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# Plant functional traits and environmental filters at a regional scale

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**Abstract.** Links between plant traits and the environment, i.e. sets of plant attributes consistently associated with certain environmental conditions, are the consequence of the filtering effect of climatic, disturbance and biotic conditions. These filters determine which components of a species pool are assembled into local communities. We aimed at testing for consistent association between plant traits and climatic conditions along a steep regional gradient, divided into 13 climatically homogeneous sectors, in central-western Argentina. We analyzed 19 vegetative and regeneration traits of the 100 most abundant species along the gradient. For each trait, we tested for homogeneity of frequencies of different categories between sectors and the regional species pool, using the  $\chi^2$  statistic. We rejected  $H_0$  in 71% of the pair-wise comparisons, which strongly suggests a ‘filtering effect’ of climatic factors on key plant functions. Vegetative traits were filtered more often than regeneration traits. Specific leaf area, life span, ramification, canopy height, leaf weight ratio, carbon investment into support tissue and pollination mode were the traits showing differences in the largest number of pair-wise comparisons.

This is probably the first attempt to detect, on a quantitative, statistically conservative basis, consistent linkages between climatic factors and numerous plant traits, over a broad spectrum of environmental conditions and plant growth forms. We discuss the advantages and limitations of this approach in predicting vegetation structure and functioning under present environmental conditions, and those expected for the next century as a consequence of global change.

**Keywords:** Argentina; Assembly rule; Climatic gradient; Climate change; Trait-environment linkage, Plant functional type.

**Nomenclature:** Cabrera (1963–1970); Correa (1969–1984).

**Abbreviations:** LWR = Leaf Weight Ratio; SLA = Specific Leaf Area.

## Introduction

The identification of consistent and predictable associations between plant traits and environmental conditions is almost as old as ecology itself. The detection of general rules underlying observed patterns is a necessary step in the development of community ecology into

an integrated science (Keddy 1992; Grime 1993). Interest in assembly rules – usually defined as generalized restrictions to coexistence – which determine which components of a species pool will form a community (Diamond 1975; Drake 1990; Wilson & Gitay 1995), is an integral part of this search for generalization. Most authors (e.g. Drake 1990; Wilson & Gitay 1995) emphasize interactions between organisms rather than with other selective forces. On the other hand, Keddy (1992) defined assembly rules in a broader sense, as filters of any kind imposed on the regional species pool. According to Keddy (1992), the best way to visualise assembly rules is a process of deletion by which the environment acts as a filter removing species which lack traits for persisting under a particular set of conditions. He mentions climatic conditions, disturbance regime and biotic interactions as examples of filters. Woodward & Diament (1991), although they do not explicitly mention the term assembly rules, consider climate, disturbance and site productivity as successive filters which select certain traits and functions out of the regional species pool.

Trait-environment linkages, consistent associations between sets of plant attributes and certain environmental conditions, irrespective of the species involved (Keddy 1992) are the consequence of the filtering effect of environmental conditions (Woodward & Diament 1991; Keddy 1992). Climatic, disturbance and interaction filters tend to act at decreasing spatial scales. At any particular site, a hierarchy of filters can be found: only those traits/functions which are viable under the prevailing climatic conditions, and then under the predominant disturbance regime, have the opportunity to be ‘filtered out’ (or not) by the interactions with other organisms.

Examples of the operation of ‘filters’ at different scales can be found in the literature. At increasing scales, one might mention the works of van der Valk (1981) focused on topographic-edaphic conditions and interactions between plants, of Noble & Slatyer (1980) and Noble & Gitay (1996) on disturbance and vital attributes and of Box (1981, 1996) and Woodward (1987) on relations between vegetation and climate at regional to global scales.

In this article, we focus on the existence of consistent trait-environment linkages, as the result of the filtering effect of variations in climatic conditions on a regional species pool. Our aims are (1) to test for consistent association between plant traits and environmental conditions along a steep climatic gradient at the regional level; and (2) to find out whether local climatic conditions act as filters, making some traits non-viable and therefore preventing the establishment of certain plant species present in the regional pool. We discuss the advantages and limitations of this approach in understanding vegetation structure and functioning at different points along the gradient.

## Material and Methods

### *Study area*

Steep gradients, in which sharp changes can be observed in relatively short distances, are particularly appropriate for the study of the relationships between natural vegetation and climatic conditions. We selected a climatic gradient in central-western Argentina (ca. 31° 25' - 32°S; 64°10' - 68° 37' W) for study, with a difference in annual precipitation of more than 800 mm, a difference in mean annual temperature of more than 11 °C, and a difference in altitude of more than 1500 m between extreme points. It stretched from the subhumid high plateaus of the Córdoba mountains to the western semiarid-arid plains, which are limited by the Sub-Andean ranges. Dry and relatively cold winters and rainfall heavily concentrated in the warm season are characteristic of the climate over the whole region.

We compiled published floristic information from 63 sites along the gradient (Cabido et al. 1989-1994). Each site was represented by the five least disturbed vegetation relevés, except for one case, in which only three relevés of undisturbed vegetation were available. The total number of original relevés considered was 313. On the basis of climatic data, we classified the sites along the gradient into 13 homogeneous sectors (Table 1). The dominant vegetation types ranged between montane grasslands (highest and wettest extreme, Sectors 1-4 in Table 1) open woodlands (intermediate points, Sectors 5-10 in Table 1), and open xerophytic shrublands (driest extreme, Sectors 11 and 12 in Table 1). Open halophytic shrublands on salt flats are scattered along the drier portion of the gradient (Sector 13). Although these sites are subjected to seasonal drought, the prevailing constraint to plant growth is chronically high salt ion concentration in the soil.

### *Selection of plant species and traits*

We selected the most abundant plant species along the whole gradient, on the basis of the aforementioned published relevés. We discarded from the analysis all vascular species which were present in less than 32 relevés (i.e. in less than 10% of all the 313 relevés). We then selected the 100 most abundant species along the whole gradient to be analyzed in terms of key functional traits. The species set comprised 30 families, numerous growth forms and eight major functional types (App. 1).

We selected 19 traits measurable at the individual plant level (Table 2). They were all easy to measure in the field or with very basic laboratory facilities. In some cases, traits were surrogates for other more quantitative labour- or technology-demanding attributes (e.g., specific leaf area as an indicator of relative growth rate). We measured most traits on field material. Information from herbaria, floras and experts was also utilised. The scales of measurement of plant traits were originally continuous or categorical, but they were all transformed into categorical scales for analysis (Table 2).

### *Data analysis*

In order to identify the association between categories of plant traits with particular sectors (sets of sites showing similar environmental conditions) along the gradient, we built a 100 species  $\times$  63 site binary matrix, obtained from the vegetation surveys mentioned above but considering only the presence or absence of each species. On that basis, we constructed 19 individual species  $\times$  site matrices, one for each trait, the data being the value (category) of the trait showed by each species (its specific leaf area, canopy height, etc.). It was then possible to assess the frequency of each trait category at each site.

For each trait, we tested for homogeneity of proportions of different categories between sectors using contingency tables with the  $\chi^2$  statistic (Agresti 1990), under the null hypothesis that there would be no significant difference between frequencies of each category in different sectors. In cases where significant differences between any pair of sectors were found, we tested for differences between the frequencies of different trait categories in each sector and those in the region as a whole (regional pool). The regional pool represented the mean frequency of each trait category in all sectors, excluding the sector being compared, thus ensuring independence of contrasts. We carried out these comparisons using the same test described above, but with a lower significance level in order to ensure simultaneous inference (Bonferroni's correction; Miller 1981).

**Table 1.** Climatically homogeneous sectors identified along a regional gradient in central-western Argentina. Vegetation in Sector 13 is determined mainly by local edaphic factors, under climatic conditions corresponding to Sectors 9-11. Meteorological data from Argentine Meteorological Services, Argentine Railways, and Palacios & Zamar (1986). Overall vegetation cover values from Cabido et al. (1989-1994). Prec. = precipitation.

Sector/ Dominant vegetation	Overall cover (%)	Altitude (m)	Mean temp (°C)	Mean min. temp. (°C)	Mean max. temp. (°C)	No. frost-free months	Annual prec. (mm)	No. dry months
1 Montane grasslands	100	2155	8.1	3.9	12.9	0	911	1
2 Montane grasslands	100	1850	8.9	5.2	15.8	0	840	1
3 Montane grasslands	100	1450	11.4	6.8	18.5	2	887	2
4 Montane grasslands	100	1000	13.1	8.8	21.6	4	996	2
5 Montane woodlands	100	900	13.1	9.4	21.9	5	996	2
6 Montane woodlands	90	750	15.6	9.2	23.8	5	826	4
7 Montane woodlands	90	600	17.5	10.7	24.5	6	662	4
8 Xerophytic woodlands	80	350	19.6	12.2	26.8	8	520	6
9 Xerophytic woodlands	70	368	19.6	12.4	25.2	8	520	7
10 Xerophytic woodlands	50	652	18.3	12.4	25.2	7	381	7
11 Xerophytic open shrublands	50	500	18.2	12.5	25.5	6	260	9
12 Xerophytic open shrublands	30	641	18.0	10.4	25.7	6	85	12
13 Halophytic open shrubland	30	350 - 400	18.2 - 19.6	12.4 - 12.5	25.2 - 25.5	6-8	260 - 520	7 - 9

**Table 2.** Traits recorded on the 100 most abundant vascular plant species along a climatic gradient in central-western Argentina. Through restricted randomization, 10 healthy-looking, sexually mature individuals were considered for measurement of traits in the field or in the laboratory. CAM = Crassulacean Acid Metabolism; LWR = Leaf Weight Ratio; SLA = Specific Leaf Area.

Trait	Description of classes
Photosynthetic pathway	CAM = 1; C4 = 2; C3 = 3
Specific leaf area (SLA) (surrogate for relative growth rate; Poorter & Bergkotte 1992, Reich et al. 1992)	Aphyllous = 0; SLA < 10 cm <sup>2</sup> /gr = 1; 10 - 100 = 2; > 100 = 3
Leaf weight ratio (LWR; photosynthetic tissue/non-photosynthetic tissue)	LWR < 1 = 0; 1 = 1; > 1 = 2
Leaf succulence (indicator of resistance to drought and/or salinity)	Non-succulent = 0; slightly succulent = 1; highly succulent = 2
Carbon storage in reserve organs (carbohydrates can be broken down and allocated to new growth) (thickened roots and stems, bulbs, rhizomes)	No specialized storage organs = 0; specialized storage organs = 1
Vegetative spread (capacity to produce expanding clones)	No evident clonal expansion = 0; evident clonal expansion = 1
Canopy height	≤ 20 cm = 1; > 20 - 60 = 2; 61 - 99 = 3; 100 - 299 = 4; 300 - 599 = 5; ≥ 600 = 6
Life span	Annual = 1; 2 - 10 yr = 2; 11 - 50 = 3; > 50 = 4
Investment into support tissue (xylem and bark)	Herbaceous monocots = 0; herbaceous dicots = 1; semi-woody dicots = 2 woody dicots with trunk and bark = 3
Ramification at the ground level (adaptive under severe drought; Carlquist 1988, Hargrave et al. 1994)	Non-woody species = 0; 1 single trunk = 1; 2 - 10 = 2; > 10 = 3
Drought avoidance (taproot and/or highly succulent stem)	No evident drought-resisting organs = 0; taproot or highly succulent stem = 1
Thorniness	No thorns = 0; slightly thorny = 1; very thorny (e.g., <i>Cactaceae</i> ) = 2
Shoot phenology (seasonality of maximum production of photosynthetic tissue)	No evident peak = 1; autumn - early spring = 2; spring - early autumn = 3 late spring - summer = 4
Seed size	Maximum length < 2 mm = 1; 2 - < 4 mm = 2; 4 - 10 = 3; > 10 = 4
Seed shape (variance of seed length, width and depth, possibly related to persistence in the soil, Thompson et al. 1993)	< 0.15 = 1; 0.15 - < 1 = 2; 1 - 5 = 3; > 5 = 4
Number of seeds per plant	< 100 seeds = 1; 100 - 999 = 2; 1000 - 5000 = 3; > 5000 = 4
Seed dispersal mode	No obvious agent = 0; animals with low mobility (ants, rodents) = 1; highly mobile animals (large mammals, bats, birds) = 2; wind = 3
Pollination mode	Anemophilous = 0; unspecialized zoophilous = 1; specialized zoophilous = 2
Reproductive phenology	No evident peak = 1; autumn - early spring = 2; spring - early autumn = 3; late spring - summer = 4

## Results

If each sector, due to its particular combination of climatic conditions, has a specific 'filtering effect' on plant traits, mean values of attributes may be poor descriptors of this process, since they may mask the real range of viable categories in each sector. Therefore, we explored the distribution of different categories of each plant trait along the gradient. The frequency distributions of categories of vegetative spread, carbon storage, seed shape and reproductive phenology showed no significant difference between sectors ( $\chi^2$ -statistic;  $p \geq 0.05$ ). For the remaining traits, the null hypothesis of trait frequency distribution in local sectors being indistinguishable from the regional pool was rejected in 71 % of the pair-wise comparisons (Table 3), strongly suggesting the existence of environmental filters. Vegetative traits were 'filtered' more often than reproductive traits (74 % and 63 % of cases, respectively). SLA, life span, ramification, canopy height, LWR, investment into support tissue and pollination mode were the traits showing differences in the largest number of comparisons between local sectors and the regional pool.

The sectors in which plant trait categories were most different from the regional pool – assumed to show the strongest 'filtering effect' – corresponded to high mountain locations, with significant differences becoming more frequent as altitude increased (Sectors 1 - 4 in Table 3). Their climate is characterised by low mean temperature, occurrence of frost throughout the growing season and positive water balance during most of the year. The 'filtering effect' of saline lowlands, with severe constraints on water uptake throughout the year (Sector 13), was also very strong. Semiarid to arid woodlands, woodland-shrublands and shrublands (Sectors 8 - 12) showed differences with the regional pool for a comparatively smaller number of traits. They did differ in several vegetative traits, but they showed no significant difference in succulence, photosynthetic pathway or vegetative phenology. In those sectors, water deficit disappears or is ameliorated during late spring to early autumn, in which frost events disappear or are very infrequent. This probably allows the survival of a relatively wide variety of trait combinations. Finally, montane woodlands in Sectors 5 - 7 were transitional between vegetation and climatic types, therefore it is not surprising that they showed comparatively few differences with the regional pool.

### Variations in vegetative traits

Variations in the frequency of different categories of the most discriminant plant traits in representative sectors are displayed in Table 4. Specific leaf area is a good

**Table 3.** Summary results of pair-wise comparisons between trait frequency distributions in local sectors and in the region considered as a whole (regional pool; see text for detailed description of analysis). \* = difference with regional pool significant at  $p < 0.05$ ; simultaneous inference; Bonferroni's correction; - = no significant difference ( $p \geq 0.05$ ). See Tables 1 and 2 for definition of sectors and traits, respectively.

Traits	Sectors												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Vegetative traits</i>													
Specific leaf area	*	*	*	*	-	*	*	*	*	*	*	*	*
Life span	*	*	*	*	*	-	*	*	*	*	*	*	*
Ramification	*	*	*	*	*	-	*	*	*	*	*	*	*
Canopy height	*	*	*	*	-	*	*	*	*	*	*	*	*
Leaf weight ratio	*	*	*	*	*	-	-	*	*	*	*	*	*
Investment into support tissue	*	*	*	*	-	*	*	-	*	*	*	*	*
Leaf succulence	*	*	*	*	*	*	*	*	-	-	-	-	-
Thorniness	*	*	*	*	*	-	*	*	*	*	-	-	-
Drought avoidance	*	*	*	*	*	-	-	-	-	*	*	*	*
Photosynthetic pathway	*	*	*	*	-	*	*	-	-	-	-	-	*
Shoot phenology	*	*	*	-	-	*	-	-	-	-	-	-	*
<i>Regeneration traits</i>													
Pollination mode	*	*	*	*	*	*	*	*	-	*	*	*	*
Seed size	*	*	*	-	-	-	-	*	*	-	*	*	*
Seed number	*	*	*	*	*	*	*	-	-	-	-	-	*
Dispersal mode	*	*	-	-	-	*	-	-	*	*	*	-	-

indicator of relative growth rate, especially when analysing a broad range of functional types (Poorter & Bergkotte 1992; Reich et al. 1992). Specific leaf areas of  $\geq 10 \text{ cm}^2/\text{gr}$  (categories 2 and 3) were very frequent in montane grasslands under cold and moist climate (Sector 1 in Table 4), becoming more rare in sectors with higher water deficit. In xerophytic (Sectors 10 and 12 in Table 4) and halophytic shrublands (Sector 13 in Table 4) plants with small, strongly protected, persistent leaves were common, together with plants whose main photosynthetic organs are green stems. In xerophytic woodlands and shrublands (Sectors 10 and 12 in Table 4) specific leaf areas of  $10\text{--}100 \text{ cm}^2/\text{gr}$  (category 2) were viable during the rainy season and corresponded to annual or summer-sprouting grasses. This was not observed in the case of the halophytic shrublands (Sector 13 in Table 4), in which severe water deficit is always present, and chronically high salt ion concentration impose serious constraints on leaf development and physiology (Crawford 1989). Dominant plants in montane woodlands (Sector 6 in Table 4) showed intermediate values of SLA, mostly between  $> 0$  and  $100 \text{ cm}^2/\text{gr}$  (categories 0 - 2).

Short-lived ( $\leq 10$  yr; categories 1 - 3) perennials predominated in montane grasslands (Sector 1 in Table 4). Longer-lived plants were more common in sectors with higher water deficit. In the case of xerophytic woodlands and shrublands (Sectors 10 and 12 in Table 4),

there was a wide spectrum of life histories, including annuals. In saline lowlands (Sector 13 in Table 4), the only viable life history among the dominants appeared to be medium- to long-lived perennials (11 - 50 yr; category 4). The high frequency of high LWR in grasslands (Sector 1 in Table 4) is not surprising and does not need further comment. In the case of halophytic shrublands (Sector 13 in Table 4), however, roughly equal proportions of photosynthetic and non-photosynthetic tissue was related to the existence of leafless plants, with photosynthetic succulent stems.

Low temperature (montane grasslands, Sector 1 in Table 4) and severe water deficit (open xerophytic and halophytic shrublands, Sectors 12 and 13 in Table 4) appeared to select for uniform canopy heights (< 300 cm, but mostly  $\leq 60$  cm, and 60-300 cm, respectively). In the case of woodlands (Sectors 6 and 10 in Table 4), taller plants were obviously more common, but there was also maximum diversity of heights. Carbon investment into xylem and degree of ramification are directly associated with woody growth forms and therefore were more common in woodlands and shrublands (Sectors 6-13 in Table 4). In woodlands (Sectors 6 and 10 in Table 4), maximum investment into support tissue was represented by trees and shrubs with nil or low degree of ramification at the ground level. In open xerophytic and halophytic shrublands (Sectors 12 and 13 in Table 4), drought-resistant shrubs showed lower investment into support tissue and a larger number of thinner branches at the ground level (probably associated with less risk of damage from cavitation, Carlquist 1988; Hargrave et al. 1994). The presence of different degrees of ramification, together with the maximum diversity of heights gave the woodlands (Sectors 6 and 10 in Table 4) the highest structural complexity along the gradient.

There was a set of species which remained active during the whole year, which tended to be evergreen, sometimes succulent, with CAM but most commonly C3 photosynthesis. There was also a less persistent set which was present or active only during the growing season. This was represented by annual herbaceous plants (mainly C4 grasses), and deciduous shrubs and trees. Although further information would be needed to assess the net annual carbon gain for these two groups of plants, deciduous types tended to predominate in the higher grasslands (Sectors 1-3 in Table 3), where the maximum seasonal differences in environmental factors were observed, whereas evergreen types predominated in chronically stressed environments (Sector 13 in Table 3), as expected on the basis of the literature (e.g. Larcher 1995). Sectors 4, 5, and 7-12 (Table 3) did not significantly differ from the regional pool in terms of shoot phenology, with deciduous and evergreen types coexisting in various proportions.

**Table 4.** Frequency distributions of different categories of plant traits in the region as a whole (regional pool) and in five selected sectors representing contrasting environmental conditions. See Table 1 for definition of sectors, Table 2 for trait classes and Table 3 for statistical significance of differences between frequency distributions in the regional pool and in each sector. Frequency distributions for the full set of sectors and trait categories considered are available on request.

	Trait	Regional	Sectors				
	categories	pool	1	6	10	12	13
Specific leaf area	1	7	1	6	14	11	25
	2	17	3	44	24	32	70
	3	59	57	44	59	55	5
	4	18	38	6	2	2	0
Life span	1	8	11	0	5	15	0
	2	53	76	61	35	15	0
	3	19	13	8	23	26	100
	4	20	0	31	36	43	0
Ramification	1	70	96	64	52	42	25
	2	14	0	33	30	23	0
	3	13	4	3	15	26	30
	4	3	0	0	3	9	45
Canopy height	1	26	56	11	9	9	0
	2	27	26	42	25	23	0
	3	17	10	11	26	11	25
	4	18	8	8	15	36	75
	5	6	0	6	13	17	0
	6	6	0	22	11	4	0
Investment in support tissue	1	12	20	36	4	2	0
	2	56	73	25	43	28	25
	3	17	7	8	22	30	75
	4	16	0	31	31	40	0
Pollination mode	1	40	50	14	34	26	75
	2	22	30	25	7	2	25
	3	39	20	61	59	72	0
Seed size	1	32	57	17	20	9	55
	2	31	23	28	34	28	20
	3	33	21	53	41	57	25
	4	3	0	3	5	6	0
Seed number	1	19	37	6	10	9	0
	2	40	43	44	33	40	0
	3	33	21	28	46	43	30
	4	8	0	22	11	8	70

### *Variations in regeneration traits*

Pollination mode, seed size, and seed number were the most discriminant among the regeneration traits considered (Table 3). Anemophily (category 0) was the most frequent pollination syndrome in grasslands and halophytic shrublands (Sectors 1 and 13 in Table 4), whereas specialized zoophilous syndromes (especially bird- and hymenopteran-pollination; category 2) predominated in woodlands and xerophytic shrublands (Sectors 6-12 in Table 4). Small seeds (< 2 mm, category 1) were common in grasslands and halophytic shrublands. In the first case (Sector 1 in Table 4), this was associated with low seed production per plant (< 1000, categories 1

and 2). In the second case (Sector 13 in Table 4), in contrast, seeds were produced in large numbers (1000 - > 5000, categories 3 and 4). In woodlands and xerophytic shrublands (Sectors 6-12 in Table 4) there was a higher variety of seed sizes and numbers, but big seeds ( $\geq 4$  mm, categories 3 and 4) were more common than in other vegetation types. These trends should be interpreted with caution, however. It is apparent from Table 3 and Table 4 that the differences between local sectors and the regional pool are less consistent for regeneration traits than for vegetative ones.

## Discussion

The results presented here quantitatively document associations - albeit not cause-effect relationships - between several plant traits and climatic conditions along a regional gradient, suggesting a 'filtering effect' of climatic factors on key plant functions and therefore the existence of assembly rules in a broad sense. These patterns are not new in the literature. Neither is the finding of recurrent associations among vegetative attributes or the trade-offs between allocation to growth vs. defence and storage. Even the partial decoupling between vegetative and regeneration traits has been repeatedly reported. However, to our knowledge, this is the first attempt to describe, on a quantitative, statistically conservative basis, consistent association between climatic factors and numerous plant traits across such wide spectra of environmental conditions and plant growth forms. The assumption of dispersal of propagules of all those species across the whole region seems to be a reasonable one, since there is no substantial geographical barrier to dispersal, the degree of habitat fragmentation is very low, and there is wide circulation of wild vertebrates and livestock.

On such a basis, our approach emphasises the links between environmental filters and key functional traits of the dominant vegetation. Although not addressed in this article, which explicitly focuses on abiotic conditions, the effects of disturbance and local biotic interactions may also be of fundamental importance (see for example Smith et al. 1997).

### *Plant traits and plant functional types*

It is extremely important to point out at this stage that traits are not filtered independently from each other, since selective pressures act on individuals as a whole (Gould & Lewontin 1979). There is evidence that plant traits tend to be associated in recurrent, predictable patterns (Grime 1977; Chapin 1980; Lambers & Poorter 1992; Reich et al. 1992; Chapin et

al. 1993). The existence of these recurrent specialization patterns allows classification of the immense diversity of plant species in natural communities into many fewer functional types, namely sets of plants exhibiting similar responses to environmental conditions and having similar effects on the dominant ecosystem processes (Walker 1992; Gitay & Noble 1997). Díaz & Cabido (1997) analyzed a species  $\times$  traits matrix similar to the one described in this article and found consistent associations between vegetative plant traits. Plants with traits associated with high investment in photosynthesis and fast growth (high LWR and SLA, short life span, short leaf longevity, shoot expansion concentrated in the most favourable season and C3 and C4 photosynthesis) and plants with traits associated with slow growth and high persistence in time and preferential allocation to storage and defence (low LWR and SLA, high longevity, evergreen or semi-deciduous and with C3 and CAM photosynthesis) were the most extreme types. That allowed Díaz & Cabido (1997) to classify the most abundant species in the regional flora into eight plant functional types (see App. 1). Regeneration traits were only loosely coupled with each other and with vegetative traits. The trade-offs between sets of traits found by these authors confirmed, over a wider spectrum of environmental conditions, the patterns described for other floras (Chapin 1980; Grime et al. 1997).

It should be stressed that neither Díaz & Cabido's (1997) classification, nor the links between plant traits and environmental conditions described here, were independent of taxonomic affiliation (see App. 1). Some sets of associated traits were restricted to certain families, and therefore not phylogenetically independent. This would seriously preclude attempts to claim that all the traits we now observe as associated to certain sectors have evolved as an adaptive response to local conditions (Harvey & Pagel 1991; Harvey et al. 1995), although they have certainly survived the predominant local filters. A considerable imprint of phylogeny has been noted by most of the authors who constructed plant functional types on the basis of several plant traits, especially on the basis of local or regional floras (Leishman & Westoby 1992; Grime et al. 1997). Also, as Westoby et al. (1995) have pointed out, a large part of the effect of habitat change is to redistribute existing lineages geographically, rather than to modify their attributes by directional selection. Since phylogenetic differentiation and current fitness are not mutually exclusive processes, the ecological relevance of plant functional traits and types should not be dismissed because of their association with phylogeny (Ackerly & Donoghue 1995; Westoby et al. 1995), provided no evolutionary interpretation is made.

This lack of phylogenetic and physiological independence between key plant traits should not be viewed

as an obstacle for their use in the analytical study of vegetation and ecosystems. Quite to the contrary, if consistent linkages are detected between a small set of key trait and environmental conditions, tight integration between traits should allow predictions about other traits not directly measured. This may prove very useful not only for practical purposes. Simplification is urgently needed in order to strengthen community ecology as an integrated and predictive science (Grime 1993). In the same direction, authors like Tucker et al. (1984), Nemani & Running (1989, 1996), Chapin (1993) or McIntyre et al. (1995) have suggested the use of only one or extremely few traits in assessing vegetation responses to changing environmental factors. Caution should be taken, however, in view of the repeated reports of only loose coupling between vegetative and regeneration attributes (Leishman & Westoby 1992; McIntyre et al. 1995; Grime et al. 1997; Díaz & Cabido 1997). Although a highly reduced set of attributes may be sufficient to predict major links between established vegetation and ecosystem processes *in situ*, seemingly we still need multiple character sets to assess responses to local disturbance and expansion/retreat over the landscape.

#### *Trait-environment linkages and ecosystem functioning*

Because dominant plant traits strongly influence ecosystem functioning (Hobbie 1992; Wilson & Agnew 1992; Schulze & Mooney 1994; Jones & Lawton 1995), the approach presented here could be seen as a first step towards the prediction of fundamental ecosystem processes on the basis of the traits of the dominant populations on a particular location. Vegetative traits tend to be associated with ecosystem processes *in situ*, whereas regeneration traits tend to influence stability, re-colonization after major disturbances and migration over the landscape (see Díaz & Cabido 1997 and references therein for further details). The global change expected for the next century (Houghton et al. 1996) will possibly modify environmental filters at all scales, including climate, disturbance regime and biotic interactions (Woodward & Diment 1991; Houghton et al. 1996). Given a certain scenario of future climatic conditions, and assuming consistent trait-environment linkages, present distribution of dominant plant traits in space - especially along steep environmental gradients - may be used as a proxy for changes in time. The works of Skarpe (1996) and of Cabido & Díaz (1997) showing associations between different plant functional types and precipitation and temperature, provide recent examples of this approach.

The use of viable plant traits or plant functional types (instead of species) under different environmental conditions provides better chances to compare and pre-

dict responses of different floras (Wilson et al. 1994) or of species now absent from the regional pool (e.g., invaders). This approach has many limitations, such as: expected changes in environmental factors to combinations with no clear equivalent at present (Woodward & Diment 1991); significant errors of global circulation models at regional scales (Rocheffort & Woodward 1992); and uncertainty about the occurrence of extreme events (Wigley 1985). However, the analysis of present spatial patterns is a useful heuristic tool in trying to predict the direction (and to a lesser extent magnitude and rate) of vegetation change under a shifting climate, and provides empirical support to modelling efforts at the regional scale.

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**App. 1.** Species considered for analysis of plant functional traits. See text for selection criteria. See Díaz & Cabido (1997) for a detailed description of plant functional types. Attributes listed in column 1 were found in > 50 % species within each plant functional type. LA = leaf area, SLA = specific leaf area, LWR = leaf weight ratio. See Table 2 for details on trait measurement. Plant family code: ACA = Acanthaceae; AMA = Amaranthaceae; AMR = Amaryllidaceae; ANA = Anacardiaceae; API = Apiaceae; APO = Apocynaceae; ASC = Asclepiadaceae; AST = Asteraceae; POR = Portulacaceae; FAB = Fabaceae; BRO = Bromeliaceae; CAC = Cactaceae; CEL = Celastraceae; CHE = Chenopodiaceae; CYP = Cyperaceae; GEN = Gentianaceae; IRI = Iridaceae; JUN = Juncaceae; LIL = Liliaceae; MAL = Malvaceae; MAP = Malpighiaceae; PLA = Plantaginaceae; POA = Poaceae; RHA = Rhamnaceae; ROS = Rosaceae; RUB = Rubiaceae; SAN = Santalaceae; SOL = Solanaceae; VER = Verbenaceae; ZYG = Zygophyllaceae.

Plant functional type (PFT)	Species	Fam.	Plant functional type (PFT)	Species	Fam.
PFT 1 Small, short-lived graminoids or dicots, with high LA, SLA, and LWR, C4 or C3 photosynthetic pathway, very low carbon accumulation, low resistance to drought, high palatability, well-defined vegetative and reproductive biomass peak in spring to early autumn, and wind pollination	<i>Agrostis montevidensis</i>	POA	PFT 4 Saxicolous or epiphytic rosettes, with high LA and LWR, very low SLA, CAM pathway, moderate carbon accumulation, high resistance to drought, and low or nil palatability, evergreen with reproductive biomass peak in early spring, and animal specialized pollination, animal and wind-assisted dispersal	<i>Deinacantho urbanianum</i>	BRO
	<i>Alchemilla pinnata</i>	ROS		<i>Dyckia floribunda</i>	BRO
	<i>Aristida adscensionis</i>	POA		<i>Tillandsia bryodes</i>	BRO
	<i>Aristida spegazzini</i>	POA		<i>Tillandsia duratii</i>	BRO
	<i>Bothriochloa laguroides</i>	POA	PFT 5 Deciduous or semi-deciduous, very long lived trees, with high to moderate LA and SLA, low LWR, C3 pathway, very high carbon accumulation, low ramification at ground level, drought avoidance, vegetative and reproductive biomass peak in spring-early autumn, animal specialized pollination, and large flattened seeds	<i>Acacia aroma</i>	FAB
	<i>Bouteloua aristoides</i>	POA		<i>Acacia caven</i>	FAB
	<i>Briza subaristata</i>	POA		<i>Acacia furcatispina</i>	FAB
	<i>Bromus unioloides</i>	POA		<i>Aspidosperma quebracho-blanco</i>	APO
	<i>Bulbostylis juncoideus</i>	CYP		<i>Bulnesia retama</i>	ZYG
	<i>Carex fuscata</i> var. <i>distenta</i>	CYP		<i>Cercidium australe</i>	FAB
	<i>Chloris retusa</i>	POA		<i>Geoffroea decorticans</i>	FAB
	<i>Cynodon dactylon</i>	POA		<i>Lithraea ternifolia</i>	ANA
	<i>Digitaria californica</i>	POA		<i>Prosopis chilensis</i>	FAB
	<i>Eragrostis lugens</i>	POA		<i>Prosopis flexuosa</i>	FAB
	<i>Juncus uruguensis</i>	JUN		<i>Schinopsis haenkeana</i>	ANA
	<i>Muehlenbergia peruviana</i>	POA	PFT 6 Evergreen, long lived shrubs and small trees, with low LA, SLA, and LWR, C3 pathway, high carbon accumulation, high resistance to drought, high ramification at ground level, very low to nil palatability, leaf biomass constant or with small peak in spring, animal specialized pollination, and large seeds	<i>Atriplex argentina</i>	CHE
	<i>Neobouteloua lophostachya</i>	POA		<i>Colletia spinosissima</i>	RHA
	<i>Papophorum caespitosum</i>	POA		<i>Condalia microphylla</i>	RHA
	<i>Piptochaetium montevidense</i>	POA		<i>Eupatorium bunifolium</i>	AST
	<i>Portulaca grandiflora</i>	POR		<i>Heterothalamus alienus</i>	AST
	<i>Relbunium richardianum</i>	RUB		<i>Jodina rhombifolia</i>	SAN
	<i>Setaria pampeana</i>	POA		<i>Larrea cuneifolia</i>	ZYG
	<i>Sorghastrum pellitum</i>	POA		<i>Larrea divaricata</i>	ZYG
PFT 2 Tussock grasses and large-leaved forbs, with high LA, SLA, and LWR, C3 pathway, moderate carbon accumulation, resistance to drought, and palatability, well-defined vegetative and reproductive biomass peak in summer, and wind pollination	<i>Sporobolus indicus</i>	POA	PFT 7 Aphyllous or scale-leaved shrubs, long-lived, with extremely low to nil LA and LWR, high carbon accumulation, numerous branches at ground level, high resistance to drought and salinity, low to nil palatability, no evident seasonal biomass peak, small and spheroidal seeds	<i>Lycium elongatum</i>	SOL
	<i>Sporobolus pyramidalis</i>	POA		<i>Maytenus vitis-idaea</i>	CEL
	<i>Stipa flexibarbata</i>	POA		<i>Trichomania usillo</i>	MAP
	<i>Stipa neesiana</i>	POA		<i>Zucagnia punctata</i>	FAB
	<i>Trifolium repens</i>	FAB	PFT 8 Globular, cylindrical, and columnar branched stem-succulents, long to very long-lived, aphyllous, with evergreen succulent stem, moderate carbon accumulation, low ramification at the ground level, high drought avoidance, nil palatability (thorns), no evident seasonal biomass peak, animal specialized pollination and dispersal.	<i>Baccharis articulata</i>	AST
	<i>Verbesina encelioides</i>	AST		<i>Senna aphylla</i>	FAB
	<i>Ambrosia tenuifolia</i>	AST		<i>Heterostachys ritteriana</i>	CHE
	<i>Cirsium vulgare</i>	AST		<i>Suaeda divaricata</i>	CHE
	<i>Deyeuxia hieronymi</i>	POA	PFT 3 Short herbaceous and semi-woody erect, creeping or rosette-like dicots, with short to moderate lifespan, high LA and LWR, intermediate SLA, C3 pathway, moderate carbon accumulation and resistance to drought, highly variable biomass peak, uncommon in mid-summer, and animal unspecialized pollination	<i>Cereus validus</i>	CAC
	<i>Festuca tucumanica</i>	POA		<i>Cleistocactus baumanii</i>	CAC
	<i>Morrenia odorata</i>	ASC		<i>Echinopsis leucantha</i>	CAC
	<i>Parthenium hysterophorus</i>	AST		<i>Gymnocalyxium spec.</i>	CAC
	<i>Paspalum dilatatum</i>	POA		<i>Opuntia sulphurea</i>	CAC
	<i>Paspalum quadrifarium</i>	POA			
	<i>Poa stuckertii</i>	POA			
	<i>Stipa tenuissima</i>	POA			
	<i>Talinum paniculatum</i>	POR			
	<i>Trichloris crinita</i>	POA			
	<i>Adesmia bicolor</i>	FAB			
	<i>Alternanthera pungens</i>	AMA			
	<i>Bidens andicola</i>	AST			
	<i>Chaptalia integerrima</i>	AST			
	<i>Diplotera tweediana</i>	ACA			
	<i>Eryngium nudicaule</i>	API			
	<i>Gentiana parviflora</i>	GEN			
	<i>Glandularia peruviana</i>	VER			
	<i>Gomphrena pulchella</i>	AMA			
	<i>Hypoxis humilis</i>	AMR			
	<i>Malvastrum coromandelianum</i>	MAL			
	<i>Margyricarpus pinnatus</i>	ROS			
	<i>Nierenbergia hippomanica</i>	SOL			
	<i>Nothoscordum inodorum</i>	LIL			
	<i>Noticastrum marginatum</i>	AST			
	<i>Oreomyrrhis andicola</i>	API			
	<i>Plantago brasiliensis</i>	PLA			
	<i>Plantago myosurus</i>	PLA			
	<i>Sisyrinchium chilense</i>	IRI			
	<i>Solanum eleagnifolium</i> var. <i>leprosum</i>	SOL			
	<i>Stenandrium dulce</i>	ACA			
	<i>Taraxacum officinale</i>	AST			
	<i>Zephyranthes longistyla</i>	AMA			

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### **Seed Size and Shape Predict Persistence in Soil**

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### **Succession in Wetlands: A Gleasonian Approach**

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### **On Misinterpreting the 'Phylogenetic Correction'**

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### **Functional Approaches to Predicting the Ecological Effects of Global Change**

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