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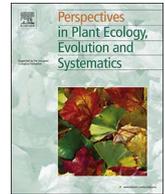
Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees

Eduardo Chacón-Madrigal[a,b,*], Wolfgang Wanek[c], Peter Hietz[d], Stefan Dullinger[a]

[a] Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria
[b] Escuela de Biología, Universidad de Costa Rica, Apdo. Postal 2060, San José, Costa Rica
[c] Department of Microbiology and Ecosystem Science, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria
[d] Institute of Botany, University of Natural Resources and Life Sciences, Gregor Mendel-Strasse 33, 1180 Vienna, Austria

ARTICLE INFO

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.

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

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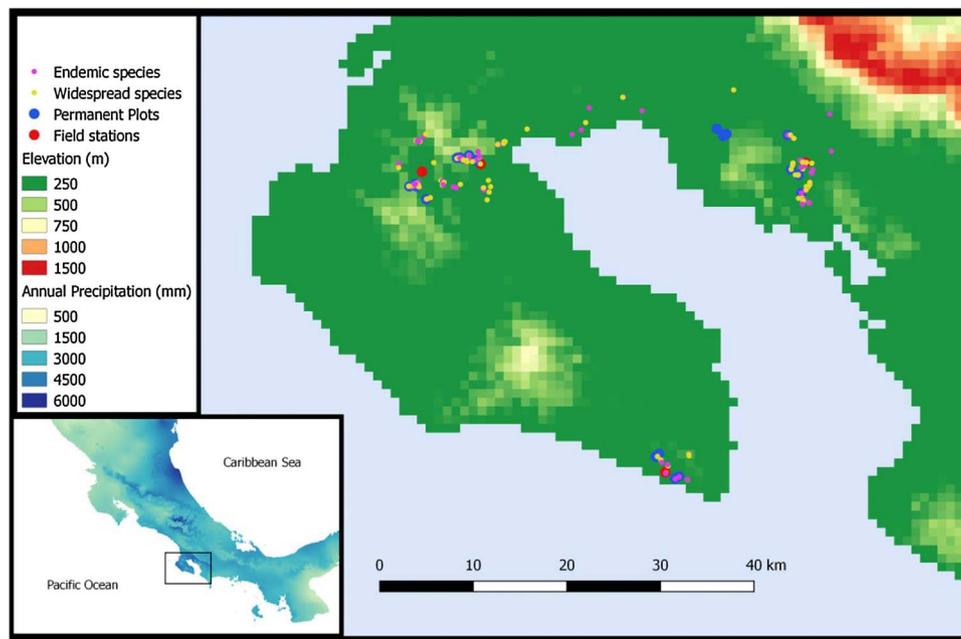
Fig. 1. Study area and sites where trees were sampled. The map in the box represents the distribution of mean annual rainfall according to Worldclim (Hijmans et al., 2005).

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 and 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, 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, 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; Diaz 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; Diaz 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.

2. Methods

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 characterized 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).

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).

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 × 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-López and Rodríguez-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).

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

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	N	Extent of Occurrence (km^2)
Annonaceae	*Guatteria amplifolia* Triana & Planch.	10	$1.02 \cdot 10^6$
Annonaceae	*Guatteria chiriquiensis* R. E. Fr.	9	$8.60 \cdot 10^3$
Annonaceae	*Guatteria pudica* N.Zamora & Maas	16	$6.87 \cdot 10^2$
Annonaceae	*Guatteria rostrata* Erkens & Maas	10	$6.45 \cdot 10^4$
Annonaceae	*Unonopsis osae* Maas & Westra	10	$7.54 \cdot 10^2$
Annonaceae	*Unonopsis theobromifolia* N. Zamora & Poveda	10	$2.81 \cdot 10^4$
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	10	$7.69 \cdot 10^6$
Araliaceae	*Dendropanax ravenii* M. J. Cannon & Cannon	10	$1.96 \cdot 10^3$
Boraginaceae	*Cordia cymosa* (Donn. Sm.) Standl.	8	$3.66 \cdot 10^5$
Boraginaceae	*Cordia liesneri* J. S. Mill.	9	$4.07 \cdot 10^3$
Burseraceae	*Protium panamense* (Rose) I. M. Johnst.	8	$1.98 \cdot 10^5$
Burseraceae	*Protium pecuniosum* D. C. Daly	10	$1.48 \cdot 10^3$
Clusiaceae	*Chrysochlamys glauca* (Oerst. ex Planch. & Triana) Hemsl.	10	$3.79 \cdot 10^5$
Clusiaceae	*Chrysochlamys skutchii* Hammel	9	$2.38 \cdot 10^4$
Clusiaceae	*Garcinia aguilari* Hammel	10	$9.43 \cdot 10^1$
Clusiaceae	*Garcinia madruno* (Kunth) Hammel	10	$9.26 \cdot 10^6$
Clusiaceae	*Garcinia magnifolia* (Pittier) Hammel	10	$1.64 \cdot 10^5$
Euphorbiaceae	*Sapium allenii* Huft	11	$8.89 \cdot 10^2$
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	10	$1.35 \cdot 10^7$
Fabaceae	*Inga skutchii* Standl.	10	$7.79 \cdot 10^3$
Fabaceae	*Inga spectabilis* (Vahl) Willd	9	$2.51 \cdot 10^6$
Lauraceae	*Ocotea mollifolia* Mez & Pittier	10	$1.14 \cdot 10^5$
Lauraceae	*Ocotea rivularis* Standl. & L. O. Williams	9	$6.68 \cdot 10^2$
Melastomataceae	*Miconia dissitinervia* Kriebel, Almeda & A. Estrada	11	$3.75 \cdot 10^3$
Melastomataceae	*Miconia donaeana* Naudin	10	$1.22 \cdot 10^6$
Melastomataceae	*Miconia osaensis* Aguilar, Kriebel & Almeda	10	$9.61 \cdot 10^1$
Melastomataceae	*Miconia trinervia* (Sw.) D. Don ex Loudon	10	$5.89 \cdot 10^6$
Myrsinaceae	*Ardisia compressa* Kunth	9	$1.44 \cdot 10^6$
Myrsinaceae	*Ardisia dunlapiana* P. H. Allen	10	$1.44 \cdot 10^3$
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	11	$1.18 \cdot 10^7$
Rubiaceae	*Faramea permagnifolia* Dwyer ex C. M. Taylor	12	$5.38 \cdot 10^1$
Sapotaceae	*Pouteria lecythidicarpa* P. E. Sánchez & Poveda	10	$1.33 \cdot 10^4$
Sapotaceae	*Pouteria subrotata* Cronquist	8	$1.72 \cdot 10^6$
Sapotaceae	*Pouteria torta* (Mart.) Radlk.	10	$1.08 \cdot 10^7$
Sapotaceae	*Pouteria triplarifolia* C. K. Allen ex T. D. Pennington	6	$2.41 \cdot 10^3$

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).

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 g^{-1} for SLA, from 195 to 472 mg 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 and A5 of

Supplementary material).

The EOO of our study species varied between $5.37 \cdot 10^1$–$2.38 \cdot 10^4$ 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

Table 2

Coefficients estimated ± 1 standard error (β), and the associated test statistics (Chi^2) 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. Significance level of p < 0.05 is indicated by an *.

Functional Trait	β	Std. Error	Chi^2	p ($>$ Chi^2)
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
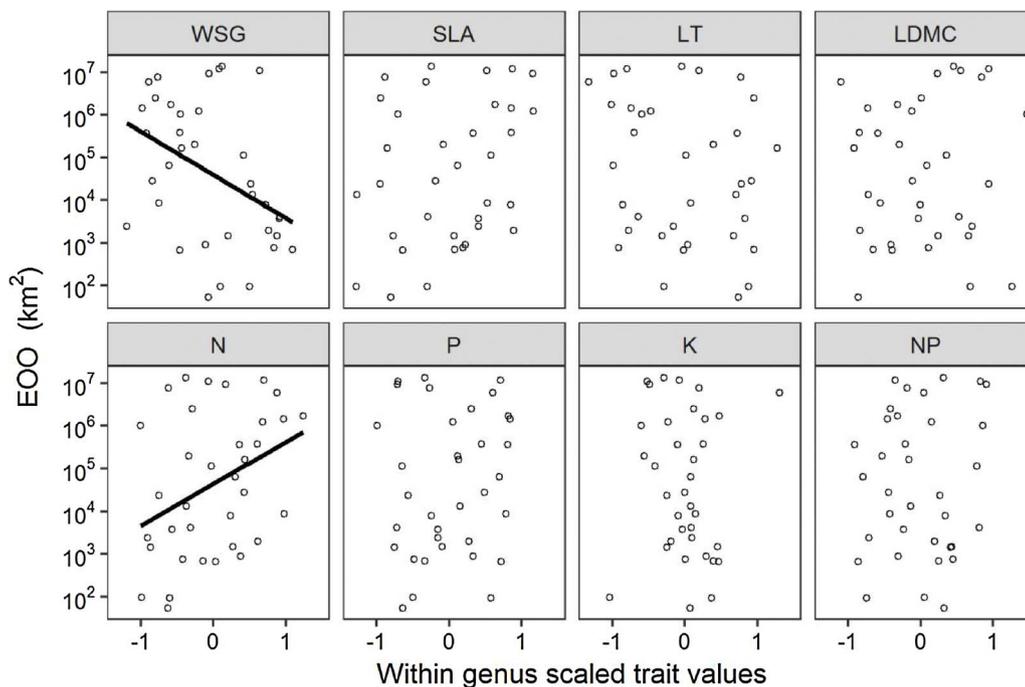
Fig. 2. The relationship between the log10-transformed extent of occurrence (EOO) and the following functional traits studied in 35 tropical tree species of Costa Rica: wood specific gravity (WSG), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content (LDMC), leaf nitrogen (N), phosphorus (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.

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 ($\beta \pm SE = 0.695 \pm 0.442$, $Chi^2 = 5.62$, $p = 0.116$) 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 ($D^2 = 0.36$).

Table 3
Coefficients estimated $\pm$ 1 standard error (β), and the associated test statistics (Chi^2) 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. Significance levels are indicated by asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Factor	Estimate	Std. Error	Chi^2	p (> Chi^2)
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*

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).

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; Swenson and Enquist, 2007) 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 relics (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
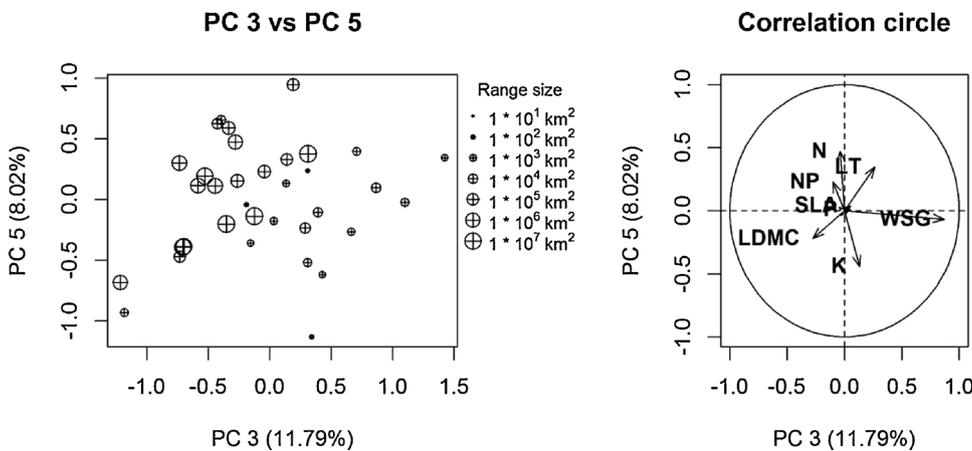
Fig. 3. Species scores and correlation plot of the third and fifth component of the principal component (PC) analysis calculated with eight functional traits (wood specific gravity, WSG; specific leaf area, SLA; leaf thickness, LT; leaf dry matter content, LDMC; leaf nitrogen content, N; leaf phosphorus 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.

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 have 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.

5. 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 colonisation 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.

Biología of the University of Costa Rica for all the logistic support and research facilities.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ppees.2018.01.003.

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