

Interspecific variation in functional traits in relation to species climatic niche optima in Andean *Polylepis* (Rosaceae) tree species: evidence for climatic adaptations

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Abstract. Plant functional traits can be genetically determined or phenotypically plastic. We assessed the degree of genetic determinism in the functional traits of Andean *Polylepis* tree species among 14 important traits that enable the species to withstand cold and dry conditions. We conducted a common garden experiment and related the species-specific means of the functional traits to the variables of climatic niche optima of the species (mean annual temperature and annual precipitation), deducing that if the interspecific variation in the functional trait is related to the species climatic niche optima according to the theoretically-expected pattern of climate-trait relationship, the variation of the trait must be genetically determined. In general, the traits were related either to species temperature or precipitation optima. For example, leaf size, maximum photosynthesis rate and root tip abundance were related to temperature, whereas light compensation and light saturation points were related to precipitation. Only leaf size showed a significant phylogenetic signal, indicating that most of the manifested climate–trait relationships are not caused purely by phylogeny, but are mainly a result of species specialisation along an environmental gradient. However, in many cases the relationships were rather weak. This suggests that important functional traits of *Polylepis* species involve both genetic and phenotypic components aiming to maximise the overall fitness of the species at high elevations.

Additional keywords: climatic niche, ecophysiology, genetic determinism, phenotypic plasticity, phylogeny, treeline.

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Introduction

The Andes are a relatively recently formed mountain chain with numerous examples of radiations in which a lowland ancestor species has adapted to high altitude conditions and subsequently diversified there. The underlying ecological adaptations have not been effectively targeted to elevation as such, but to physiologically meaningful environmental gradients that are correlated with elevation such as reductions in mean annual air and soil temperatures and in air CO₂ concentration and increases in clear sky radiation and in diurnal temperature variation (Körner 2003). Precipitation shows a more complex relationship with elevation, being affected by orography and prevailing wind directions (e.g. Killeen *et al.* 2007). Generally, precipitation increases with elevation up to the main cloud condensation layer and then decreases again, so that the highest mountain habitats may suffer from water stress (Leuschner 2000). However, there are strong regional variations in this pattern. As a response to these changes, high elevation plants show

different sets of genetically determined adaptations and phenotypically plastic acclimations in their functional traits involving interactions and trade-offs driven by plant energy economy (Grime and Pierce 2012). Trees are especially susceptible to the multi-stress conditions of high elevations owing to their high stature and open architecture, which couple them more directly to atmospheric climatic conditions than herbs and shrubs (Körner 2012).

The most commonly documented response of tree functional traits to climate is probably a reduction in tree aboveground structures with decreasing temperature and increasing drought, manifested for example in reduced leaf size and specific leaf area (e.g. Cordell *et al.* 1998; Moser *et al.* 2007; Hertel and Wesche 2008; Macek *et al.* 2009). On the contrary, the size of tree belowground parts and their relative proportion in relation to aboveground structures has been reported to respond positively to decreasing temperature (Hertel and Wesche 2008; Hertel and Schöling 2011; Moser *et al.* 2011) and increasing drought (Gaul

et al. 2008; Hertel *et al.* 2008). Maximum photosynthesis rate has been shown to relate positively to temperature (e.g. Cabrera *et al.* 1998; Zhang *et al.* 2005; Azócar *et al.* 2007). However, increase in leaf thickness, and consequently N concentration per leaf area, with decreasing temperature may compensate the effect of Rubisco inactivation at low temperatures (Wittich *et al.* 2012) (Table 1).

Genetically determined traits are typically unresponsive to the environmental variation, whereas plastic traits respond to the varying environmental conditions (e.g. Clausen *et al.* 1940; Bradshaw 1965; Schlichting 1986; Sultan 2000). Therefore, by growing individuals of different species in the same environment,

the eventually observed interspecific variation in a given trait must be genetically determined. One can apply this logic in practice by investigating experimentally if the genetically determined interspecific variation in a given trait has evolved as a response to a certain environmental factor. This examination becomes possible if one knows the preferred condition of each species along the gradient of the environmental factor. A correlation between the interspecific variation in the trait and the interspecific variation in the preferred environmental condition is in concordance with the proposition that the evolutionary adaptation of the species along the gradient of the environmental factor has included genetically determined

Table 1. Expected relationships between tree functional traits and temperature/precipitation and their functional explanations

Note: '+' indicates positive relationship with temperature and precipitation, '-' indicates negative relationship and '±' no relationship; LA, single leaf area; SLA, specific leaf area; SRA, specific root area; SRL, specific root length; RT, root tip abundance; A_{mass} , mass-based maximum photosynthesis; A_{area} , area-based maximum photosynthesis; g , stomatal conductance; E , total leaf transpiration; $C_i : C_a$, ratio of intercellular to ambient CO_2 concentration; α , quantum use efficiency; R_d , dark respiration; LSP, light saturation point; LCP, light compensation point

Trait	Expected relationship to:	Functional explanation of the relationship	References
Temperature			
LA	+	Reduced cell number in plant organs at low temperatures due to energy economical reasons	Cordell <i>et al.</i> (1998); Körner <i>et al.</i> (1989); Hertel and Wesche (2008)
SLA	+	Reduced leaf size due to reduced number of cells and increased leaf thickness (especially epidermal cell walls) at low temperatures	Rundel <i>et al.</i> (2003); Hertel and Wesche (2008); Macek <i>et al.</i> (2009); van de Weg <i>et al.</i> (2009)
SRA, SRL, RT	-	Response to decreased soil nutrient availability, constrained nutrient uptake or a compensation for a lower mycorrhizal infections at low temperatures	Ostonen <i>et al.</i> (2007); Hertel and Wesche (2008); Hertel <i>et al.</i> (2008)
A_{mass}	+	Decreased activity of Rubisco enzyme and consequently decreased rate of carboxylation at low temperatures.	Wittich <i>et al.</i> (2012)
A_{area} , $C_i : C_a$	±	Increase in leaf thickness and consequently higher N and Rubisco concentration per leaf area at low temperatures may affect area-based CO_2 uptake and other area-based measures so that a positive relationship with temperature is not detected	Benecke <i>et al.</i> (1981); Körner and Diemer (1987); Bresson <i>et al.</i> (2009); Wieser <i>et al.</i> (2010); Wittich <i>et al.</i> (2012)
g , E	+	Defined via positive response to vapour pressure deficit until a threshold limit in which stomata close	Benecke <i>et al.</i> (1981); Körner <i>et al.</i> (1986)
R_d	+	Depends mainly on the demand for metabolites for maintenance and growth. Exponential increase with temperature, but can acclimate over a long-term.	Larigauderie and Körner (1995); Reich <i>et al.</i> (1997); Wright <i>et al.</i> (2006)
LCP, LSP	+	Adaptation of light response to lower temperatures at low light levels in colder environments. Consequently LSP has also a positive relationship with temperature.	Körner (2003)
α	-	Due to a positive relationship between temperature and LCP/LSP, light use efficiency decreases (slower response of CO_2 assimilation to increased light intensity) with increasing temperature	
Precipitation			
LA, SLA	+	Decreased carbon gain due to higher stomatal limitation in dry environments (resistance against desiccation), adaptation to longer leaf lifespan in dry environments	Li <i>et al.</i> (2000); Colmenares-Arteaga <i>et al.</i> (2005)
SRA, SRL, RT	-	Response to decreased water availability in soil to improve water absorption	Bakker <i>et al.</i> (2006); Hertel <i>et al.</i> (2008)
A_{mass} , A_{area} , g , E , $C_i : C_a$	+	Defined via positive response to vapour pressure deficit until a threshold limit in which stomata close	Benecke <i>et al.</i> (1981); Körner <i>et al.</i> (1986); Rada <i>et al.</i> (2009)
LSP, LCP, α , R_d	±	No functional explanation which would be directly related to precipitation	Wright <i>et al.</i> (2006)

modifications of the trait. However, it is possible that maternal effects may influence the outcome of common garden experiments.

The Andean tree genus *Polylepis* (Rosaceae) offers an excellent opportunity to study interspecific variation in traits in relation to species climatic optima, because the genus contains ~30 species (Schmidt-Lebuhn *et al.* 2006) adapted to different temperature and moisture conditions (Simpson 1986). These adaptations are relatively new in evolutionary terms, because the genus evolved and diversified during the uplift of the Andes in the Plio-Pleistocene (Simpson 1986; Kerr 2003) in response to the emergence of new high elevation habitats (Gregory-Wodzicki 2000). In this study, we specifically asked whether the variation in several functional traits potentially associated with temperature and/or precipitation among nine *Polylepis* tree species can be attributed to genetically determined adaptations, and whether the physiological traits are genetically more strongly controlled than morphological traits. It has been suggested that physiological traits, photosynthesis in particular, would be more fixed (less plastic) than morphological traits due to the conservative inheritance of physiological traits caused by their complex genetic basis (e.g. Müller *et al.* 2012). Genetically determined variation in a trait may also be induced by purely phylogenetic reasons. Therefore, we also asked whether the studied functional traits show a phylogenetic signal. To answer these research questions, we tested the following hypotheses:

- (i) that species-specific average values in the functional traits are related to the climatic niche optima of the species (defined by mean annual temperature and annual precipitation) according to the theoretical patterns listed in Table 1;
- (ii) that physiological traits are more strongly related to the climatic niche optima than morphological traits due to the conservative inheritance of physiological traits; and
- (iii) that closely related species are functionally more similar than distantly related species, i.e. functional traits show a phylogenetic signal.

Materials and methods

Species distribution and climate data

We studied nine species of *Polylepis* originating from five geographical regions in central and southern Andes. These species grow under a wide range of climatic conditions ranging from humid montane forests to dry high-elevation habitats. Four of the species form the natural alpine treelines whereas the other five occur at lower elevations (Fig. 1). Plants were obtained from the *Polylepis* collection at the greenhouses of the Experimental Botanical Garden of the University of Göttingen. Provenances held in the botanical garden were grown from seeds (in the case of *Polylepis pauta* Hieron. and *Polylepis microphylla* (Wedd.) Bitter.), or from seedling and/or root suckers. Due to logistical reasons (e.g. very restricted

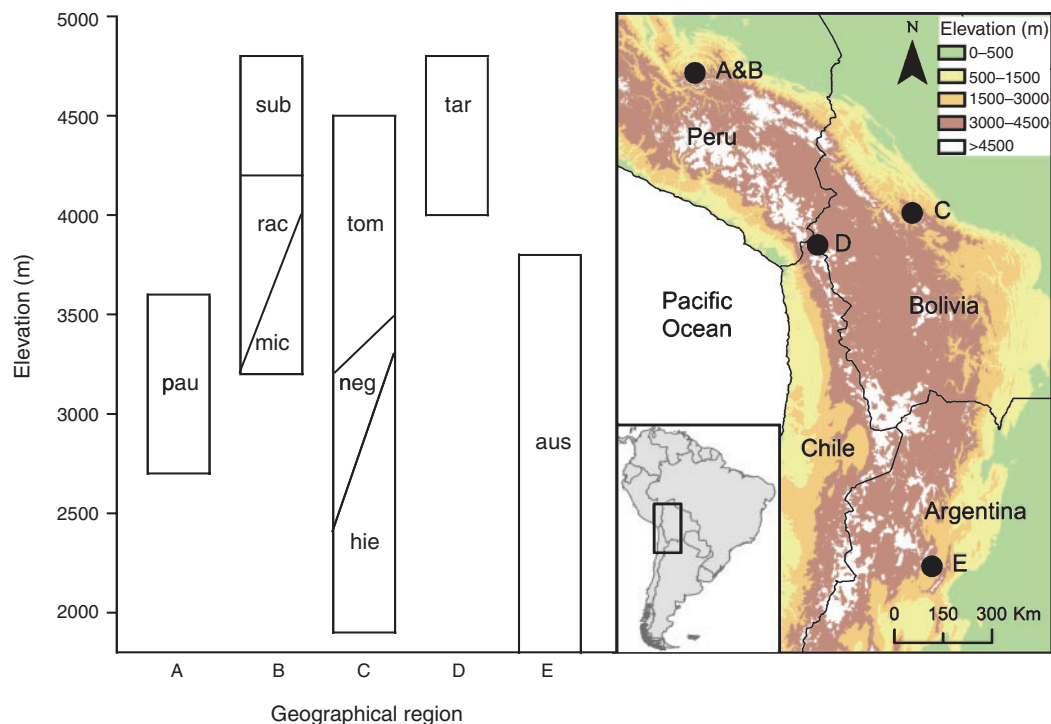


Fig. 1. Species geographical regions (A–E) and their elevation ranges: A, humid eastern Andes of southern Peru, including *P. pauta* (pau); B, semi-dry eastern Andes of southern Peru, including the species *P. microphylla* (mic), *P. racemosa* (rac) and *P. subsericans* (sub); C, humid eastern Andes of central Bolivia, including *P. hieronymi* (hie), *P. neglecta* (neg) and *P. tomentella* (tom); D, dry western Andes of central Bolivia, including *P. tarapacana* (tar); and E, semi-dry eastern Andes of Argentina, including *P. australis* (aus).

accessibility of respective populations), individuals of each species represent one population, which comes from a geographically limited area (Table 2).

To define the climatic niche optima of the species, we extracted the climate data for the localities of species occurrence from WorldClim global modelled climate data (<http://www.worldclim.org>, accessed 1 February 2011) at the spatial resolution of $\sim 1 \text{ km}^2$ (Hijmans *et al.* 2005). The localities of species occurrence were obtained during field trips reported in Kessler (1995) and Toivonen *et al.* (2011). We obtained additional georeferenced occurrence information from specimen location data in the GBIF (<http://www.gbif.org/>, accessed 1 November 2010) and Tropicos (<http://www.tropicos.org/>, accessed 1 November 2010) databases and scientific publications reporting *Polylepis* species locations. Before using all this legacy data, we manually cleaned it. For the species with a large distribution range we included only climate records near the areas of the provenances used in this study to ensure the correspondence between the climate data and species ecophysiological data. For the species with a narrow distribution range, all the climate records were used.

WorldClim climate data includes 19 climatic variables, of which we used mean annual temperature and total annual precipitation because they are readily interpretable and statistically uncorrelated variables ($r = -0.022$, $P = 0.955$). In our dataset, these two variables captured a large proportion of the variation in climatic niche optima between the species. In a principal component analysis (PCA) made for all 19 bioclim variables, total annual precipitation had the highest score in PCA component 1 (0.981) and mean annual temperature had the highest score in PCA component 2 (0.992), and PCA components 1 and 2 together captured 88.6% of the total variation. We calculated species-specific means for mean annual temperature (Mmat) and for total annual precipitation (Mtap) from the species occurrence locations. We also calculated mean minimum values of mean annual temperature and total annual precipitation (Minmat and Mintap) for each species based on the lowest 10% of the mean values, and an interaction term of climatic stress, Climstress ($-Mmat \times Mtap$) standardised to mean 0 and variance 1. High climatic stress is characterised by the conditions of low temperature and precipitation, and therefore the interaction term was multiplied by -1 , so that the

climatic stress increases when the value of the variable increases. We were aware of the uncertainties in the modelled climate data (Killeen *et al.* 2007; Soria-Auza *et al.* 2010) and possible spatial errors in species occurrence records. These could have caused a certain degree of inaccuracy in our estimates for species-specific means, but we do not have any reason to expect systematic biases in the data (Table 2).

Common garden experiment

We raised 15–20 individuals per species, which were grown at constant greenhouse conditions of 20°C of daytime and 8°C of night-time temperature with regular watering regime and a light intensity of $\sim 700 \text{ PAR}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) for 12 h per day, for 18 months. These conditions were chosen because they were relatively easy to maintain and we considered that all the species would perform reasonably well in them. Saplings were grown in the pots of the same size (1.5 L), which were placed in the greenhouse in a randomised block design with all species being present in each block with the same number of individuals being so that possible differences in growth would have affected the different species to the same extent. At the time of the measurements the saplings were 1.5–8 years old and 10–50 cm tall.

As aboveground morphological traits we measured single leaf area (LA, cm^2) and specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$). We randomly extracted one intact and fully expanded leaf from the upper branches of 12 different individuals of each *Polylepis* species, scanned them with a digital flatbed scanner and measured the leaf area from the scanned images using a WinFolia software (Régent Instruments Inc., Québec, Canada). To determine SLA, we dried leaves to constant weight at 70°C and related the single leaf area to the dry weight (DW) (Table S2 in available as Supplementary Material to this paper).

As belowground traits we measured specific root area (SRA, $\text{cm}^2 \text{ g}^{-1}$), specific root length (SRL, m g^{-1}) and the abundance of root tips, (RT, n mg^{-1}). We extracted randomly one representative intact living rootlet from the soil of 12 or six *Polylepis* individuals of each species and took digital images of the rootlets under water with a special transmitted light scanner to measure root surface area, root length and abundance of root tips from the scanned

Table 2. Species, the provenance of accession of seeds, seedlings and root suckers for the cultivation, and species environmental data including the number of species occurrence localities used to obtain climate data (*n*), species elevation ranges (adapted from Kessler (1995) and Toivonen *et al.* (2011), and species-specific mean values \pm s.e. for climate variables (obtained from modelled global climate data of WorldClim)

Mmat, mean for mean annual temperature; Minmat, mean minimum for mean annual temperature; Mtap, mean for total annual precipitation; Mintap, mean minimum for total annual precipitation. Mean minimum values, Minmat and Minmap, are calculated as a mean of the lowest 10% of the mean values

Species	Provenance	<i>n</i>	Elevation (m)	Species environmental data			
				Mmat (°C)	Minmat (°C)	Mtap (mm)	Mintap (mm)
<i>Polylepis pauta</i>	Cuzco, Peru	16	2670–3600	10.98 \pm 0.48	8.90 \pm 0.13	737 \pm 58	459 \pm 0
<i>Polylepis microphylla</i>	Cuzco, Peru	10	3300–4000	9.17 \pm 0.46	7.66 \pm 0.25	730 \pm 26	651 \pm 12
<i>Polylepis racemosa</i>	Cuzco, Peru	24	3200–4200	9.08 \pm 0.38	6.28 \pm 0.06	704 \pm 16	557 \pm 58
<i>Polylepis subsericans</i>	Cuzco, Peru	36	4200–4800	5.52 \pm 0.17	3.48 \pm 0.39	773 \pm 3	754 \pm 0.3
<i>Polylepis hieronymi</i>	Tarija, Bolivia	31	1900–3300	16.10 \pm 0.23	13.62 \pm 0.66	625 \pm 21	437 \pm 42
<i>Polylepis neglecta</i>	Santa Cruz, Bolivia	17	2400–3500	14.40 \pm 0.33	12.07 \pm 0.11	690 \pm 22	511 \pm 14
<i>Polylepis tomentella</i>	Cochabamba, Bolivia	139	3200–4500	10.06 \pm 0.21	5.75 \pm 0.14	370 \pm 14	143 \pm 3
<i>Polylepis tarapacana</i>	Oruro, Bolivia	49	4000–4800	4.38 \pm 0.22	1.95 \pm 0.04	181 \pm 22	58 \pm 0.9
<i>Polylepis australis</i>	Córdoba, Argentina	22	1800–3800	12.85 \pm 0.39	9.07 \pm 0.08	356 \pm 23	255 \pm 6

images using the WinRhizo software (Régent Instruments Inc.). We dried the roots to constant weight at 70°C and calculated the specific root area, specific root length and root tips abundance relating the measured surface area, length and root tip data to DW of the rootlets (Table S3).

The photosynthetic performance of the species was measured as light response curves with a portable gas-exchange system (LI-6400, Li-Cor Biosciences, Lincoln, NE, USA) with an integrated gas analyser and a standard leaf chamber equipped with a LED red/blue light source (type 6400-02B). We measured 1–4 intact and fully expanded upper branch leaves per individual. The number of individuals per species varied from one to eight, because at the moment of the measurement we did not have the same number of individuals with sufficiently healthy leaves necessary for the measurements. Measurements were done in constant CO₂ partial pressure of 350 μmol mol⁻¹ and leaf temperature of 18°C. First, the plant leaf was exposed to the maximum light intensity of 1500 PAR for ~15–20 min until CO₂ level in the leaf chamber stabilised and leaves showed the maximum rate of photosynthesis (μmol of CO₂ m⁻² s⁻¹). Then we ran an automatic light response program, where the light intensity was gradually lowered from 1500 to 1200, 1000, 800, 600, 400, 200 and zero PAR, and CO₂ assimilation rate was measured in each light intensity level after the CO₂ level had stabilised within a minimum waiting time of 2 min. The last measurement at zero PAR was used to estimate dark respiration. We fitted the light response curve to the measured data using non-linear regression, which describes leaf photosynthesis, A_1 as a rectangular hyperbolic function of photosynthetic photon flux density, Q :

$$A_1 = A_{\max} \alpha Q / (A_{\max} + \alpha Q) - R_d, \quad (1)$$

where A_{\max} represents the asymptotic value of gross photosynthesis with respect to Q , α is the quantum use efficiency and R_d the apparent dark respiration rate (Meir *et al.* 2007). We calculated the following parameters from the light response data:

A_{area} (μmol CO₂ m⁻² s⁻¹), leaf area-based maximum net photosynthesis rate;

A_{mass} (nmol CO₂ g⁻¹ s⁻¹), leaf mass-based maximum net photosynthesis rate calculated through specific leaf area;

g (mol H₂O m⁻² s⁻¹), stomatal conductance to water vapour in maximum light conditions;

R_d (μmol CO₂ m⁻² s⁻¹), dark respiration rate;

E (mol H₂O m⁻² s⁻¹), leaf transpiration rate;

$C_i : C_a$ (mol CO₂ mol CO₂⁻¹), ratio of intercellular to ambient CO₂ concentration;

α , quantum use efficiency, this is the coefficient of the initial slope of light response curve indicating the efficiency of light use in CO₂ assimilation;

LSP (μmol photons m⁻² s⁻¹), light saturation point: this refers to the PAR value where 90% of maximum net photosynthesis is reached and carbon assimilation rate can no longer increase because of the limited carboxylation; and

LCP (μmol photons m⁻² s⁻¹), light compensation point: this is the PAR value where photosynthesis and respiration are balanced, so that the rate of CO₂ assimilation matches the rate of CO₂ released from respiration (Table S1).

Statistical analyses

To explore the relationships among the traits, we used Pearson's correlation analysis. To relate the traits with estimated climatic optima of the species, we used ordinary linear regressions, where species-specific mean for each trait was used in turn as a response variable and species-specific means for occurrence points along climatic variables (Mmat and Mtap) and their interaction term, climatic stress (Climstress), as explanatory variables.

To illustrate the relationships among the functional traits and between functional traits and climate, we conducted a redundancy analysis (RDA), where we used all 14 functional traits as response variables and Mmat, Mtap and their interaction Climstress as an explanatory variable. Due to a low sample size ($n = 9$ species), it is not meaningful to report type 1 error probabilities for RDA models that have more than one explanatory variable. The RDA was carried out with the statistical software Canoco 4.5 (ter Braak and Smilauer 1998).

We also made RDA separately for morphological and physiological traits to study whether the selected physiological traits are in general better explained by climatic niche variables than morphological traits. If so, that would prove higher degrees of genetic determinism in physiological traits compared with morphological traits due to more complex genetic basis of physiological traits. As above, we report statistics with one explanatory variable in turn (Mmat, Mtap or Climstress).

To study the phylogenetic signal in functional traits, we calculated phylogenetic distances between the species based on the phylogenetic tree by Schmidt-Lebuhn *et al.* (2006) that was calculated by successive reweighting of morphological characters in combination with molecular AFLP (Amplified Fragment Length Polymorphism) data. The tree is not time-calibrated and therefore time-scaled evolutionary distances could not be calculated. Instead, we calculated the phylogenetic distances as number of bifurcations between the species. We then calculated dissimilarity matrices based on Euclidean distances separately for each functional trait. These matrices were then compared with the phylogenetic distance matrix with a Mantel test of matrix correspondence (Smouse *et al.* 1986). Distance matrices and Mantel tests were calculated with the statistical software PC-ORD 6 (Peck 2010).

Results

Several functional traits were intercorrelated. For example, area- and mass-based maximum CO₂ assimilation rates (A_{mass} , A_{area}), stomatal conductance (g) and leaf transpiration (E) were strongly positively intercorrelated. Similarly, light compensation and light saturation points (LCP and LSP) and dark respiration (R_d) were strongly positively intercorrelated. Also, LCP and LSP were marginally negatively correlated with quantum use efficiency (α). Specific root area and root length (SRA and SRL) and root tip abundance (RT), were strongly positively intercorrelated. Additionally, RT and single leaf area (LA) were marginally negatively intercorrelated. Specific leaf area (SLA) neither single leaf area (LA) correlated with CO₂ assimilation rates (A_{mass} , A_{area}). Instead, SLA correlated negatively with LCP, LSP and R_d . (Table 3).

We noted some significant and some marginally significant relationships between the interspecific variation in functional

traits and climatic niche variables (Mmat, Mtap and Climstress), but in many cases the relationships were not significant (Table 4). The strongest relationships were the increase in LA with increasing mean annual temperature, the reduction in LA with increasing climatic stress, and the decrease in light compensation point of photosynthesis (LCP) with increasing

precipitation. Mass-based photosynthesis rate A_{mass} was marginally related to Mmat, but area-based photosynthesis rate (A_{area}) not, as we expected. Also, specific leaf area (SLA) was not related to Mmat neither to Mtap even though it was positively correlated with LCP, which showed a strong relation with Mtap. Similarly, even the root morphological traits

Table 3. Pearson's correlation coefficients among species-specific mean values for functional traits

Correlations with $C_i : C_a$ are Spearman's correlation coefficient. Significant differences are indicated: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; +, $P < 0.1$. A_{area} , area-based maximum photosynthesis; A_{mass} , mass-based maximum photosynthesis; R_d , dark respiration; g , stomatal conductance; E , total leaf transpiration; $C_i : C_a$, ratio of intercellular to ambient CO_2 concentration; α , quantum use efficiency; LSP, light saturation point; LCP, light compensation point; SLA, specific leaf area; LA, single leaf area; SRA, specific root area; SRL, specific root length; RT, root tip abundance

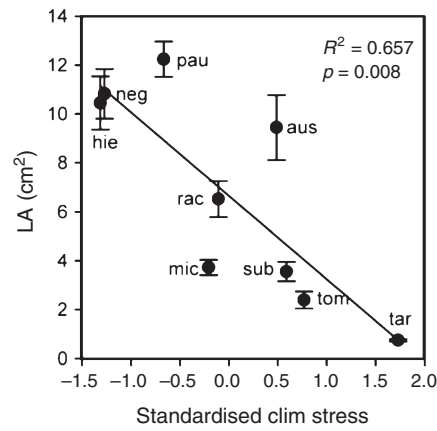
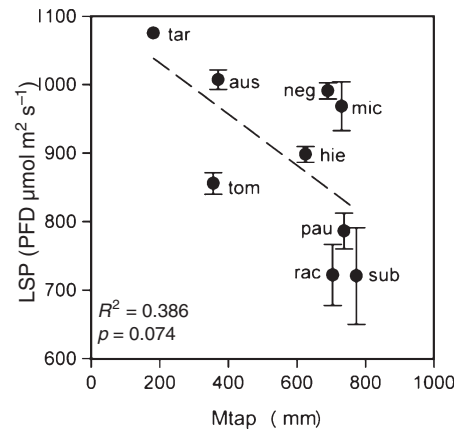
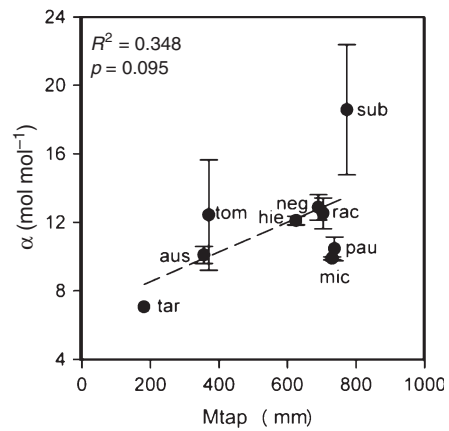
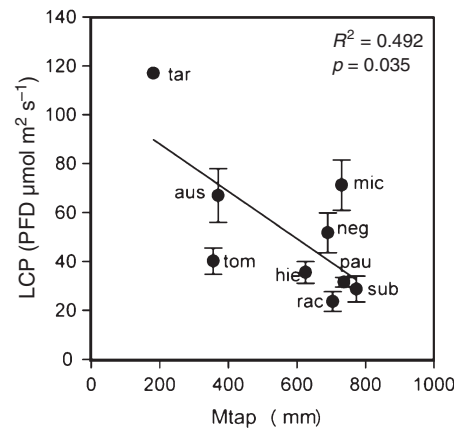
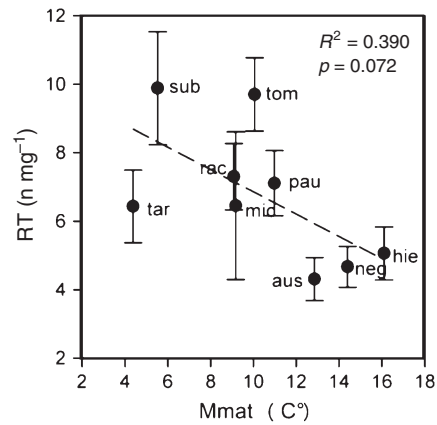
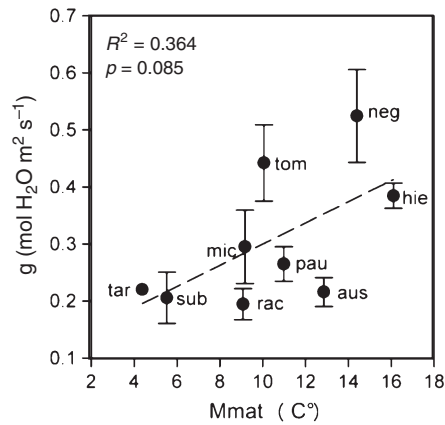
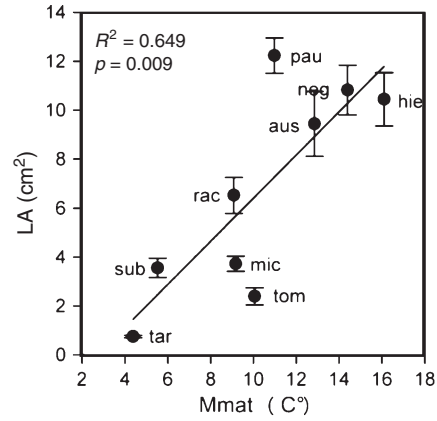
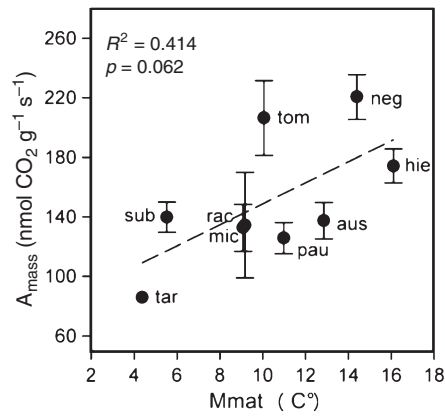
	A_{mass}	R_d	g	E	$C_i : C_a$	α	LSP	LCP	SLA	LA	SRA	SRL	RT
A_{area}	0.940***	0.580	0.954***	0.930***	0.199	0.267	0.462	0.039	-0.325	0.104	-0.073	0.006	-0.051
A_{mass}		0.321	0.894**	0.898**	0.157	0.400	0.193	-0.267	0.014	0.305	0.116	0.202	-0.023
R_d			0.554	0.523	0.221	-0.221	0.883**	0.795*	-0.818**	-0.587+	-0.345	-0.263	0.151
g				0.986***	0.451	0.074	0.531	0.082	-0.295	0.254	-0.170	-0.066	-0.171
E					0.461	0.090	0.470	0.035	-0.210	0.262	-0.098	-0.015	-0.099
$C_i : C_a$						-0.758*	0.550	0.309	-0.101	0.356	-0.464	-0.380	-0.486
α							-0.591+	-0.635+	0.295	0.030	0.674*	0.670*	0.525
LSP								0.864**	-0.809**	-0.344	-0.644+	-0.580	-0.259
LCP									-0.851**	-0.641+	-0.550	-0.535	-0.044
SLA										0.594+	0.498	0.508	0.039
LA											-0.030	-0.023	-0.584+
SRA												0.974***	0.769*
SRL													0.804**

Table 4. Explained proportion of variance (R^2) in inter-specific variation of functional traits in ordinary linear regressions and their statistical significance (p) using climatic niche variables Mmat (mean for mean annual temperature), Mtap (mean for total annual precipitation) and their interaction term Climstress as explanatory variables

[+] and [-] symbols indicate the direction of the relationship. Statistically significant R^2 -values are indicated: **, $P < 0.01$; *, $P < 0.05$; +, $P < 0.1$. A_{area} , area-based maximum photosynthesis; A_{mass} , mass-based maximum photosynthesis; R_d , dark respiration; g , stomatal conductance; E , total leaf transpiration; $C_i : C_a$, ratio of intercellular to ambient CO_2 concentration; α , quantum use efficiency; LSP, light saturation point; LCP, light compensation point; SRA, specific root area; SRL, specific root length; RT, root tip abundance; SLA, specific leaf area; LA, single leaf area

Trait	Mmat			Mtap			Climstress		
	Slope	R^2	P -value	Slope	R^2	P -value	Slope	R^2	P -value
A_{area}	[+]	0.259	0.162	[+]	0.003	0.893	[+]	0.164	0.279
A_{mass}	[+]	<u>0.414</u>	0.062+	[+]	0.044	0.588	[+]	0.284	0.140
R_d	[-]	0.042	0.595	[-]	0.222	0.200	[-]	0.116	0.370
g	[+]	<u>0.364</u>	0.085+	[+]	0.004	0.879	[+]	0.263	0.158
E	[+]	0.325	0.109	[+]	0.016	0.747	[+]	0.272	0.150
$C_i : C_a$	[+]	0.248	0.172	[-]	0.064	0.512	[+]	0.101	0.404
α	[-]	0.001	0.951	[+]	<u>0.348</u>	0.095+	[+]	0.048	0.572
LSP	[+]	0.001	0.946	[-]	<u>0.386</u>	0.074+	[-]	0.046	0.579
LCP	[-]	0.198	0.230	[-]	<u>0.492</u>	0.035*	[-]	0.345	0.096+
SRA	[-]	0.020	0.718	[+]	0.171	0.268	[+]	0.000	0.974
SRL	[-]	0.035	0.627	[+]	0.071	0.488	[-]	0.007	0.832
RT	[-]	<u>0.390</u>	0.072+	[+]	0.015	0.750	[-]	0.191	0.239
SLA	[+]	0.097	0.415	[+]	0.212	0.212	[+]	0.112	0.378
LA	[+]	<u>0.649</u>	0.009**	[+]	0.182	0.253	[+]	<u>0.657</u>	0.008**

Fig. 2. Significant or marginally significant relationships between species-specific mean values in functional traits (\pm s.e.) and climatic niche variables. A_{mass} is the mass-based maximum photosynthesis; g is stomatal conductance; LA is single leaf area; RT is root tip abundance; LCP is the light compensation point; LSP is the light saturation point; α is quantum use efficiency; Mmat is the species-specific mean for mean annual temperature; and Mtap is the species-specific mean for total annual precipitation. Standardised Climstress is calculated as an interaction between Mmat and Mtap, multiplied by -1 and standardised to mean 0 and variance 1. Solid trend lines indicate statistically significant relationships ($P < 0.05$) and dashed trend lines marginally significant relationships ($P < 0.1$).



(SRA, SRL and RT) were strongly intercorrelated, only root tip abundance (RT) showed a significant relationship (even though marginal) to Mmat (Table 4; Figs 2, 3).

Physiological traits were not in general better explained by climatic niche variables than morphological traits. When relating all morphological and all physiological traits respectively to climatic niche variables, no significant relationships were detected (Table 5).

Single leaf area (LA) was the only trait showing a significant phylogenetic signal. Phylogenetic distances among the species were positively correlated with Euclidean distances based on LA ($r=0.33$, $P<0.05$) (Table 6).

Discussion

In this study, our aim was to assess (i) whether the functional traits that enable *Polylepis* species from tropical and subtropical Andes to cope with cold and dry conditions are genetically determined, (ii) whether the morphological traits are more plastic than the physiological traits, and (iii) whether the functional traits show a phylogenetic signal. We found some significant relationships between the interspecific variation in functional traits and temperature and/or precipitation optima of the species,

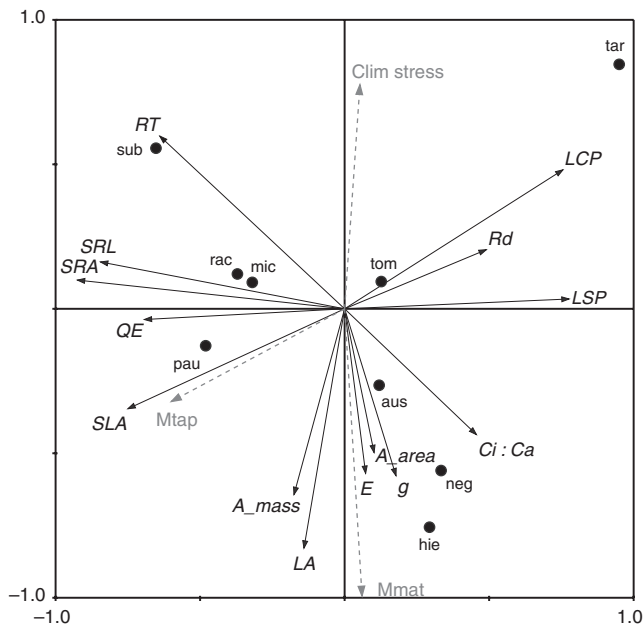


Fig. 3. Redundancy analysis (RDA) triplot with three explanatory variables (Mmat is the mean for mean annual temperature; Mtap is the mean for total annual precipitation; Climstress is climatic stress calculated as an interaction between Mmat and Mtap, multiplied by -1); and all 14 functional traits as response variables (A_{area} is area-based maximum photosynthesis; A_{mass} is mass-based maximum photosynthesis; R_d is dark respiration; g is stomatal conductance; E is total leaf transpiration; $C_i : C_a$ is the ratio of intercellular to ambient CO_2 concentration; QE is quantum use efficiency (α); LSP is the light saturation point; LCP is the light compensation point; SRA is specific root area; SRL is specific root length; RT is root tip abundance; SLA is specific leaf area; and LA is single leaf area). Species (= samples) are marked as black dots (pau=*P. pautia*, mic=*P. microphylla*, rac=*P. racemosa*, sub=*P. subsericans*, hie=*P. hieronymi*, neg=*P. neglecta*, tom=*P. tomentella*, tar=*P. tarapacana*, aus=*P. australis*).

indicating genetically determined climatic adaptations to cold and dry conditions respectively. However, several climate-trait relationships that we expected to see, based on theories and previous empirical evidence, were not observed. Our results did not support the hypothesis about the conservative inheritance of physiological traits, i.e. physiological traits were not genetically more strongly controlled than morphological traits among the traits and species that we studied. The role of phylogenetic relationships determining the inter-specific variation in the functional traits was limited and significant only for single leaf area.

Genetically determined adaptive traits

Adaptive traits are assumed to have a genetic basis and have been consistently linked to the environment during the species evolution, in the case of *Polylepis* species since Plio-Pleistocene (Simpson 1986; Kerr 2003). In our study, these associations can be seen in strong relationships between the inter-specific variation of a trait and climatic niche optima.

We found the expected increase in species-specific mean of single leaf area (LA) and decrease in root tip abundance (RT) with increasing mean annual temperature optima (Mmat). These findings are in concordance with the well known size reduction in tree aboveground parts, and more recently detected increase in the size of tree belowground parts with decreasing temperature, which also results in corresponding changes in above- and belowground biomass allocation patterns (e.g. Hertel *et al.* 2008; Hertel and Schöling 2011; Moser *et al.* 2011). Positive responses of root systems to decreased temperatures are explained by low nutrient supply at low temperatures due to reduced water viscosity and liquid diffusion and low microbial activity (e.g. Sveinbjörnsson *et al.* 1992; Tanner *et al.* 1998; Hertel and Wesche 2008; Hertel and Schöling 2011). The direct mechanisms underlying the reduction in leaf area with decreasing temperature remain unclear, but are likely to be linked to leaf energy economy and increasing leaf thickness. Körner (2003) highlighted the role of the developmental control of cell wall structures, increased lipid concentration in particular, as a reason for increased leaf thickness at low temperatures. In thick leaves, more carbon is invested per unit of photosynthesising leaf area than in thin leaves. Consequently, leaf size decreases with increasing thickness, because it would be energetically too expensive to develop and maintain large and thick leaves.

Also, according to our expectations, mass-based maximum photosynthetic rate was positively related to Mmat. The positive relationship between CO_2 assimilation and temperature is commonly related to the activation of the Rubisco enzyme (Berry and Björkman 1980; Yamori *et al.* 2005). Generally, all nine species studied showed relatively high rates of maximum area-based photosynthesis rates in comparison to other *Polylepis* species measured *in situ* (e.g. Rada *et al.* 1996; García-Núñez *et al.* 2004; Azócar *et al.* 2007). We believe this was partially an effect of optimum laboratory conditions and elevated CO_2 partial pressure, which was almost twice as high as the one *Polylepis* species are exposed to in their high mountain habitats.

Reduction in A_{mass} with decreasing Mmat may be interpreted as an evidence that tree growth is limited by carbon acquisition at

Table 5. Statistics of redundancy analysis made with one explanatory variable (Mmat, Mtap or Climstress), being either ‘all functional traits together as response variables’, ‘only morphological traits’, or ‘only physiological traits as response variables’

Mmat, species-specific mean for mean annual temperature; Mtap, species-specific mean for total annual precipitation; Climstress, interaction between Mmat and Mtap

	R ²	P-value
<i>All functional traits</i>		
Mmat	0.22	0.096 ⁺
Mtap	0.16	0.286
Climstress	0.15	0.357
<i>Morphological traits</i>		
Mmat	0.24	0.136
Mtap	0.12	0.936
Climstress	0.18	0.246
<i>Physiological traits</i>		
Mmat	0.21	0.157
Mtap	0.18	0.243
Climstress	0.13	0.391

Table 6. Coefficients of correlation (r) and their level of significance (P-value) between the matrices of functional dissimilarities and phylogenetic distances among the nine species in the Mantel test of matrix correspondence

Significant differences are indicated: **, $P < 0.01$; *, $P < 0.05$; +, $P < 0.1$. A_{area} , area-based maximum photosynthesis; A_{mass} , mass-based maximum photosynthesis; R_d , dark respiration; g , stomatal conductance; E , total leaf transpiration; $C_i : C_a$, ratio of intercellular to ambient CO₂ concentration; α , quantum use efficiency; LSP, light saturation point; LCP, light compensation point; SRA, specific root area; SRL, specific root length; RT, root tip abundance; SLA, specific leaf area; LA, single leaf area

Trait	r	P-value
A_{area}	-0.161	0.237
A_{mass}	-0.073	0.402
R_d	0.260	0.076 ⁺
g	-0.266	0.068 ⁺
E	-0.222	0.128
$C_i : C_a$	-0.263	0.177
α	-0.247	0.193
LSP	0.066	0.323
LCP	0.253	0.184
SRA	-0.101	0.277
SRL	-0.041	0.457
RT	-0.262	0.079 ⁺
SLA	0.181	0.210
LA	0.327	0.031*

high elevations, and not only by metabolic constraints related to the carbon investment into tree organs at low temperatures (Körner 1998; Hoch and Körner 2005). This finding is in agreement to recent ecophysiological studies on trees under *in situ* conditions at high elevation treelines (Wieser *et al.* 2010; Wittich *et al.* 2012).

Unexpectedly, we found that inter-specific variation in light compensation and light saturation points (LCP, LSP) was

negatively and quantum use efficiency (α) positively related to species-specific mean for total annual precipitation (Mtap). This may be interpreted as an indirect response of these photosynthetic traits to light conditions as a result of prevailing cloud cover and precipitation at the natural growth sites of the species. It is possible that species from areas of frequent cloud cover and high precipitation may better exploit available light and reach positive carbon balance and maximum CO₂ assimilation rate at lower light intensities than species from areas of clear sky conditions, and consequently lower precipitation. This assumption is supported by the observation that among Amazonian cloud forest trees maximum photosynthesis rate may be negatively affected by cloud cover due to low light intensity levels and leaf wetness (Letts and Mulligan 2005). However, it has been shown that sun leaves have higher saturated photosynthesis rate and light compensation point than shade leaves of the same plant (e.g. Boardman 1977), calling this interpretation into question. It has also been shown among several tropical tree species that photosynthetic features and functional leaf traits do not differ between the species of different shade tolerance (Coste *et al.* 2005), and that leaves may also be able to acclimate to changed light conditions (Mooney 1977). We did not find a decrease in species-specific maximum photosynthesis rate in relation to increased mean annual precipitation optima, even though light compensation and light saturation points of photosynthesis (LCP, LSP) and quantum use efficiency (α) were affected.

Traits showing no relationships with climatic niche variables

We did not detect the commonly reported decrease in specific leaf area (SLA) with decreasing Mmat (e.g. Cordell *et al.* 1998; Moser *et al.* 2007; Hertel and Wesche 2008; Macek *et al.* 2009). Neither was the relationship with Mtap statistically significant, even though the expected trend was visible. We expected that area-based photosynthetic rate (A_{area}) would respond to changes in SLA so that an increase in SLA with decreasing temperature would compensate the temperature-related decrease in A_{area} , via increase in N concentration per leaf area, eventually leading A_{area} to show no relationship with temperature optima of the species. We indeed observed this lack of relationship. However, the assumed compensation effect was not manifested in our study because SLA did not decrease with increasing temperature optimum. This suggests that A_{area} is not controlled solely by SLA.

Also the root traits, SRA and SRL in particular, showed no relationship with climatic niche variables. We expected these traits to be negatively related to precipitation and temperature due to the necessity to improve water absorption in arid conditions (Bakker *et al.* 2006; Hertel *et al.* 2008) and to improve nutrient uptake at low temperatures (Sveinbjörnsson 2000; Ostonen *et al.* 2007; Hertel and Wesche 2008). However, only root tip abundance (RT) showed the expected negative relationship with temperature. SRA and SRL were unresponsive to both climatic niche variables. This may partially be a consequence of possible inaccuracies in species-specific mean values, due to the intra-specific variation and limited number of measured individuals per species. In addition, we used individuals of one population only, but as the used climate records also came from

the proximity of the studied provenances, we believe the maternal effect has only a minor effect on the results.

Dark respiration (R_d) was expected to relate positively to temperature, but no relationship with precipitation was found (Wright *et al.* 2006). In contrast, interspecific variation in R_d should relate positively to the variation in maximum photosynthesis rate and associated leaf traits because high photosynthesis rates have substantial maintenance costs (Reich *et al.* 1997). We found no relationship between interspecific variation in dark respiration and M_{mat} in *Polylepis* species grown in uniform experimental conditions. This may confirm the acclimation tendency of R_d to prevailing temperature conditions (Larigauderie and Körner 1995; Körner 2003; Atkin *et al.* 2006). Instead, inter-specific variation in dark respiration showed a slight negative trend in relation to M_{tap} , but owing to the weak statistical significance of this relationship, it remains unclear whether or not *Polylepis* species of drier habitats would respire more than species from humid habitats. However, our results showed a high respiration rate for *P. tarapacana*, the species with the most stressful climatic niche optima (the driest and the coldest) in relation to its mean maximum photosynthesis rates. So, even though the variation in R_d among the nine species was not related to the variation in average climatic stress conditions that the species face, it seems that the respiration cost for this specific species is especially high because of the stressful climatic conditions where it comes from, and this trait was apparently maintained in the common garden experiment.

The role of phylogeny and ecological specialisation

Genetically determined interspecific variation in traits may also reflect phylogenetic distances among species so that trait value differences increase together with phylogenetic distances. In our study, single leaf area was the only trait that showed a significant positive phylogenetic signal indicating that closely related species have similar single leaf area. Therefore, among our study species the interspecific variations in traits that were significantly related to climatic niche optima of the species seem to be mainly a result of species-specific preferences to different environmental conditions. This can be interpreted as an evidence of ecological specialisation along environmental gradient in the course of species evolution within the genus *Polylepis*. It has been shown earlier that the phylogenetically basal grade of species within the genus *Polylepis* grows in humid habitats and that there is a successive adaptation of species to increasingly arid environments (Simpson 1986; Schmidt-Lebuhn *et al.* 2006, 2010). Instead, cold climate species (treeline species) are dispersed fairly evenly in the phylogenetic tree, indicating that adaptations to cold climate within the genus would have happened several times independently.

Conclusions

The results of our study indicate that some of potentially relevant functional traits that enable high Andean *Polylepis* species to withstand cold and dry conditions show genetically determined variation among species. Therefore, these traits appear to have been important objects of selection during evolution of the species. Physiological traits were not more fixed than

morphological traits among the studied traits and species, leading to the rejection the hypothesis regarding the conservative inheritance of physiological traits. A phylogenetic signal was significant only for single leaf area, indicating that the relationships between species-specific means in the studied traits and climatic niche optima result largely from environmental adaptations.

The results of our study agree with earlier findings (Chapin *et al.* 1993; Westoby *et al.* 2002) that plant functional responses to climate form a complex network of interactions and trade-offs, where plants aim to the optimal combination of traits to maximise their overall fitness. Therefore, it is possible that not all of the individual traits studied are manifested optimally in relation to the species-specific climatic niche variables. Consequently, predictions about species functional responses to increasing temperatures due to climate change or changes in the high elevation treeline position should be made very carefully.

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