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A hyper arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not belowground resource acquisition strategies

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Abstract.

1. The fast–slow plant economics spectrum predicts that because of evolutionary and biophysical constraints, different plant organs must be coordinated to converge in a unique ecological strategy within a continuum that shifts from fast to slow resource acquisition and conservation. Therefore, along a gradient of aridity, taxa with different strategies will be expected to be successful because selection pressures for slow resource acquisition become stronger as the environment becomes drier. In extremely arid and seasonal environments, however, a slow strategy may become disadvantageous because slow traits are costly to maintain. Additionally, as the availability of water decreases, selection pressures increase, reducing the variation in ecological strategies.
2. Using shrub assemblages along an aridity gradient in the Atacama Desert, we test the hypothesis that selection pressures imposed by hyper aridity act simultaneously on the variation and coordination of trait attributes, leading to an inverse pattern in the fast – slow plant economics spectrum, where strategies shift from slow to fast as the environment becomes drier.
3. We established 20 to 22 plots at each of four sites along the gradient to estimate plant community structure and functional variation. For all species recorded we quantified a set of leaf, stem and, root traits.
4. Results revealed an inverse pattern of the fast–slow economics spectrum for leaf and stem traits, but not for root traits; that is, as aridity further increased, aboveground

traits exhibited a shift from a slow to a fast strategy with some level of coordination. Belowground traits, however, did not shift accordingly with our prediction, rather they showed more complex pattern of shift and coordination with aboveground traits along the gradient. We also found that trait variation showed an idiosyncratic pattern of variation along the gradient, indicating that ecological strategies are driven by local processes within sites.

5. *Synthesis*: Our results increase our understanding of the fast–slow plant economics spectrum by showing that environmental gradients, as well as local process can simultaneously shape different below- and above-ground resource acquisition strategies in extremely poor resource environments.

Keywords: Aridity gradient, Atacama Desert, ecological strategies, functional traits, leaf, root, shrub communities, stem, trait functional variation.

INTRODUCTION

The fast–slow plant economics spectrum (Fast–slow PES hereafter) is a whole-plant ecological strategy framework that postulates that along gradients of resource availability such as water, carbon and nutrients, the trade-off between acquisition and conservation of resources translates into different successful ecological strategies for plant communities at different points along a gradient (Pérez-Ramos *et al.* 2012; Reich 2014; de la Riva *et al.* 2016b). Accordingly, along gradients of water availability, plants with traits that allow them to acquire and use water quickly (i.e., a fast strategy) are only successful in environments with high-water input; in contrast, having slow water-acquisition traits (i.e., a slow strategy) is advantageous in low-water input environments

because it promotes water conservation, which in turn enhances plant survival (Chapin 1991; Reich 2014; Carvajal *et al.* 2017). However, some studies have suggested that when the environment becomes extremely arid and highly seasonal, a slow strategy (for leaf traits at least) may not be beneficial because maintaining slow traits for long time periods involves a greater energetic expenditure than maintaining fast traits, ultimately decreasing plant survival (Mooney & Dunn 1970; Nilsen & Muller 1981). Consequently, having traits for fast acquisition and use of water in these environments may allow plants to take advantage of the periods of high water availability (Nilsen & Muller 1981; Mooney 1982; Ackerly 2004).

A prerequisite for a fast–slow PES to occur is that traits of the different plant organs (e.g., leaf, stems and roots) must be coordinated because of evolutionary and biophysical constraints (Reich *et al.* 1999; Freschet *et al.* 2010; Reich 2014). That is, to acquire resources efficiently, being fast or slow at the leaf level, also involves being fast or slow at the stem and root levels; otherwise, a plant may not be able to establish in a given locality (Reich 2014). While some studies bear out this expectation (e.g., Freschet *et al.* 2010; Liu *et al.* 2010; Méndez-Alonzo *et al.* 2012; de la Riva *et al.* 2016b), others do not (e.g., Baraloto *et al.* 2010; Fortunel, Fine & Baraloto 2012; Kramer-Walter *et al.* 2016; Butterfield *et al.* 2017). For example, studying Amazonian trees Baraloto *et al.* (2010) found orthogonal leaf and stem traits; that is, leaf and stem traits represented independent strategies of resource acquisition. The level of coordination between root and leaf traits can be multidimensional, meaning that certain root traits are coordinated with leaf traits, while others vary independently in determining resource acquisition strategies (Fort, Jouany & Cruz 2013; Kramer-Walter *et al.* 2016; Butterfield *et al.* 2017). Weak or lack of coordination among traits can occur because different plant

organs respond to different selection pressures, respond to the same selection pressures but in different ways, or because of different constraints on different plant organs (Withington *et al.* 2006; Kembel & Cahill 2011; Weemstra *et al.* 2016; Bergmann *et al.* 2017). All of these alternatives result in specific trait combinations that allow plants to enhance their fitness in a given locality (Valverde-Barrantes & Blackwood 2016; Messier *et al.* 2017). In hyper arid environments, however, plant traits are expected to be highly coordinated because the strong selection pressure imposed by aridity will restrict the suits of trait attributes that allow plants to cope with local environmental conditions (Chapin 1991; Reich 2014).

Different plant species can have different ecological strategies within a single point along a resource gradient (i.e., within particular communities) because factors such as plant-plant interactions, microenvironmental variability or perturbation, among others, can promote trait variation (Stubbs & Wilson 2004; Grime 2006; Ackerly & Cornwell 2007; Maestre *et al.* 2009; Butterfield & Briggs 2011; Adler *et al.* 2013; Morales *et al.* 2015; Butterfield *et al.* 2017). For example, Ackerly and Cornwell (2007) found that in Mediterranean woody plant communities of Coastal California, the effect of perturbation, as well as below- and above-ground partitioning of resources on trait variation among coexisting species, promoted different ecological strategies. From a geographical perspective, low diversity of ecological strategies along a resource gradient is expected to occur in sites where there is low input of water because as the harshness of the environment increases, aboveground competition among coexisting species decreases (e.g., Grime *et al.* 1997; Swenson & Enquist 2007; Coyle *et al.* 2014; but see Butterfield *et al.* 2017). Therefore, a shift from high to low trait variation along aridity gradients should occur as the environment becomes drier.

Woody shrub communities of the Coastal Atacama Desert constitute an ideal system to test the fast–slow economics spectrum hypothesis because water is considered the main resource limiting plant abundance and distribution (Squeo *et al.* 1998). This desert, which constitutes a hyper-arid environment according to De Martonne’s aridity index (De Martonne 1926), exhibits a north to south (between 23° S and 30° S) increase in rainfall from less than 1 mm·yr⁻¹ to 82 mm·yr⁻¹ (Rundel *et al.* 1991; Squeo *et al.* 2006); therefore, within this hyper-arid desert, there is a marked north to south aridity gradient biologically relevant at both the community and intraspecific levels (e.g., Squeo *et al.* 1994; Sotomayor & Gutiérrez 2015; López *et al.* 2016; Carvajal *et al.* 2017).

In this study, we used leaf, stem and root traits that have functional significance for woody shrub species, to test the hypothesis that as aridity increases in a hyper-arid environment, selection pressures act simultaneously on trait attributes, variation and coordination to promote an inverse pattern in the fast–slow PES. Specifically, we predict that in the most arid end of a hyper-arid aridity gradient (1) shrub assemblages will exhibit trait values that reflect a water acquisition strategy at the whole plant level; (2) traits will be highly coordinated across different plant organs and; (3) low variation in ecological strategies will predominate among shrub assemblages.

MATERIAL AND METHODS

Study area

We conducted this study during 2015 in four sites (listed from north to south) along the Coastal Atacama Desert: Quebrada El León (QL), Norte de Llanos de Challe (LLCHA), Chañaral de Aceituno (CHA) and Romeral (ROM) (Fig. S1). Mean annual precipitation at these sites ranges between 14 and 80 mm, mean annual temperature is relatively

constant along the gradient and fluctuates between 15 and 17°C (Table 1). Most of this rainfall falls in very few pulses interspersed with long periods of drought, which can range from 10 months in the wettest sites (Carvajal *et al.* 2014), to many years in the driest sites (Dirección General de aguas, Chile - <http://www.dga.cl>). The area is also affected by El Niño Southern Oscillation cycle (ENSO), which promotes high inter-annual variability of rainfall (Houston 2006) that increases towards the north (Carvajal, Loayza & Squeo 2015; Carvajal *et al.* 2017). For each site, we calculated De Martonne's aridity index (De Martonne 1926) ($DEMAI = MAP/[MAT + 10]$), where *MAP* and *MAT* represent mean annual precipitation and temperature, respectively. A decrease in values of DEMAI is indicative of an increase in aridity and values below 5 indicate hyper-aridity. Accordingly, all sites studied are in a hyper-arid region (Table 1).

Sampling design

To avoid variation caused by factors other than the one produced by aridity, all sites were located on sandy soils (stabilized dunes) of west-facing slopes of less than 5%. At each of the four sites, we installed 20 50 × 2 m plots separated by at least 100 m (N=20/site, except QL that had 22 plots), which we used to identify the dominant shrub species. We recorded all species present at each plot, as well as the number of individuals per species. Shrub richness decreased from 19 at Romeral (least dry site) to 10 at Quebrada el León (most arid site; table S1). Species diversity followed the same pattern, being highest at the least dry site and gradually decreasing as aridity increased (table S1). To quantify the functional structure (i.e., trait composition at the community level) of the shrub assemblages, we selected those species that collectively represented approximately 90% of the total abundance at each site (see Table S1 for the list of species selected and their relative abundance per site). The number of individuals of the selected species was used to estimate relative species abundance at each plot.

Traits measurements

We measured a set of leaf, stem, as well as fine and coarse root traits (see table S2 for a description of the functional significance of traits) that have been previously linked with plant ecological strategies following standardized protocols (Pérez-Harguindeguy *et al.* 2013). At each site, we haphazardly selected 50 individuals to measure aboveground traits, except for one species at QL whose abundance was very low (10 sampled individuals). For stem and leaf chemistry traits we sampled five individuals per species per site. Within 1 to 2 h after harvest, all fully expanded leaves per plant were scanned (Scanner HP Scanjet 200; maximum resolution of 2400×4800 dpi) and their fresh weight (g) was measured using an analytical balance (ADAM PGL 203). Leaves were then oven-dried at 60°C (Binder FED 53 - 720) for 48 h to measure dry weight. We measured leaf area (LA [cm^2]) using ImageJ (Schneider, Rasband & Eliceiri 2012) and calculated specific leaf area (SLA; the ratio of leaf area to leaf mass [$\text{cm}^2 \text{g}^{-1}$]) and leaf dry matter content (LDMC; the ratio of leaf dry mass to fresh mass [mg g^{-1}]). We used the water displacement method, to estimate stem wood density (WDs; the ratio of oven dry mass to green volume [$\text{g}\cdot\text{cm}^{-3}$]) in a short section (i.e., 5-7 cm) of stem before removing its bark (Osazuwa-Peters, Zanne & PrometheusWiki contributors).

Because root trait quantification involves a destructive procedure, for coarse-root traits (roots with diameter ≥ 2 mm) we only measured three individuals per species per site, and five individuals for fine-root traits (roots with diameter < 2 mm). Root depth distribution, described by the beta index [β], was estimated by excavating adjacent to each shrub, a trench 1 m deep that extended outwards 1.6 m from the plant. Then, starting at the center of each shrub, we collected a total of 100 $20 \times 20 \times 10$ cm blocks of soil samples from the trench walls (Fig. S2). To determine root biomass, we separated roots according to their diameter into fine, medium and coarse roots ($\emptyset < 1$,

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1–2 and >2 mm, respectively), and dried them in an oven at 60°C in order to stabilize their weight and be able to weigh them. Total root mass of each shrub was estimated by considering the root mass within the trench to be a proportion (~4%) of the total root biomass in a cylinder (1.6 m radius and 1 m depth; Morales *et al.* 2014). β was estimated from the asymptotic equation: $Y = 1 - \beta^d$, where, Y is the accumulated proportion of root biomass from the soil surface down to d depth (Gale & Grigal 1987). Higher values of β indicate a greater proportion of roots deep in the soil (Gale & Grigal 1987). We used roots of about 5 mm in diameter to estimate root wood density (WDr; the ratio of oven-dried mass to green volume [$\text{g}\cdot\text{cm}^{-3}$]) using the same methodology as for stems. Within two hours after harvesting, fine roots from each individual were cleaned with distilled water, scanned (Scanner HP Scanjet 200) and their fresh weight (g) recorded using an analytical balance (ADAM PGL 203). Roots were then oven-dried at 60 °C (Binder FED 53 - 720) for 48 h to record their dry weight. We estimated root dry matter content (RDMC; the ratio of root dry mass to fresh mass [$\text{mg}\cdot\text{g}^{-1}$]) and specific root length (SRL; the ratio of root dry mass to length [$\text{g}\cdot\text{cm}^{-1}$]). From root images, we measured total root length using ImageJ (Schneider, Rasband & Eliceiri 2012). Finally, leaf nitrogen concentration (LNC [%]), foliar carbon isotope ratio ($\delta^{13}\text{C}$ [‰]) and root nitrogen concentration (RNC [%]) was quantified using an isotope ratio mass spectrometer at Laboratorio de Biogeoquímica e Isotopos Estables Aplicados (LABASI) at the Pontificia Universidad Católica de Chile.

Community level metrics

To examine shift and variation in fast–slow ecological strategies at the community level, we calculated two community-level metrics. First, we estimated community-weighted mean traits (Garnier *et al.* 2004) as $CWM = \sum_{i=1}^s p_{ik} x_{ik}$, where p_{ik} is the relative abundance of species i at site k and x_{ik} is the trait value of species i at site k . CWM was estimated for each trait, within each plot of every site because it represents the dominant trait value of plants in a given community and thus allows us to identify how plants use and acquire resources under different aridity regimes. Second, we quantified the community-weighted trait variance (Sonnier, Shipley & Navas 2010) as $CWV = \sum_{i=1}^s p_{ik} (x_{ij})^2 - (CWMjk)^2$, where p_{ik} is the relative abundance of species i at site k , x_{ij} is the trait value j of species i and, $CWMjk$ is the community weighted mean of trait j at site k . CWV quantifies the variability of trait attributes around the mean trait value of the community. CWV was estimated for each trait, within each plot of every site and used as indicative of the variation in ecological strategies.

Statistical analyses

To evaluate the shift in the functional structure of shrub assemblages in different plant organs along the aridity gradient we performed separate Principal Component Analyses (PCAs) for leaf and root traits. We used PCAs because the first axis explains a high proportion of the CWM variation, thus the scores of these axis can be used as a proxy for the fast–slow PES given that they represent gradients of trait variation across sites (Freschet *et al.* 2010; de la Riva *et al.* 2016b). Because WDs was the only stem trait, we conducted a linear regression between DEMAI and the CWM of WDs to assess how WDs values change along the aridity gradient. Moreover, to assess how CWM values of

each leaf and root trait change along the aridity gradient we conducted separate linear regressions with quadratic components ($Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \epsilon_i$), using DEMAI as an independent variable (X_i) and CWM values of each root and leaf traits as response variables (Y_i). To test the effects of aridity on CWM, we performed a non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson & Walsh 2013) using sites as independent factors. To quantify whether variation in functional structure of shrub assemblages along the gradient was mediated by changes in species co-occurrences or by changes in species abundance, we decomposed species turnover by estimating the relative importance of species co-occurrence and species abundance following de la Riva *et al.* (2016a). Briefly, for each plant organ we calculated three parameters: 1) a “*fixed*” trait value, which indicates the effect of species turnover, estimated as the CWM trait values averaged across all sites where a species was found (i.e., site-independent trait value); 2) an “*unweighted*” trait value across all sites where a species was found, which indicates the effect of species co-occurrences and; 3) *species-abundance* as the difference between “*fixed*” and “*unweighted*” values and reveals the pure effects of species abundances. Next, following Leps *et al.* (2011), we conducted an individual PERMANOVA for each parameter (i.e., *fixed*, *unweighted* and *species abundance*) using sites as independent factors and extracted the sum of squares (SS) from each model (SS_{fixed} , $SS_{unweighted}$, and $SS_{species\ abundance}$, respectively). SS_{fixed} represents total trait variation due to species turnover, $SS_{unweighted}$ and $SS_{species\ abundance}$ represent the contributions of species co-occurrences and species abundance to species turnover, respectively. Because species co-occurrences and species abundances could be responding to environmental factors in the same (= positive covariation) or opposite directions (= negative covariation), we also calculated the covariation component as $SS_{cov} = SS_{fixed} - SS_{unweighted} - SS_{species\ abundance}$.

To assess whether pairs of traits were perfectly coordinated (i.e., the slope of the relationship equal to one) at different spatial scales, we performed standardized major axis (SMA) regressions (Warton *et al.* 2012) at regional (i.e., considering all sites) and local scales (i.e., within each site). Given that the only plant organ that showed a clear differentiation within the fast–slow PES along the first PCA axis were leaves (leaf traits hereafter), we used the scores of this axis to regress against the CWM of WDs and each of the CWM of root traits. Coordination between stem and root traits was assessed by conducting SMA regressions between the CWM of WDs and each of the CWM of root traits. We used SMA regressions because these are useful when the aim is not to predict a dependent variable from an independent one, but rather to summarise the relationship between two variables (Warton *et al.* 2006). Finally, to examine the effects aridity on trait variation (CWV), we performed a series (one per trait) of General linear models (GLMs; Crawley 2007), using a Gaussian error distribution (link function “identity”). For all GLMs we considered aridity as a main factor and the CWV of each trait as the response variable. All statistical analyses were performed using the R statistical environment (R Development Core Team 2014).

RESULTS

Aridity had a significant effect on the CWM of leaf traits (PERMANOVA: $F_{3,78} = 64.73$, $R^2 = 0.71$, $P < 0.0001$). The first PCA axis accounted for 49.5 % of the total variation across sites (Table S3). Specifically, the three drier sites had high values (positive PCA scores) of SLA and low values of LDMC and LNC (Fig. 1a, Fig. 2, table S4), suggesting that for morphological traits at least, ecological strategies shift from slow to fast as aridity increases. The second PCA axis was related to high values of $\delta^{13}\text{C}$

and low values (negative PCA scores) of LA, which were associated with QL and CHA respectively (Fig. 1a, Fig. 2, table S4). The CWM of root traits was also significantly affected by aridity (PERMANOVA: $F_{3,78} = 18.37$, $R^2 = 0.41$, $P < 0.0001$). The first PCA axis, which accounted for 36.5% of the total CWM variation across sites (Table S3) revealed that the two least arid sites (ROM and CHA) were associated with high values of SRL and RDMC, and with low WDr and RNC (Fig. 1b, Fig. 2, table S4). The second PCA axis, which accounted for 25% of the total CWM variation across sites, showed high values of β associated with QL and ROM (Fig. 1b, Fig. 2, table S4). These results reveal that the pattern of variation in root traits along an aridity gradient is complex and cannot be associated to a particular strategy within the fast–slow PES. WDs showed a significant negative relationship with aridity (Fig. 1c), suggesting a change from slow (high WDs values) to fast (low WDs values) resource acquisition as aridity increases.

The decomposition of species turnover into its components revealed that among-site averaged leaf trait values varied mainly due to changes in species occurrence (93.3%), rather than by changes in species abundance (10.1%) (Fig. 3). In addition, only a fraction of the variation in averaged leaf traits values was because of a decrease in abundances resulting from changes in species occurrence (negative covariation of -4.1%; Fig. 3). Thus, changes in SLA, LNC, LA, $\delta^{13}\text{C}$ and, LDMC results mainly from changes in occurrence across sites. The response of WDs to aridity is also mainly explained by changes in species occurrences (69.5%), rather than by changes in species abundance (2.9%). In this case, however, there was a positive covariation (27.6%) between these two components of species turnover (Fig. 3), suggesting that the decrease in the averaged WDs values associated to changes in occurrence along the gradient is in part also explained by a correlated decrease in the abundance of species with high

values of WDs. The change in averaged root traits values along the gradient was explained both by changes in species occurrences (33.1%) and abundances (22.6%), and the change was intensified by the joint positive effect of components (positive covariation of 44.3%; Fig. 3), suggesting that changes in mean trait values of SRL, RDMC, β , RNC and, WDr are influenced by both the contribution of species occurrences and species abundance.

The SMA regressions between the first PCA axis of leaf traits and CWM values of SRL, RDMC, β and WDs was negative at the regional scale (Fig. 4, Table S5). At local scale, the relationship between the first PCA axis of leaf traits with the above-mentioned root traits was negative in some sites, but unrelated in others. Specifically, there was a relationship between leaf traits and SRL only at LLCHA (Fig. 4, Table S5), between leaf traits and RDMC only at ROM and CHA (the least arid sites), and between leaf traits and β and WDs at QL and LLCHA (the most arid sites; Fig. 4, Table S5). There was no relationship between leaf traits and WDr and RNC at the regional scale (Fig. 4, Table S5). However, at a local scale, the relationship between leaf traits and WDr was negative in the most arid sites (QL and LLCHA; Fig. 4, Table S5). The relationship between leaf traits and RNC was negative in the most arid site (QL) and positive in the least arid ones (ROM and CHA). The slope of the above relationships, except SRL in CHA and LLCHA at local scale, was statistically different from -1 or $+1$ (Table S5), revealing that these organs are not perfectly coordinated.

At the regional scale, the SMA regression revealed a positive relationship between CWM values of WDs and CWM values of RDMC and β , and a negative relationship between WDr and RNC (Fig. 5, Table S6). Moreover, there was no relationship between WDs and SRL (Fig. 5, Table S6). At a local scale, the relationship between

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WDs with RDMC was positive only in QL (the most arid site) and unrelated in the other sites (Fig. 5, Table S6). The relationship between WDs with β was positive in LLCHA, CHA and ROM; there was no relationship between these variables in QL. The relationship between WDs and WDr was positive in LLCHA, negative in CHA and non-significant in the other sites (Fig. 5, Table S6); with RNC, the relationship was positive in ROM (least arid sites) and non-significant in the other sites. At the local scale, the relationship between WDs and SRL was a negative only at ROM (Fig. 5, Table S6). The slope of the relationships between WDs and roots traits was statistically different from -1 or $+1$ (Table S6) in all sites, except for RNC in LLCHA and ROM and WDr at CHA. Again, these results suggest that WD and other root traits are not perfectly coordinated.

Aridity had significant effects on the variation of all CWV trait values, except LNC (Table 2). RNC, WDr, β and WDs were more variable at the most arid site (QL) than in the other sites (Fig. 6). Conversely, SRL had a higher variability at the least arid site (ROM). Variation of LDMC and $\delta^{13}\text{C}$ tended to be higher in the three drier sites than in the least arid one (ROM; Fig. 6). Variation of LA and SLA was lowest at LLCHA and CHA, respectively than in the other sites (Fig 6). RDMC was more variable at LLCHA than in either end of the aridity gradient (Fig. 6).

DISCUSSION

Our results reveal three important findings. First, that most of the leaf traits, as well as WDs, responded to aridity by shifting from a slow to a fast resource acquisition strategy as aridity increased; that is, shrub assemblages along the Coastal Atacama

Desert adopt a faster aboveground strategy as the environment turns drier. In contrast, belowground traits showed a more complex pattern of shift along the aridity gradient that cannot be associated to a particular strategy within the fast–slow PES. Second, there was some level of coordination among traits from different plant organs. Third, except for SRL, trait variation did not decrease as aridity increased. Together, these results partially support the hypothesis that as aridity increases in a hyper-arid environment, selection pressures act simultaneously on trait attributes, variation and coordination to promote an inverse pattern in the fast–slow PES. Although several studies have shown shifts in the fast–slow PES at both the species and community levels (e.g., Pérez-Ramos *et al.* 2012; Reich 2014; de la Riva *et al.* 2016b), to our knowledge this is the first study that reports an inverse pattern of the spectrum.

Our prediction that in the most arid end of a hyper-arid aridity gradient shrub assemblages will exhibit trait values that reflect a water acquisition strategy at the whole plant level was partially supported. Changes in both leaf traits and WDs values reflect a shift from a slow to a fast strategy as aridity increased; this shift was determined mainly by changes in species occurrences across sites. Shifts in the functional structure of plant assemblages associated with changes in species occurrences have been related to habitat filtering because those species having sets of traits unsuitable to cope with particular environmental conditions tend to be eliminated (Keddy 1992; de la Riva *et al.* 2016a). We propose that selection pressures imposed by the hyper-aridity of this system, in conjunction with the short growing season, which increases from south to north (Rundel *et al.* 1991), lead to an inverse pattern of the fast–slow PES spectrum. Under these extreme conditions, a fast strategy may be beneficial because it allows plants to take advantage of the short periods of high resource availability (Mooney & Dunn 1970;

Nilsen & Muller 1981), thus increasing their probability of survival (Nilsen & Muller 1981; Mooney 1982; Ackerly 2004). The only aboveground trait that departed from a fast strategy was LNC; this trait depends on soil nitrogen availability, which in arid ecosystems is not only low, but also highly dependent on soil moisture (Ward 2009; Yu *et al.* 2017). Consequently, low levels of LNC may not have been determined by the net nitrogen acquisition rate, rather than by soil nitrogen availability. Conversely, belowground traits did not exhibit a clear pattern within the fast–slow PES along the aridity gradient. Moreover, belowground mean trait variation across sites was determined by changes in species occurrences and abundance, suggesting that both habitat filtering and local biotic processes determine the functional structure of root traits. Therefore, the apparent lack of functional adjustment to aridity at the root level may result to some extent from the hyper-aridity of this system, but also from local biotic processes, such as competition and/or facilitation (Cahill 1999; López *et al.* 2016), which increase trait dissimilarity and allow plant coexistence by way of niche differentiation (Bernard-Verdier *et al.* 2012; de la Riva *et al.* 2016a).

At the regional scale leaf traits showed a negative relationship with WDs, indicating that fast resource use by leaves is accompanied by fast water conduction by the stem; therefore, aboveground traits respond concordantly to aridity promoting rapid resource acquisition. Our results are in line with other studies that show some degree of coordination between leaf and stem traits (Freschet *et al.* 2010; Méndez-Alonzo *et al.* 2012). With respect to the coordination between leaf and root traits, we found negative relationships between leaf traits and RDMC, SRL and β . In other words, fast resource use by leaves was associated with shallow root systems (low β values), low root length investment per root mass (low SRL values) and roots with low tissue investment in fine roots (low RDMC values). WDs was positively related to RDMC and β , meaning that

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fast water conduction by the stem is accompanied by a shallow root system and low tissue investment. In water-limited ecosystems, shallow root systems may be more relevant than deep root systems because: (1) both water and nitrogen availability concentrate in shallow soil layers, which are available only during brief time periods, followed by long periods of low resource supply (Noy-Meir 1973; Jobbágy & Jackson 2001; Reynolds *et al.* 2004) and, (2) shallow root systems are cheaper to construct and maintain than deep root systems (Adiku *et al.* 2000; Schenk & Jackson 2002).

Therefore, in arid and semiarid environments, shallow root systems have been indicated as a resource acquisition trait (Fort, Jouany & Cruz 2013) because after small rainfall events, they enable plants to use water from shallow soil layers faster than deep root systems (Moreno-Gutiérrez *et al.* 2012). Additionally, it has been suggested that roots with low values of RDMC and SRL have an increased lifespan and therefore they increase the duration of the growing season (Withington *et al.* 2006; Weemstra *et al.* 2016; Zhou *et al.* 2018). On the other hand, WDs was negatively with WDr and RNC. The negative relationship with RNC indicates that fast water transport by the stem is accompanied by fast fine root metabolism because high nitrogen content increases respiration rates (Guo *et al.* 2008), which in turn suggests that these traits are coordinated to have a fast rate of resource acquisition. The relationship between WDs and WDr is opposite from what is expected by theory (see Fortunel *et al.* 2012); that is, we showed that as WDs increases (fast resource acquisition) WDr decreases (slow resource acquisition). High wood density is associated with a high resistance to mechanical damage (Van Gelder, Poorter & Sterck 2006) and low tissue mortality (King *et al.* 2006); therefore, a decrease in WDr may promote plant persistence by maintaining the viability of coarse root tissue. Finally, the absence of a relationship between WDs and SRL, and between leaf traits with RNC and WDr indicated that these

pair of traits are orthogonal, probably because of different selection pressures or constraints on these particular traits (Kembel & Cahill 2011; Weemstra *et al.* 2016). In summary, at the regional scale most traits tend to show some degree of coordination, but the functional significance of this coordination differs from what is expected under the fast–slow PES framework.

At local scales, coordination among traits was found in some sites, but not others. This may result from the occurrence of local processes, such as environmental heterogeneity and biotic interactions that promote a broader range of ecological strategies. For example, Kembel and Cahill (2011), suggested that environmental heterogeneity within communities may promote trait coordination because it leads to the coexistence of species with different trait values. Conversely, the lack of coordination suggests that above- and belowground traits represent different ecological strategies that promote independent axes of niche differentiation for plant organs (Ackerly 2004; Ackerly & Cornwell 2007).

The pattern of among-site trait variation reveals a mixture of different ecological strategies within each shrub assemblage along the aridity gradient, yet these are not segregated according to the gradient; rather, they showed an idiosyncratic pattern of variation. Our results differ from those of previous empirical studies in which trait variation decreased in poor-resource environments (Grime *et al.* 1997; Swenson & Enquist 2007; Coyle *et al.* 2014) or alternatively, in which variability increased with aridity (e.g., Butterfield & Callaway 2013, Butterfield *et al.* 2017). The pattern of trait variation we observed here could have resulted if different assembly processes at each site determine different traits. In this light, although several processes could explain our results, local biotic interactions, as well as environmental heterogeneity are the most plausible ones for two reasons. First, because López *et al.* (2016) found support for the

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stress gradient hypothesis in the Coastal Atacama Desert, meaning that facilitation increased and competition decreased as the environment become drier. Both facilitation and competition can increase functional trait variation in plant communities (Kraft, Valencia & Ackerly 2008; Butterfield & Briggs 2011; Butterfield & Callaway 2013) and thus could have promoted a broader range of ecological strategies. Second, spatial and temporal environmental-resource heterogeneity has been suggested as a promoter of high trait diversity because it reduces interspecific niche overlap (Chesson 2000; Chesson *et al.* 2004; Adler *et al.* 2013). The few studies that have assessed how traits vary with resource heterogeneity have found a positive relationship between both variables (Butterfield *et al.* 2017; Price *et al.* 2017). For example, Price *et al.* (2017) studying grassland communities in Europe, found that high variation in leaf area, leaf dry matter content and specific root length were related to heterogeneity in soil depth, a variable that has been related to spatial heterogeneity of soil resources (Gazol *et al.* 2012). Therefore, trait variability at different sites could be determined both by plant-plant interactions and within-site heterogeneity in soil resource availability.

The main conclusion of this study is that, contrary to what is predicted by the fast-slow PES framework, a strong environmental filter, such as aridity, does not necessarily lead to an integrated whole-plant economics spectrum. Biotic processes can also be important drivers in determining resource acquisition strategies, particularly for belowground traits. Given that the relative importance of assembly processes driving trait variation differs between above and belowground traits, the interaction between habitat filtering and biotic processes can thus result in different above- and belowground strategies, which change the functional significance of trait coordination.

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AUTHORS' CONTRIBUTIONS

D.E.C., A.P.L., and F.A.S. designed the study. D.E.C and C.A.D collected data. D.E.C. analysed all data and was the primary writer of the manuscript. R.S.R., A.P.L and F.A.S contributed to writing and revising the manuscript.

DATA ACCESSIBILITY

Data associated with this manuscript are deposited in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.p9b92jh> (Carvajal *et al.* 2018).

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Table 1. Location and climatic characteristics of the four study sites. The De Martonne aridity index (DEMAI) was calculated as $MAP / (MAT + 10)$; thus, the lower the index value, the greater the aridity. Climate data (Mean annual precipitation, MAP; Mean annual temperature, MAT) were obtained from Dirección General de Aguas, Chile (www.dga.cl) and from CEAZA-Met weather station (www.ceazamet.cl).

Locality	Site Acronym	Coordinates	MAP (mm)	MAT (°C)	DEMAI
Quebrada El León	QL	26° 57' 53" S - 70° 45' 59" W	14	17.2	0.5
Norte Llanos de Challe	LLCHA	27° 59' 21" S - 71° 07' 22" W	28	16.6	1.1
Chañaral de Aceituno	CHA	29° 06' 16" S - 71° 27' 18" W	45	16.1	1.7
Romeral	ROM	29° 43' 48" S - 71° 19' 24" W	80	15.3	3.2

Table 2. Results of the general linear models (GLM) for the community weighted variance (CWV) of traits. Significant values are in bold. Trait acronyms: LA= Leaf area, LDMC= Leaf dry matter content, SLA= Specific leaf area, $\delta^{13}\text{C}$ = Carbon isotope discrimination, LNC= Leaf nitrogen content, RNC= Root nitrogen content, RDMC= Root dry matter content, SRL= Specific root length, WDr= Wood density of root, β index= Beta index, WDs= Wood density of stem.

CWV of trait	χ^2	<i>P</i> -value
LA	449.02	0.0007
LDMC	70806570	0.0002
SLA	4135473	0.004
$\delta^{13}\text{C}$	18.5471	<0.0001
LNC	0.02	0.15
RNC	35.197	<0.0001
RDMC	215561719	<0.0001
SRL	2440.7	0.0004
WDr	7.4442	<0.0001
β index	14.575	<0.0001
WDs	4.8407	<0.0001

Figure legends

Figure 1. a) Principal components analysis for the community-weighted mean (CWM) of leaf and b) root traits. c) Linear regression of the CWM of WDs with aridity. Vectors represent the relative contribution of each plant trait to the axes. Symbols denote the plots sampled at each site. Trait acronyms: LA= Leaf area, SLA= Specific leaf area, LDMC= Leaf dry matter content, $\delta^{13}\text{C}$ = Carbon isotope discrimination, LNC= Leaf nitrogen content, SRL= Specific root length, RDMC= Root dry matter content, WDr= Wood density of root, β index= Beta index, RNC= Root nitrogen concentration, WDs= Wood density of stem.

Figure 2. Linear regressions with quadratic components ($Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \epsilon_i$) between the community-weighted mean (CWM) of plant traits and the degree of aridity in the Atacama Desert as indicated by DEMAI (De Martonne aridity index). Lower index values indicate greater aridity. Site acronyms: QL = Quebrada El León, LLCHA= Norte Lanos de Challe, CHA= Chañaral de Aceituno, ROM= Romeral. Traits acronyms: LA= Leaf area, SLA= Specific leaf area, LDMC= Leaf dry matter content, $\delta^{13}\text{C}$ = Carbon isotope discrimination, LNC= Leaf nitrogen content, SRL= Specific root length, RDMC= Root dry matter content, WDr= Wood density of roots, β index= Beta index, RNC= Root nitrogen concentration.

Figure 3. Decomposition of species turnover into species occurrences, abundance and their covariation for leaf traits, Wood density of stems (WDs) and root traits.

Figure 4. Standardized major axis regression between the first PCA of leaf traits and a) SRL, b) RDMC, c) WDr, d) β index, e) RNC and, f) WDs. Black lines represent a significant SMA regression at a regional scale. Colored lines represent significant SMA

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regressions at local scales. Arrows represent the change in leaf trait values from a slow to a fast strategy. Values are represented the community weighted mean of each trait. Trait acronym: SRL= Specific root length, RDMC= Root dry matter content, WDr= Wood density of root, β index= Beta index, RNC= Root nitrogen concentration, WDs= Wood density of stem. Regression lines and R^2 are represented only for those significant regressions.

Figure 5. Standardized major axis regression between WDs and a) SRL, b) RDMC, c) WDr, d) β and, e) RNC. Black lines represent a significant SMA regression at a regional scale. Colored lines represent significant SMA regressions at local scales. Arrows represent the change in WDs values from a slow to a fast resource acquisition. Values are represented the community weighted mean of each trait. Trait acronym: SRL= Specific root length, RDMC= Root dry matter content, WDr= Wood density of root, β index= Beta index, RNC= Root nitrogen concentration. Regression lines and R^2 are represented only for those significant regressions.

Figure 6. Box plot showing change in community-weighted variance (CWV) with different levels of aridity for a) LA= Leaf area, b) LDMC= Leaf dry matter content, c) SLA= Specific leaf area, d) $\delta^{13}\text{C}$ = Carbon isotope discrimination, e) LNC= Leaf nitrogen content, f) RNC= Root nitrogen concentration, g) RDMC= Root dry matter content, h) SRL= Specific root length, i) WDr= Wood density of root, j) β index= Beta index and, k) WDs= Wood density of stem. Lowercase letters indicate significant differences among sites.

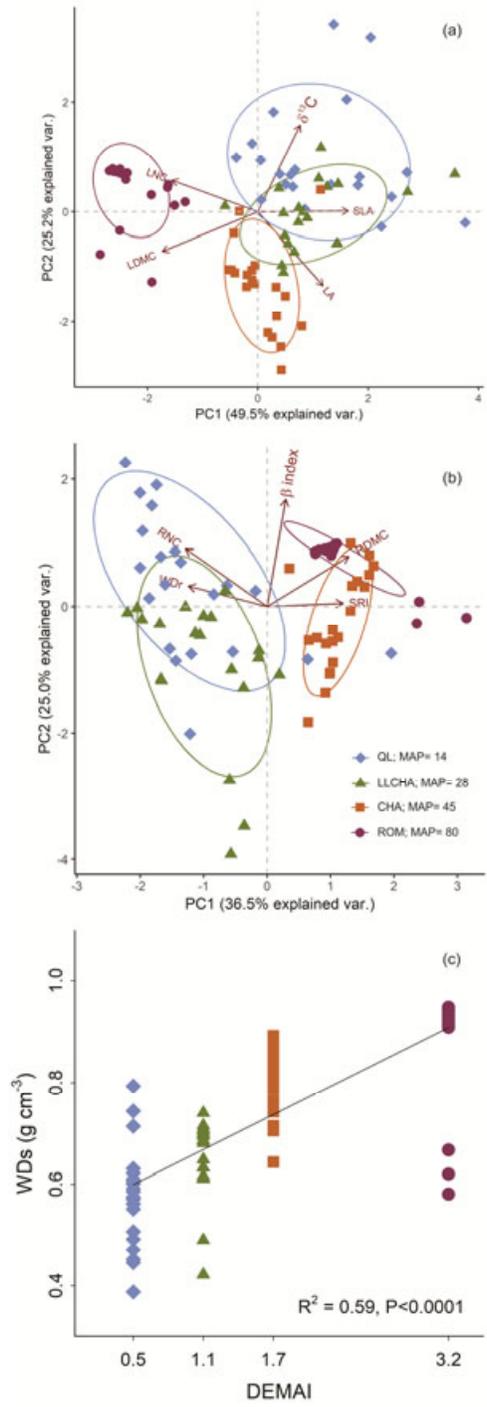


Figure 1.

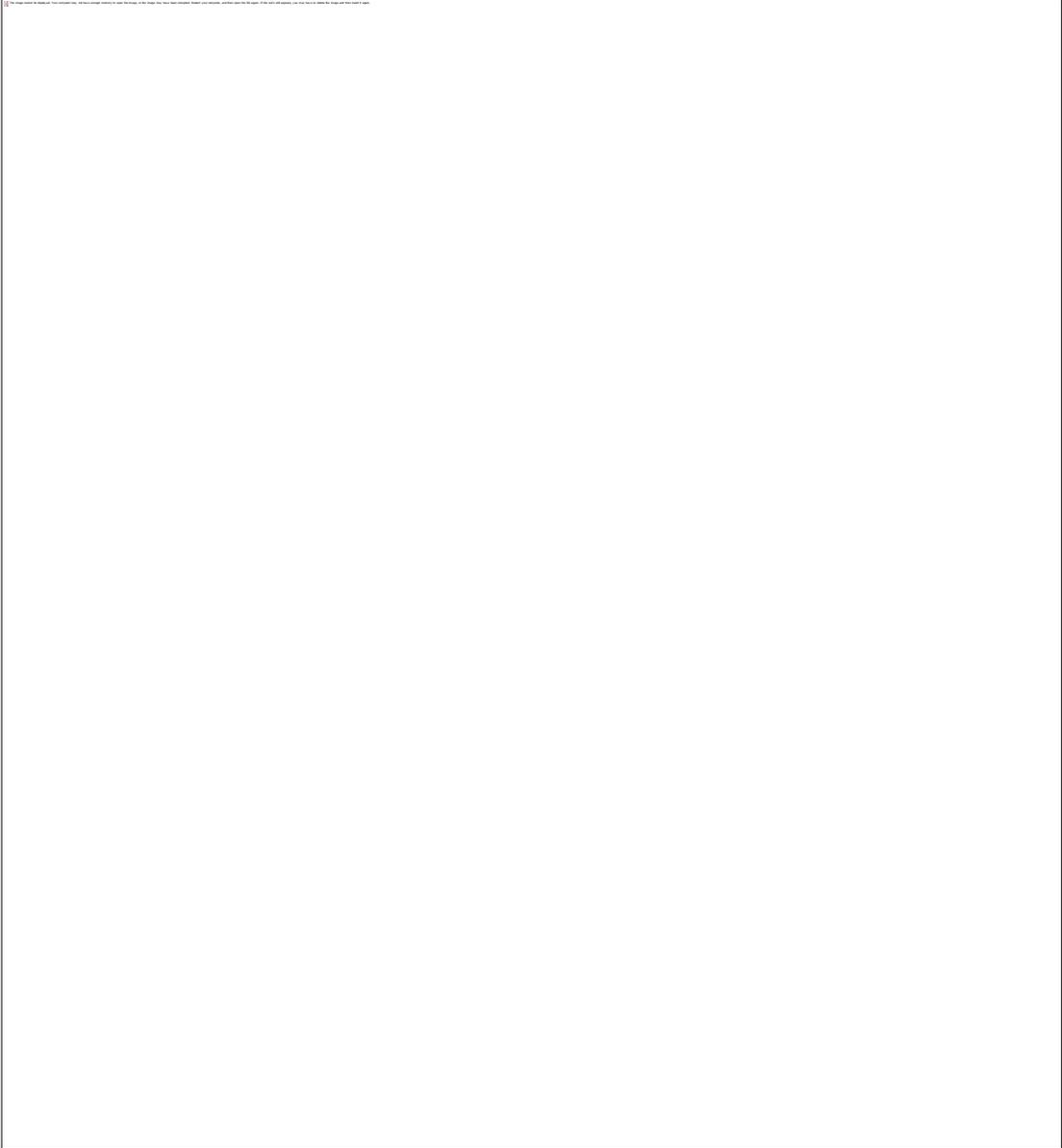


Figure 2.

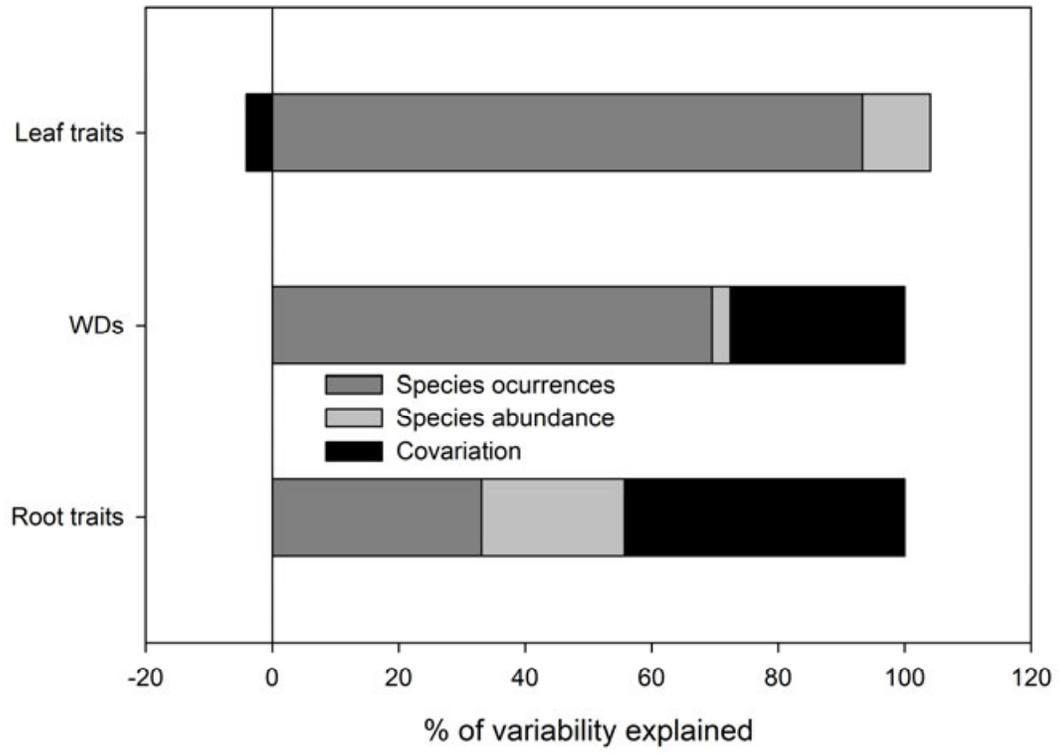


Figure 3.

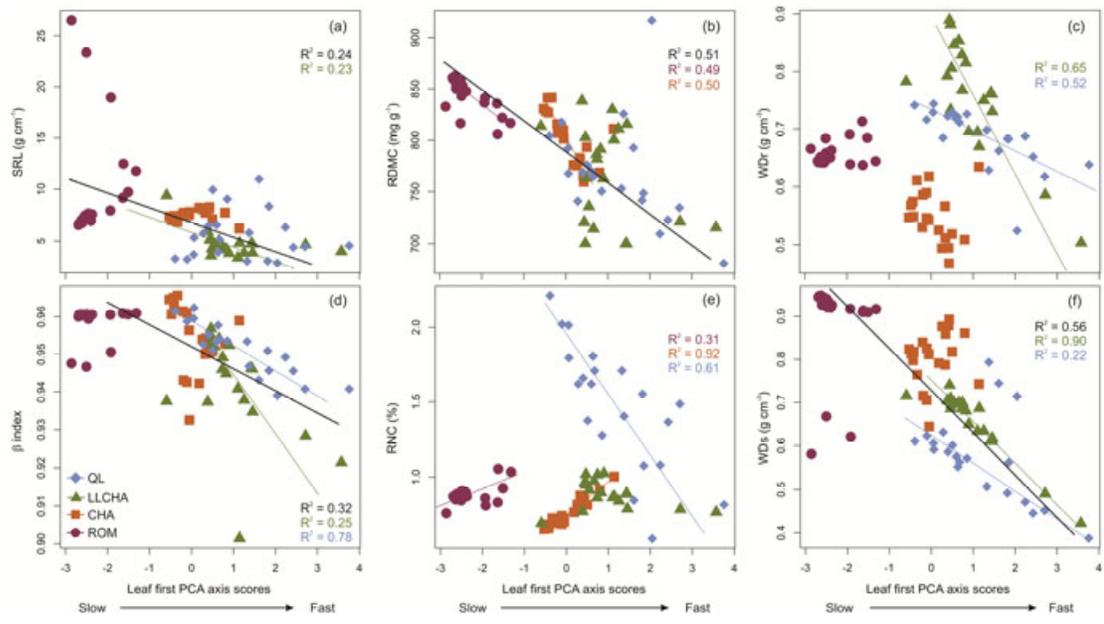


Figure 4.

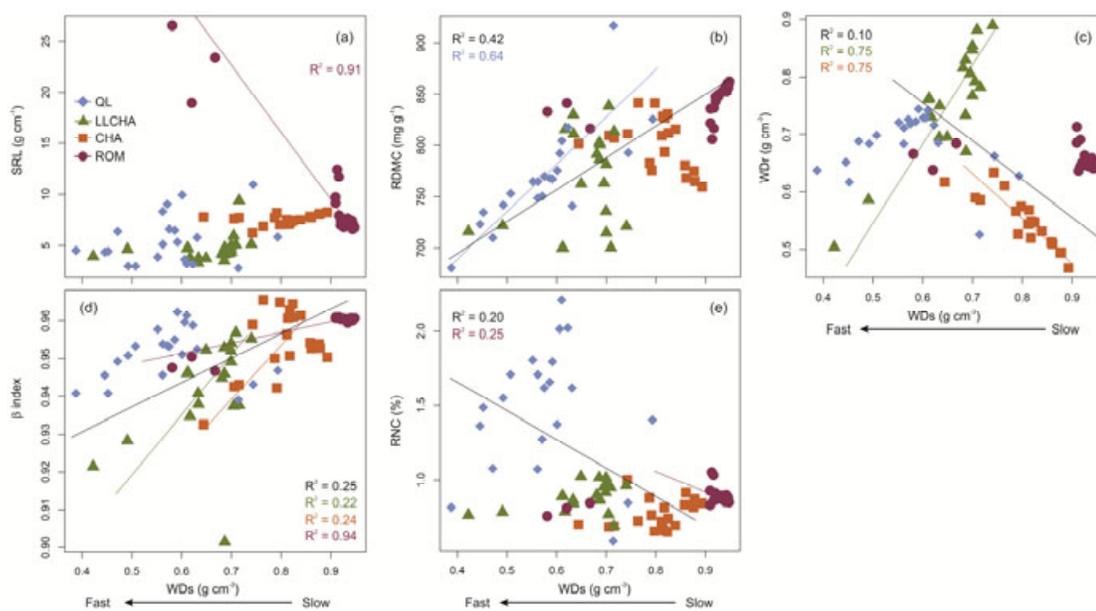


Figure 5.

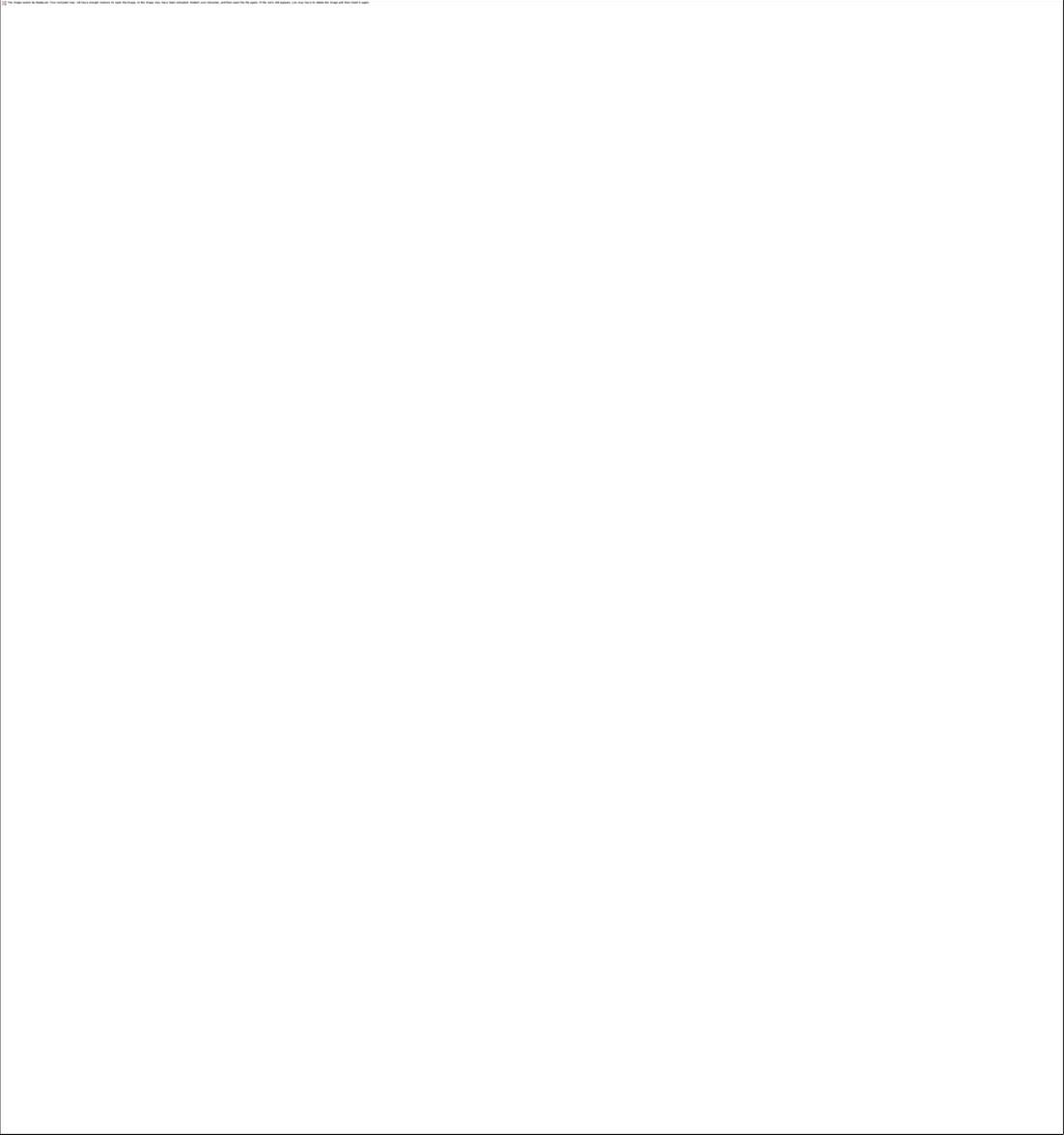


Figure 6.