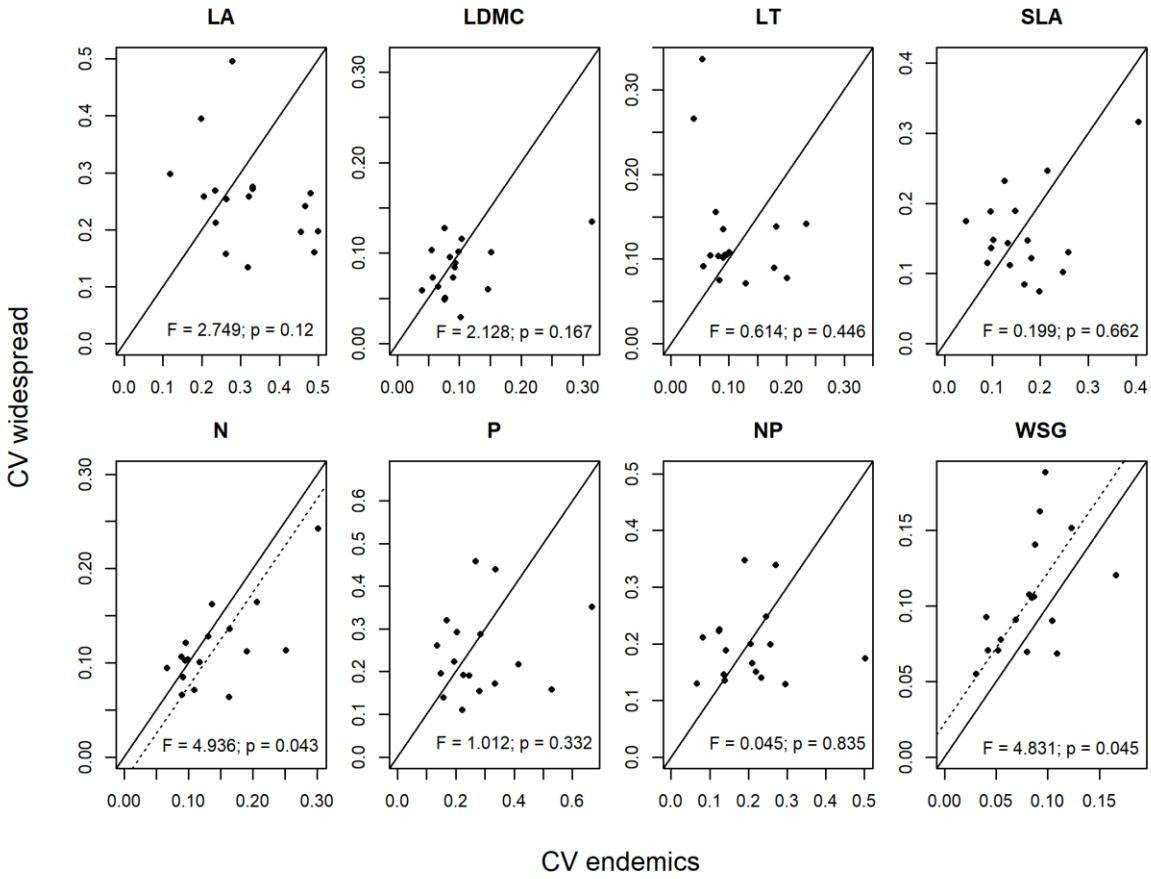
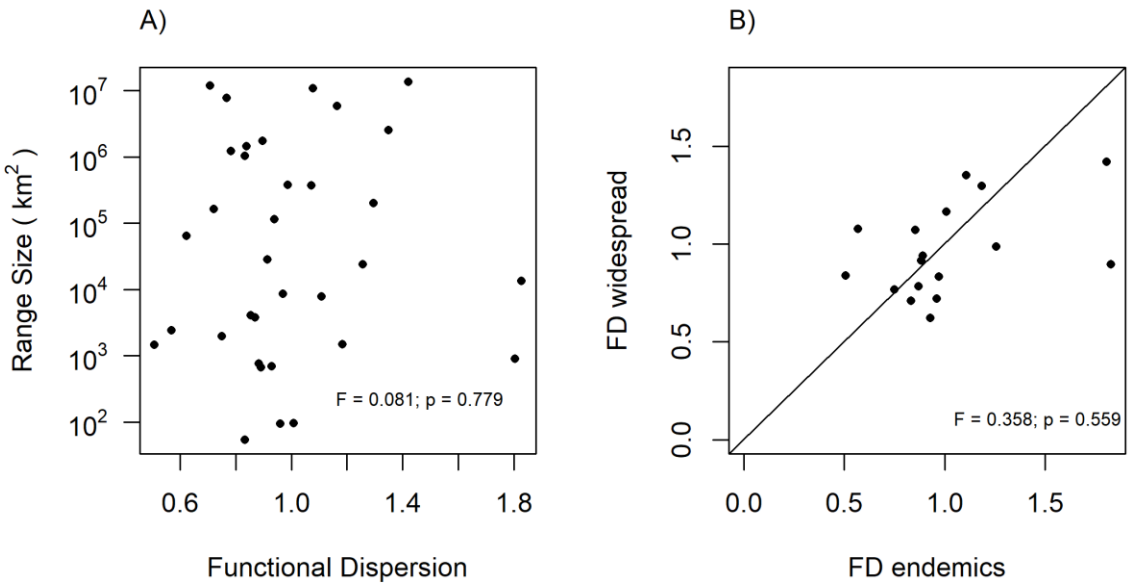


Fig 4. Coefficients of variation (CV) in eight functional traits of 17 congeneric pairs of endemic neotropical tree species and their widespread congeners. Functional traits: leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N),leaf phosphorus content (P), N:P ratio (NP), and wood specific gravity (WSG). Each point represents one pair (endemic, widespread). The continuous diagonal represents the null model, i.e. positioning of points along the line indicates equal trait variability of both species in a pair. Points above the line represent pairs with CV higher in widespread species, and points below the line pairs with CV higher in endemic species. The dotted diagonal represents the mean difference between pairs in case this difference was statistically significant.


A)
Range Size (km^2)
10^7
10^6
10^5
10^4
10^3
10^2
F = 0.081; p = 0.779
0.6
1.0
1.4
1.8
Functional Dispersion
B)
FD widespread
0.0
0.5
1.0
1.5
F = 0.358; p = 0.559
0.0
0.5
1.0
1.5
FD endemics

2.8 Tables

Table 1. The species used in the analysis, their classification as either widespread or endemic, their extent of occurrence (in km²) and the number of individuals sampled (N).

Family	Species name	Range size class	N	Extent of Occurrence
Annonaceae	*Guatteria amplifolia* Triana & Planch.	widespread	10	$1.02 \cdot 10^6$
Annonaceae	*Guatteria chiriquiensis* R. E. Fr.	endemics	9	$8.60 \cdot 10^3$
Annonaceae	*Guatteria pudica* N.Zamora & Maas	endemics	16	$6.87 \cdot 10^2$
Annonaceae	*Guatteria rostrata* Erkens & Maas	widespread	10	$6.45 \cdot 10^4$
Annonaceae	*Unonopsis osae* Maas & Westra	endemics	10	$7.54 \cdot 10^2$
Annonaceae	*Unonopsis theobromifolia* N. Zamora & Poveda	widespread	10	$2.81 \cdot 10^4$
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	widespread	10	$7.69 \cdot 10^6$
Araliaceae	*Dendropanax ravenii* M. J. Cannon & Cannon	endemics	10	$1.96 \cdot 10^3$
Boraginaceae	*Cordia cymosa* (Donn. Sm.) Standl.	widespread	8	$3.66 \cdot 10^5$
Boraginaceae	*Cordia liesneri* J. S. Mill.	endemics	9	$4.07 \cdot 10^3$
Burseraceae	*Protium panamense* (Rose) I. M. Johnst.	widespread	8	$1.98 \cdot 10^5$
Burseraceae	*Protium pecuniosum* D. C. Daly	endemics	10	$1.48 \cdot 10^3$
Clusiaceae	*Chrysochlamys glauca* (Oerst. ex Planch. & Triana) Hemsl.	widespread	10	$3.79 \cdot 10^5$
Clusiaceae	*Chrysochlamys skutchii* Hammel	endemics	9	$2.38 \cdot 10^4$
Clusiaceae	*Garcinia aguilari* Hammel	endemics	10	$9.43 \cdot 10^1$
Clusiaceae	*Garcinia magnifolia* (Pittier) Hammel	widespread	10	$1.64 \cdot 10^5$
Euphorbiaceae	*Sapium allenii* Huft	endemics	11	$8.89 \cdot 10^2$
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	widespread	10	$1.35 \cdot 10^7$
Fabaceae	*Inga skutchii* Standl.	endemics	10	$7.79 \cdot 10^3$
Fabaceae	*Inga spectabilis* (Vahl) Willd	widespread	9	$2.51 \cdot 10^6$
Lauraceae	*Ocotea mollifolia* Mez & Pittier	widespread	10	$1.14 \cdot 10^5$
Lauraceae	*Ocotea rivularis* Standl. & L. O. Williams	endemics	9	$6.68 \cdot 10^2$
Melastomataceae	*Miconia dissitinervia* Kriebel, Almeda & A. Estrada	endemics	11	$3.75 \cdot 10^3$
Melastomataceae	*Miconia donaeana* Naudin	widespread	10	$1.22 \cdot 10^6$
Melastomataceae	*Miconia osaensis* Aguilar, Kriebel & Almeda	endemics	10	$9.61 \cdot 10^1$
Melastomataceae	*Miconia trinervia* (Sw.) D. Don ex Loudon	widespread	10	$5.89 \cdot 10^6$
Primulaceae	*Ardisia compressa* Kunth	widespread	9	$1.44 \cdot 10^6$
Primulaceae	*Ardisia dunlapiana* P. H. Allen	endemics	10	$1.44 \cdot 10^3$
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	widespread	11	$1.18 \cdot 10^7$
Rubiaceae	*Faramea permagnifolia* Dwyer ex C. M. Taylor	endemics	12	$5.38 \cdot 10^1$
Sapotaceae	*Pouteria lecythidicarpa* P. E. Sánchez & Poveda	endemics	10	$1.33 \cdot 10^4$
Sapotaceae	*Pouteria subrotata* Cronquist	widespread	8	$1.72 \cdot 10^6$
Sapotaceae	*Pouteria torta* (Mart.) Radlk.	widespread	10	$1.08 \cdot 10^7$
Sapotaceae	*Pouteria triplarifolia* C. K. Allen ex T. D. Pennington	endemics	6	$2.41 \cdot 10^3$

Chapter 3: What property of the species functional traits defines better the realized niche breadth of tropical trees: the central position or the variation?

Abstract

What determines realized niche size is a central question in biogeography. Both intra-specific variability of functional traits and species' mean trait values have been supposed to contribute to variation in niche breadth. However, empirical evidence for both ideas is mixed and comparative analysis of whether trait variability or mean trait states are more important in this context has not yet been conducted. We compiled data from different sources for three functional traits of tropical trees distributed in tropical America: wood density (WD), specific leaf area (SLA), and leaf nitrogen content (N). For species with five or more documented values for at least one of these traits, we searched for occurrences in the Global Biodiversity Information Facility. Based on these occurrences, we extracted six uncorrelated climatic variables from WorldClim and calculated realized climatic niche breadth by means of a hypervolume approach. We tested for relationships between niche breadth and trait means or trait coefficients of variation (CV), respectively, by means of both ordinary least-squares regressions and phylogenetically corrected regression models. Five or more values for at least one of the three traits were available for 521 species (2969 WD values of 271 species, 4291 N values of 274 species and 4731 SLA values of 288 species). In general, both trait means and trait variability explained only a low to moderate fraction of the variance in climatic niche breadth (2 to 22%). Results for trait means suggest that a 'ruderal' strategy with fast maximal growth rates fosters broader niches. However, in univariate models relationships of niche breadth with trait CV were much stronger in case of N and SLA, and approximately equally strong in case of WD. In multivariate models for a subset of 90 species, CVs of WD and SLA remained significantly correlated to niche breadth but trait means were uncorrelated. Results were consistent between models with and without phylogenetic correction. Our results corroborate that in neotropical tree species parameters of intra-specific functional trait distribution are indeed related to the realized niche breadth. Among these parameters, trait variability is apparently more important than mean trait states for explaining the breadth of realized niches, even if trait values related to fast acquisitive resource strategies seem to additionally foster realized niche breadth.

Keywords: climatic niche, coefficient of variation, intraspecific trait variation, leaf nitrogen content, specific leaf area, wood density

3.1 Introduction

Protection of the world's biodiversity rests, in part, on our ability to rank species according to their extinction risk. Such ranking is facilitated by identifying properties, or traits, of species that are correlated with levels of threat. Range size is known as one of the main predictors of extinction risk (Purvis et al., 2000; Harris & Pimm, 2008; Pimm et al., 2014) al. 2014), but for many species range size is unsufficiently documented (Meyer et al., 2015, 2016). The factors that, in turn, determine range size are under debate (Brown et al., 1996; Slatyer et al., 2013). Among these factors, numerous studies support that species with broad environmental tolerances, i.e. generalists with the ability to exploit more different resources, can satisfy their requirements at more different localities. Ergo, species with broader niches commonly have wider ranges (Boulangeat et al., 2012; Slatyer et al., 2013). The relationship between niche breadth and range size is maintained across taxonomic groups and therefore is considered a general pattern in ecology (Slatyer et al., 2013). However, the probability of extinction seems to be associated more with the species ability to fill their potential ranges (realised niche) than with their inherent tolerance limits (fundamental niche) (Saupe et al., 2015). Consequently, identifying traits and properties that determine species' realised niche breadth is of particular interest for conservation biology and biogeography.

The environmental space occupied, i.e. the realised niche breadth, tends to correlate with the variability of phenotypes and genotypes at the level of communities, species and individuals (Ackerly, 2003; Bolnick et al., 2003; Messier et al., 2010; McKown et al., 2014). Consequently, species with higher intraspecific trait variation should tolerate broader environmental conditions (Bradshaw, 1965), that is, have broader environmental niches. However, the relationship between niche breadth and intra-specific variability in phenotypic expression is less clear-cut empirically than it might appear theoretically. In fact, both, studies supporting that relation (Sides et al., 2014) and others with inconsistent or even contradictory results (Matesanz et al., 2009; Dostál et al., 2016, 2017; Mitchell et al., 2017) have recently been published.

Besides phenotypic variability, the average phenotype of a species ("common phenotype") could also affect niche breadth. For example, Stahl et al., (2014) demonstrated for temperate tree species of North America that the means of functional traits like wood density, seed mass, and maximum height are correlated to the species' realized niche breadths and determine the climatic limits of species' ranges. Analogous to the "general purpose genotype" (Baker, 1965), a general purpose phenotype could be hypothesised as one way in which a species could occupy a broad ecological niche (Richards et al., 2006). For instance, an individual with determinate genotype and phenotype can tolerate and survive in an array of

different environmental conditions (Bolnick et al., 2003). This general purpose phenotype should represent trait values that maximize tolerance of different environmental conditions or the ability to use different resources (Bolnick et al., 2003).

The relative contributions of the different parameters of trait value distribution (e.g. mean, variance, maximum and minimum) to explaining the realised niche breadth of species have been little explored so far. Here, we use tropical tree species, as a model-group, to compare relationships between the realised climatic niche breadth and the location (e.g. means) and scale (coefficient of variation) parameters of three functional traits, wood density, specific leaf area and leaf nitrogen content. These traits are known to be related to different ecological strategies of trees (Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016; Kunstler et al., 2016). We hypothesise that both trait mean and trait variability affect the species' niche breadth. We suppose, however, that the relationship of realized niches with trait means could even be stronger than with trait variability because trait means often also affect the competitive ability of tree species (Kunstler et al., 2016) which is, in turn, important for realized niche breadth (Connell, 1983). Our tentative assumption hence is, that realized niche breadths of tropical trees are significantly correlated to both the mean and variance of the selected traits, but that trait means will explain more of the variance in niche breadths than trait variability.

3.2 Methods

We focus our study on the Neotropics, a region particularly rich in tree species (Gentry, 1988). First, we assembled an updated list of tree species in the Neotropics searching for tree species names for each one of 26 countries (Argentina, Barbados, Belize, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Ecuardor, El Salvador, Guatemala, Guayna, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Peru, Puerto Rico, Republica Dominicana, Surinam, Uruguay, Venezuela) in the Global Tree Search Database (GTSD) (Beech et al., 2017). We complemented the resulting list with further species from the Amazonian tree species database (ATD)(ter Steege et al., 2016). The GTSD defines a tree as a woody plant, at least two meters in height, with at least a single vertical stem five centimetres in diameter at breast height. This definition has also been applied for selecting additional species from the ATD (ter Steege et al., 2016). The final tree species list was used to filter data of functional traits from different sources.

We compiled data for three functional traits, wood density (WD), specific leaf area (SLA), and leaf nitrogen content (N), the total nitrogen content per unit of leaf dry mass (mg g^{-1}). These traits have been frequently used in ecological studies because they are related to main plant strategies (Díaz et al., 2016), and in particular to the economic spectrum of plants (Wright et al.,

2004; Chave et al., 2009). Information on these traits has accumulated in recent years for the Neotropics (Enquist et al., 2016).

Data on WD for our study species were taken from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) complemented with data available in the BIEN database (Enquist et al., 2016) using the R-package "bien" (Maitner et al., 2017). For SLA and N, we used the data available in BIEN, complemented with records of foliar nutrient contents for 140 neotropical tree species whose ranges include Costa Rica (measured at the Centro de Investigaciones Agronómicas (CIA) of the University of Costa Rica), and with information from other sources (see Appendix S1). Because some of the databases used are in turn compilations (e.g. BIEN, (Maitner et al., 2017), we carefully checked for duplicated data based on the reference and removed them. For all traits, we checked the species names using the Taxonomic Name Resolution Service (version 4.0)(Boyle et al., 2013).

For each trait, we estimated the mean and the coefficient of variation for all the species with at least five trait values. Because species varied in the number of trait values available in our compilation, we used an unbiased estimator of the coefficient of variation ($\widehat{CV}^*$ the estimator corrects the coefficient of variation (CV) according to the sample size (n) as follows: $\widehat{CV}^* = \left(1 + \frac{1}{4n}\right) CV$ (Sokal & Rohlf, 1995). The unbiased estimator $\widehat{CV}^*$ will be abbreviated as CV in the rest of the paper.

For each species with at least five traits values, we collected occurrence records from the Global Biodiversity Information Facility (GBIF) (Appendix S2, GBIF_Citation.xlsx) using the R package "rgbif" (Chamberlain, 2017). We used standard procedures to clean obvious errors in GBIF (García-Roselló et al., 2014). In particular, we removed the following kinds of entries: a) localities without coordinates, b) coordinates equal to 0°(García-Roselló et al., 2014), c) localities with coordinates without decimals (integers), d) duplicate occurrences inside the same cell of a raster map with a resolution of 30 arc-seconds (http://www.worldclim.org/bioclim) (Hijmans et al., 2005), e) localities outside of the Americas and f) localities in which a label noted that the plant was cultivated. The set of species used in the subsequent analysis was then further reduced to those a) for which 30 or more different occurrence records were available, and b) which had more than 90% of their occurrence records within the tropics (23.43° N, 23.43° S). The occurrences collected were distributed all across the Neotropics (Fig. 1).

For each occurrence point, we used data from WorldClim (Hijmans et al., 2005) to estimate the climatic niche breadth. First, we checked for correlations of the 19 bioclimatic variables provided by WorldClim within tropical America and retained six of them with collinearity (Spearman's correlation coefficient) lower than 0.7: BIO1 = Annual Mean

Temperature, BIO2 = Mean Diurnal Range, BIO3 = Isothermality, BIO12 = Annual Precipitation, BIO15 = Precipitation Seasonality and BIO18 = Precipitation of Warmest Quarter (S3 Table). The values of these six layers were normalized using z-scores. Subsequently, we extracted the normalized values for each occurrence point of each species. Based on the extracted values, we estimated the realized climatic niche breadth of each species using the R-package hypervolume (version 2.0.7) (Blonder et al., 2017). We thereby used the one-class support vector machine (SVM) method with the parameters v = 0.1 and γ = 0.5. The parameters were chosen because they were slightly more conservative than the default parameters in previous tests of the method (Blonder et al., 2017). The first parameter v determines the upper and lower bound on the fraction of misclassification errors, and the second parameter defines the influence of a single point in the estimation. All subsequent analyses were performed with log 10 transformations of the thus calculated niche breadths. Log-transformations were used to improve symmetry of niche breadth value distributions (S4 Fig).

For each trait, we performed ordinary univariate linear regression analysis with niche breadth as the response and either the trait mean or the trait CV as the predictor variable. We compared the models by means of coefficients of determination (R^2) and the Akaike Information Criterion. We moreover included both the mean and CV of each trait into a bivariate model to assess the unique variance explained by the two parameters (calculated as R^2 of the bivariate model minus R^2 of the model with means only in case of CV, and with CV only in case of means).

To account for phylogenetic relationships among species, we repeated the same analyses using phylogenetic regression instead of ordinary least-squares models. We recovered phylogenies using the PHYLOMATIC v.3 utility (Webb & Donoghue, 2005) via the R package *brranching* (Chamberlain, 2016). The underlying phylogenetic tree was published by (Zanne et al., 2009), and is based on a rooted vascular plant tree with divergence times calibrated by means of molecular phylogeny (Soltis et al., 2011) and fossil calibration points. Phylogenetic regressions were performed by means of the function *pyhlom* within the R-package *phylolm* (Ho et al., 2016). The phylolm function calculates the likelihood with an algorithm that is linear in the number of tips (branches) in the phylogenetic tree (Ho & Ané, 2014). Coefficients of determination for these models were computed with the *rr2* function within the R-package *rr2* (Ives, 2017).

3.3 Results

We analysed data for 521 tropical tree species in total (S5 List of species). We used 2969 WD values of 271 species, 4291 N_{mass} values of 274 species and 4731 SLA values of 288 species, respectively. Across species, trait means were normally distributed in case of WD and

SLA, and slightly right skewed in case of foliar N (S6 Fig). Trait variation was lowest for WD (mean = 0.13, max = 0.38), intermediate for N (mean = 0.17, max = 0.45) and highest for SLA (mean = 0.26, max = 0.78). Trait CVs were not, or only very loosely correlated in the case of SLA, with the number of trait values available per species (S6 Fig). To estimate the niche breadth we used 167 928 localities of occurrence distributed across the Neotropics (Fig. 1, S5 List of species).

Means of all three traits were statistically significantly correlated with niche breadths in univariate ordinary least-squares models (Table 1, Fig. 2). Species with lower WD and higher SLA and N tended to have broader realized niches. However, model goodness of fit was very low for all three trait means. Models with phylogenetic correction provided a somewhat better fit but relationships with trait means remained statistically significant in case of WD and N only.

Similar to trait means, CVs of all traits were significantly correlated to species' niche breadth in both the models with and without phylogenetic correction (Table 1, Fig. 2). In all three cases, species with higher trait CVs had broader realized niches. Coefficients of determination were still low to moderate, but considerably higher than for models with trait means as predictors in case of SLA and N. For those two traits, AIC values were also lower by 10 at least for models with CVs than for models with means as predictors, irrespective of whether phylogenies were accounted for or not. Although, the variance explained by bivariate models was slightly higher, it was relatively similar to the variance explained only by CVs. The variance explained by trait CV was much larger than the variance uniquely explained by trait means in case of SLA and N (8 and 2% or 11 and 6% with phylogenetic correction, respectively, in case of SLA; and 14 and 3% or 17 and 10% with phylogenetic correction, respectively, in case of N). Only in case of WD, trait means and trait CVs contributed about equally to explaining species' niche breadth (Table 1, Fig. 2).

Multivariate models are not strictly comparable to uni- and bivariate ones because a minimum of five trait values for all three traits simultaneously was only available for 90 species. However, the results are qualitatively consistent insofar as in this much smaller species set trait variability was still more closely correlated to niche breadth than trait means. In multivariate models with all three trait means as predictors, none of theses traits were significantly correlated to realized niche breadths, independent of whether phylogenetic relationships were accounted for or not (Table 2). By contrast, CVs of WD and SLA remained significantly correlated to niche breadth in multivariate models, and CV of N was marginally significant ($p=0.07$); would be significant in a one-sided test). Figure 3 demonstrates that species with narrow realized niches actually tend to have low variability in terms of both WD and SLA. As a consequence, the multivariate CV model explained realized niche breadths of these 90 species much better than

the multivariate model of trait means (R^2 = 0.22 and 0.03, AIC = 291 and 311, respectively). Again, models with and without phylogenetic correction provided very similar results (Table 2).

3.4 Discussion

Our results suggest that in neotropical tree species parameters of intra-specific functional trait distribution are indeed related to realized niche breadth. They hence corroborate both older hypotheses about the correlation between niche breadth and trait plasticity (Darwin, 1859; Bradshaw, 1965) and more recent ideas about relationships between particular trait states and the range of colonized environments (Stahl et al., 2014; Kunstler et al., 2015). However, in a direct comparison, trait plasticity turned out to be more closely related to realized niche breadth than trait means, at least for two of the three functional traits analyzed. Flexible adaptation to varied environments hence seems more important for biogeographical success than possession of a 'general purpose phenotype' or of trait states that confer particular competitive abilities, at least in neotropical tree species.

Detected relationships between mean trait states and realized niche breadths are not only weak, they are moreover difficult to interpret in a functional context. High wood density and low specific leaf area have been found to be associated with both high competitive response and competitive ability in tree species (Kunstler et al., 2016). By contrast, our data suggest that broader realized niches are associated with lower wood density and higher SLA. Our results thus provide no indication for a positive effect of competitive ability on realized niche breadth. Similarly, high wood density and low specific leaf area can also increase the species' ability to cope with extreme environmental conditions. Trees with denser wood can tolerate more stressful environments such as dry, nutrient and light-poor habitats (Augspurger, 1984; Poorter & Markesteijn, 2008; Valladares & Niinemets, 2008) and lower SLA tends to be associated with economical use of resources which also is particularly widespread under stressful conditions (Reich et al., 1998; Li et al., 2000; Wright et al., 2001). As a corollary, the detected relationships between mean wood density or specific leaf area, respectively, and realized niche breadth are also inconsisent with the idea that tolerance of more extreme conditions would foster expansion of realized niche breadths. In terms of plant strategies (Grime, 2001), neither strong competitive abilities nor tolerance of extreme condtions seem to foster large realized niches in tropical trees. Rather, our results suggest that a 'ruderal' strategy, i.e. the capability of rapidly colonizing disturbed sites and efficiently profiting from a transient low-competitive situation, could facilitate biogeographical success. Indeed, fast maximum growth rate, a feature particularly characteristic of ruderal plants (Grime, 2001), is generally coupled with low wood density and high specific leaf area in trees (Kunstler et al., 2016), and was also found to be related to higher leaf nitrogen

content (Reich et al., 1997; Thomas & Vesk, 2017). All these trait states were also positively related to increasing niche breadth in our species set.

Evidence supporting the relationship between trait variability and niche breadth was both stronger and more consistent and easily interpretable. Indeed, species with broader realized niches were more variable with respect to all three of the analysed traits. While this result is not particularly surprising from a theoretical perspective (e.g. Sexton et al., 2017), it contradicts the findings of other recently published studies. In particular, Dostál et al., (2017) and Mitchell et al., (2016) could not find such a relationship in temperate grassland species and along a temperate wetland – dryland gradient, respectively. However, among the four traits tested by Mitchell et al., (2016), specific leaf area actually was both the only one also included in our study and the only one that was more variable in species with wider tolerance along this gradient in their study. In fact, these results hence are not contradictory but suggest that the relationship between plasticity and niche breadth may not be valid for all traits in the same way, or may vary in magnitude according to particular combinations of traits and ecological gradients or ecosystems. Most obviously, the importance of trait plasticity for realized niche breadth will depend on the adaptive value of trait variation along a specific ecological gradient (van Kleunen et al., 2011). In our data, a clear hierarchy among the three traits analysed does not emerge: while leaf N content showed the strongest relationship with realized niche breadth in univariate models, it was least correlated with niche breadth in the multivariate model. In fact, variation in all three of these traits have been shown to be of adaptive value in tropical trees (e.g. Chave et al., 2006; Messier et al., 2010; Brenes-Arguedas et al., 2013). However, these traits are phylogenetically conserved to a different degree (Kraft & Ackerly, 2010) and hence likely also differ in intraspecific adaptive plasticity. We indeed found that the extent of trait variablity in our species was distinct among the three traits in a way consistent with the known extent of phylogenetic variablity (wood density more conserved than specific leaf area, Kraft & Ackerly, 2010). We hence speculate that the low inherent adaptive plasticity of wood density was responsible for the lower correlation of the CV of this trait and niche breadth in our univariate models.

Although variation in trait values was more closely related to niche breadth than to trait means, coefficients of determination of all models were low to moderate at best. There are several reasons which, in combination, likely explain this low model fit. First, our analysis focused on three particular traits and disregarded many others that may be equally or even more important for realized niche breadth, mainly for reasons of data availability. We did not, for example, include dispersal-relevant traits which have been shown to be related to range size and, implicitly, also to niche breadths (e.g. Dullinger et al., 2012). We also did not account for maximum species height, a trait known as important for ecological strategies in trees (Morin &

Chuine, 2006; Dexter & Chave, 2016; Kunstler et al., 2016) and also related to dispersal capacity (Thomson et al., 2011). Second, there are other factors and processes which determine realized niche breadths in addition to traits. In particular, environmental history and associated contingencies of temporal range dynamics have been shown to importantly contribute to current distribution patterns of tree species (e.g. Svenning & Skov, 2004, 2007). Third, we have measured niche breadth only in terms of climatic niche dimensions. While climatic niches capture a considerable part of large-scale tree distribution patterns (Boucher-Lalonde et al., 2012), other abiotic (e.g. soils) and biotic (e.g mutualists) factors represent important additional niche axes that may modify 'multi-dimensional' niche breadth hierarchies among species. Fourth, our estimates of trait means and variances are based on sample sizes that are small, and hence likely not fully representative, for many species. Moreover, individual trait values are compiled from large databases with individual entries not necessarily complying with common measurement protocols and standards.

3.4.1 Conclusions

Many naturalists have assumed that higher phenotypic variation allows species to exist in a more diverse range of environments (Darwin, 1859; Bradshaw, 1965; Sides et al., 2014). Nevertheless, empirical support of this hypothesis remains mixed so far. Our study corroborates this idea for the case of neotropical tree species and for the three analyzed traits known to be functionally important and of adaptive value in this group of species. In particular, our data suggest that trait variability is more important than trait means for explaining the breadth of realized niches, even if trait values related to fast acquisitive resource strategies seem to additionally foster realized niche breadth.

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3.7 Figures

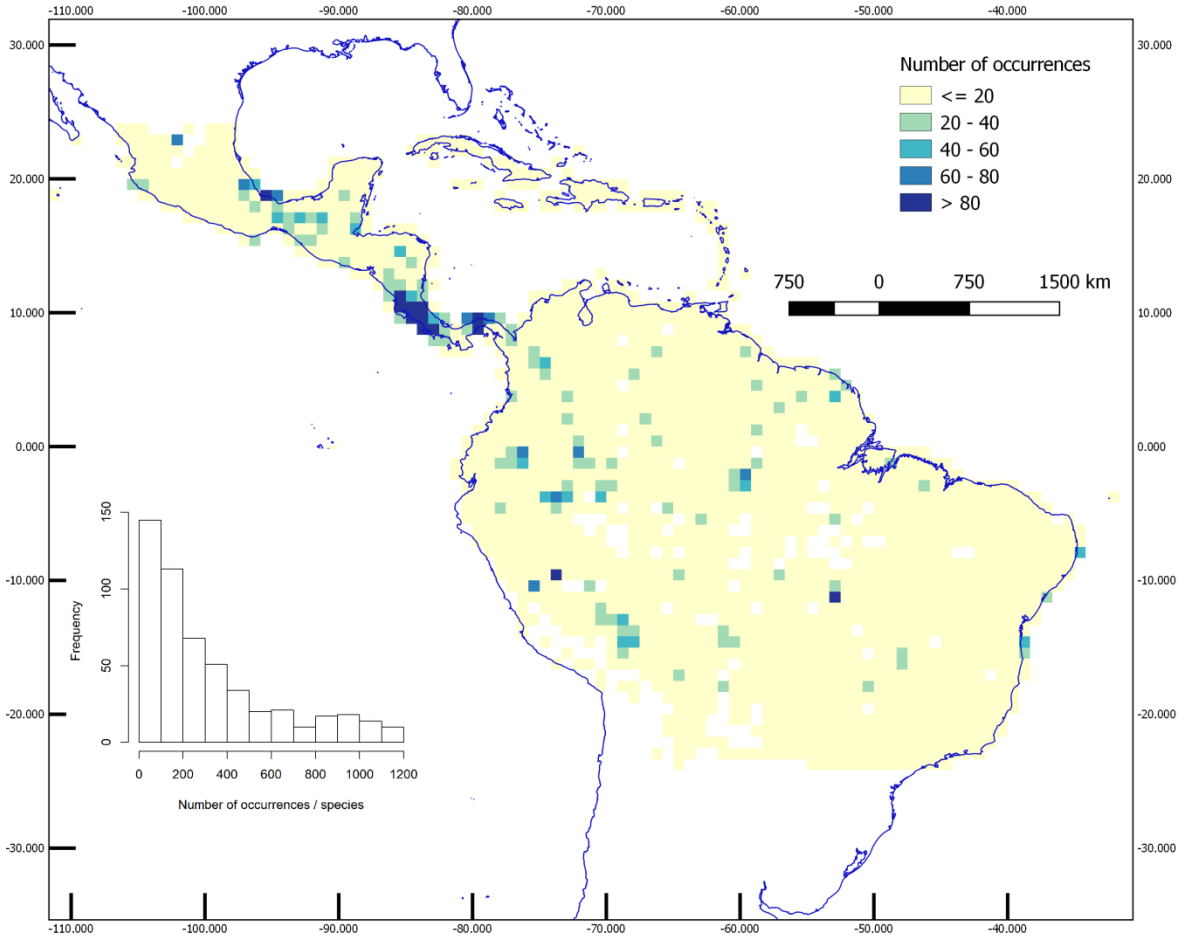

Fig. 1. Geographic distribution of the number of occurrences extracted from the Global Biodiversity Information Facility for the 521 tropical tree species considered in the Neotropics. The insert provides a histogram of the occurrence numbers per species..

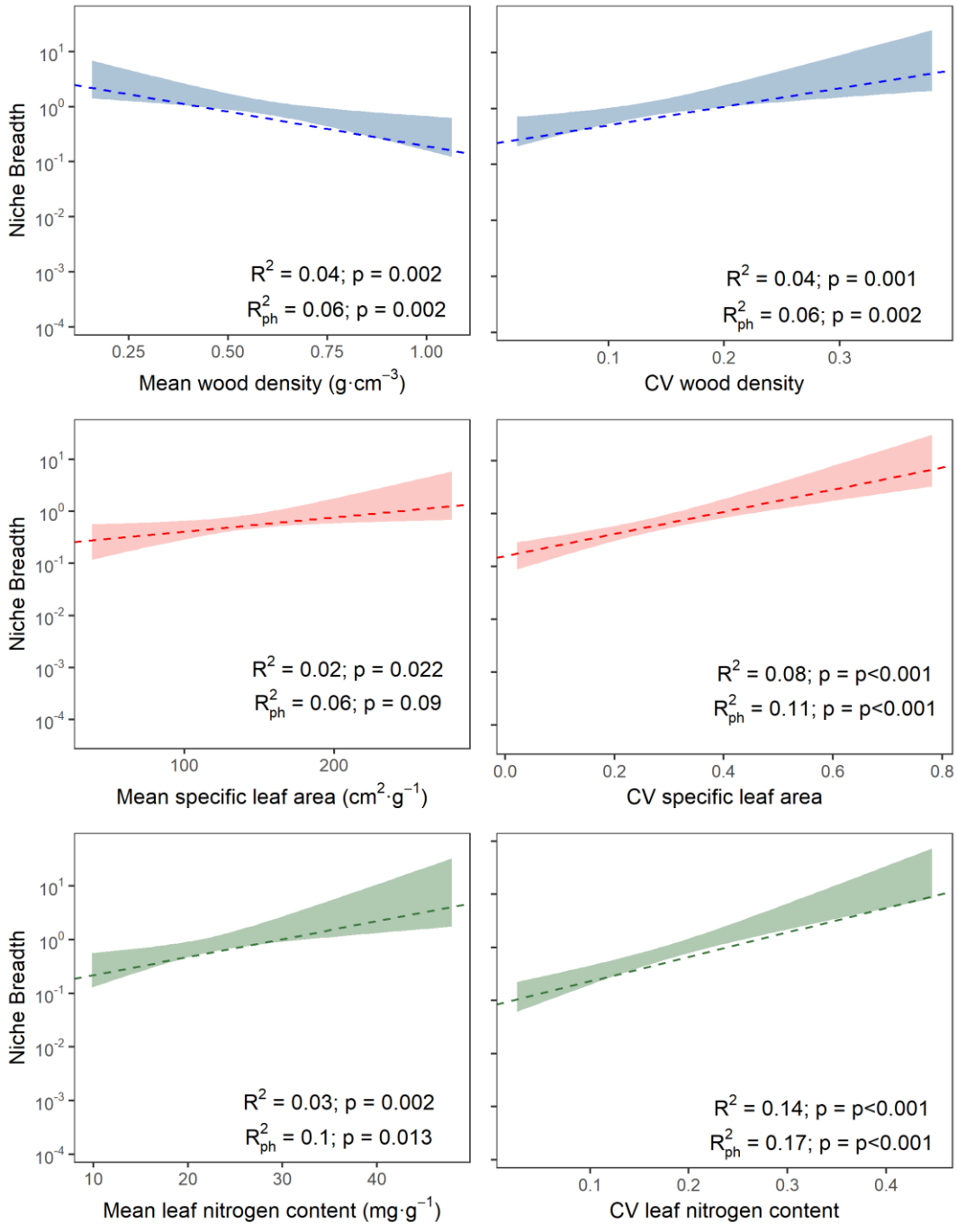

Fig. 2. Relationship between niche breadth and the means or CVs, respectively, of wood density, specific leaf area and leaf nitrogen content according to either univariate least squares regression models or univariate phylogenetic regression models. Shaded areas represent 95% confidence limits for regression lines calculated without phylogenetic correction, and dashed lines represent regression lines computed with phylogenetic correction. R^2 and R^2_{ph} are the coefficients of determination of the models without and with phylogenetic correction, respectively.

Table 1. Results of univariate linear regression models relating climatic niche breadth (NB) of neotropical tree species to means and coefficients of variation or three functional traits: wood density (WD), specific leaf area (SLA) and leaf nitrogen content (N).

		Without phylogenetic correction						With phylogenetic correction					
Model	Factors	Estimate	Std. Error	t value	p. value	R2	AIC	Estimate	Std. Error	T value	p. value	R2	AIC
Log10(NB) = β+WDmean	WDmean	-1.16	0.36	-3.17	0.002	0.04	800.26	-1.26	0.39	-3.19	0.002	0.06	795.05
Log10(NB) = β +WDcv	WDcv	3.53	1.07	3.30	0.001	0.04	799.49	3.30	1.06	3.11	0.002	0.06	795.44
Log10(NB)= β +WDcv+WDmean	WDcv	2.84	1.10	2.59	0.01	0.06	795.57	2.62	1.09	2.41	0.02	0.08	791.25
	WDmean	-0.91	0.37	-2.43	0.02			-1.01	0.40	-2.49	0.01		
Log10(NB) = β +SLAmean	SLAmean	0.004	0.002	2.31	0.02	0.02	905.86	0.003	0.002	1.70	0.09	0.06	896.89
Log10(NB) = β +SLAcv	SLAcv	2.37	0.46	5.12	< 0.001	0.08	885.94	2.09	0.46	4.56	< 0.001	0.11	879.70
Log10(NB) = β +SLAcv+SLAmean	SLAcv	2.30	0.46	4.98	< 0.001	0.10	883.86	2.07	0.46	4.52	< 0.001	0.12	879.09
	SLAmean	0.003	0.002	2.02	0.03			0.003	0.002	1.62	0.11		
Log10(NB) = β +Nmean	Nmean	0.04	0.01	3.13	0.002	0.03	862.84	0.03	0.01	2.49	0.01	0.10	844.38
Log10(NB) = β +Ncv	Ncv	5.53	0.84	6.55	< 0.001	0.14	832.44	4.60	0.85	5.39	< 0.001	0.17	823.53
Log10(NB) = β +Ncv+Nmean	Ncv	5.37	0.83	6.43	0.004	0.16	825.90	4.55	0.85	5.38	< 0.001	0.19	819.59
	Nmean	0.03	0.01	2.93	< 0.001			0.03	0.01	2.47	0.01		

Table 2. Results of multiple linear regression models relating climatic niche breadth (NB) of neotropical tree species to means and coefficients of variation of three functional traits: wood density (WD), specific leaf area (SLA) and leaf nitrogen content (N).

		Without phylogenetic correction						With phylogenetic correction					
	Factors	Estimate	Std. Error	t value	p. value	R^2	AIC	Estimate	Std. Error	T value	p. value	R^2	AIC
$Log_{10}(NB) = \beta + WD_{mean} + SLA_{mean} + N_{mean}$	WD_{mean}	-0.66	0.87	-0.77	0.45	0.03	310.7	-1.30	0.89	-1.46	0.15	0.08	307.62
	SLA_{mean}	0.00	0.00	0.78	0.44			0.00	0.00	0.63	0.53		
	N_{mean}	0.01	0.04	0.17	0.86			0.01	0.04	0.22	0.82		
$Log_{10}(NB) = \beta + WD_{cv} + SLA_{cv} + N_{cv}$	WD_{cv}	5.56	2.37	2.35	0.02	0.22	291.0	5.65	2.34	2.41	0.02	0.23	292.07
	SLA_{cv}	1.97	0.93	2.12	0.04			1.99	0.91	2.19	0.03		
	N_{cv}	3.06	1.69	1.81	0.07			2.45	1.71	1.44	0.15		

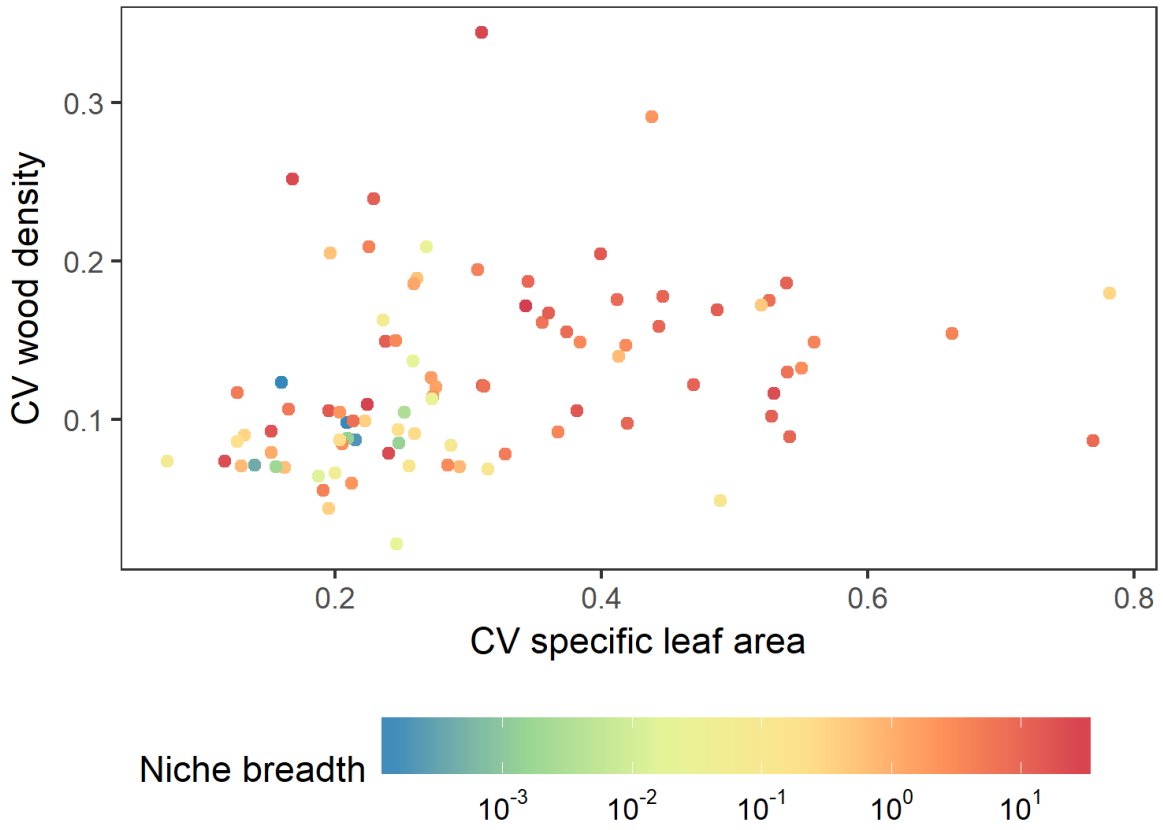

Fig. 3. Relationship between niche breadth (colors) of 90 neotropical trees species and coefficients of variation of wood density and specific leaf area.

Appendices

4.1 Supplementary Material Chapter 1, Appendix A:

Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees

Table A1: Seed size (length x width), seed volume, seed mass and dispersers of the species used in the analysis. The dispersers are based on literature about the genus, B: Birds, M: mammals.

Family	Species name	Seed Size (mm)	Seed Volume (mm^3)[a]	Seed mass (g)[b]	Dispersers	Ref.
Annonaceae	*Guatteria amplifolia*	10 x 6	132.70	0.130	B, M	1
Annonaceae	*Guatteria pudica*	8 x 4	49.76	0.078	B, M	1
Annonaceae	*Guatteria rostrata*	15 x 7	292.70	0.174	B, M	1
Annonaceae	*Guatteria chiriquiensis*	8 x 4	49.76	0.052	B, M	1
Annonaceae	*Unonopsis osae*	12 x 6	167.95	0.345	B	2
Annonaceae	*Unonopsis theobromifolia*	10 x 6	132.70		B	2
Araliaceae	*Dendropanax arboreus*	5 x 4	27.99		B	3
Araliaceae	*Dendropanax ravenii*	6 x 4	34.56		B	3
Boraginaceae	*Cordia cymosa*	9	251.92		B, M	4
Boraginaceae	*Cordia liesneri*	15 x 10	539.96		B	5
Burseraceae	*Protium panamense*	13 x 8	304.80	0.260	M, B	6
Burseraceae	*Protium pecuniosum*	2.1 x 1	830.24	0.793	M, B	7
Clusiaceae	*Chrysochlamys glauca*	10 x 4	67.73	0.026	B	6
Clusiaceae	*Chrysochlamys skutchii*	10 x 4	67.73	0.060	B	8
Clusiaceae	*Garcinia aguilari*	35	14816.54		M	8
Clusiaceae	*Garcinia madruno*	25	5399.61	1.407	M	8
Euphorbiaceae	*Garcinia magnifolia*	30	9330.53		M	9
Euphorbiaceae	*Sapium allenii*	5 x 5	43.20	0.032	B	9
Fabaceae	*Sapium glandulosum*	5 x 5	43.20	0.033	B	9
Fabaceae	*Inga skutchii*	15	172.79		M	10
Lauraceae	*Inga spectabilis*	35	1749.47		M	10
Lauraceae	*Ocotea mollifolia*	4 x 1.8	5231.32	1.519	B	11
Melastomataceae	*Ocotea rivularis*	1.1 x 0.6	149.81		B	11
Melastomataceae	*Miconia dissitinervia*	0.5	0.04		B	12
Melastomataceae	*Miconia donaeana*	0.6	0.07		B	12
Melastomataceae	*Miconia osaensis*	0.5	0.04		B	13
Myrsinaceae	*Miconia trinervia*	0.9	0.25		B	12
Myrsinaceae	*Ardisia compressa*	4	22.12	0.021	B	14
Rubiaceae	*Ardisia dunlapiana*	3	9.33		B	14
Rubiaceae	*Faramea occidentalis*	10	345.58	0.065	B	6
Sapotaceae	*Faramea permagnifolia*	13	759.23	0.055	B	15
Sapotaceae	*Pouteria lecytidicarpa*	29	4148.63		M	16
Sapotaceae	*Pouteria subrotata*	22	2759.33		M	16
Sapotaceae	*Pouteria torta*	32	3526.34	0.596	M	16
Sapotaceae	*Pouteria triplarifolia*	30	3244.35		M	16

[a] Seed volume estimated according to Eriksson et al. (2000).

[b] Seed mass obtained from herbarium specimens at the University of Costa Rica herbarium (USJ)

[1] Maas et al. 2015; [2] Maas et al. 2007,[3] Cannon & Cannon 1989, [4] Miller 1987, [5] Miller 1988, [6] Paton & Calderón 2016, [7] Daly 2007, [8] Hammel 2010, [9] González 2010, [10] Zamora 2010, [11]

González & Hammel 2007, [12] Almeda 2007, [13] Kriebel et al. 2008, [14] Morales 2007, [15] Taylor 1996, [16] Morales 2015.

Herbarium specimens from USJ: R. Aguilar 12313; J. M. Ley 85; R. Aguilar 12317; E. Chacón 671; J. M. Ley 42; R.Aguilar 11220; P. Juárez 704; González 32; J. Gómez-Laurito 12172; T. Robles n.n., A. Ruiz 539; J. M. Ley 85; P. Juárez 749; R. Soto 3554; Kernan 1252; J. M. Ley 3; Marin 532.

Appendix A1: Analysis of seed size differences

To assess possible differences in seed sizes among the congeneric endemic and widespread species we used data from Table A1 to compute a seed volume assuming that seeds have an ellipsoid shape. We used the equation for the volume of an ellipsoid following the method described by Eriksson et al. (2000). Similar to these authors, in cases where thickness was missing, we used an approximation with T = 0.66W. The equation used was $V = \frac{4}{3}\pi ab^2$ with $a = L/2$ and $b = (W + T)/4$.

We also tried to support our volume estimation with seed mass data. We collected seed mass data from herbarium specimens at the University of Costa Rica herbarium (USJ) as long as they could be taken without damaging the specimen. We collected seed mass data for 16 of the 34 species used in our analysis. We correlated seed mass with the calculated seed volume in these 16 species. Both variables were highly and significantly correlated (Pearson r = 0.92, $p<0.01$; Fig A2-a).

We randomly paired one of the species with narrow range size with another congeneric species with large range size and used a linear mixed effects model with the difference of seed volume (widespread-endemic) as response variable and only the intercept on the predictor side of the regression equation (i.e. the model tested whether the difference in seed volumes between widespread and endemic species was different from zero, on average). We used genus as a random intercept term to account for the phylogenetic structure of the data. The results provided no indication for any difference in seed volumes between widespread and endemic congeneric species (Intercept = -35.08 ± 563.73, t-value = -0.06, p=0.95; Fig A2-B).

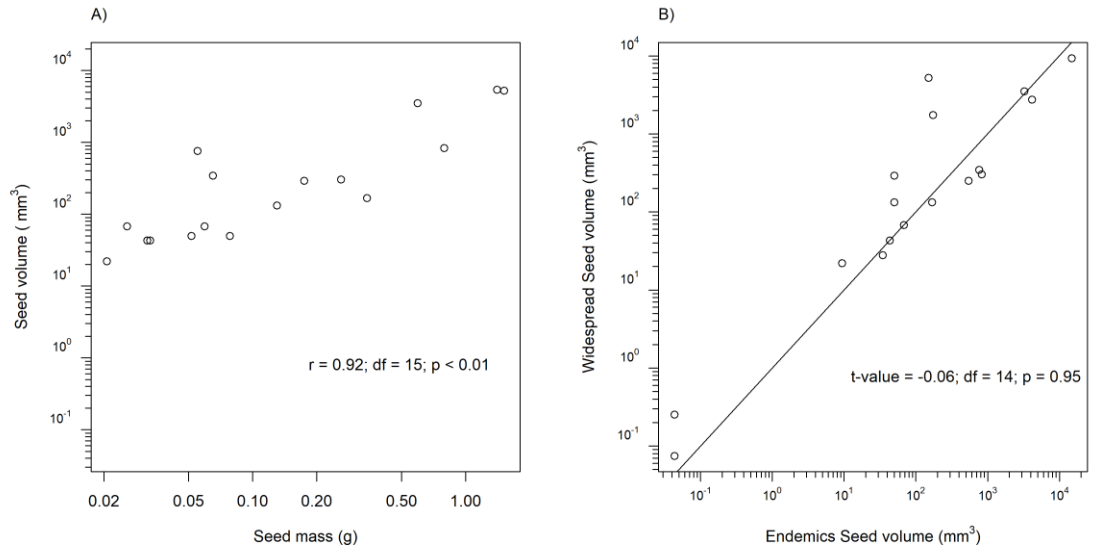

Figure A1: (A): Correlation between seed mass and seed volume for the 35 neotropical tree species analysed. (B): Seed volumes of congeneric pairs of endemic and widespread species. T- and p-values are from a linear mixed effects model assessing statistical difference in seed volumes between widespread and endemic congeners (see text for details).

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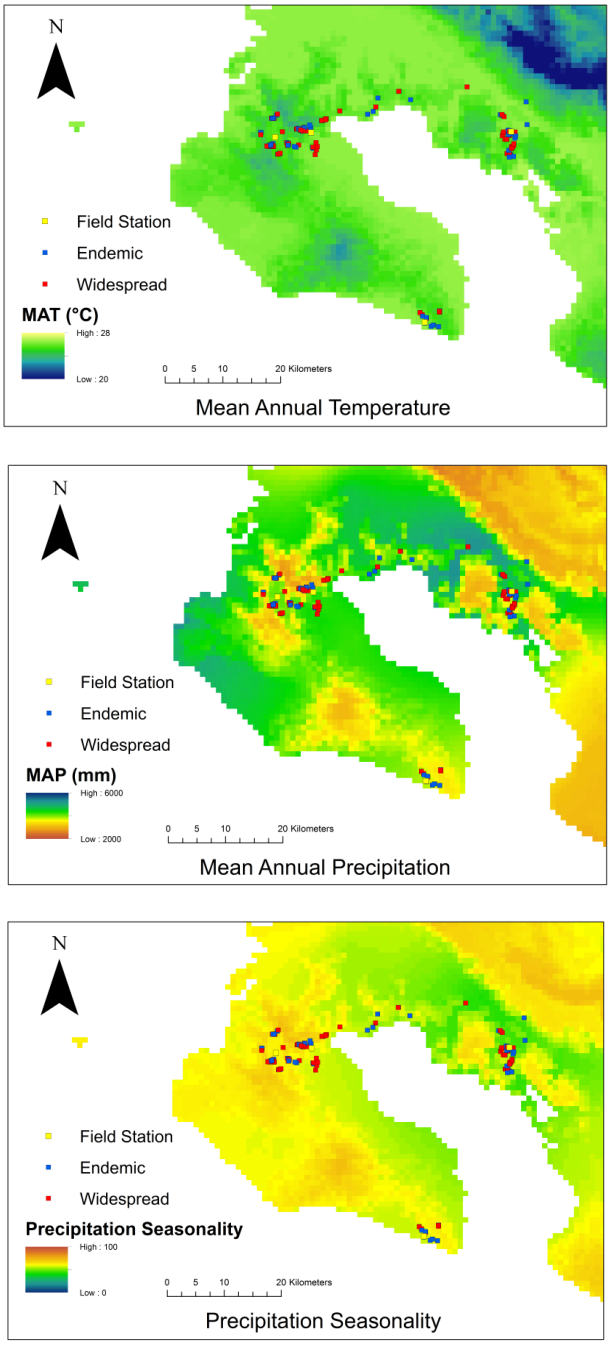

Figure A2: Mean annual temperature, mean annual precipitation and precipitation seasonality (coefficient of variation) according to Hijmans et al. (2005) in the study region.

Table A2: Mean of the nearest distance from a tree to another conespecific tree for each species studied. Shaded are the species with small range size within each genus.

Species	Mean of nearest distance between individuals (km)
Ardisia compressa	0.21
Ardisia dunlapiana	0.38
Chrysochlamys glauca	4.40
Chrysochlamys skutchii	0.86
Cordia cymosa	1.80
Cordia liesneri	2.34
Dendropanax arboreus	1.92
Dendropanax ravenii	0.34
Faramea occidentalis	0.63
Faramea permagnifolia	0.55
Garcinia aguilarii	0.88
Garcinia madruno	1.05
Garcinia magnifolia	5.54
Guatteria amplifolia	1.10
Guatteria chiriquiensis	1.56
Guatteria pudica	0.83
Guatteria rostrata	3.99
Inga skutchii	0.66
Inga spectabilis	0.74
Miconia dissitinervia	3.10
Miconia donaeana	0.32
Miconia osaensis	2.07
Miconia trinervia	1.89
Ocotea mollifolia	1.42
Ocotea rivularis	0.51
Pouteria lecytidicarpa	0.29
Pouteria subrotata	4.61
Pouteria torta	0.33
Pouteria triplarifolia	0.60
Protium panamense	1.40
Protium pecuniosum	0.91
Sapium allenii	0.74
Sapium glandulosum	1.13
Unonopsis osae	0.59
Unonopsis theobromifolia	1.13

Table A3: Linear mixed effects-models testing six climatic variables between localities where widespread species and endemic species were collected. Diff. = mean difference (widespread species-endemic species), DF = degrees of freedom.

Climatic variable	Diff. ± Std. Error	DF	F-value	p-value
Mean annual temperature	-0.449 ± 0.566	1/330	0.63	0.428
Mean diurnal temperature range	0.086 ± 0.379	1/330	0.05	0.821
Isothermality (ratio of day-to-night temperature oscillation to summer-to-winter oscillation)	0.071 ± 0.087	1/330	0.81	0.418

Mean annual precipitation	-38.646 ± 38.813	1/330	0.991	0.32
Precipitation seasonality	0.154 ± 0.60	1/330	0.064	0.8
Precipitation of warmest quarter	-3.824 ± 10.02	1/330	0.146	0.703

Appendix A2: Field methods and trait measurements.

For all collected trees, we measured diameter at breast height (DBH) using a diametric tape, height using a clinometer and a Leica Disto E7100i distance measurer, slope of growing sites (by means of a clinometer), and crown exposure to light using an index from 0 to 5 (0: crown receives no direct light, 1: crown receives direct light from the top or one side, 2: direct light from the top and one side or two sides without the top, 3: direct light from the top and two sides, 4: direct light from the top and three sides and 5: crown receives direct light from all directions (Bechtold 2003). Moreover, we took geographical coordinates by means of a GPS device (Garmin 60 CSX, mean RSE: 6 m).

We collected five leaves and a wood core from each tree. Leaves were taken with a pole or with a saw chain raised with cords from the highest accessible branch at the outer side of the crown. The collected leaves were completely expanded and mature, healthy, entire and without signs of herbivory. We only selected leaves older than the second fully exposed leaf to assure maturity. When less than five leaves on the collected branch fulfilled these criteria, we took the remaining ones from the next lower branch. Leaves were maintained in zip-loc bags with moistened paper towels and were measured within 24 hours after collection. Before weighing, leaves were carefully washed and wiped to remove epiphylls and subsequently dried with a cloth or absorbent paper.

Leaf thickness was measured using a Mitutoyo 7321 dial thickness gauge (readability 0.01 mm). We took the average of three measurements, at the proximal, medium and distal part of the leaf lamina, avoiding major veins.Leaf fresh weight and dry weight (after drying 72 hours at 70 ºC) were measured using a Radwag WTB 200 Precision Balance (readability 1 mg). The leaves of species with compound leaves (genera *Inga* and *Protium*) were weighed with petiole, because it was difficult to differentiate from the rachis; the leaves within a genus were always either compound or simple but never mixed among species. Leaf area was measured using a LICOR-3100 area meter; the values used are the average of three measurements. SLA was calculated as leaf fresh area measured in cm^2 divided by the leaf dry weight measured in mg. LDMC was estimated as leaf dry weight measured in mg divided by leaf fresh weight measured in g.

For each tree individual, leaf N, P and K contents (% dry matter) were measured after pooling the five individual leaves and grinding. Leaf N content was determined by dry combustion in an autoanalyzer, P, K, Ca and Mg content by wet digestion with HNO_3 and inductively coupled plasma-optical emission spectrometry (ICP-OES) at the laboratory of the Agronomic Research Center (Centro de Investigaciones Agronómicas) of the University of Costa Rica.

Wood specific gravity (WSG) was estimated as dry weight divided by the fresh volume of each wood core and corrected by the water density at 26 ºC, which was the average temperature in the laboratory; therefore the values are expressed as WSG without units (Williamson & Wiemann 2010). The fresh volume was measured using the Archimedes

principle. After drying for 72 hours at 103 ºC, wood samples were weighed on a precision balance (to 1 mg).

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Table A4: Means and standard deviations of wood specific gravity (WSG), leaf thickness (LT), specific leaf area (SLA) and leaf dry matter content (LDMC) in 35 tropical tree species. Shaded are the species with small range size within each genus.

Species	WSG	LT (mm)	SLA ($cm^2 \cdot g^{-1}$)	LDMC ($mg \cdot g^{-1}$)
Ardisia compressa	0.58 ± 0.05	0.25 ± 0.03	167.98 ± 22.23	249.92 ± 28.05
Ardisia dunlapiana	0.84 ± 0.03	0.3 ± 0.02	118.64 ± 11.26	306.92 ± 31.15
Chrysochlamys glauca	0.57 ± 0.05	0.25 ± 0.02	228.97 ± 29.07	195.21 ± 16
Chrysochlamys skutchii	0.63 ± 0.06	0.37 ± 0.07	102.18 ± 25.74	286.44 ± 25.74
Cordia cymosa	0.26 ± 0.05	0.39 ± 0.06	159.53 ± 38.11	290.21 ± 28.28
Cordia liesneri	0.55 ± 0.05	0.31 ± 0.02	137.97 ± 28.95	349.54 ± 51.49
Dendropanax arboreus	0.43 ± 0.05	0.29 ± 0.03	145.92 ± 16.37	284.37 ± 17.48
Dendropanax ravenii	0.54 ± 0.04	0.22 ± 0.02	220.19 ± 19.39	232.35 ± 15.01
Faramea occidentalis	0.63 ± 0.04	0.29 ± 0.03	160.95 ± 13.19	405.56 ± 11.44
Faramea permagnifolia	0.62 ± 0.07	0.37 ± 0.04	110.39 ± 18.08	301.95 ± 30.33
Garcinia aguilarii	0.79 ± 0.02	0.38 ± 0.04	79.69 ± 11.49	428.95 ± 23.3
Garcinia madruno	0.77 ± 0.04	0.27 ± 0.03	114.54 ± 13.63	412.07 ± 21.23
Garcinia magnifolia	0.75 ± 0.04	0.62 ± 0.06	66.41 ± 12.25	369.33 ± 37.06
Guatteria amplifolia	0.42 ± 0.04	0.23 ± 0.02	130.97 ± 13.02	419.01 ± 24.52
Guatteria chiriquiensis	0.4 ± 0.03	0.27 ± 0.03	165.52 ± 39.97	310.12 ± 44.18
Guatteria pudica	0.53 ± 0.05	0.33 ± 0.06	152.77 ± 29.77	304.82 ± 27.11
Guatteria rostrata	0.41 ± 0.04	0.21 ± 0.02	153.89 ± 11.13	344.58 ± 24.57
Inga skutchii	0.68 ± 0.06	0.16 ± 0.03	236.33 ± 39.95	387.73 ± 35.48
Inga spectabilis	0.52 ± 0.07	0.35 ± 0.05	99.51 ± 14.19	388.09 ± 33.52
Miconia dissitinervia	0.61 ± 0.05	0.39 ± 0.03	165.19 ± 16.5	340.76 ± 18.97
Miconia donaeana	0.55 ± 0.04	0.29 ± 0.03	200.58 ± 28.95	336.58 ± 23.91
Miconia osaensis	0.57 ± 0.04	0.39 ± 0.03	85.94 ± 8.07	403.81 ± 29.96
Miconia trinervia	0.51 ± 0.05	0.22 ± 0.02	131.34 ± 24.16	288.52 ± 35.82
Ocotea mollifolia	0.42 ± 0.07	0.32 ± 0.04	147.55 ± 33.4	343.69 ± 31.93
Ocotea rivularis	0.37 ± 0.03	0.32 ± 0.03	108.44 ± 13.29	320.47 ± 26.47
Pouteria lecytidicarpa	0.85 ± 0.03	0.25 ± 0.02	74.05 ± 13.11	413.2 ± 39.79
Pouteria subrotata	0.77 ± 0.05	0.18 ± 0.01	125.95 ± 14.86	429.58 ± 42.08
Pouteria torta	0.86 ± 0.07	0.23 ± 0.06	122.88 ± 20.91	465.45 ± 26.65
Pouteria triplarifolia	0.73 ± 0.04	0.21 ± 0.01	119.68 ± 5.15	471.84 ± 18.02
Protium panamense	0.49 ± 0.07	0.23 ± 0.07	123.17 ± 17.08	418.82 ± 19.61
Protium pecuniosum	0.53 ± 0.06	0.19 ± 0.01	125.52 ± 16.16	433.66 ± 32.4
Sapium allenii	0.36 ± 0.06	0.26 ± 0.06	185.81 ± 73.75	233.38 ± 71.75
Sapium glandulosum	0.37 ± 0.04	0.26 ± 0.04	156.57 ± 48.32	288.29 ± 37.88
Unonopsis osae	0.61 ± 0.03	0.2 ± 0.01	168.09 ± 22.46	435.68 ± 32.62
Unonopsis theobromifolia	0.51 ± 0.03	0.31 ± 0.03	160.57 ± 17.51	429.76 ± 21.11

Table A5: Means and standard deviations of leaf macronutrient concentrations (% dry mass) in 35 tropical tree species: Leaf nitrogen (N), phosphorus (P), potassium (K), and the leaf N:P ratio. Shaded are the species with small range size within each genus.

Species	N	P	K	N:P
Ardisia compressa	1.87 ± 0.17	0.1 ± 0.02	1.25 ± 0.39	20.29 ± 4.45
Ardisia dunlapiana	1.17 ± 0.08	0.05 ± 0.01	1 ± 0.54	23.79 ± 2.91
Chrysochlamys glauca	2.09 ± 0.49	0.1 ± 0.03	0.58 ± 0.2	22.08 ± 4.27

Chrysochlamys skutchii	1.28 ± 0.37	0.06 ± 0.04	0.49 ± 0.16	24.52 ± 6.12
Cordia cymosa	2.05 ± 0.25	0.12 ± 0.03	1.18 ± 0.44	18.2 ± 3.93
Cordia liesneri	1.87 ± 0.24	0.06 ± 0.01	1.27 ± 0.5	32.38 ± 3.92
Dendropanax arboreus	1.53 ± 0.18	0.07 ± 0.01	1.71 ± 0.68	23.18 ± 3.39
Dendropanax ravenii	1.79 ± 0.17	0.08 ± 0.02	1.51 ± 0.29	24.84 ± 5.33
Faramea occidentalis	1.39 ± 0.14	0.06 ± 0.01	0.41 ± 0.11	24.33 ± 3.46
Faramea permagnifolia	1.18 ± 0.11	0.04 ± 0.01	0.45 ± 0.4	26.78 ± 3.57
Garcinia aguilarii	1.24 ± 0.13	0.07 ± 0.02	0.78 ± 0.31	18.63 ± 5.38
Garcinia madruno	1.34 ± 0.12	0.05 ± 0.01	0.54 ± 0.17	27.71 ± 3.72
Garcinia magnifolia	1.37 ± 0.1	0.06 ± 0.01	0.71 ± 0.32	21.81 ± 2.73
Guatteria amplifolia	1.67 ± 0.1	0.06 ± 0.01	0.48 ± 0.19	30.17 ± 5.53
Guatteria chiriquiensis	2.32 ± 0.37	0.1 ± 0.02	0.66 ± 0.17	23.71 ± 3.29
Guatteria pudica	1.95 ± 0.19	0.07 ± 0.01	0.72 ± 0.33	27.12 ± 3.67
Guatteria rostrata	2.1 ± 0.21	0.1 ± 0.02	0.64 ± 0.22	21.87 ± 2.88
Inga skutchii	3.07 ± 0.27	0.11 ± 0.02	0.7 ± 0.33	27.86 ± 5.6
Inga spectabilis	2.92 ± 0.3	0.13 ± 0.03	0.77 ± 0.23	23.73 ± 4.59
Miconia dissitinervia	1.58 ± 0.14	0.07 ± 0.02	0.73 ± 0.28	25.41 ± 5.22
Miconia donaeana	1.92 ± 0.16	0.07 ± 0.01	0.64 ± 0.14	27.94 ± 4.51
Miconia osaensis	1.46 ± 0.17	0.06 ± 0.01	0.26 ± 0.09	27.29 ± 7.21
Miconia trinervia	1.97 ± 0.19	0.08 ± 0.04	1.35 ± 0.39	27.28 ± 9.01
Ocotea mollifolia	1.94 ± 0.21	0.07 ± 0.01	0.87 ± 0.27	28.31 ± 3.58
Ocotea rivularis	1.96 ± 0.36	0.1 ± 0.02	1.16 ± 0.31	20.17 ± 1.33
Pouteria lecytidicarpa	1.61 ± 0.32	0.08 ± 0.04	0.79 ± 0.3	24.6 ± 12.06
Pouteria subrotata	2.29 ± 0.37	0.1 ± 0.02	0.91 ± 0.44	22.9 ± 3.87
Pouteria torta	1.73 ± 0.23	0.06 ± 0.02	0.61 ± 0.14	33.33 ± 6.86
Pouteria triplarifolia	1.38 ± 0.22	0.07 ± 0.01	0.79 ± 0.18	19.3 ± 1.53
Protium panamense	1.69 ± 0.26	0.11 ± 0.02	0.65 ± 0.18	16.31 ± 2.21
Protium pecuniosum	1.85 ± 0.25	0.1 ± 0.04	1.04 ± 0.43	20.36 ± 4.65
Sapium allenii	2.48 ± 0.61	0.25 ± 0.08	1.3 ± 0.63	10.58 ± 1.97
Sapium glandulosum	2.12 ± 0.23	0.19 ± 0.08	0.99 ± 0.39	12.74 ± 4.32
Unonopsis osae	1.82 ± 0.16	0.07 ± 0.02	0.65 ± 0.31	28 ± 6.71
Unonopsis theobromifolia	1.95 ± 0.13	0.09 ± 0.03	0.65 ± 0.16	22.08 ± 5.35

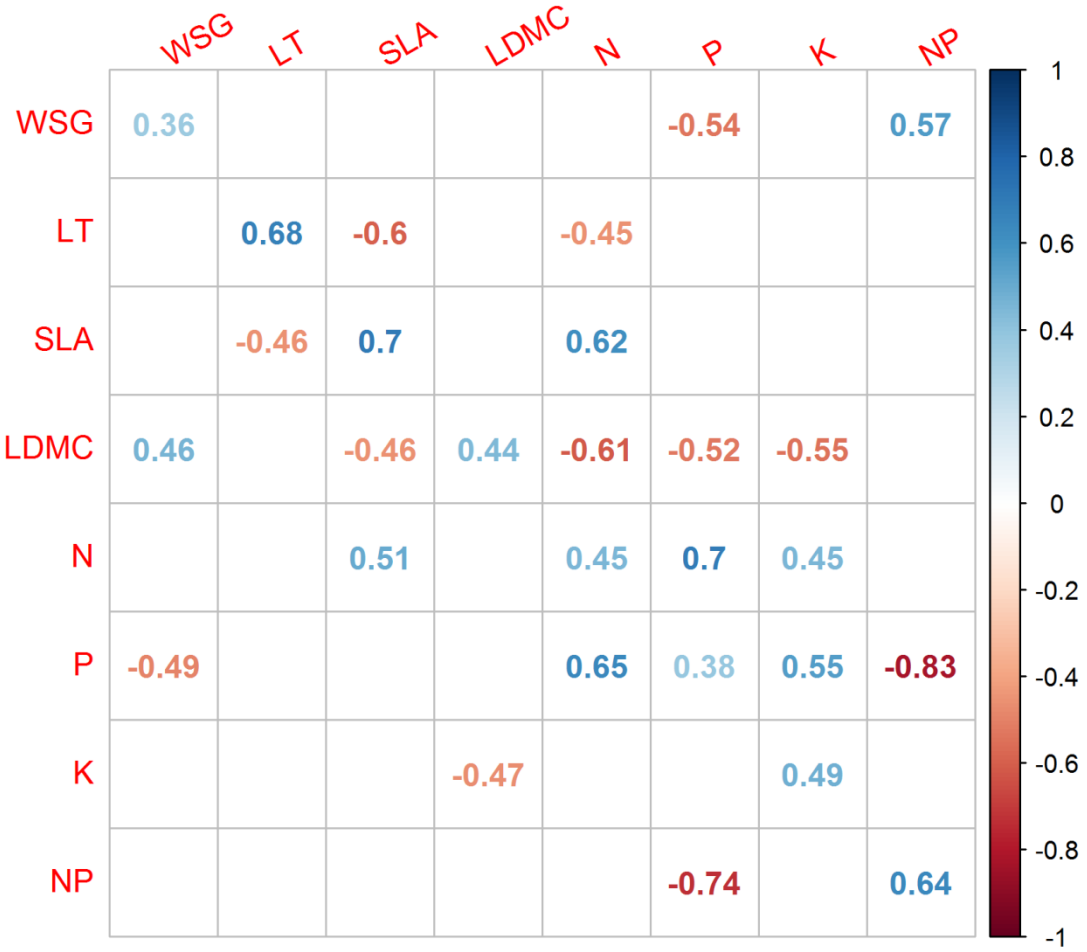

Figure A3: Pearson correlation coefficients between eight functional traits (wood specific gravity, WSG; specific leaf area, SLA; leaf thickness, LT; leaf dry matter content, LDMC; leaf nitrogen content, N; leaf phosphorus content, P; leaf potassium content, K; and leaf N:P ratio, NP) using data from 35 tropical tree species. Above diagonal, correlations based on the within-genus scaled data. Below diagonal, correlations based on raw data. In the diagonal, correlations between the raw data and the within-genus scaled data. Numbers indicate only correlations with $p<0.05$.

Table A6: Principal component analysis (PCA) made with eight functional traits (wood specific gravity, WSG; specific leaf area, SLA; leaf thickness, LT; leaf dry matter content, LDMC; leaf nitrogen content, N; leaf phosphorus content, P; leaf potassium content, K; and leaf N:P ratio, NP) of 35 tropical tree species. The PCA was made with traits scaled among the individuals within each genus.

PC	Eig.	% of variance	Cum. % variance	WSG	LT	SLA	LDMC	N	P	K	NP
1	3.10	40.90	40.90	2.89	6.69	12.99	**-16.70**	**17.65**	**20.73**	12.77	-9.57
2	1.44	19.03	59.93	5.23	**-30.31**	**20.79**	0.00	1.96	-11.97	0.00	**29.74**
3	0.89	11.79	71.73	**80.76**	7.52	0.31	-8.13	-0.16	0.29	1.78	-1.05
4	0.75	9.92	81.65	5.89	-7.21	5.31	**21.51**	0.40	10.09	**-34.94**	**-14.65**
5	0.61	8.02	89.66	-0.72	**19.02**	0.24	-7.61	**34.44**	0.01	**-29.87**	8.08

4.2 Supplementary Material Chapter 1, Appendix B:

Citations of Global Biodiversity Information Facility's providers of the localities of occurrences of the species studied.

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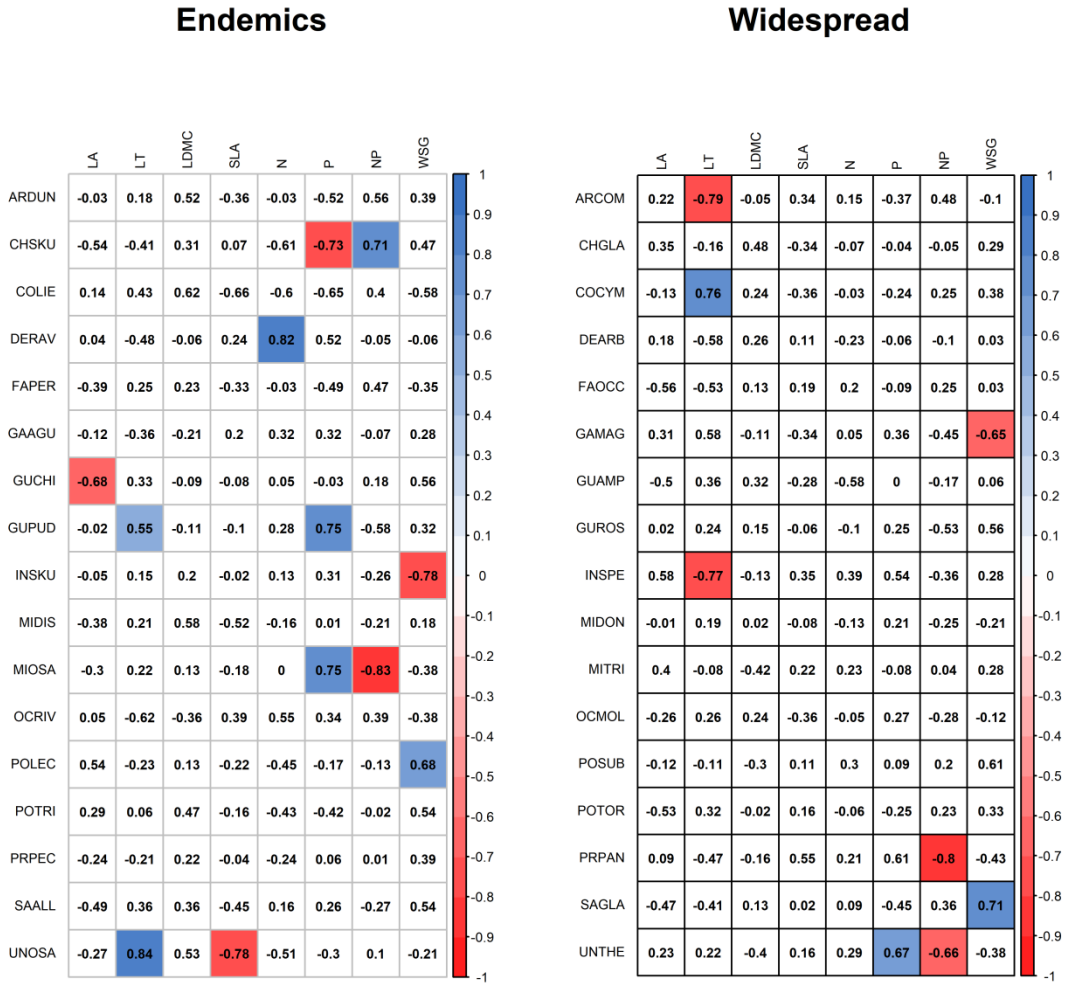
Data accessibility Chapter 1

All trait data reported in this manuscript are available in the Plant Trait Database via the link: https://www.try-db.org/TryWeb/Data.php#12, DOI: 10.17871/TRY.12.

4.3 Supporting information Chapter 2:

Is local trait variation related to total range size of tropical trees?



S1 Fig. Pearson's correlation coefficients between tree size (diameter at breast height) and eight functional traits in 34 neotropical tree species. Correlation coefficients significantly different from zero ($p<0.05$, 20 out of 272) are presented with color.

S2 File. Methods of functional trait measurements.

See Appendix A2: Field methods and trait measurements, page 83.

S3 Table. Correlation between bioclimatic variables within the tropical region (23.5° N-23.5°S) in America.

	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
BIO1 = Annual Mean Temperature	1.000																		
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))	-0.530	1.000																	
BIO3 = Isothermality (BIO2/BIO7) (* 100)	0.435	-0.478	1.000																
BIO4 = Temperature Seasonality (standard deviation *100)	-0.511	0.499	-0.846	1.000															
BIO5 = Max Temperature of Warmest Month	0.699	0.030	-0.085	-0.098	1.000														
BIO6 = Min Temperature of Coldest Month	0.901	-0.777	0.623	-0.648	0.419	1.000													
BIO7 = Temperature Annual Range (BIO5-BIO6)	-0.571	0.920	-0.764	0.727	0.058	-0.830	1.000												
BIO8 = Mean Temperature of Wettest Quarter	0.838	-0.354	0.125	-0.181	0.740	0.652	-0.309	1.000											
BIO9 = Mean Temperature of Driest Quarter	0.951	-0.622	0.531	-0.600	0.595	0.950	-0.676	0.686	1.000										
BIO10 = Mean Temperature of Warmest Quarter	0.905	-0.423	0.159	-0.206	0.799	0.743	-0.367	0.938	0.807	1.000									
BIO11 = Mean Temperature of Coldest Quarter	0.963	-0.565	0.571	-0.678	0.602	0.933	-0.657	0.710	0.966	0.785	1.000								
BIO12 = Annual Precipitation	0.491	-0.544	0.546	-0.679	0.143	0.623	-0.628	0.251	0.576	0.284	0.582	1.000							
BIO13 = Precipitation of Wettest Month	0.476	-0.424	0.418	-0.560	0.243	0.560	-0.485	0.222	0.572	0.300	0.557	0.887	1.000						
BIO14 = Precipitation of Driest Month	0.270	-0.625	0.523	-0.471	-0.207	0.489	-0.674	0.190	0.325	0.154	0.314	0.694	0.408	1.000					
BIO15 = Precipitation Seasonality (Coefficient of Variation)	-0.261	0.577	-0.445	0.466	0.101	-0.437	0.607	-0.218	-0.295	-0.175	-0.296	-0.616	-0.280	-0.899	1.000				
BIO16 = Precipitation of Wettest Quarter	0.482	-0.416	0.424	-0.583	0.251	0.561	-0.482	0.224	0.574	0.295	0.568	0.911	0.986	0.419	-0.308	1.000			
BIO17 = Precipitation of Driest Quarter	0.308	-0.644	0.523	-0.510	-0.159	0.522	-0.686	0.209	0.372	0.186	0.357	0.756	0.483	0.988	-0.917	0.498	1.000		
BIO18 = Precipitation of Warmest Quarter	-0.120	-0.040	0.072	-0.093	-0.212	-0.087	-0.068	0.005	-0.180	-0.155	-0.114	0.455	0.275	0.452	-0.472	0.300	0.471	1.000	
BIO19 = Precipitation of Coldest Quarter	0.557	-0.694	0.577	-0.625	0.114	0.734	-0.743	0.301	0.668	0.403	0.625	0.765	0.652	0.720	-0.638	0.660	0.769	0.098	1.000

S4 Table. Coefficients estimated (β) ± 1 standard error and the associated test statistics for mixed effects models evaluating the effect of the sample size on the coefficient of variation for eight functional traits analysed in 34 neotropical trees species.

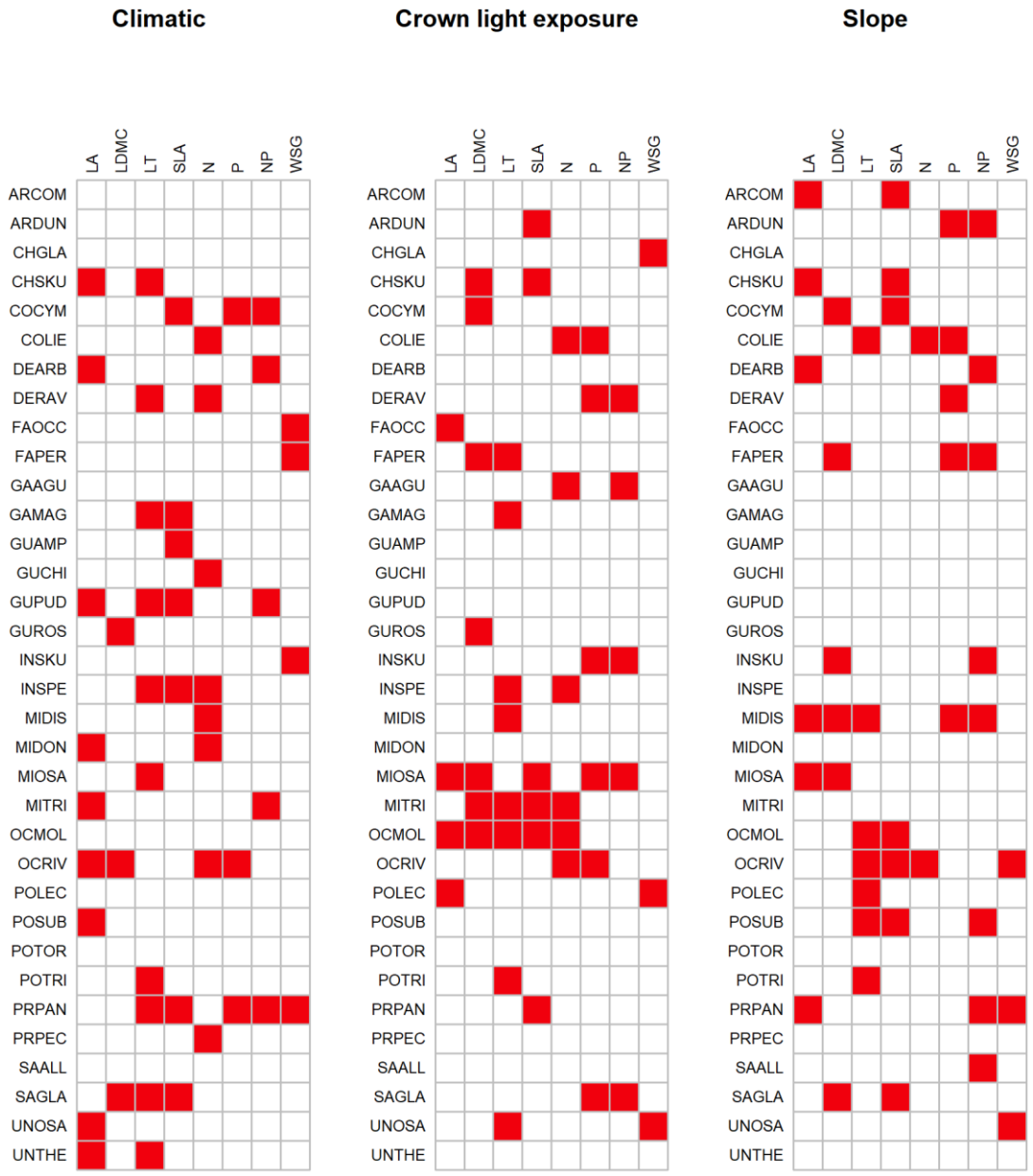
Trait	β	Std. Error	DF	t. value	p. value
LA	0.003	0.0022	198	1.386	0.167
LT	-0.0005	0.0007	198	-0.71	0.476
SLA	-0.0011	0.0009	198	-1.13	0.259
LDMC	0.0001	0.0006	198	0.228	0.819
N	0.0012	0.0011	198	1.108	0.269
P	0.0022	0.0018	198	1.261	0.208
NP	0.0019	0.0012	198	1.618	0.107
WSG	0.0001	0.0006	198	0.103	0.917

Method: For each trait and each species, we calculated the coefficient of variation (CV) for subsamples of incremental size, starting with n=4 until n=all samples taken (10, in most cases). Subsamples were randomly selected. For each trait, we subsequently fitted a linear mixed effects model of the effect of the sample size on CV, using species identity as a random factor. Estimated coefficents are the fixed effect estimates of this linear mixed effects model.

S5 Table. Principal component analysis of six functional traits measured in 335 individual trees of 34 species. The functional traits included in the analysis were: Leaf area (LA), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N), leaf phosphorus content (P), and wood specific gravity (WSG).

	PC 1	PC 2	PC 3	PC 4	PC 5
Variance	2.699	1.514	1.032	0.739	0.55
% of variance	38.554	21.622	14.736	10.554	7.86
Cumulative % of Variance	38.554	60.177	74.913	85.467	93.327

S6 File. Global Biodiversity Information Facility Data Providers: See Supplementary Material Chapter 1, Appendix B, page 89.

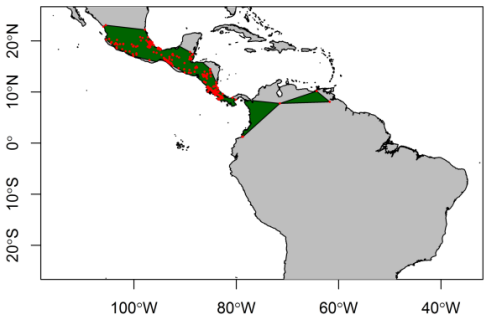


S7 Fig. Graphical display of the univariate linear regression models of eight functional traits against three environmental variables (climate, crown light exposure and slope inclination of growing site). Red squares indicate models with p-value< 0.1. Functional traits are abbreviated as follows: leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N), leaf phosphorus content (P), leaf nitrogen to phosphorus ratio (N:P) and wood specific gravity (WSG). Species codes are in File S9.

S8 File. Maps of the geographic ranges of the 34 tree species studied.

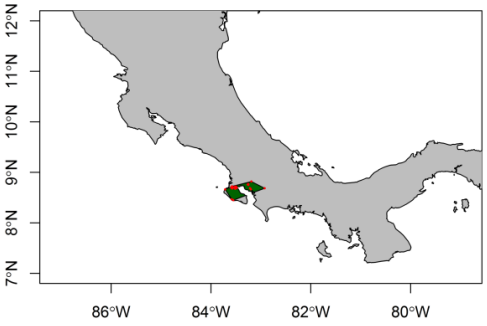
Maps represent occurrences derived from different sources plotted as red points. The green polygon was constructed using an alpha-hull algorithm with 8 as alpha value. Maps in the same row belong to species in the same genus, maps on the right side are for endemic species and maps on the left side are for widespread species. Below the map is the amount of records available for each species.

Ardisia compressa



n=876

Ardisia dunlapiana



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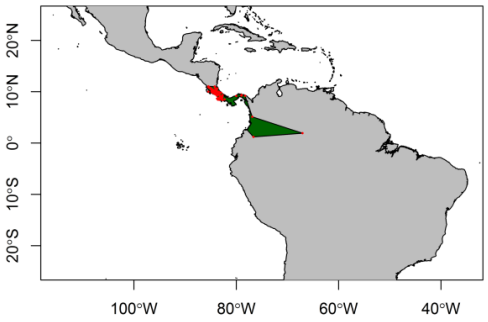

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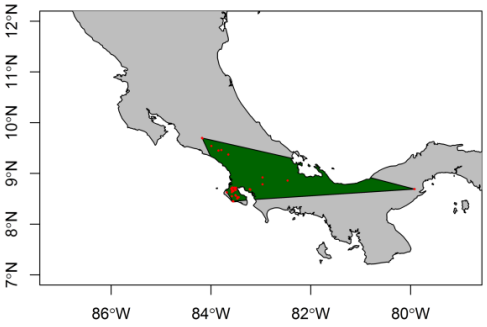

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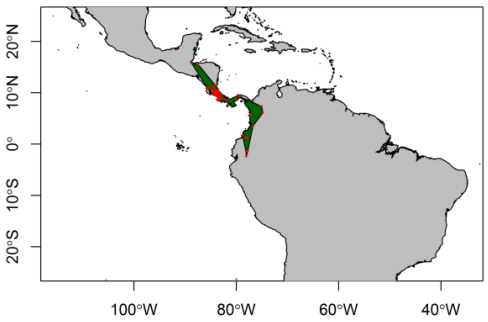

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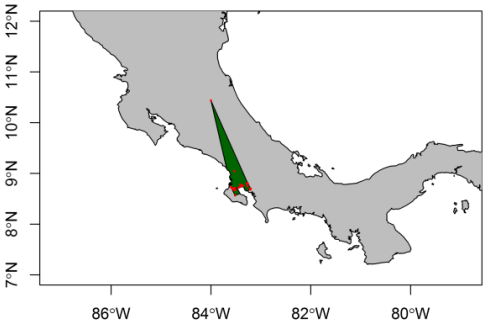

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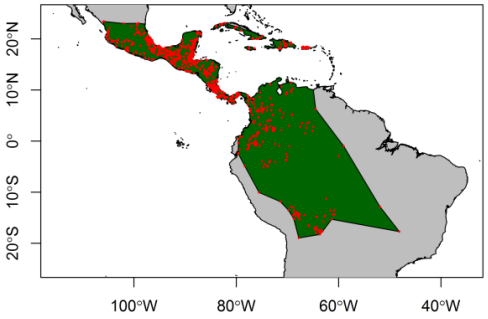

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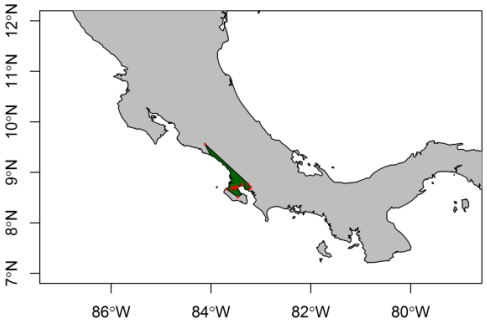

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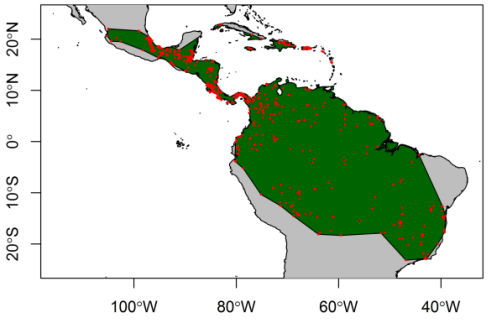

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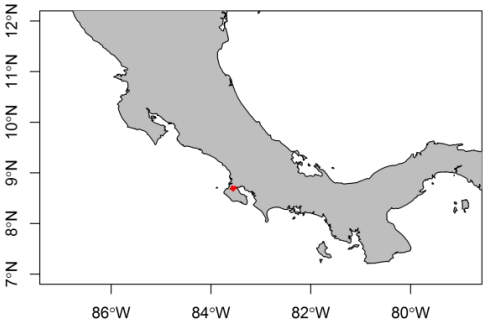

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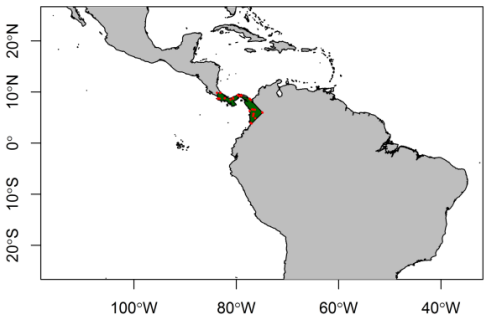

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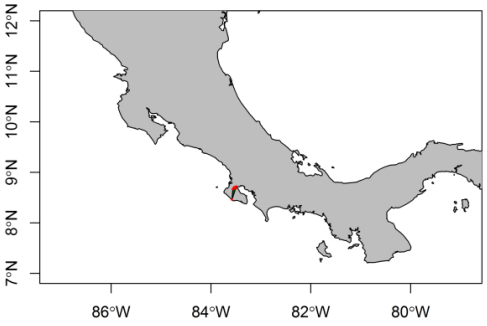

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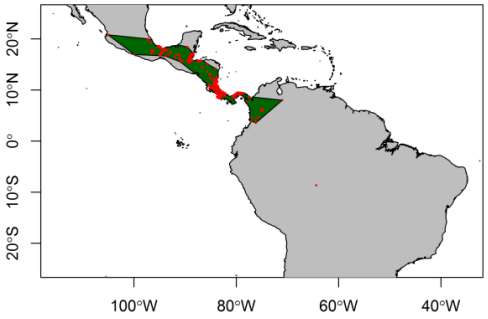

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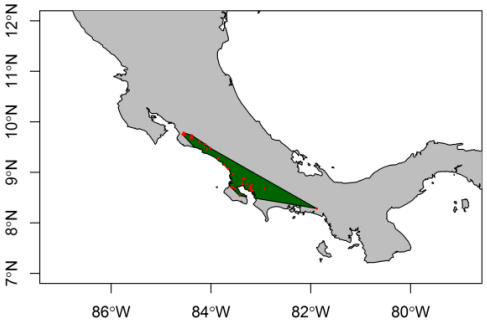

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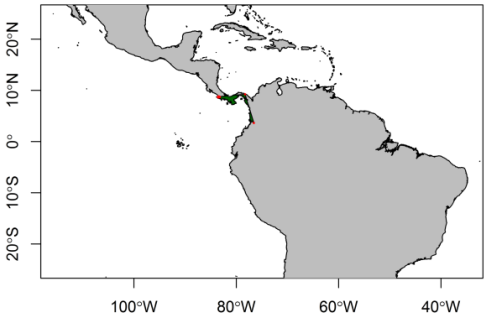

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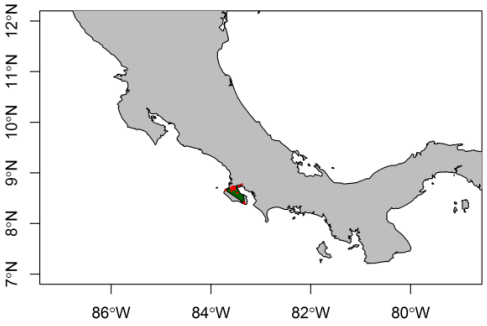

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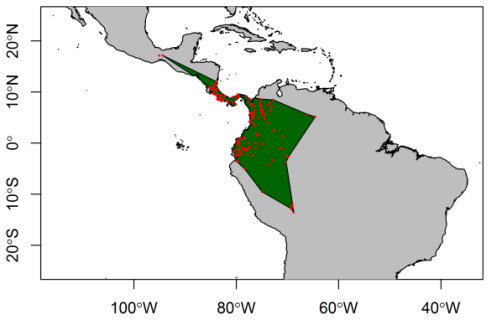

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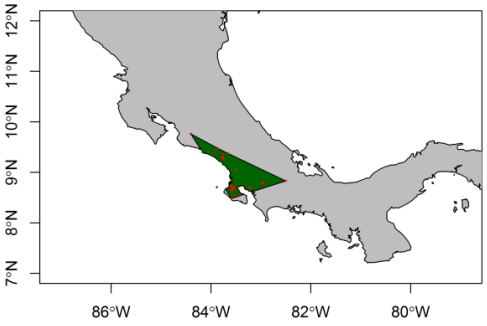

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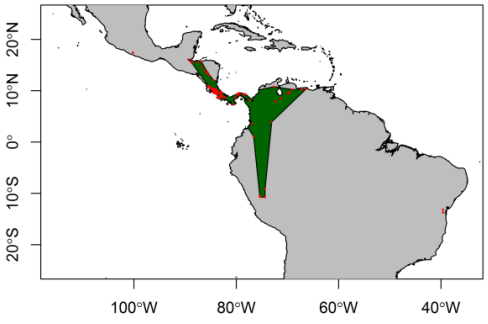

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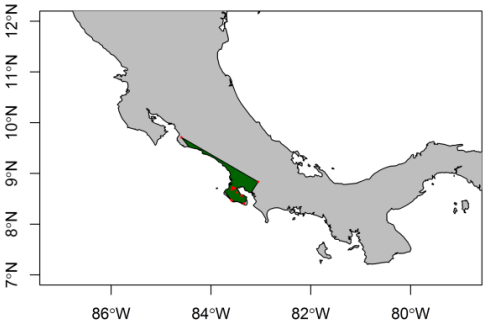

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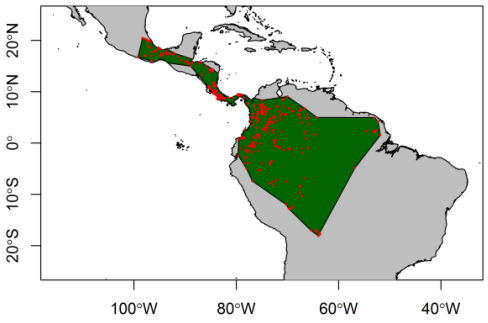

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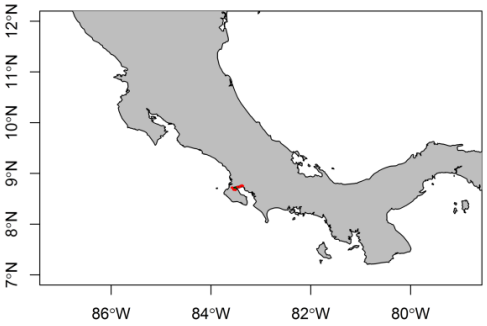

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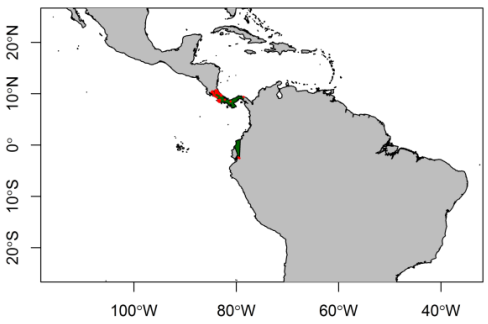

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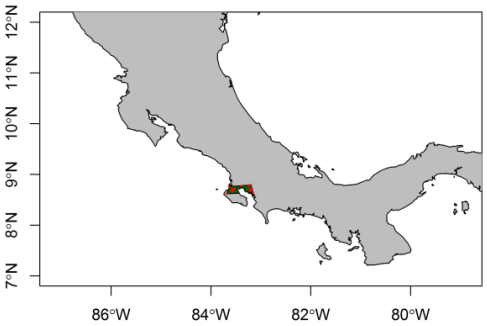

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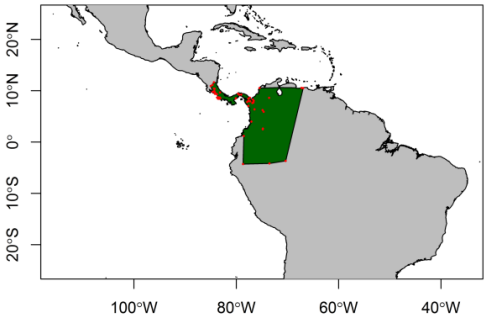

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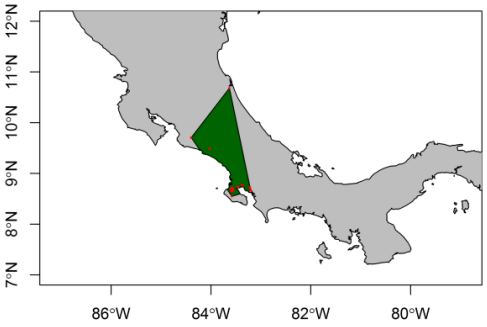

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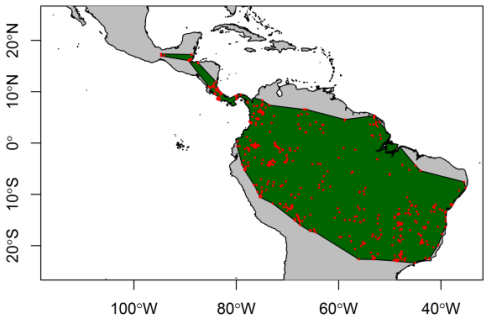
Pouteria torta



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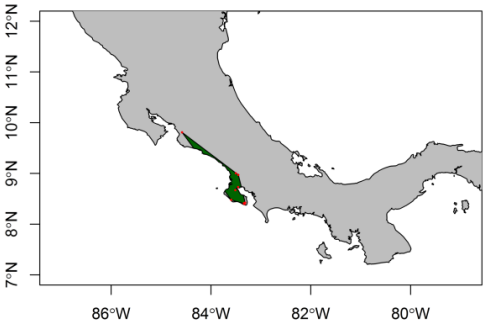

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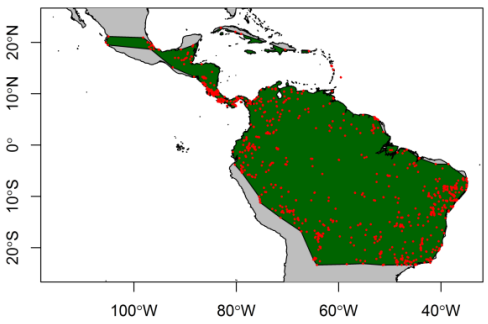

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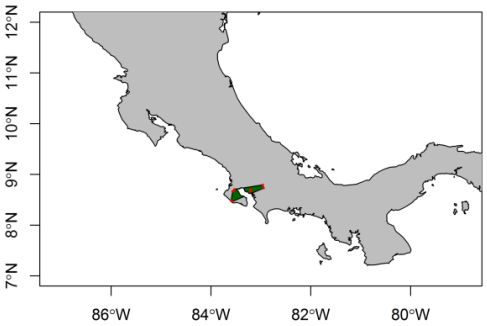

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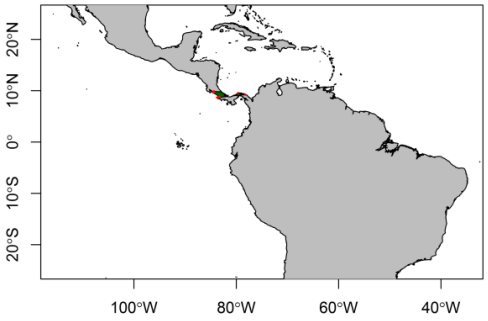

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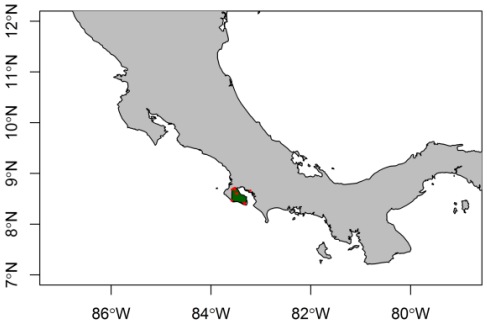


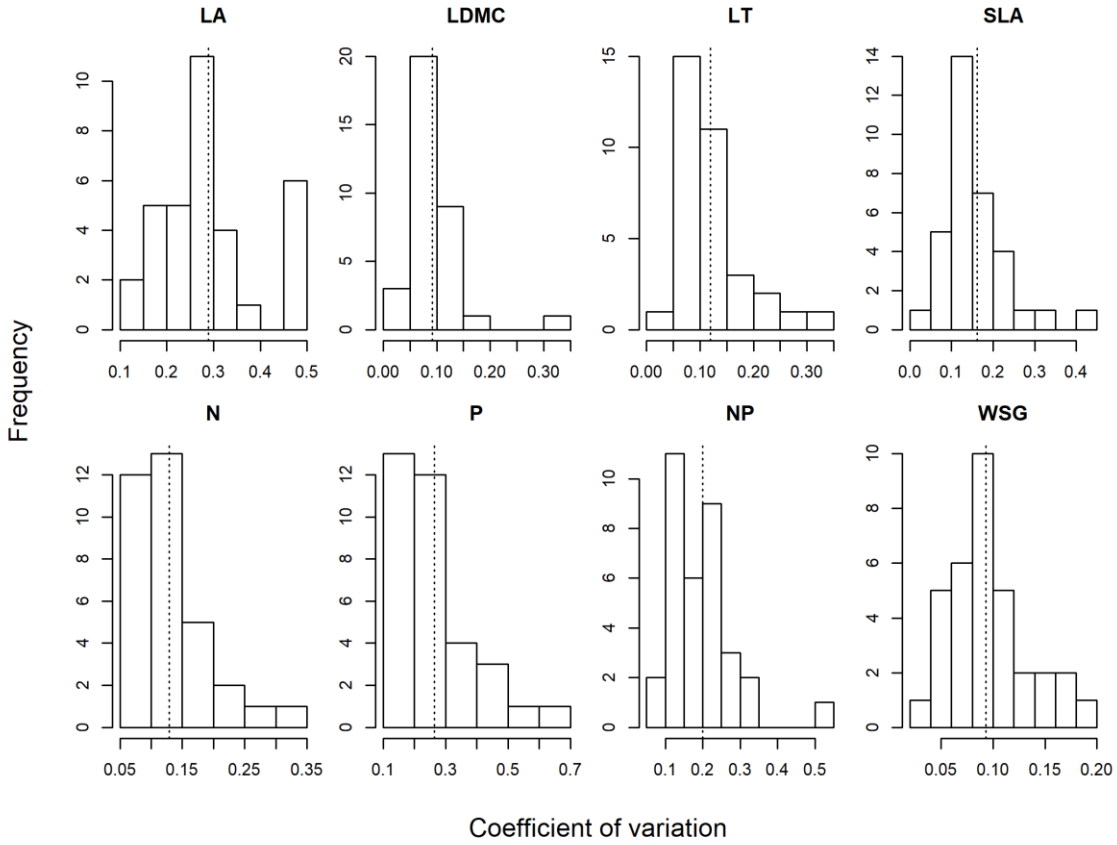
n=32

S9 Table. Coefficients of variation of eight functional traits and multivariate functional dispersion (FD) for 34 neotropical tree species. Traits: Leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N) , leaf phosphorus content (P), leaf N:P ratio (NP) and wood specific gravity (WSG).

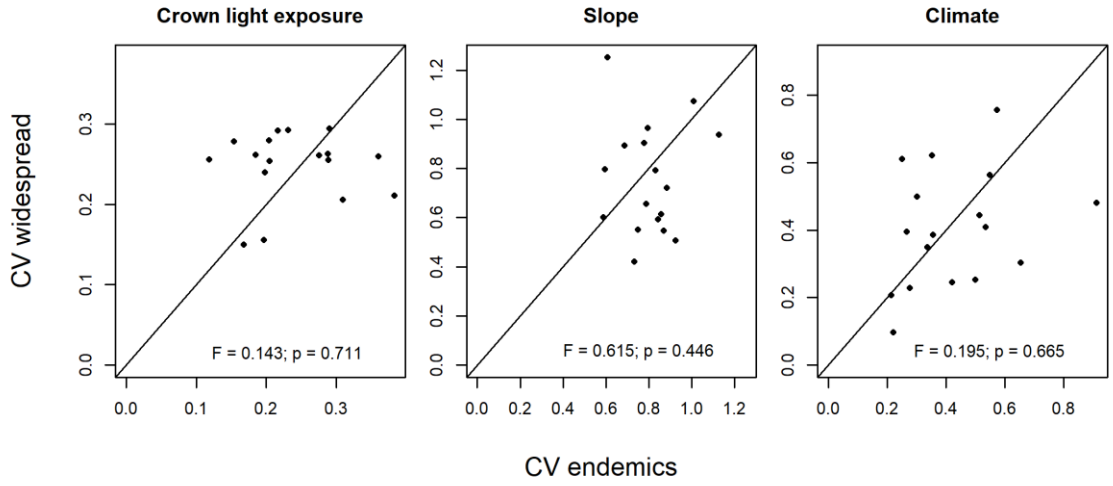
Species Code	LA	LDMC	LT	SLA	N	NP	P	WSG	FD
ARCOM	0.212	0.115	0.103	0.136	0.095	0.225	0.260	0.092	0.839
ARDUN	0.237	0.104	0.082	0.097	0.067	0.125	0.137	0.041	0.507
CHGLA	0.264	0.084	0.078	0.130	0.242	0.198	0.352	0.090	0.986
CHSKU	0.480	0.092	0.202	0.259	0.302	0.257	0.666	0.104	1.257
COCYM	0.133	0.100	0.156	0.246	0.128	0.223	0.292	0.188	1.072
COLIE	0.319	0.151	0.077	0.216	0.131	0.124	0.204	0.098	0.854
DEARB	0.268	0.063	0.105	0.115	0.121	0.150	0.191	0.108	0.767
DERAV	0.235	0.066	0.094	0.090	0.096	0.220	0.225	0.082	0.750
FAOCC	0.258	0.029	0.108	0.084	0.103	0.146	0.139	0.068	0.708
FAPER	0.206	0.103	0.100	0.167	0.095	0.136	0.158	0.109	0.833
GAAGU	0.456	0.056	0.096	0.148	0.110	0.296	0.334	0.031	0.960
GAMAG	0.196	0.103	0.105	0.189	0.071	0.128	0.172	0.055	0.721
GUAMP	0.298	0.060	0.071	0.102	0.063	0.188	0.190	0.105	0.832
GUCHI	0.120	0.146	0.129	0.248	0.164	0.142	0.246	0.085	0.970
GUPUD	0.332	0.090	0.178	0.198	0.099	0.139	0.149	0.087	0.929
GUROS	0.275	0.073	0.089	0.074	0.103	0.135	0.195	0.106	0.623
INSKU	0.264	0.094	0.183	0.173	0.089	0.206	0.195	0.088	1.108
INSPE	0.254	0.089	0.138	0.147	0.106	0.200	0.224	0.141	1.350
MIDIS	0.331	0.057	0.090	0.102	0.092	0.211	0.281	0.080	0.869
MIDON	0.271	0.073	0.102	0.148	0.085	0.166	0.154	0.070	0.784
MIOSA	0.467	0.076	0.069	0.096	0.118	0.271	0.269	0.069	1.008
MITRI	0.241	0.127	0.104	0.189	0.101	0.339	0.459	0.091	1.163
OCMOL	0.258	0.095	0.135	0.232	0.112	0.130	0.110	0.163	0.938
OCRIV	0.322	0.085	0.090	0.126	0.191	0.068	0.222	0.092	0.891
POLEC	0.489	0.099	0.084	0.181	0.207	0.502	0.528	0.042	1.828
POSUB	0.160	0.101	0.075	0.122	0.164	0.174	0.158	0.070	0.896
POTOR	0.496	0.059	0.266	0.174	0.136	0.211	0.320	0.078	1.078
POTRI	0.280	0.040	0.040	0.045	0.164	0.082	0.170	0.054	0.568
PRPAN	0.395	0.048	0.337	0.143	0.162	0.140	0.216	0.151	1.295
PRPEC	0.200	0.077	0.054	0.132	0.137	0.234	0.415	0.123	1.184
SAALL	0.500	0.314	0.234	0.406	0.251	0.191	0.337	0.166	1.805
SAGLA	0.197	0.135	0.141	0.316	0.113	0.348	0.439	0.120	1.420
UNOSA	0.263	0.077	0.056	0.137	0.090	0.246	0.284	0.052	0.884
UNTHE	0.157	0.050	0.091	0.112	0.066	0.248	0.287	0.071	0.914

Species codes: *Ardisia compressa* (ARCOM), *Ardisia dunlapiana* (ARDUN), *Chrysochlamys glauca* (CHGLA), *Chrysochlamys skutchii* (CHSKU), *Cordia cymosa* (COCYM), *Cordia liesneri* (COLIE), *Dendropanax arboreus* (DEARB), *Dendropanax ravenii*

(DERAV), *Faramea occidentalis* (FAOCC), *Faramea permagnifolia* (FAPER), *Garcinia aguilarii* (GAAGU), *Garcinia magnifolia* (GAMAG), *Guatteria amplifolia* (GUAMP), *Guatteria chiriquiensis* (GUCHI), *Guatteria pudica* (GUPUD), *Guatteria rostrata* (GUROS), *Inga skutchii* (INSKU), *Inga spectabilis* (INSPE), *Miconia dissitinervia* (MIDIS), *Miconia donaeana* (MIDON), *Miconia osaensis* (MIOSA), *Miconia trinervia* (MITRI), Ocotea *mollifolia* (OCMOL), *Ocotea rivularis* (OCRIV), *Pouteria lecytidicarpa* (POLEC), *Pouteria subrotata* (POSUB), *Pouteria torta* (POTOR), *Pouteria triplarifolia* (POTRI), *Protium panamense* (PRPAN), *Protium pecuniosum* (PRPEC), *Sapium allenii* (SAALL), *Sapium glandulosum* (SAGLA), *Unonopsis osae* (UNOSA), *Unonopsis theobromifolia* (UNTHE).



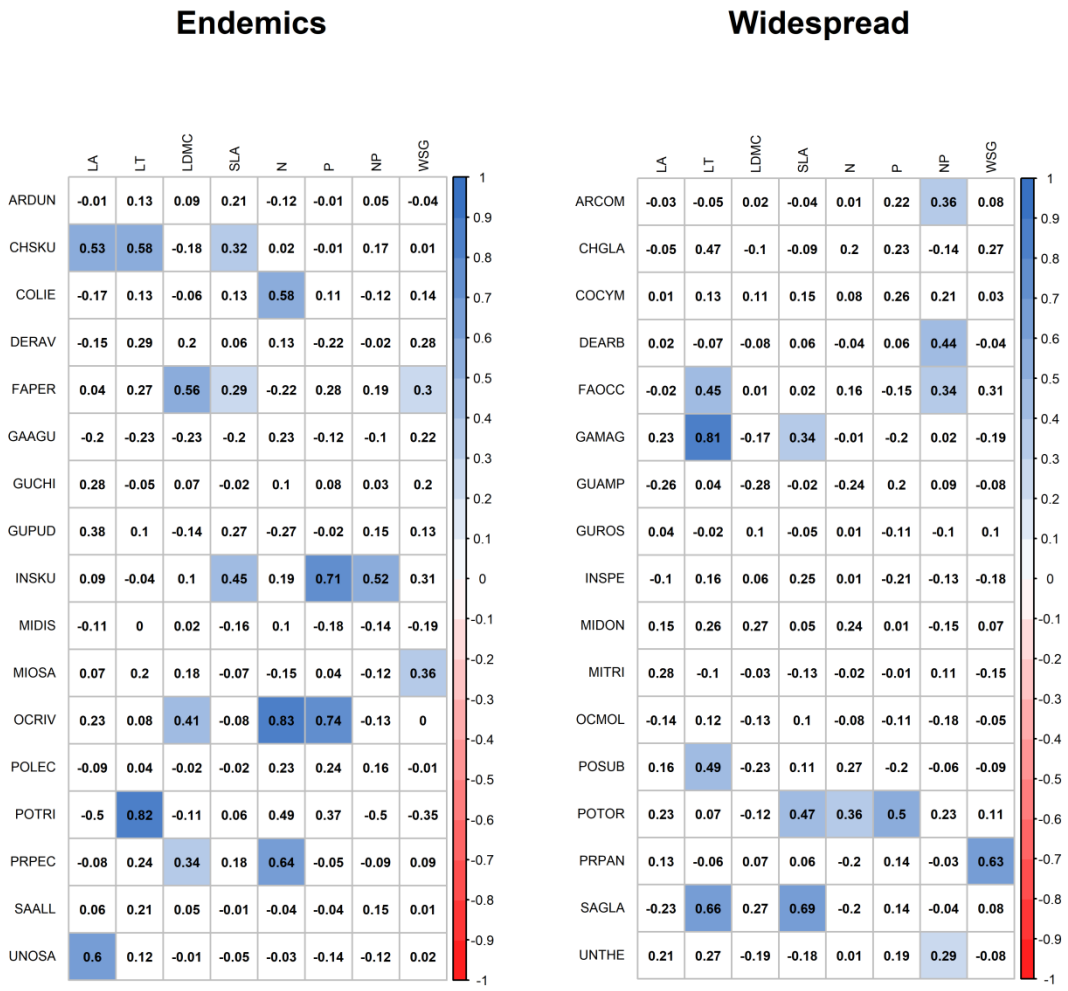
S10 Fig. Frequency distributions of the coefficients of variation of eight functional traits in 34 tropical trees species. The dotted vertical line indicates the mean of the coefficients of variation. Leaf area (LA), leaf dry matter content (LDMC), leaf thickness (LT), specific leaf area (SLA), leaf nitrogen content (N), leaf phosphorus content (P), leaf N:P ratio (NP) and wood specific gravity (WSG).



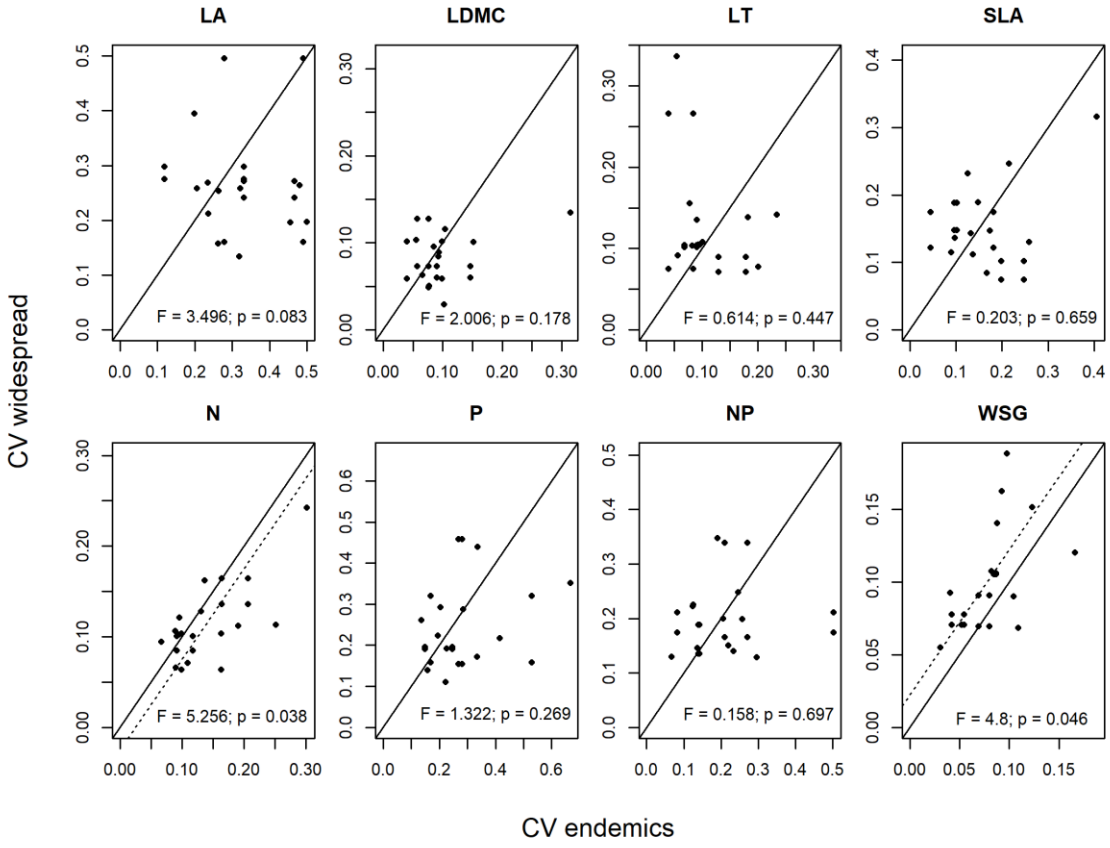
S11 Fig. Coefficients of variation (CV) of three environmental variables used to characterize the sampled trees' growing sites: crown light exposure, the slope of the growing sites and local climate. Each point represents one pair of congeneric endemic and widespread species. The diagonal represents the null model, i.e. positioning of points along the line indicates equal environmental variability among the sampled trees of both species in a pair. Points above the line represent pairs with environmental CV higher in widespread species and points below the line pairs with CV higher in endemic species.

S12 Table. Fixed effects coefficients (β ± 1 standard error), derived from linear mixed effects models, for the effects of environmental variables measured on eight functional traits in 335 individual trees of 34 species, using species identity as a random effect. The functional traits included in the analysis were: Leaf area (LA), leaf thickness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (N), leaf phosphorus content (P), leaf nitrogen phosphorus ratio (NP) and wood specific gravity (WSG). Statistically significant results (Ho: β=0) are in bold.

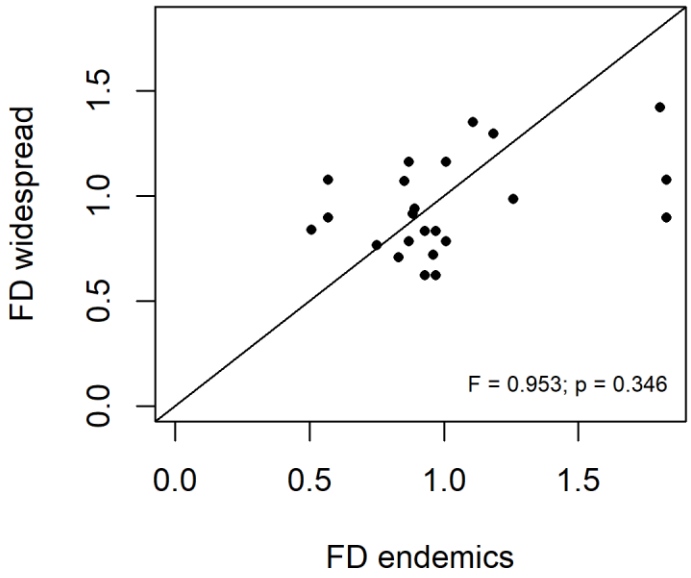
		Climatic PC1				Crown Light Exposure				Inclination of growing sites			
Trait	DF	β	Std.Error	t.value	p.value	β	Std.Error	t.value	p.value	β	Std.Error	t.value	p.value
LA	300	-5.530	5.062	-1.092	0.276	12.683	10.836	1.170	0.243	-0.892	0.526	-1.697	0.091
LDMC	300	0.199	1.113	0.179	0.858	7.806	2.339	3.338	0.001*	-0.149	0.116	-1.288	0.199
LT	300	0.003	0.001	2.580	0.010*	0.007	0.003	2.593	0.010*	0.000	0.000	-1.894	0.059
SLA	300	0.706	0.920	0.767	0.444	-7.567	1.923	-3.935	<0.001*	0.122	0.096	1.264	0.207
N	287	0.001	0.009	0.116	0.908	0.009	0.020	0.460	0.646	0.000	0.001	-0.149	0.882
P	287	0.000	0.001	0.086	0.932	0.001	0.002	0.361	0.719	0.000	0.000	-0.210	0.833
NP	287	-0.121	0.175	-0.691	0.490	-0.342	0.379	-0.902	0.368	-0.004	0.018	-0.206	0.837
WSG	298	0.005	0.002	3.143	0.002*	0.003	0.004	0.883	0.378	0.000	0.000	-0.130	0.896



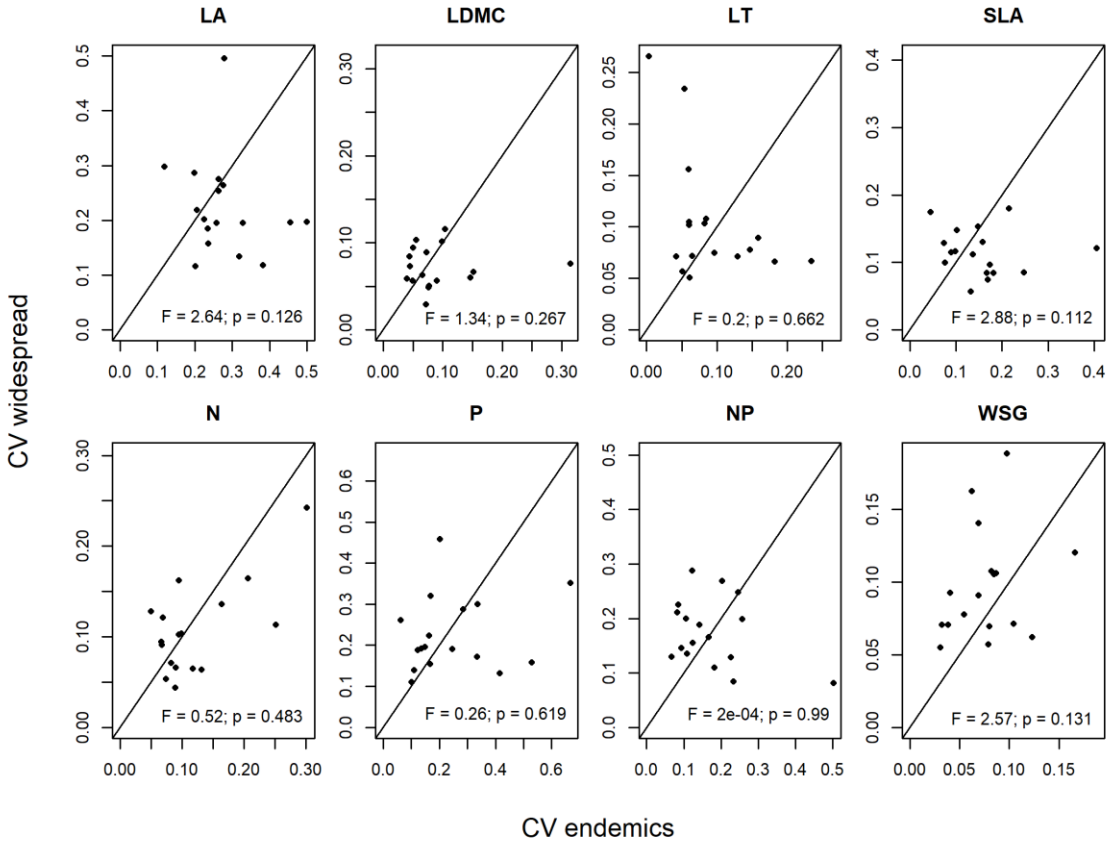
S13 Fig. Mantel tests (based on Pearson's correlation coefficient) between the geographical distance of individuals and the absolute difference between the trait values of the individuals for eight functional traits in 34 neotropical tree species. Correlation coefficients significantly different from zero ($p<0.05$) are presented with color.



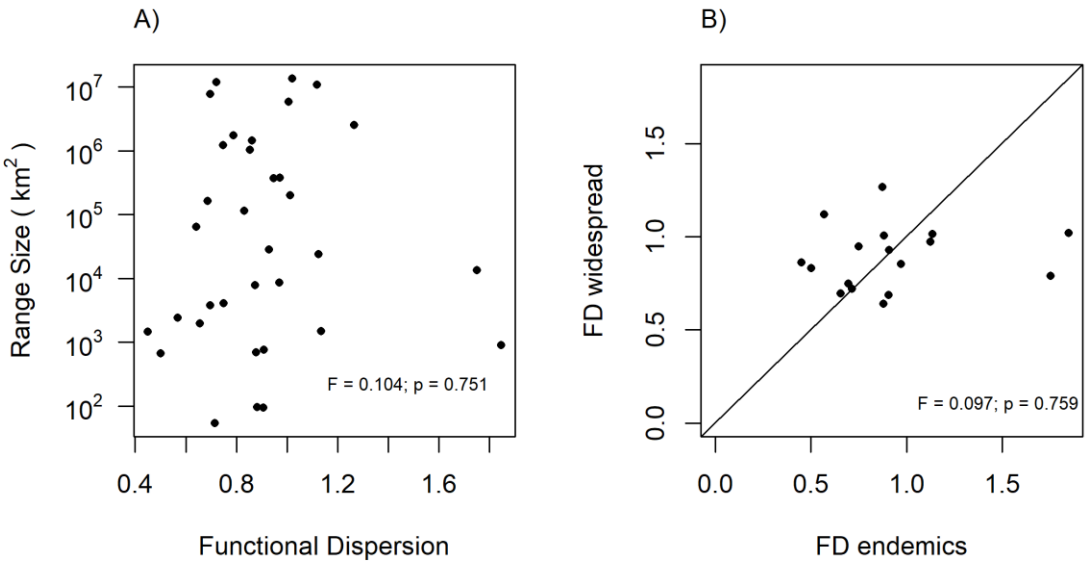
S14 Fig. Coefficients of variation (CV) in eight functional traits using all combinations of possible pairs of endemic and widespread congeners from 17 genera of neotropical tree species.



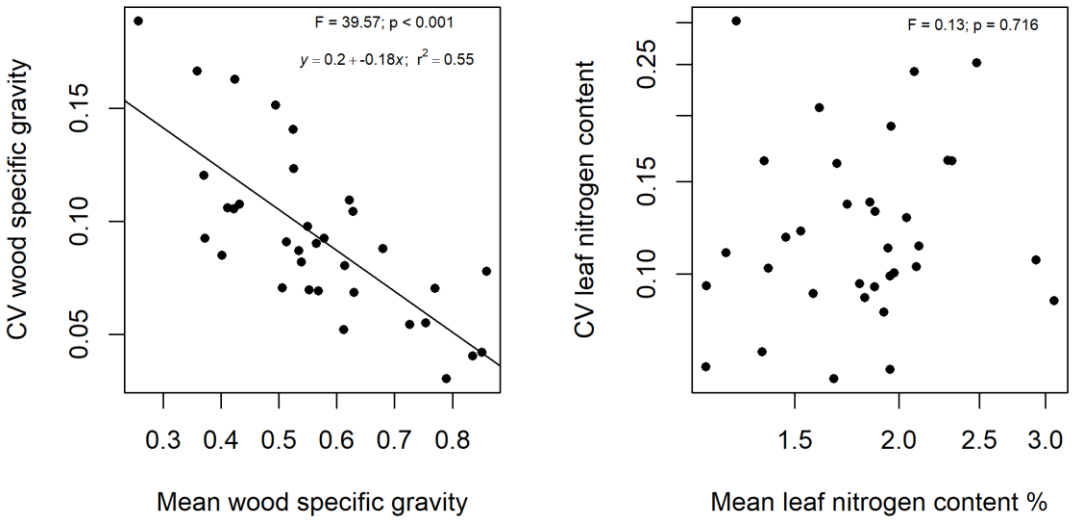
S15 Fig. Functional dispersion (FD) of 17 congeneric pairs of endemic neotropical tree species and their widespread congeners, using all combinations of possible pairs of endemic and widespread congeners from 17 genera of neotropical tree species.



S16 Fig. Coefficients of variation (CV) in eight functional traits. Leaf area (LA), leaf thickness (LT), specific leaf area (SLA) and leaf dry matter content (LDMC), wood specific gravity (WSG), leaf nitrogen content (N) and leaf phosphorus content (P), and N:P ratio of endemic neotropical tree species and their widespread congeners after removing variation related to variation in environmental variables. Each point represents one congeneric pair of species (endemic, widespread). The diagonal represents the null model, i.e. positioning of points along the line indicates equal trait variability of both species in a pair. Points above the line represent pairs with CV greater in widespread species, and points below the line pairs with CV greater in endemic species. The p-value is for the associated statistics testing if the intercept = 0.



S17 Fig. Functional dispersion calculated from six functional traits after removing variation attributable to variation in measured environmental variables for the studied 34 tropical tree species. A) Functional dispersion in relation to the range size. B) Functional dispersion (FD) of 17 congeneric pairs of endemic species and their widespread congeners. In Fig 5B each point represents one pair (endemic, widespread). The diagonal represents the null model, i.e. positioning of points along the line indicates equal functional dispersion of both species in a pair. Points above the line represent pairs with FD higher in widespread species, and points below the line pairs with FD higher in endemic species.



S18 Fig. Linear relationships between the mean and the coefficient of variation of wood specific gravity and leaf nitrogen content among the 34 neotropical tree species analyzed. The regression line is represented by a solid line when the effect of the regressor was significantly different from zero, and with a dotted line when it was not significant.

S19 Table. Estimated ages of species included in the present analysis according to available phylogenies (Erkens et al., 2007; Li & Wen, 2013; Fine et al., 2014).

Family	Species name	Range size class	Extent of Occurrence	Age clade Million years	Reference
Annonaceae	*Guatteria amplifolia*	widespread	1.02 • 106	1.6 ± 0.6	Erkens et al. 2007
Annonaceae	*Guatteria chiriquiensis*	endemics	8.60 • 103	<1.6	Erkens et al. 2007
Annonaceae	*Guatteria pudica*	endemics	6.87 • 102	<1.6	Erkens et al. 2007
Annonaceae	*Guatteria rostrata*	widespread	6.45 • 104	5-1.6	Erkens et al. 2007
Araliaceae	*Dendropanax arboreus*	widespread	7.69 • 106	< 10	Li et al. 2013
Araliaceae	*Dendropanax ravenii*	endemics	1.96 • 103	< 10	Li et al. 2013
Burseraceae	*Protium panamense*	widespread	1.98 • 105	< 5	Fine et al. 2014
Burseraceae	*Protium pecuniosum*	endemics	1.48 • 103	< 5	Fine et al. 2014

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S20 Table. Seed size (length x width) and seed dispersers of the 34 neotropical tree species used in the analysis. B: Birds, M: mammals.

Family	Species name	Seed Size (mm)	Dispersers	Ref.
Annonaceae	*Guatteria amplifolia*	10 x 6	B, M	1
Annonaceae	*Guatteria pudica*	8 x 4	B, M	1
Annonaceae	*Guatteria rostrata*	15 x 7	B, M	1
Annonaceae	*Guatteria chiriquiensis*	8 x 4	B, M	1
Annonaceae	*Unonopsis osae*	12 x 6	B	2
Annonaceae	*Unonopsis theobromifolia*	10 x 6	B	2
Araliaceae	*Dendropanax arboreus*	5 x 4	B	3
Araliaceae	*Dendropanax ravenii*	6 x 4	B	3
Boraginaceae	*Cordia cymosa*	9 x 9	B, M	4
Boraginaceae	*Cordia liesneri*	15 x 10	B	5
Burseraceae	*Protium panamense*	13 x 8	M, B	6
Burseraceae	*Protium pecuniosum*	21 x 10	M, B	7
Clusiaceae	*Chrysochlamys glauca*	10 x 4	B	6
Clusiaceae	*Chrysochlamys skutchii*	10 x 4	B	8
Clusiaceae	*Garcinia aguilarii*	35 x 35	M	8
Clusiaceae	*Garcinia magnifolia*	30 x 30	M	9
Euphorbiaceae	*Sapium allenii*	5 x 5	B	9
Euphorbiaceae	*Sapium glandulosum*	5 x 5	B	9
Fabaceae	*Inga skutchii*	15 x 5	M	10
Fabaceae	*Inga spectabilis*	35 x 10	M	10
Lauraceae	*Ocotea mollifolia*	40 x 18	B	11
Lauraceae	*Ocotea rivularis*	11 x 6	B	11
Melastomataceae	*Miconia dissitinervia*	0.5 x 0.5	B	12
Melastomataceae	*Miconia donaeana*	0.6 x 0.6	B	12
Melastomataceae	*Miconia osaensis*	0.5 x 0.5	B	13
Melastomataceae	*Miconia trinervia*	0.9 x 0.9	B	12
Myrsinaceae	*Ardisia compressa*	4 x 4	B	14
Myrsinaceae	*Ardisia dunlapiana*	3 x 3	B	14
Rubiaceae	*Faramea occidentalis*	10 x 10	B	6
Rubiaceae	*Faramea permagnifolia*	13 x 13	B	15
Sapotaceae	*Pouteria lecytidicarpa*	29 x 20	M	16
Sapotaceae	*Pouteria subrotata*	22 x 19	M	16
Sapotaceae	*Pouteria torta*	32 x 17	M	16
Sapotaceae	*Pouteria triplarifolia*	30 x 18	M	16

[1] Maas et al., 2015; [2] Maas et al., 2007; [3] Cannon & Cannon, 1989; [4] Miller, 1987; [5] Miller, 1988; [6] Paton & Calderón, 2016; [7] Daly, 2007; [8] Hammel 2010; [9] González, 2010; [10] Zamora, 2010; [11] González & Hammel, 2007; [12] Almeda, 2007; [13] Kriebel et al., 2008; [14] Morales, 2007; [15] Taylor, 1996; [16] Morales, 2015.

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4.4 Supporting information Chapter 3:

What property of the species functional traits defines better the realized niche breadth of tropical trees: the central position or the variation?

Appendix S1. References of the sources of data for nitrogen leaf content and specific leaf area

Leaf Nitrogen content

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S3. Correlation between bioclimatic variables within the tropical region (23.5° N-23.5°S) in America (See table S3, page 103

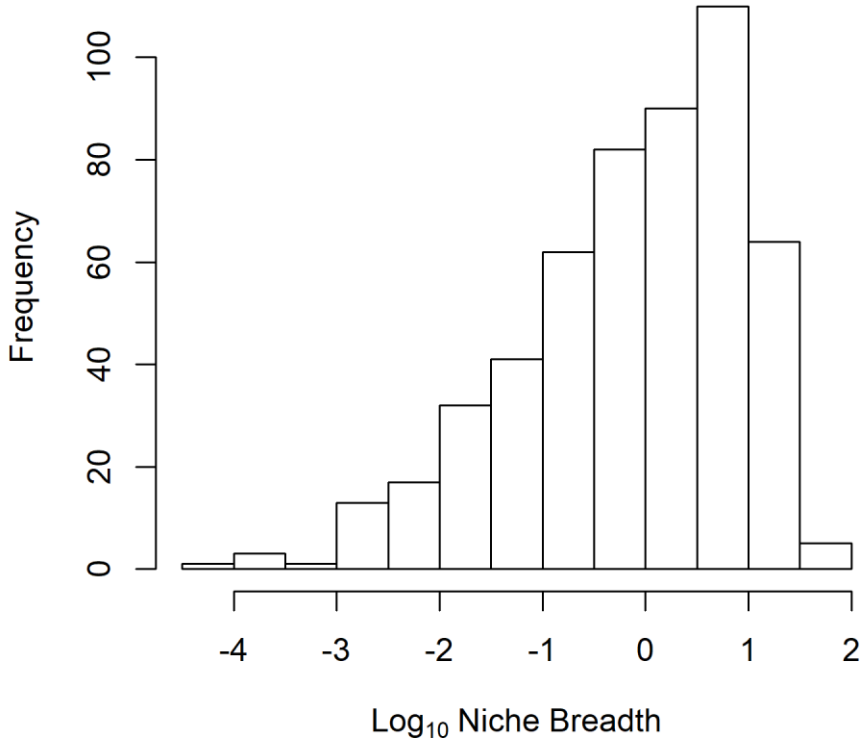

Figure S4. Frequency distribution of the log-transformed niche breadth values for 521 tropical tree species.

Table S5. List of tropical tree species included in tha analysis with the number of trait values for each trait (N:Leaf nitrogen content, SLA: Specific leaf area, WD: Wood density) and the number of occurrences (N.occ).

Family	Species	WD	N	SLA	N.occ
Actinidiaceae	Saurauia yasicae Loes.			11	383
Adoxaceae	Viburnum costaricanum Hemsl.		5	10	307
Adoxaceae	Viburnum venustum C.V.Morton			5	81
Anacardiaceae	Anacardium excelsum (Bertero ex Kunth) Skeels	8	15	7	272
Anacardiaceae	Anacardium giganteum Hancock ex Engl.	7			78
Anacardiaceae	Anacardium occidentale L.	6			466
Anacardiaceae	Anacardium spruceanum Benth. ex Engl.	6		7	45
Anacardiaceae	Astronium graveolens Jacq.	16	16	10	703
Anacardiaceae	Astronium lecointei Ducke	9			89
Anacardiaceae	Spondias mombin L.	18	10	8	148
Anacardiaceae	Spondias purpurea L.		7		661
Anacardiaceae	Spondias radlkoferi Donn.Sm.			5	257
Anacardiaceae	Tapirira guianensis Aubl.	18	12	11	957
Anacardiaceae	Tapirira obtusa (Benth.) J.D.Mitch.			7	289
Annonaceae	Bocageopsis multiflora (Mart.) R.E.Fr.	5			283
Annonaceae	Cymbopetalum costaricense (Donn.Sm.) R.E.Fr.			6	128
Annonaceae	Desmopsis bibracteata (B.L.Rob.) Saff.		5		114
Annonaceae	Duguetia calycina Benoist			7	97
Annonaceae	Duguetia surinamensis R.E.Fr.		7	13	66
Annonaceae	Fusaea longifolia (Aubl.) Saff.		5	11	304
Annonaceae	Guatteria amplifolia Triana & Planch.	11	13	51	701
Annonaceae	Guatteria chiriquiensis R.E.Fr.	9	9	45	42
Annonaceae	Guatteria pudica N.Zamora & Maas	16	10	80	32
Annonaceae	Guatteria wachenheimii Benoist		5	11	42
Annonaceae	Unonopsis pittieri Saff.	8			136
Annonaceae	Unonopsis rufescens (Baill.) R.E. Fr.		5	23	44
Annonaceae	Unonopsis theobromifolia N. Zamora & Poveda	10	10	50	45
Annonaceae	Xylopia aromatica (Lam.) Mart.	5			991
Annonaceae	Xylopia nitida Dunal	6	20	25	59
Apocynaceae	Ambelania acida Aubl.		10	24	114
Apocynaceae	Aspidosperma album (Vahl) Benoist ex Pichon	7	7	6	55
Apocynaceae	Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	5			165
Apocynaceae	Aspidosperma desmanthum Benth. ex Müll.Arg.		9	21	217
Apocynaceae	Aspidosperma excelsum Benth.	5	7	11	302
Apocynaceae	Aspidosperma megalocarpon Müll.Arg.	7			306
Apocynaceae	Aspidosperma polyneuron Müll.Arg.	9			171
Apocynaceae	Couma macrocarpa Barb.Rodr.	6			257
Apocynaceae	Geissospermum laeve (Vell.) Miers			5	40
Apocynaceae	Lacmellea aculeata (Ducke) Monach.			10	144

Family	Species	WD	N	SLA	N.occ
Apocynaceae	Lacmellea panamensis (Woodson) Markgr.	9			230
Apocynaceae	Lacmellea zamorae J.F.Morales			38	43
Apocynaceae	Macoubea guianensis Aubl.			8	216
Apocynaceae	Parahancornia fasciculata (Poir.) Benoist	7			38
Apocynaceae	Tabernaemontana arborea Rose ex J.D.Sm.	13			189
Araliaceae	Dendropanax arboreus (L.) Decne. & Planch.	51	21	63	975
Araliaceae	Dendropanax caucanus (Harms) Harms			12	177
Araliaceae	Dendropanax querceti Donn.Sm.		10		120
Araliaceae	Oreopanax xalapensis (Kunth) Decne. & Planch.		9	5	912
Araliaceae	Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	16	7	5	685
Araliaceae	Schefflera rodriguesiana Frodin			10	100
Arecaceae	Oenocarpus mapora H.Karst.		17		100
Arecaceae	Synechanthus warscewiczianus H.Wendl.			10	82
Betulaceae	Alnus acuminata Kunth	14	211		951
Bignoniaceae	Handroanthus capitatus (Bureau & K.Schum.) Mattos	6			67
Bignoniaceae	Handroanthus chrysanthus (Jacq.) S.O.Grose	10			655
Bignoniaceae	Handroanthus guayacan (Seem.) S.O.Grose	7			201
Bignoniaceae	Handroanthus ochraceus (Cham.) Mattos		6		604
Bignoniaceae	Handroanthus serratifolius (Vahl) S.O.Grose	35			395
Bignoniaceae	Jacaranda copaia (Aubl.) D.Don	27	17	23	604
Bignoniaceae	Jacaranda obtusifolia Bonpl.	6			225
Bignoniaceae	Roseodendron donnell-smithii (Rose) Miranda	11			106
Bignoniaceae	Tabebuia insignis (Miq.) Sandwith	5			195
Bignoniaceae	Tabebuia ochracea A.H. Gentry		8	8	152
Bignoniaceae	Tabebuia rosea (Bertol.) Bertero ex A.DC.	9	10		933
Bixaceae	Cochlospermum vitifolium (Willd.) Spreng.		13	7	1206
Boraginaceae	Cordia alliodora (Ruiz & Pav.) Oken	19	52	13	60
Boraginaceae	Cordia bicolor A.DC.	31		6	380
Boraginaceae	Cordia cymosa (Donn.Sm.) Standl.	8	13	40	131
Boraginaceae	Cordia dwyeri Nowicke	8			75
Boraginaceae	Cordia liesneri J.S.Mill.	8	9	45	32
Boraginaceae	Cordia panamensis L.Riley			6	320
Boraginaceae	Cordia sagotii I.M.Johnst.		13	20	67
Burseraceae	Bursera simaruba (L.) Sarg.	8	17	15	593
Burseraceae	Dacryodes nitens Cuatrec.		8	7	82
Burseraceae	Protium apiculatum Swart		5	10	181
Burseraceae	Protium decandrum (Aubl.) Marchand		12	26	144
Burseraceae	Protium demerarense Swart		13	12	34
Burseraceae	Protium glabrum (Rose) Engl.			8	316
Burseraceae	Protium heptaphyllum (Aubl.) Marchand	10			916
Burseraceae	Protium opacum Swart		20	38	285
Burseraceae	Protium pallidum Cuatrec.		9	9	40
Burseraceae	Protium panamense (Rose) I.M.Johnst.	11	10	44	147

Family	Species	WD	N	SLA	N.occ
Burseraceae	Protium pecuniosum D.C. Daly	10	14	50	39
Burseraceae	Protium pittieri (Rose) Engl.	13			103
Burseraceae	Protium sagotianum Marchand		19	24	370
Burseraceae	Protium subserratum (Engl.) Engl.			5	215
Burseraceae	Protium tenuifolium (Engl.) Engl.	8		5	319
Burseraceae	Protium trifoliolatum Engl.		9	15	261
Burseraceae	Tetragastris altissima (Aubl.) Swart	7	12	14	293
Burseraceae	Tetragastris panamensis (Engl.) Kuntze	16	33	17	610
Burseraceae	Trattinnickia rhoifolia Willd.	7			85
Calophyllaceae	Calophyllum brasiliense Cambess.	22	41		1070
Calophyllaceae	Caraipa densifolia Mart.	5			326
Calophyllaceae	Marila laxiflora Rusby			5	237
Cannabaceae	Trema micrantha (L.) Blume	5	8	10	1178
Capparaceae	Capparidastrum frondosum (Jacq.) Cornejo & Iltis			7	418
Capparaceae	Capparis indica (L.) Druce		5		347
Cardiopteridaceae	Dendrobangia boliviana Rusby		21	27	275
Caryocaraceae	Caryocar costaricense Donn.Sm.		26		61
Caryocaraceae	Caryocar glabrum (Aubl.) Pers.	10	20	20	295
Caryocaraceae	Caryocar villosum (Aubl.) Pers.	6			52
Celastraceae	Cheiloclinium cognatum (Miers) A.C.Sm.		5	7	831
Celastraceae	Maytenus guyanensis Klotzsch ex Reissek			15	165
Celastraceae	Maytenus oblongata Reissek			6	41
Celastraceae	Maytenus segoviarum Standl. & L.O.Williams		5		115
Celastraceae	Maytenus woodsonii Lundell			15	54
Chrysobalanaceae	Couepia bracteosa Benth.		7	13	63
Chrysobalanaceae	Couepia guianensis Aubl.	5	7	10	185
Chrysobalanaceae	Couepia parillo DC.			5	79
Chrysobalanaceae	Hirtella bicornis Mart. & Zucc.		5	6	171
Chrysobalanaceae	Hirtella glandulosa Spreng.		9	9	399
Chrysobalanaceae	Hirtella racemosa Lam.			6	1141
Chrysobalanaceae	Licania alba (Bernoulli) Cuatrec.	6	37	46	37
Chrysobalanaceae	Licania canescens Benoist		47	61	155
Chrysobalanaceae	Licania heteromorpha Benth.	5	16	13	645
Chrysobalanaceae	Licania hypoleuca Benth.	5		8	389
Chrysobalanaceae	Licania majuscula Sagot		6	6	43
Chrysobalanaceae	Licania membranacea Sagot ex Laness.		42	52	36
Chrysobalanaceae	Licania oblongifolia Standl.	5			40
Chrysobalanaceae	Licania sparsipilis S.F.Blake			10	56
Chrysobalanaceae	Parinari campestris Aubl.	5			63
Chrysobalanaceae	Parinari excelsa Sabine	16			215
Clethraceae	Clethra mexicana DC.		5		1079
Clusiaceae	Chrysochlamys allenii (Maguire) Hammel		9		92
Clusiaceae	Chrysochlamys glauca (Oerst. ex Planch. & Triana) Hemsl.	10	11	50	312

Family	Species	WD	N	SLA	N.occ
Clusiaceae	Chrysochlamys skutchii Hammel	9	8	45	34
Clusiaceae	Garcinia intermedia (Pittier) Hammel		14	25	448
Clusiaceae	Garcinia madruno (Kunth) Hammel	13	18	67	547
Clusiaceae	Garcinia magnifolia (Pittier) Hammel	10	10	50	75
Clusiaceae	Moronobea coccinea Aubl.		17	15	69
Clusiaceae	Platonia insignis Mart.	7			81
Clusiaceae	Symphonia globulifera L.f.	20	11	8	976
Clusiaceae	Tovomita longifolia (Rich.) Hochr.			7	159
Combretaceae	Buchenavia tetraphylla (Aubl.) R.A.Howard	8			316
Combretaceae	Terminalia amazonia (J.F.Gmel.) Exell	13	58	9	664
Cunoniaceae	Weinmannia fagaroides Kunth		6		324
Cunoniaceae	Weinmannia pinnata L.			15	745
Dichapetalaceae	Tapura guianensis Aubl.			6	163
Dilleniaceae	Curatella americana L.			5	968
Ebenaceae	Diospyros capreifolia Mart. ex Hiern			6	73
Elaeocarpaceae	Sloanea brenesii Standl.			10	37
Elaeocarpaceae	Sloanea guianensis (Aubl.) Benth.	5			497
Elaeocarpaceae	Sloanea terniflora (Moc. & Sessé ex DC.) Standl.		5		267
Erythroxylaceae	Erythroxylum citrifolium A.St.-Hil.			6	814
Erythroxylaceae	Erythroxylum macrophyllum Cav.			24	40
Euphorbiaceae	Alchornea latifolia Sw.	9			949
Euphorbiaceae	Alchorneopsis floribunda (Benth.) Müll.Arg.	10			249
Euphorbiaceae	Conceveiba guianensis Aubl.		17	26	321
Euphorbiaceae	Conceveiba pleiostemona Donn.Sm.	11	5		47
Euphorbiaceae	Croton megistocarpus J.A.González & Poveda			13	58
Euphorbiaceae	Croton schiedeanus Schltdl.		5		909
Euphorbiaceae	Glycydendron amazonicum Ducke		5	6	110
Euphorbiaceae	Gymnanthes riparia (Schltdl.) Klotzsch			9	215
Euphorbiaceae	Hevea brasiliensis (Willd. ex A.Juss.) Müll.Arg.	8			251
Euphorbiaceae	Hevea guianensis Aubl.	9	12	14	337
Euphorbiaceae	Hura crepitans L.	16			463
Euphorbiaceae	Mabea excelsa Standl. & Steyerm.			5	50
Euphorbiaceae	Maprounea guianensis Aubl.	5			752
Euphorbiaceae	Pausandra trianae (Müll.Arg.) Baill.		6		391
Euphorbiaceae	Pera bicolor (Klotzsch) Müll.Arg.	5			112
Euphorbiaceae	Pogonophora schomburgkiana Miers ex Benth.		31	32	318
Euphorbiaceae	Sandwithia guyanensis Lanj.		38	43	35
Euphorbiaceae	Sapium glandulosum (L.) Morong	9	14	55	1098
Euphorbiaceae	Sapium laurifolium (A.Rich.) Griseb.			5	261
Euphorbiaceae	Sapium marmieri Huber	5			214
Fabaceae	Abarema jupunba (Willd.)Britton & Killip	8	9	7	538
Fabaceae	Albizia guachapele (Kunth)Dugand		6		210
Fabaceae	Albizia niopoides (Benth.)Burkart	5			404

Family	Species	WD	N	SLA	N.occ
Fabaceae	Albizia pedicellaris (Dc.)L.Rico	10	5		320
Fabaceae	Albizia saman (Jacq.) F. Muell.		17		395
Fabaceae	Alexa grandiflora Ducke	6			36
Fabaceae	Amburana cearensis (Allemao)A.C.Sm.	9			278
Fabaceae	Anadenanthera colubrina (Vell.)Brenan	10			1039
Fabaceae	Andira inermis (Wright)DC.	9	9		1000
Fabaceae	Apuleia leiocarpa (Vogel)J.F.Macbr.	18			440
Fabaceae	Balizia elegans (Ducke)Barneby & J.W.Grimes	8			33
Fabaceae	Bowdichia nitida Benth.	6			40
Fabaceae	Caesalpinia coriaria (Jacq.)Willd.	5			272
Fabaceae	Caesalpinia eriostachys Benth.		6		180
Fabaceae	Cedrelinga cateniformis (Ducke)Ducke	15			167
Fabaceae	Centrolobium paraense Tul.	8			49
Fabaceae	Cojoba arborea (L.)Britton & Rose	7			607
Fabaceae	Copaifera multijuga Hayne	6			57
Fabaceae	Dalbergia nigra (Vell.)Benth.	8			139
Fabaceae	Dalbergia retusa Hemsl.	9	52		168
Fabaceae	Dialium guianense (Aubl.)Sandwith	14	27	6	993
Fabaceae	Dinizia excelsa Ducke	10			56
Fabaceae	Diphysa americana (Mill.)M.Sousa		5		308
Fabaceae	Diplotropis purpurea (Rich.)Amshoff	26	5		125
Fabaceae	Dipteryx odorata (Aubl.)Willd.	16			178
Fabaceae	Dipteryx oleifera Benth.		40		136
Fabaceae	Enterolobium cyclocarpum (Jacq.)Griseb.	10	15		535
Fabaceae	Enterolobium schomburgkii (Benth.)Benth.	12			269
Fabaceae	Eperua grandiflora (Aubl.)Benth.		30	31	52
Fabaceae	Eperua leucantha Benth.		15		69
Fabaceae	Eperua purpurea Benth.		10		67
Fabaceae	Gliricidia sepium (Jacq.)Walp.	5			1178
Fabaceae	Haematoxylum campechianum L.	5			386
Fabaceae	Hymenaea courbaril L.	21	36	7	1075
Fabaceae	Hymenaea oblongifolia Huber	9			176
Fabaceae	Hymenaea parvifolia Huber	5			116
Fabaceae	Inga acreana Harms			6	160
Fabaceae	Inga alba (Sw.)Willd.	20	19		456
Fabaceae	Inga coruscans Willd.			5	147
Fabaceae	Inga densiflora Benth.		5		365
Fabaceae	Inga edulis Mart.	11			890
Fabaceae	Inga leiocalycina Benth.		5		266
Fabaceae	Inga mortoniana J. León		5		82
Fabaceae	Inga multijuga Benth.			5	192
Fabaceae	Inga paraensis Ducke			7	79
Fabaceae	Inga pezizifera Benth.	16	6	12	288

Family	Species	WD	N	SLA	N.occ
Fabaceae	Inga punctata Willd.		5	13	1154
Fabaceae	Inga rubiginosa (Rich.)DC.			7	71
Fabaceae	Inga sapindoides Willd.		5		535
Fabaceae	Inga skutchii Standl.	10	10	50	38
Fabaceae	Inga spectabilis (Vahl)Willd.	14	12		284
Fabaceae	Inga thibaudiana DC.		8		994
Fabaceae	Lonchocarpus guatemalensis Benth.		5		836
Fabaceae	Lonchocarpus heptaphyllus (Poir.)DC.			6	317
Fabaceae	Lonchocarpus minimiflorus Donn.Sm.		8		263
Fabaceae	Machaerium salvadorense (Donn.Sm.)Rudd			5	168
Fabaceae	Macrolobium acaciifolium (Benth.)Benth.	5			512
Fabaceae	Macrolobium costaricense W.C.Burger			6	70
Fabaceae	Myroxylon balsamum (L.)Harms	7			283
Fabaceae	Myroxylon peruiferum L.f.	6			133
Fabaceae	Ormosia coccinea (Aubl.)Jacks.	7			190
Fabaceae	Ormosia paraensis Ducke	6			86
Fabaceae	Parkia multijuga Benth.	5			138
Fabaceae	Parkia nitida Miq.	11	7		184
Fabaceae	Parkia pendula (Willd.)Walp.	15			259
Fabaceae	Peltogyne catingae Ducke	6			37
Fabaceae	Peltogyne paniculata Benth.	8			106
Fabaceae	Pentaclethra macroloba (Willd.)Kuntze	62	8		266
Fabaceae	Pithecellobium dulce (Roxb.)Benth.	6			707
Fabaceae	Platymiscium pinnatum (Jacq.)Dugand	22			293
Fabaceae	Platymiscium trinitatis Benth.	10			42
Fabaceae	Platypodium elegans Vogel	11			524
Fabaceae	Prioria copaifera Griseb.	7			123
Fabaceae	Prosopis juliflora (Sw.)DC.	16			485
Fabaceae	Pseudopiptadenia psilostachya (DC.)G.P.Lewis & M.P.Lima		6	6	151
Fabaceae	Pseudopiptadenia suaveolens (Miq.) J.W. Grimes	7	12	11	80
Fabaceae	Pterocarpus acapulcensis Rose	7			176
Fabaceae	Pterocarpus officinalis Jacq.	9			215
Fabaceae	Pterocarpus rohrii Vahl	7		5	647
Fabaceae	Schizolobium parahyba (Vell.)S.F.Blake	19	39		304
Fabaceae	Senegalia polyphylla (DC.) Britton	10			923
Fabaceae	Senna siamea (Lam.)H.S.Irwin & Barneby	8			147
Fabaceae	Stryphnodendron microstachyum Poepp.	12			95
Fabaceae	Swartzia benthamiana Miq.	19	6		107
Fabaceae	Swartzia panacoco (Aubl.) R.S. Cowan	13			85
Fabaceae	Swartzia polyphylla DC.		6	7	254
Fabaceae	Swartzia simplex (Sw.)Spreng.			26	894
Fabaceae	Tachigali versicolor Standl. & L.O.Williams		18		33
Fabaceae	Vatairea erythrocarpa (Ducke)Ducke			5	45

Family	Species	WD	N	SLA	N.occ
Fabaceae	Vatairea guianensis Aubl.	7			103
Fabaceae	Vouacapoua americana Aubl.	8	29	37	51
Fagaceae	Quercus costaricensis Liebm.		12	14	98
Fagaceae	Quercus oleoides Schltdl. & Cham.		6		203
Fagaceae	Quercus seemannii Liebm.		12		177
Goupiaceae	Goupia glabra Aubl.	16	31	20	350
Hernandiaceae	Gyrocarpus americanus Jacq.	5			274
Hernandiaceae	Hernandia didymantha Donn.Sm.	19			103
Humiriaceae	Endopleura uchi (Huber) Cuatrec.	7			46
Humiriaceae	Humiria balsamifera Aubl.	13			438
Humiriaceae	Sacoglottis guianensis Benth.	7			193
Humiriaceae	Vantanea parviflora Lam.	6	5	6	67
Hypericaceae	Vismia japurensis Rchb.f.		8		197
Hypericaceae	Vismia lauriformis (Lam.) Choisy		6		89
Hypericaceae	Vismia macrophylla Kunth	9			619
Icacinaceae	Poraqueiba guianensis Aubl.		13	43	52
Lamiaceae	Gmelina arborea Roxb.		156		45
Lamiaceae	Tectona grandis L.f.		362		123
Lauraceae	Aniba canelilla (Kunth) Mez	7			76
Lauraceae	Aniba rosaeodora Ducke	7			37
Lauraceae	Licaria cannella (Meisn.) Kosterm.	8	6		173
Lauraceae	Nectandra umbrosa (Kunth) Mez	5		39	247
Lauraceae	Ocotea aciphylla (Nees & Mart.) Mez	5	8		566
Lauraceae	Ocotea argyrophylla Ducke		5	6	76
Lauraceae	Ocotea atirrensis Mez & Donn.Sm.			5	460
Lauraceae	Ocotea floribunda (Sw.) Mez	6	6		279
Lauraceae	Ocotea glomerata (Nees) Mez	5			240
Lauraceae	Ocotea guianensis Aubl.	6			250
Lauraceae	Ocotea insularis (Meisn.) Mez		11	8	442
Lauraceae	Ocotea leucoxylon (Sw.) Laness.			6	488
Lauraceae	Ocotea mollifolia Mez & Pittier	10	11	50	84
Lauraceae	Ocotea veraguensis (Meisn.) Mez		8	8	342
Lauraceae	Persea americana Mill.		6		967
Lauraceae	Rhodostemonodaphne grandis (Mez) Rohwer			6	56
Lauraceae	Rhodostemonodaphne kunthiana (Nees) Rohwer		6	8	269
Lauraceae	Sextonia rubra (Mez) van der Werff	17	19	22	52
Lecythidaceae	Allantoma decandra (Ducke) S.A.Mori,Ya Y.Huang & Prance	8			61
Lecythidaceae	Bertholletia excelsa Bonpl.	9			176
Lecythidaceae	Cariniana micrantha Ducke	5			42
Lecythidaceae	Couratari guianensis Aubl.	9	5	7	272
Lecythidaceae	Couratari multiflora (Sm.) Eyma		8	11	59
Lecythidaceae	Couratari stellata A.C.Sm.	7			55
Lecythidaceae	Eschweilera chartaceifolia S.A.Mori			5	45

Family	Species	WD	N	SLA	N.occ
Lecythidaceae	Eschweilera decolorans Sandwith		26	28	85
Lecythidaceae	Eschweilera micrantha (O.Berg) Miers		5	9	140
Lecythidaceae	Eschweilera parviflora (Aubl.) Miers		5	18	168
Lecythidaceae	Eschweilera parvifolia Mart. ex DC.	5			281
Lecythidaceae	Eschweilera pedicellata (Rich.) S.A.Mori		6	7	332
Lecythidaceae	Eschweilera sagotiana Miers		38	41	76
Lecythidaceae	Eschweilera subglandulosa (Steud. ex O.Berg) Miers	5			180
Lecythidaceae	Gustavia hexapetala (Aubl.) Sm.		30	75	418
Lecythidaceae	Lecythis ampla Miers	5			68
Lecythidaceae	Lecythis chartacea O.Berg		6		159
Lecythidaceae	Lecythis corrugata Poit.	7	8	13	231
Lecythidaceae	Lecythis idatimon Aubl.	7	9	9	101
Lecythidaceae	Lecythis pisonis Cambess.	8			248
Lecythidaceae	Lecythis poiteaui O.Berg		20	30	49
Lecythidaceae	Lecythis zabucajo Aubl.	6	7	8	95
Linaceae	Hebepetalum humiriifolium (Planch.) Benth.		9	9	139
Loranthaceae	Gaiadendron punctatum (Ruiz & Pav.) G.Don			14	745
Malpighiaceae	Byrsonima arthropoda A.Juss.	14			271
Malpighiaceae	Byrsonima crassifolia (L.) Kunth	11		8	1179
Malvaceae	Apeiba albiflora Ducke	5			57
Malvaceae	Apeiba glabra Aubl.	13	7	9	326
Malvaceae	Apeiba membranacea Spruce ex Benth.	12			515
Malvaceae	Apeiba petoumo Aubl.		5		39
Malvaceae	Apeiba tibourbou Aubl.		7		1152
Malvaceae	Ceiba pentandra (L.) Gaertn.	35		6	426
Malvaceae	Goethalsia meiantha (Donn.Sm.) Burret	40			123
Malvaceae	Guazuma ulmifolia Lam.	14	18	9	925
Malvaceae	Hampea appendiculata (Donn.Sm.) Standl.	16			248
Malvaceae	Luehea candida (Moc. & Sessé ex DC.) Mart.		5		469
Malvaceae	Luehea seemannii Triana & Planch		6	9	462
Malvaceae	Luehea speciosa Willd.		5	10	1020
Malvaceae	Ochroma pyramidale (Cav. ex Lam.) Urb.	14			497
Malvaceae	Pachira aquatica Aubl.	5			1062
Malvaceae	Pachira humilis Spruce ex Decne.		5		39
Malvaceae	Pachira quinata (Jacq.) W.S.Alverson	9	11		151
Malvaceae	Scleronema micranthum (Ducke) Ducke	9			139
Malvaceae	Sterculia apetala (Jacq.) H.Karst.	12			466
Malvaceae	Sterculia pruriens (Aubl.) K.Schum.	5	24	35	102
Malvaceae	Theobroma subincanum Mart.		19	35	470
Melastomataceae	Bellucia grossularioides (L.) Triana		6		611
Melastomataceae	Miconia acuminata (Steud.) Naudin		6	6	33
Melastomataceae	Miconia affinis DC.	5			268
Melastomataceae	Miconia argentea (Sw.) DC.		8	5	452

Family	Species	WD	N	SLA	N.occ
Melastomataceae	Miconia dispar Benth.		5		183
Melastomataceae	Miconia donaeana Naudin	10	11	50	134
Melastomataceae	Miconia elata (Sw.) DC.	6			298
Melastomataceae	Miconia multispicata Naudin	10			180
Melastomataceae	Miconia punctata (Desr.) D. Don ex DC.			10	499
Melastomataceae	Miconia tonduzii Cogn.		9		288
Melastomataceae	Miconia trinervia (Sw.) D. Don ex Loudon	11	12	52	693
Melastomataceae	Mouriri gleasoniana Standl.	5	7	35	116
Melastomataceae	Mouriri myrtilloides (Sw.) Poir.		6		357
Melastomataceae	Mouriri sagotiana Triana			5	51
Meliaceae	Carapa guianensis Aubl.		10	5	76
Meliaceae	Guarea glabra Vahl	6	17	25	784
Meliaceae	Guarea guidonia (L.) Sleumer	19	8	14	1050
Meliaceae	Guarea kunthiana A.Juss.	7			1051
Meliaceae	Guarea scabra A.Juss.			9	52
Meliaceae	Ruagea glabra Triana & Planch.			15	341
Meliaceae	Swietenia macrophylla King	12	29		422
Meliaceae	Trichilia cipo (A.Juss.) C.DC.		8	10	113
Meliaceae	Trichilia martiana C.DC.		6		813
Meliaceae	Trichilia micrantha Benth.			9	251
Meliaceae	Trichilia pallida Sw.		6	9	891
Meliaceae	Trichilia schomburgkii C.DC.			11	104
Meliaceae	Trichilia septentrionalis C.DC.	6			442
Moraceae	Bagassa guianensis Aubl.	9			33
Moraceae	Brosimum acutifolium Huber	7			91
Moraceae	Brosimum alicastrum Sw.	10	12	10	679
Moraceae	Brosimum guianense (Aubl.) Huber ex Ducke	11	19	30	837
Moraceae	Brosimum lactescens (S.Moore) C.C.Berg	18	80		532
Moraceae	Brosimum parinarioides Ducke	8			63
Moraceae	Brosimum rubescens Taub.	16	8	6	235
Moraceae	Brosimum utile (Kunth) Oken	15	37	7	86
Moraceae	Castilla elastica Cerv.		5	8	179
Moraceae	Clarisia biflora Ruiz & Pav.		5	9	460
Moraceae	Clarisia racemosa Ruiz & Pav.	21			313
Moraceae	Ficus insipida Willd.	12	14		1034
Moraceae	Helicostylis tomentosa (Poepp. & Endl.) J.F.Macbr.	10	5		496
Moraceae	Helicostylis tovarensis (Klotzsch & H.Karst.) C.C.Berg			9	263
Moraceae	Maclura tinctoria (L.) D.Don ex Steud.	17		6	1102
Moraceae	Maquira calophylla (Poepp. & Endl.) C.C.Berg			5	148
Moraceae	Maquira coriacea (H.Karst.) C.C.Berg	5			107
Moraceae	Maquira guianensis Aubl.		10	10	377
Moraceae	Naucleopsis naga Pittier	5			98
Moraceae	Poulsenia armata (Miq.) Standl.	8	5	7	379

Family	Species	WD	N	SLA	N.occ
Moraceae	Pseudolmedia glabrata (Liebm.) C.C.Berg			29	337
Moraceae	Pseudolmedia laevigata Trécul	6			490
Moraceae	Pseudolmedia laevis (Ruiz & Pav.) J.F.Macbr.	9			466
Moraceae	Trophis involucrata W.C. Burger			6	89
Myristicaceae	Compsoneura excelsa A.C.Sm.			26	108
Myristicaceae	Iryanthera hostmannii (Benth.) Warb.		16	19	182
Myristicaceae	Iryanthera juruensis Warb.	6			732
Myristicaceae	Iryanthera sagotiana (Benth.) Warb.		68	121	50
Myristicaceae	Osteophloeum platyspermum (Spruce ex A.DC.) Warb.	7	6	6	377
Myristicaceae	Otoba parvifolia (Markgr.) A.H.Gentry	6			394
Myristicaceae	Virola guatemalensis (Hemsl.) Warb.			5	101
Myristicaceae	Virola koschnyi Warb.	19	37		148
Myristicaceae	Virola macrocarpa A.C. Sm.			10	69
Myristicaceae	Virola michelii Heckel	8	48	60	115
Myristicaceae	Virola multiflora (Standl.) A.C.Sm.	6			79
Myristicaceae	Virola sebifera Aubl.	46	22	6	1028
Myristicaceae	Virola surinamensis (Rol. ex Rottb.) Warb.	11			103
Myrtaceae	Eugenia acapulcensis Steud.			24	661
Myrtaceae	Eugenia basilaris McVaugh		5		39
Myrtaceae	Eugenia patrisii Vahl			5	233
Myrtaceae	Myrcia decorticans DC.			7	164
Myrtaceae	Myrciaria floribunda (H.West ex Willd.) O.Berg		5	12	843
Nyctaginaceae	Neea floribunda Poepp. & Endl.		8	8	158
Ochnaceae	Cespedesia spathulata (Ruiz & Pav.) Planch.	20			367
Ochnaceae	Lacunaria panamensis (Standl.) Standl.	6			39
Ochnaceae	Quiina macrophylla Tul.			11	131
Olacaceae	Heisteria concinna Standl.		17	14	118
Olacaceae	Minquartia guianensis Aubl.	24	27	25	418
Olacaceae	Ptychopetalum olacoides Benth.		5	16	35
Oleaceae	Chionanthus panamensis (Standl.) Stearn			10	106
Opiliaceae	Agonandra silvatica Ducke			6	82
Pentaphylacaceae	Cleyera theoides (Sw.) Choisy			5	411
Phyllanthaceae	Margaritaria nobilis L.f.		9		1098
Phyllanthaceae	Richeria dressleri G.L.Webster			24	66
Phytolaccaceae	Gallesia integrifolia (Spreng.) Harms	6			206
Pinaceae	Pinus caribaea Morelet	6			191
Podocarpaceae	Retrophyllum rospigliosii (Pilg.) C.N.Page	6			88
Polygonaceae	Triplaris weigeltiana (Rchb.) Kuntze	7			94
Primulaceae	Ardisia compressa Kunth	9	13	45	1121
Primulaceae	Ardisia glandulosomarginata Oerst.		11		124
Primulaceae	Ardisia revoluta Kunth		6		567
Proteaceae	Roupala montana Aubl.	9	10	7	902
Putranjivaceae	Drypetes variabilis Uittien	6	13	14	92

Family	Species	WD	N	SLA	N.occ
Rhizophoraceae	Cassipourea guianensis Aubl.		11	5	851
Rubiaceae	Alibertia edulis (Rich.) A.Rich. ex DC.			10	1198
Rubiaceae	Arachnothryx buddleioides (Benth.) Planch.		7		459
Rubiaceae	Calycophyllum candidissimum (Vahl) DC.			5	341
Rubiaceae	Chimarrhis turbinata DC.		11	15	50
Rubiaceae	Chione venosa (Sw.) Urb.		8	10	580
Rubiaceae	Coussarea caroliana Standl.			18	121
Rubiaceae	Coussarea loftonii (Dwyer & M.V.Hayden) Dwyer			11	81
Rubiaceae	Faramea occidentalis (L.) A.Rich.	14	22	65	1075
Rubiaceae	Genipa americana L.	12	6	8	1209
Rubiaceae	Guettarda macrosperma Donn.Sm.		7		339
Rubiaceae	Posoqueria coriacea M.Martens & Galeotti			6	236
Rubiaceae	Posoqueria latifolia (Rudge) Schult.		7	9	1112
Rubiaceae	Tocoyena pittieri (Standl.) Standl.	8			100
Rutaceae	Zanthoxylum ekmanii (Urb.) Alain	7			119
Salicaceae	Casearia arborea (Rich.) Urb.	60	9	13	1066
Salicaceae	Casearia arguta Kunth		6	6	490
Salicaceae	Casearia corymbosa Kunth		10		1074
Salicaceae	Casearia javitensis Kunth		5	11	840
Salicaceae	Casearia sylvestris Sw.	5	7	15	1010
Salicaceae	Laetia procera (Poepp.) Eichler	43	17	13	309
Salicaceae	Lunania mexicana Brandegee			7	260
Salicaceae	Salix humboldtiana Willd.	24			956
Salicaceae	Tetrathylacium johansenii Standl.			14	61
Sapindaceae	Cupania glabra Sw.	5			403
Sapindaceae	Cupania guatemalensis (Turcz.) Radlk.		6		191
Sapindaceae	Cupania scrobiculata Rich.		10	20	261
Sapindaceae	Dilodendron costaricense (Radlk.) A.H.Gentry & Steyerm.		5		90
Sapindaceae	Matayba apetala (Griseb.) Radlk.			6	129
Sapindaceae	Talisia hexaphylla Vahl			6	98
Sapindaceae	Thouinidium decandrum (Humb. & Bonpl.) Radlk.		6		241
Sapindaceae	Vouarana guianensis Aubl.			6	67
Sapotaceae	Chrysophyllum argenteum Jacq.		14	13	611
Sapotaceae	Chrysophyllum brenesii Cronquist		8		135
Sapotaceae	Chrysophyllum cuneifolium (Rudge) A.DC.		5	5	51
Sapotaceae	Chrysophyllum prieurii A.DC.	5	11	9	110
Sapotaceae	Chrysophyllum sanguinolentum (Pierre) Baehni	5	12	11	226
Sapotaceae	Ecclinusa guianensis Eyma	7			89
Sapotaceae	Manilkara bidentata (A.DC.) A.Chev.	15	27	24	327
Sapotaceae	Manilkara chicle (Pittier) Gilly		6	6	191
Sapotaceae	Manilkara huberi (Ducke) Standl.	11	8	6	60
Sapotaceae	Micropholis egensis (A.DC.) Pierre		5	6	214
Sapotaceae	Micropholis guyanensis (A.DC.) Pierre	11	33	28	641

Family	Species	WD	N	SLA	N.occ
Sapotaceae	Micropholis venulosa (Mart. & Eichler ex Miq.) Pierre	5	14	13	554
Sapotaceae	Pouteria bangii (Rusby) T.D.Penn.		5	5	174
Sapotaceae	Pouteria bilocularis (H.J.P.Winkl.) Baehni		7	7	202
Sapotaceae	Pouteria caimito (Ruiz & Pav.) Radlk.	8			527
Sapotaceae	Pouteria cuspidata (A.DC.) Baehni		8	8	397
Sapotaceae	Pouteria durlandii (Standl.) Baehni	11	7	9	302
Sapotaceae	Pouteria egregia Sandwith	6	6	5	36
Sapotaceae	Pouteria eugeniifolia (Pierre) Baehni		9	8	66
Sapotaceae	Pouteria filipes Eyma		5	5	74
Sapotaceae	Pouteria gongrijpii Eyma	5	45	45	38
Sapotaceae	Pouteria guianensis Aubl.	6	23	20	504
Sapotaceae	Pouteria hispida Eyma		9	8	183
Sapotaceae	Pouteria laevigata (Mart.) Radlk.		6	6	85
Sapotaceae	Pouteria macrophylla (Lam.) Eyma	5		5	166
Sapotaceae	Pouteria reticulata (Engl.) Eyma		6	6	654
Sapotaceae	Pouteria subrotata Cronquist	8	9	45	83
Sapotaceae	Pouteria torta (Mart.) Radlk.	6	35	66	575
Scrophulariaceae	Buddleja nitida Benth.			15	131
Simaroubaceae	Simaba cedron Planch.		12	15	239
Simaroubaceae	Simaba polyphylla (Cavalcante) W.W. Thomas			8	81
Simaroubaceae	Simarouba amara Aubl.	48	14	22	654
Simaroubaceae	Simarouba versicolor A. St.-Hil.	5			199
Siparunaceae	Siparuna cristata (Poepp. & Endl.) A.DC.			5	192
Siparunaceae	Siparuna decipiens (Tul.) A.DC.			14	446
Staphyleaceae	Turpinia occidentalis (Sw.) G.Don		6		1217
Stemonuraceae	Discophora guianensis Miers			17	528
Styracaceae	Styrax argenteus C.Presl		8		536
Ulmaceae	Ampelocera macrocarpa Ferero & Gentry	5			76
Ulmaceae	Phyllostylon rhamnoides (J.Poiss.) Taub.	6			118
Urticaceae	Cecropia insignis Liebm.	9			103
Urticaceae	Cecropia peltata L.		7	5	771
Urticaceae	Cecropia sciadophylla Mart.	7			219
Urticaceae	Myriocarpa longipes Liebm.			5	821
Urticaceae	Pourouma bicolor Mart.	20	15	10	180
Urticaceae	Pourouma melinonii Benoist			5	79
Urticaceae	Pourouma minor Benoist	9	18	27	398
Urticaceae	Pourouma villosa Trécul		15	18	39
Urticaceae	Urera caracasana (Jacq.) Gaudich. ex Griseb.		5		753
Verbenaceae	Rehdera trinervis (S.F.Blake) Moldenke		11		157
Violaceae	Amphirrhox longifolia (A.St.-Hil.) Spreng.		5	6	306
Violaceae	Leonia glycycarpa Ruiz & Pav.		5	6	545
Violaceae	Rinorea crenata S.F. Blake			39	50
Violaceae	Rinorea deflexiflora Bartlett		7		137

Family	Species	WD	N	SLA	N.occ
Violaceae	Rinorea hummelii Sprague			5	424
Vochysiaceae	Erisma uncinatum Warm.	12		6	144
Vochysiaceae	Qualea albiflora Warm.		9	12	44
Vochysiaceae	Qualea paraensis Ducke	9			185
Vochysiaceae	Vochysia allenii Standl. & L.O.Williams			9	41
Vochysiaceae	Vochysia ferruginea Mart.	39	20		406
Vochysiaceae	Vochysia guatemalensis Donn. Sm.	12	62		397
Winteraceae	Drimys granadensis L.f.		6	9	709
Ximeniaceae	Ximenia americana L.		5		707
	Total species	271	274	288	521
	Total trait values	2969	4291	4731	
	Total occurrences				167928

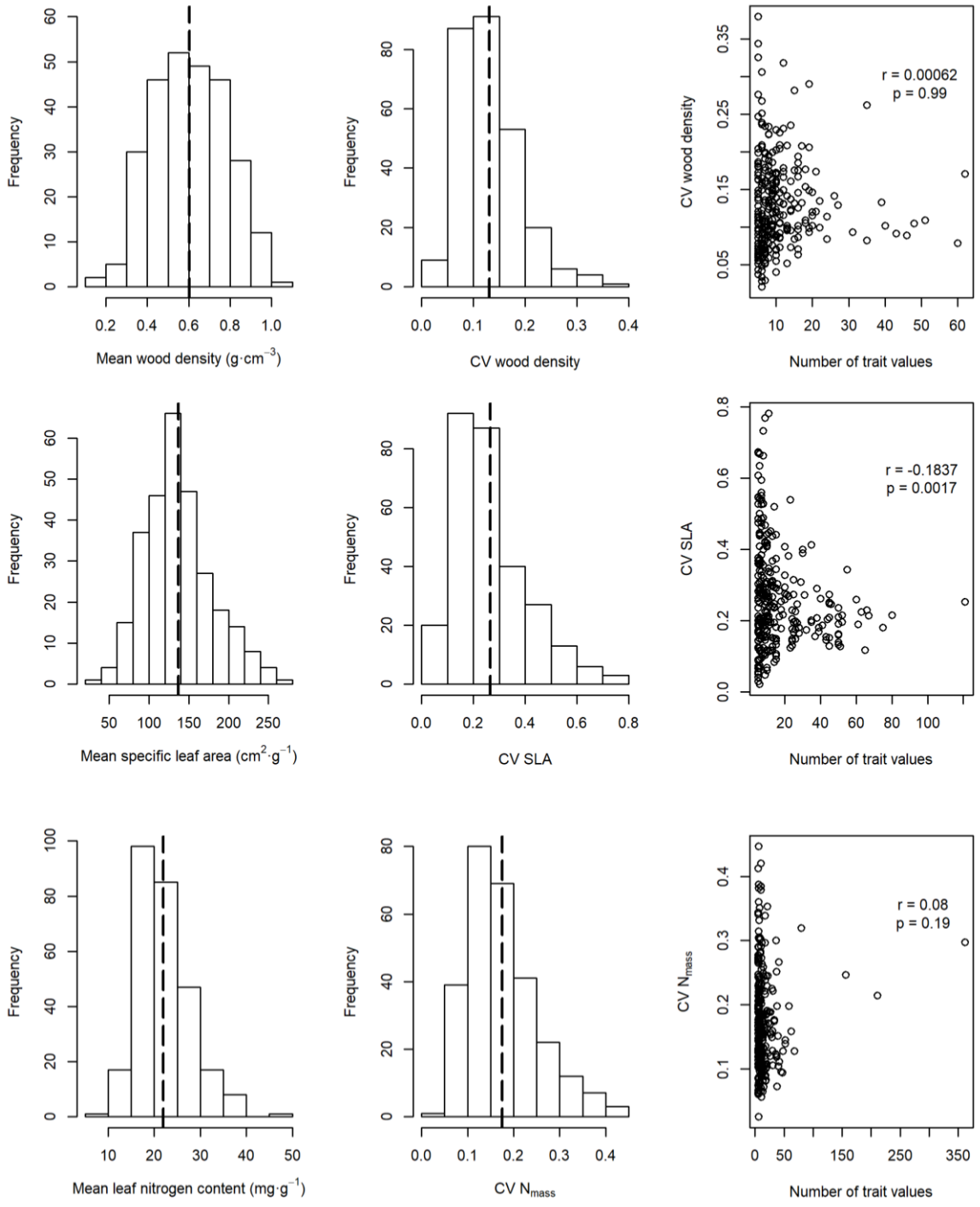

Figure S6. Frequency distributions of the means and coefficients of variation for each trait analysed, and the relation between the number of trait values and the coefficient of variation. The vertical line in the frequency distribution plots represents the mean of the trait values means or the mean of the coefficient of variations.