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Changes in traits of shrub canopies across an aridity gradient in northern Patagonia, Argentina

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Abstract

Low and highly variable precipitation pulses exert a strong selective pressure on plant traits and this might provide axes of ecological differentiation among plant species in arid ecosystems. We asked whether aridity contributes to maintain high diversity of species and morphotypes in shrub canopies. We selected eleven study sites evenly distributed across a 400-km transect in northern Patagonia, Argentina. Precipitation is low and highly variable within and between years but almost homogeneous across the transect (125–150 mm). Mean annual temperature varied, however, ranging from 8 °C (west) to 13.5 °C (east) creating a west–east gradient of aridity (aridity index from 3.7 to 7.3, respectively). Sheep grazing commenced in the early 1900s at a similar intensity across the transect. We recorded the richness and cover of shrubs by species and by morphotypes (drought deciduous tall shrubs, evergreen tall shrubs, medium shrubs, and dwarf shrubs), and further calculated the species and morphotype Shannon diversity index at each site. We assessed the presence of spiny leaves, leaf pubescence, thorny stems, and photosynthetic stems in shrub species of all morphotypes and collected green leaves of the dominant shrub species (more than 80% of the total shrub cover) to assess the leaf area, leaf mass per unit area, N-, lignin- and soluble phenolic-concentrations per species at each site. Richness and diversity of shrub species and morphotypes were positively associated with aridity. The richness and diversity of shrub species with pubescent leaves and thorny stems, and nitrogen concentration in green leaves of dominant shrubs increased with increasing aridity. We conclude that our findings on increased diversification in life history traits, species and morhotypes in shrub canopies with increasing aridity support the hypothesis that variability in aridity provides axes of ecological differentiation among shrub species facilitating their coexistence.

Zusammenfassung

Geringe und hochgradig variable Niederschlagspulse üben einen starken Selektionsdruck auf die Merkmale von Pflanzen aus und könnten eine Leitlinie für die ökologische Differenzierung bei Pflanzenarten in ariden Ökosystemen darstellen. Wir fragten, ob die Trockenheit dazu beiträgt eine hohe Diversität der Arten und Morphotypen in Buschgemeinschaften zu erhalten. Wir wählten elf Untersuchungsflächen aus, die sich gleichverteilt entlang eines 400-km-Transektes in Nordpatagonien, Argentinien, befanden. Der Niederschlag ist gering und hochgradig variabel innerhalb und zwischen den Jahren aber fast homogen entlang des Transektes (125–150 mm). Die mittlere Jahrestemperatur variierte jedoch und reichte von 8 °C (Westen) bis 13,5 °C (Osten) und erzeugte einen West-Ost-Gradienten der Trockenheit (der Trockenheitsindex variierte von 3,7 bis 7,3). In den frühen 1900er Jahren begann die Schafbeweidung bei gleichbleibender Intensität. Wir erfassten den Artenreichtum und die Deckung der Sträucher auf der Arten- und auf der Morphotypenebene (große laubwerfende Sträucher,

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große immergrüne Sträucher, mittlere Sträucher und Zwergsträucher) und berechneten darüber hinaus den Shannon Diversitätsindex für die Arten und Morphotypen für jede Probefläche. Wir schätzten die Anwesenheit von dornigen Blättern, Blattbehaarung, dornigen Stämmen und photosynthetisch aktiven Stämmen bei den strauchigen Arten aller Morphotypen und sammelten grüne Blätter der dominanten Straucharten (mehr als 80% der gesamten Strauchdeckung) um die Blattflächen, die Blattmassen pro Flächeneinheit, N-, Lignin- und lösliche Phenol-Konzentrationen für die Arten jeder Probefläche zu ermitteln. Artenreichtum und Diversität der Straucharten und Morphotypen waren mit der Aridität positiv assoziiert. Der Artenreichtum und die Diversität der Straucharten mit behaarten Blättern und dornigen Stämmen sowie die Stickstoffkonzentration in den grünen Blättern der dominanten Sträucher nahmen mit zunehmender Aridität zu. Wir schließen daraus, dass unsere Erkenntnisse über die zunehmende Diversifikation der Entwicklungsgeschichten, der Arten und Morphotypen in den Strauchschichten mit zunehmender Aridität die Hypothese unterstützt, dass die Variabilität unter Aridität eine Leitlinie der ökologischen Differenzierung bei Straucharten darstellt und ihre Koexistenz fördert.

Introduction

The study of variation in plant traits and species diversity across regional and global climate or land use gradients contributes to our understanding of ecosystem functioning under changing environments (Rosenzweig & Abramsky 1993; Wright et al. 2004; Bertiller et al. 2006; Oyarzabal, Paruelo, del Pino, Oesterheld, & Lauenroth 2008). A central issue that has been addressed in several studies is the relationship between diversity and ecosystem functioning. A common pattern emerging from these studies is that species diversity varies with productivity following a hump-shaped or unimodal distribution. Accordingly, species diversity increases with productivity at low productivity levels (Rosenzweig & Abramsky 1993). Most of these studies included a wide range of environmental variation from humid to dry ecosystems. Few of them have addressed these relationships across more constrained environmental gradients such as those occurring in arid ecosystems.

Low and highly variable precipitation in arid ecosystems exert a strong selective pressure on morphological, physiological and life history traits allowing plants to tolerate or avoid extremely dry conditions (Noy Meir 1973). Drought tolerant perennial plants usually have long lasting tissues with large accumulations of carbon-based secondary metabolites which not only increase tolerance to water shortage but also provide resistance to herbivores (Grace 1998; Hartley & Jones 1998). Other xeromorphic plant traits associated with drought tolerance are small leaves with wax deposits and reflective surfaces, aphyllous photosynthetic stems, low plant stature, and deep root systems, among others (Grace 1998). On the other hand, drought-avoiding perennial plants usually have the ability to shed leaves during drought and produce leaves with low defenses against water shortage and high N concentration which makes them prone to herbivore attack. These leaves are usually protected from herbivores by spines or other plant structures (e.g., thorny stems) (Grace 1998). Different combinations of traits to tolerate or avoid extreme dry conditions could result in phenological asynchronism and differences in responses to changing environment among plant species (Reynolds, Kemp, Ogle, & Fernandez 2004). Accordingly, a wide range of variation in traits facilitating survival and growth in water-limited ecosystems among coexisting species might reduce species competition and promote diversity (Chesson et al. 2004).

The effects of wild and domestic herbivory on the patterns of plant responses or adaptations to aridity should also be taken into consideration when analyzing vegetation changes across climatic gradients (Díaz et al. 2007). Herbivory effects can usually be identified by changing plant traits of individual species, replacement of species with different plant traits, varying proportion of woody and herbaceous plants, and shifting in life history, height or habit of herbaceous plants (Bisigato & Bertiller 1997; Díaz et al. 2007). However, several studies have reported null or negative effects of grazing on plant species richness and diversity of a wide range of plant life forms of arid ecosystems (Milchunas, Lauenroth, & Burke 1998; Adler, Milchunas, Sala, Burke, & Lauenroth 2005; Tadey 2006).

Shrubs and perennial grasses are the most conspicuous life forms in arid ecosystems of the world (Sala, Golluscio, Lauenroth, & Soriano 1989; Montaña, Seghieri, & Cornet 2001). Perennial grasses have an almost unique morphology and are mostly opportunistic (relative to water inputs) and drought-avoiding species. In contrast, shrubs display a diversity of structural and chemical traits enabling them to avoid or tolerate desiccation during periods of water shortage (Bertiller, Beeskow, & Coronato 1991; Bertiller, Sain, Carrera, & Vargas 2005; Lambers, Chapin, & Pons 2000, Carrera, Bertiller, Sain, & Mazzarino 2003; Díaz et al. 2007). These characteristics make shrubs an interesting plant group with which to explore the role of aridity in the maintenance of a wide range of coexisting species with contrasting life history (low degree of convergence in life history traits). We asked whether aridity influences diversity of species and morphotypes in shrub canopies.

Materials and methods

Study area

We selected eleven study sites evenly separated across an east–west transect, approximately 400 km long and 90 km, wide located in northern Patagonia, Argentina (Fig. 1). The transect included dominant functional biozones in the southern portion of the Monte Phytogeographical Province (Monte steppes 1 and 2) and in the northern portion of the Central District of the Patagonian Phytogeographical Province (Semideserts 1, Shrub grass steppes, and Shrub steppes) (Cabrera 1976; Paruelo, Jobbágy, & Sala 1998). Vegetation in the Monte steppes is characterized by xeromorphic tall shrublands while the semideserts and shrub or shrub grass steppes are represented by xeromorphic shrublands dominated by medium shrubs (Ares et al. 1990).

Climatic conditions differ across the study area (Cabrera 1976; Paruelo et al. 1998). We used data of the period 1931–1960 to characterize the climate of the transect as there are no recent climatic data for all sites. Past climatic trends described for the Monte in the last decades provided evidence of warming in the periods 1920–1944 and 1977–2001 ($0.15\,°C$ and $0.16\,°C\,decade^{-1}$) and a positive long term increase of precipitation in summer during the interval 1985–2001 (Labraga & Villalba 2009). These trends do not suggest drastic changes in the aridity indexes over the last decade, however, and traits of shrub canopies across the transect probably have been shaped over very long (centuries) time periods (Vasek 1980). Although mean annual precipitation does not vary considerably across the transect, mean annual temperature varies from $8\,°C$ to $13.5\,°C$ (Soriano 1950; Paruelo et al. 1998; Mitchell & Jones 2005). This creates a west–east gradient of aridity (Fig. 1). In the eastern portion of the transect, precipitation occurs as discrete events evenly distributed across the year whereas towards the west precipitation events are concentrated in the cold season (autumn–winter) (Cabrera 1976). Desiccation of the upper soil layers might be higher in the eastern than in the western portion of the transect due to the combination of non-seasonal precipitation and high temperatures (Coronato & Bertiller 1996, 1997). Precipitation has high intra-annual variation across the transect. The ratio mean^{2}/variance of the annual precipitation varies from 3.5 to 4.5 across the transect (Barros & Rivero 1982).
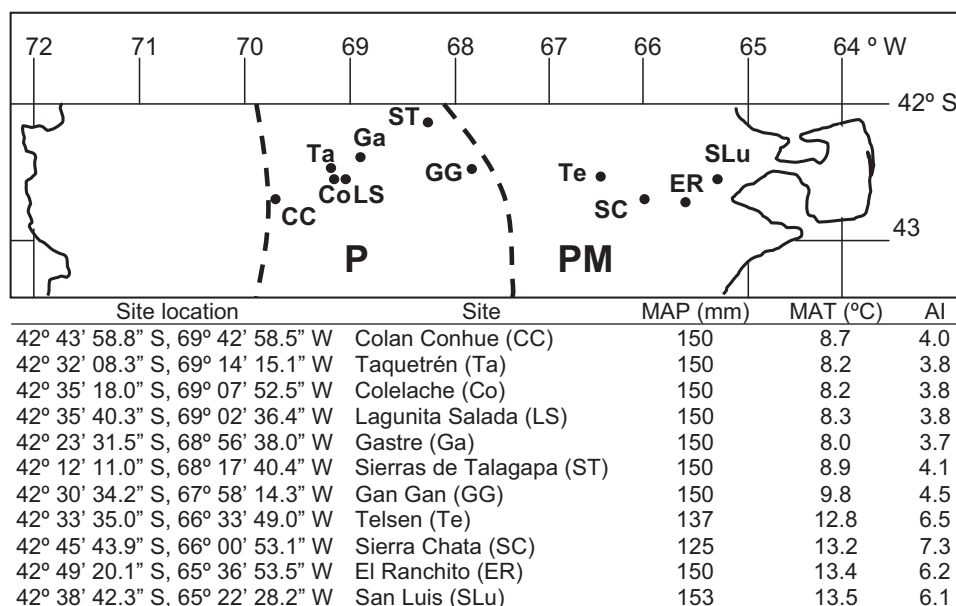
As with other Patagonian ecosystems, the study area has been grazed by sheep since the early 1900s (Ares et al. 1990). Mean historical stocking rates (period 1960–1991) in the transect were $0.24 \pm 0.02\,sheep\,ha^{-1}$ (eastern portion of the transect), $0.20 \pm 0.04\,sheep\,ha^{-1}$ (central portion of the transect), and $0.24 \pm 0.03\,sheep\,ha^{-1}$ (western portion of the transect) (Chubut Province 1960–1970–1978–1991). Sheep and wild ungulates have stronger effects on herbaceous plants (forbs and grasses) than on shrubs (Bisigato & Bertiller 1997; Baldi, Albon, & Elston 2001; Pazos, Bisigato, & Bertiller 2007).

Sampling

Sampling was carried out in November–December 2003 (late vegetative-early reproductive growth period of shrubs). Sampling sites were located in physiognomically and floristically homogeneous areas representative of each biozone. We selected a representative vegetation stand of about 1 ha (minimal area *sensu* Mueller-Dombois & Ellenberg 1974) to perform the vegetation sampling at each site (Bertiller and Ares 2008). We recorded species richness (the total number of species found in the minimal area of the selected stand) and the total and per species absolute and relative cover of shrubs (Mueller-Dombois & Ellenberg 1974) at each site. Cover was visually estimated using 1% cover intervals (Bertiller & Ares 2008). We assessed the presence/absence of spiny leaves, leaf pubescence, thorny stems, and photosynthetic stems on three randomly selected individuals of similar size (crown diameter, height) of each shrub species at each sampling site. We further assigned each species to one of the following shrub morphotypes: deciduous tall shrubs (DTS), shrubs more than 1 m tall with drought deciduous leaves; evergreen tall shrubs (ETS), shrubs more than 1 m tall with evergreen leaves; medium shrubs (MS), shrubs from 0.25 to 1 m tall; dwarf shrubs (DS), shrubs of less than 0.25 m height. We did not find deciduous drought avoiding species among medium and dwarf shrubs. These morphotypes defined by aboveground plant stature and leaf deciduousness also differ in other life history traits, including their root systems. Evergreen tall shrubs are characterized by deep root systems (more than 3 m) but are also able to develop active fine root systems in the upper soil layer (Peláez, Distel, Boó, Elia, & Mayor 1994; Rodríguez, Bertiller, & Bisigato 2007). Deciduous tall shrubs could either have deep or shallow rooting depth, but all drop their leaves and rest in the warm dry season (Campanella & Bertiller 2008). The medium and dwarf shrubs have mostly shallow root systems (Fernández and Paruelo 1988; Bertiller et al. 1991; Bucci, Scholtz, Goldstein, Meinzer, & Arce 2009).

We randomly selected three individuals of the modal size (most frequent crown diameter and height) of each dominant shrub species at each sampling site. Dominant shrub species accounted for more than 80% of the total shrub cover at each site (Appendix A: Table 1). We collected fully expanded young to medium aged green leaves (Bertiller et al. 2006) from five branches of the external canopy crown (sunny and partially sunny leaves) of each individual. Collected leaves per branch, individual, species, and site were air dried and stored at $20\,°C$ for later analysis. We randomly selected one totally expanded leaf per branch of each individual, re-hydrated the leaf up to full expansion and placed it on the flat bed of a HP ScanJet ADF scanner and scanned it. Leaf area was calculated from the images obtained by means of the AxioVision 4 program. Then, leaves were oven dried at $60\,°C$ for 48 h, and weighed to assess leaf dry mass. We further calculated the mean leaf mass per area (LMA) of each dominant shrub species at each site. The rest of the totally

Site location	Site	MAP (mm)	MAT (ºC)	AI
42º 43' 58.8" S, 69º 42' 58.5" W	Colan Conhue (CC)	150	8.7	4.0
42º 32' 08.3" S, 69º 14' 15.1" W	Taquetrén (Ta)	150	8.2	3.8
42º 35' 18.0" S, 69º 07' 52.5" W	Colelache (Co)	150	8.2	3.8
42º 35' 40.3" S, 69º 02' 36.4" W	Lagunita Salada (LS)	150	8.3	3.8
42º 23' 31.5" S, 68º 56' 38.0" W	Gastre (Ga)	150	8.0	3.7
42º 12' 11.0" S, 68º 17' 40.4" W	Sierras de Talagapa (ST)	150	8.9	4.1
42º 30' 34.2" S, 67º 58' 14.3" W	Gan Gan (GG)	150	9.8	4.5
42º 33' 35.0" S, 66º 33' 49.0" W	Telsen (Te)	137	12.8	6.5
42º 45' 43.9" S, 66º 00' 53.1" W	Sierra Chata (SC)	125	13.2	7.3
42º 49' 20.1" S, 65º 36' 53.5" W	El Ranchito (ER)	150	13.4	6.2
42º 38' 42.3" S, 65º 22' 28.2" W	San Luis (SLu)	153	13.5	6.1

Fig. 1. Geographical location of the eleven study sites along the transect encompassing the northern portion of the Central District of the Patagonian Phytogeographical Province (P) and the Patagonian Monte (PM) corresponding to the southern portion of the Monte Phytogeographical Province, Argentina. The mean annual precipitation (MAP) of each site (series 1931–1960) was taken from Barros & Rivero (1982). Mean annual air temperature (MAP) of each site was calculated for the same time series from the dataset CRU TS 2.1 (Mitchell & Jones 2005). The aridity index (AI) of each site was computed as PET/ MAP, with PET the mean annual potential evapotranspiration (PET = 69.4 × MAT) (UNESCO 1979; Le Houérou 1990). High AI-values indicate high aridity conditions.

expanded green leaves without signs of deterioration (uniformity in the coloration and absence of damage by herbivores or pathogens) were oven dried at 60 °C over 48 h. We assessed N concentration by semi-micro Kjeldahl, total soluble phenolics by the Folin-Ciocalteu method using 50% methanol as extract solution and tannic acid as standard (Waterman & Mole 1994), and lignin by the van Soest (1963) procedure in the leaves of each individual of each species at each site. We used field data to compute the following groups of response variables: (1) shrub species richness (number of species), (2) Shannon diversity index (Begon, Harper, & Townsend 1996) of shrub species, and (3) the richness, and the Shannon diversity index of shrub species with pubescent leaves, thorny stems, spiny leaves, or photosynthetic stems by site and by morphotype and site.

We used the relative cover of each dominant species of each morphotype at each site to weight the mean values of leaf traits of species (Bertiller & Ares 2008) to calculate mean leaf structural (area and LMA) and chemical (N, soluble phenolic, and lignin concentrations) attributes in the dominant shrub canopy. These latter constituted the groups of response variables 4 and 5, respectively. The morphological and chemical plant traits selected were those identified as relevant in relation to aridity (Bertiller et al. 2005, 2006). In particular, leaf traits of shrubs are strongly related to abiotic conditions although some traits selected could be also relevant in relation to herbivory (Hartley & Jones 1998; Díaz et al. 2007).

Statistical analyses

We compared means of morphotype traits in the whole transect by one-way ANOVA. Regression analyses were used to relate plant traits and aridity. Variables were transformed to meet the assumptions of the above statistical tests. We used the Bonferroni sequential correction to reduce type one error when applying multiple tests of regression (Sokal & Rohlf 1995). Unless otherwise noted, the significance level was set at $p \leq 0.05$ throughout the study. Statistical analyses were performed with the statistical package SPSS 7.5 for Windows (Norusis 1997).

Results

General attributes of shrub morphotypes in the study area

We found the largest proportion of species with pubescent leaves, thorny stems and photosynthetic stems among deciduous tall shrubs. Species of this morphotype also had the highest N concentration in leaves. Evergreen tall shrubs displayed leaves with high LMA, and the highest concentration of soluble phenolics. This plant morphotype had the lowest proportion of species with pubescent leaves. Medium shrubs had high LMA and lignin concentration in green leaves. Dwarf shrubs showed the largest proportion of species with

Table 1. Proportion of species with pubescent leaves, thorny stems, spiny leaves, and photosynthetic stems by shrub morphotype, and mean values ± one standard error of leaf area, leaf mass per area (LMA), and concentrations of lignin, soluble phenolics, and N by shrub morphotype in the whole transect. DTS: deciduous tall shrubs, ETS: evergreen tall shrubs, MS: medium shubs, and DS: dwarf shrubs. Different lower case letters indicate significant differences among morphotypes (Bonferroni test).

	Morphotype			
	DTS	ETS	MS	DS
Structural traits				
Proportion of species (%) with:				
Pubescent leaves	71.43	30.00	46.67	61.90
Thorny stems	78.57	20.00	0.00	0.00
Spiny leaves	0.00	20.00	33.33	66.67
Photosynthetic stems	42.86	10.00	6.67	23.81
Leaf area, LMA and chemical traits				
Leaf area (mm^2)	$9.41 \pm 1.02a$	$36.98 \pm 4.07b$	$40.77 \pm 5.73b$	$5.65 \pm 0.90a$
LMA ($mg\,mm^{-2}$)	$0.14 \pm 0.02a$	$0.23 \pm 0.004b$	$0.25 \pm 0.01b$	$0.19 \pm 0.02ab$
Lignin ($mg\,g^{-1}$)	$82.08 \pm 17.08ab$	$60.84 \pm 5.17a$	$101.28 \pm 7.79b$	$119.02 \pm 8.96b$
Soluble phenolics ($mg\,g^{-1}$)	$53.78 \pm 7.58a$	$141.64 \pm 10.58b$	$41.48 \pm 6.57a$	$42.09 \pm 2.89a$
N ($mg\,g^{-1}$)	$24.23 \pm 1.78b$	$14.58 \pm 1.14a$	$11.47 \pm 0.56a$	$12.20 \pm 0.46a$

spiny leaves and high lignin concentration in green leaves (Table 1).

Richness and diversity of species and morphotypes

We found a significant increase in shrub species richness (all morphotypes) with increasing aridity index (AI) (Fig. 2A). This was attributable to increasing species richness of deciduous and evergreen tall shrubs with increasing AI (DTS: $r^2 = 0.73$, $p = 0.0008$ and ETS: $r^2 = 0.71$, $p = 0.0012$, respectively, significant after the Bonferroni sequential adjustment). The species richness of the other morphotypes did not vary significantly with AI (data not shown). Shannon diversity of shrub species in the shrub canopy also increased significantly with increasing AI (Fig. 2B) and this was explained by the increase in species diversity of evergreen tall shrubs with increasing AI (ETS: $r^2 = 0.55$, $p = 0.008$; significant after the Bonferroni sequential adjustment). The species richness of the other morphotypes did not vary significantly with AI (data not shown). Morphotype richness did not vary significantly with the AI but morphotype diversity increased significantly with increasing AI (Figs. 2C and D).

Structural shrub traits

The richness of species with pubescent leaves (Fig. 3A) increased significantly with increasing AI due to increasing richness of deciduous and evergreen tall shrubs with pubescent leaves with increased AI (DTS: $r^2 = 0.51$, $p = 0.013$, and ETS: $r^2 = 0.81$, $p = 0.0002$, respectively, significant after the Bonferroni sequential adjustment).

The richness of species with thorny stems (Fig. 3B) increased with increasing AI due to increasing richness of deciduous tall shrubs with thorny stems (DTS: $r^2 = 0.51$, $p = 0.0067$, significant after the Bonferroni sequential adjustment). The richness of species with spiny leaves and photosynthetic stems (all morphotypes) did not vary significantly with AI (Fig. 3C and D). However, the richness of species with photosynthetic stems in deciduous tall shrubs increased with AI (richness DTS: $r^2 = 0.65$, $p = 0.003$, significant after the Bonferroni sequential adjustment). Shannon diversity of species with pubescent leaves, thorny stems, spiny leaves, and photosynthetic stems yielded virtually the same results as species richness (Appendix A: Fig. 1A–D).

Leaf area, LMA and chemical plant traits

Mean values of leaf area, LMA, and concentrations of lignin, and soluble phenolics of the whole canopy of dominant shrub species did not vary significantly with AI (Fig. 4). However, soluble phenolics increased with increasing aridity in evergreen tall shrub canopy ($r^2 = 0.78$, $p = 0.047$, power function; non significant after the sequential Bonferroni adjustment). Nitrogen concentration in the whole canopy of dominant shrub species (Fig. 4E) increased significantly with increasing AI due to increasing N concentration of evergreen tall shrub canopy ($r^2 = 0.98$, $p = 0.003$, significant after the Bonferroni sequential adjustment).

Discussion

Aridity was positively associated with species richness and diversity of evergreen and deciduous tall shrubs as reported for other arid ecosystems (Barboni et al. 2004). These morphotypes have strong xeromorphic adaptations and structural/chemical defenses. Most of these plant traits could be associated with adaptations to water shortage but some of
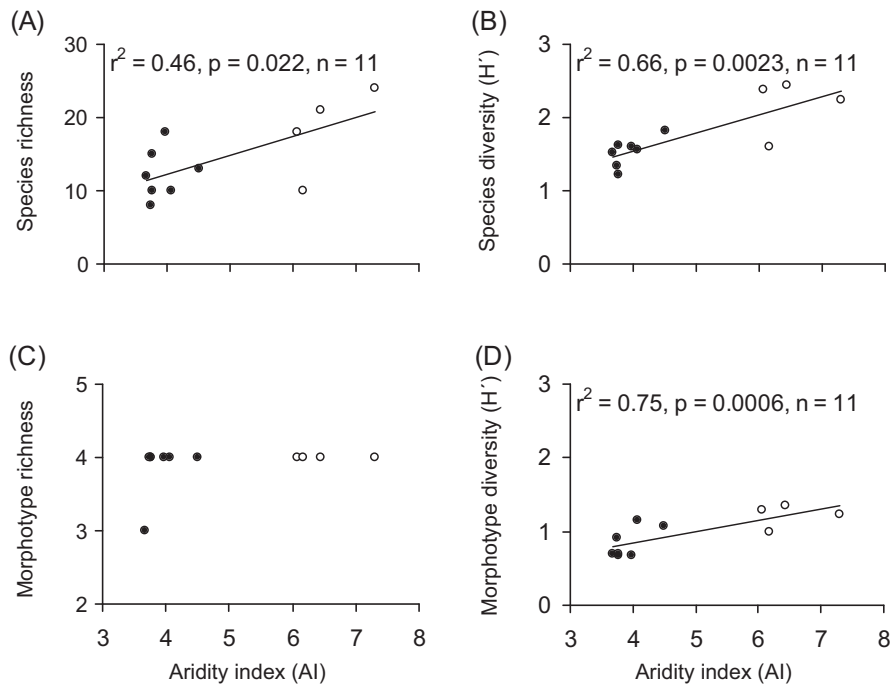
Fig. 2. Species richness (number of species: A), species diversity (*H'*): B), morphotype richness (number of morphotypes: C), and morphotype diversity (*H'*): D) along the aridity gradient. Solid circles: Patagonian sites, open circles: Patagonian Monte sites.

them are also traits which could result from herbivory adaptations (Díaz et al. 2007). Increased pubescence in leaves with aridity could be an advantage to reduce water losses (Ehleringer & Mooney 1978; Grace 1998) but could also serve to reduce attack by small herbivores and pathogens (Woodman & Fernandes 1991). High richness or diversity of deciduous tall shrubs with thorny stems at the driest extreme of the gradient could be an adaptation to water shortage
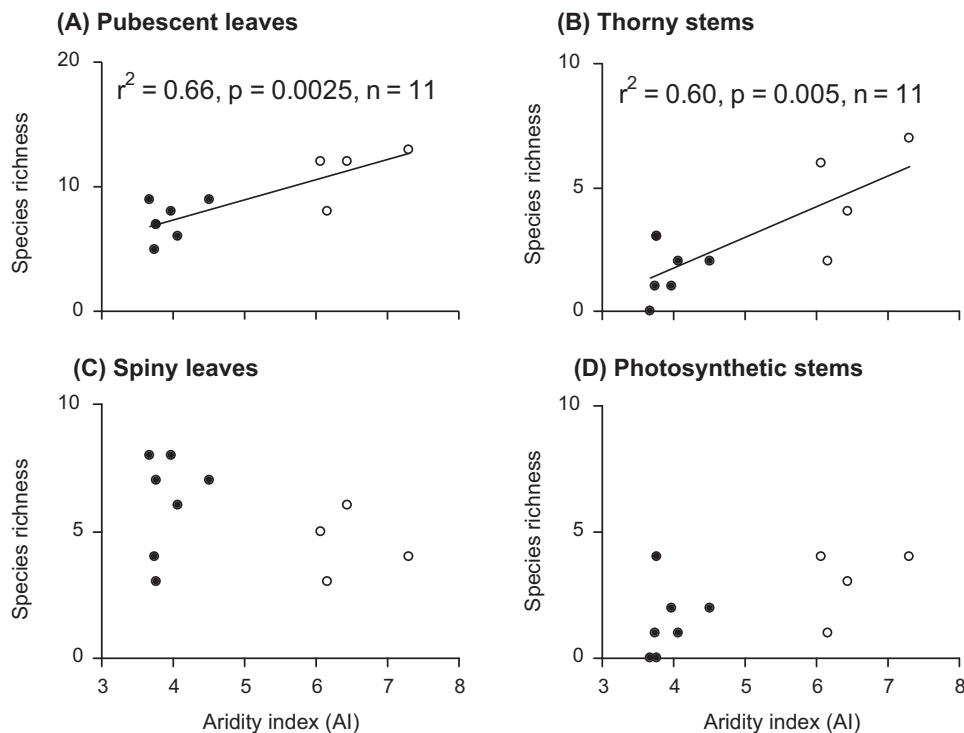
Fig. 3. Mean values of species richness of morphotypes along the aridity gradient. Solid circles: Patagonian sites, open circles: Patagonian Monte sites.

(A) Leaf area

(B) LMA

(C) Lignin

(D) Soluble phenolics

(E) Nitrogen

$r^2 = 0.43, p = 0.0269, n = 11$
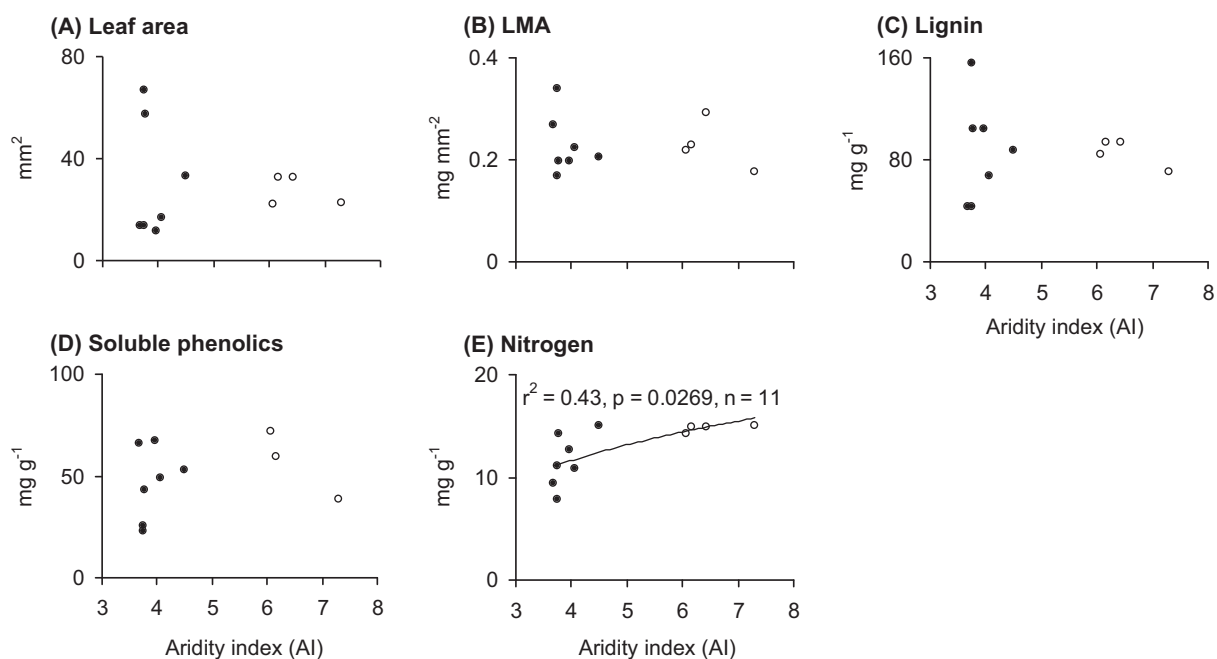
Fig. 4. Mean values of (A) leaf area, (B) leaf mass per unit area (LMA), (C) lignin concentration, (D) soluble phenolic concentration, and (E) N concentration in green leaves of dominant shrubs along the aridity gradient. Solid circles: Patagonian sites, open circles: Patagonian Monte sites.

(deciduousness) but thorny stems could also protect short lived leaves with the highest N concentration from herbivore damage (Hartley & Jones 1998; Pérez-Harguindeguy et al. 2003). Increased soluble phenolics in leaves of evergreen tall shrub canopies with increasing aridity could be associated with increased defenses against both water shortage and herbivores (Wright & Westoby 2003; Campanella & Bertiller 2009). However, we assumed that patterns of diversification of life history traits of shrubs observed are mostly plant adaptations or responses more related to water shortage than to grazing because contrasts in climate are greater than those in the ecological history of domestic grazing across the gradient. This assumption is further supported by studies reporting no changes in species richness and diversity due to herbivory in other arid ecosystems (Milchunas et al. 1998; Adler et al. 2005).

As with other arid ecosystems of the world (Noy Meir 1973; Reynolds et al. 2004), increasing aridity is related to decreasing productivity and increasing variability in intra- and interannual water pulsing in Patagonian ecosystems (Barros & Rivero 1982; Austin & Sala 2002). The relationship between species richness/diversity and aridity found in our study differs from the general hump-shaped pattern (Rosenzweig & Abramsky 1993) in which species richness peaks at intermediate levels of productivity. This difference could be attributed to the fact that most of described hump-shaped functions relating species richness and productivity correspond to gradients of precipitation/productivity along geographical areas or precipitation intervals many-fold wider than our relatively constrained aridity gradient. In this sense, our results might refer to just a section of an extended

hump-shaped pattern over an area including less productive ecosystems.

Our findings support the hypothesis that aridity helps maintain richness/diversity of species with different morpho-functional and life history traits in shrub canopies. Proposed mechanisms sustaining the coexistence of a large number of species in arid ecosystems are separation of water use in space and time and differences in plant responses to resource pulsing, among others (Ehleringer, Phillips, Schuster, & Sandquist 1991; Chesson et al. 2004; Reynolds et al. 2004). These mechanisms are consistent with phenological asynchronism and differences in rooting depth among species of the morphotypes described in our study (Fernández & Paruelo 1988; Bertiller et al. 1991; Rodríguez et al. 2007; Campanella & Bertiller 2008; Bucci et al. 2009). Evergreen tall shrubs and deep-rooted deciduous tall shrubs are expected to access a more stable water source than medium and dwarf shrubs (Bertiller et al. 1991; Coronato & Bertiller 1997). Also, the positive relationship of plant species richness/diversity and aridity observed in our study is consistent with the hypothesis of increasing environmental heterogeneity with decreasing precipitation proposed to explain the decreasing end of the hump-shaped pattern (Rosenzweig & Abramsky 1993; Chesson et al. 2004). In more arid sites, the non-seasonal pattern of precipitation along with the highest temperatures probably has a stronger effect on the desiccation of the upper soil layers than in the least arid sites (Coronato & Bertiller 1996, 1997). Due to these characteristics, precipitation pulses could be less biologically effective in more arid sites (Reynolds et al. 2004) increasing spatial and temporal water heterogeneity in the soil profile (Coronato

& Bertiller 1996, 1997). Also, increasing vegetation patchiness and species richness/diversity of tall shrub morphotypes induced by aridity could lead to the increase of spatial heterogeneity in soil water, evaporative demand and soil fertility (Bertiller et al. 2002) thus further supporting the environmental heterogeneity hypothesis. We conclude that our results on increasing richness and diversity of shrub species with different life history traits with increasing water shortage support the idea that aridity provides axes of ecological differentiation among shrub species that facilitate shrub coexistence in water limited ecosystems.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2010.09.002.

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