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Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina

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Abstract. This paper deals with theoretical concepts, methodological steps, and case studies related to the use of plant functional traits in the assessment of vegetation responses to climate and land use. Trait-environment links are considered, and special emphasis is put on the links between vegetation structure and ecosystem function, and on the role of disturbance history in determining vegetation responses to land use at present. As a basis for discussion, published and new case studies from central-western Argentina are presented. Similar plant traits measured with different levels of precision are utilized in the description of ecosystem structure in different land-use situations along a steep regional climatic gradient. The general protocol followed in the case studies represents a data-driven, non-hierarchical, low-tech approach, that can be applied to a wide range of spatial scales, from plots to regions. Climatic factors (including extreme events and seasonality), disturbance frequency and intensity, and disturbance history are suggested as key factors to be considered in global comparisons of vegetation responses to land use and in predictive models of ecosystem dynamics.

Keywords: Climate; Disturbance; Environmental filter; Global change; Grazing; Trait-environment link.

Introduction

This paper deals with the use of plant functional traits in assessing vegetation responses to different environmental factors, such as climate, disturbance or land-use. Climate and land use are interpreted as successive filters acting upon the regional species pool. The main emphasis is on the links between plant traits, vegetation structure, and ecosystem functioning, and on the role of disturbance history in determining plant responses to land use. These ideas are illustrated with previous and new findings in central-western Argentina.

Plant assemblages, environmental filters and global change

According to some authors (Woodward & Diament 1991; Keddy 1992; Díaz et al. 1998a, b) the assemblage of plant genotypes found at any given location can be interpreted as the product of the 'filtering' effect of climatic conditions, disturbance regime, and biotic interactions. These effects represent a hierarchy of factors, which tend to operate at increasingly finer spatial scales. Only those genotypes that are not 'filtered out' by the prevailing climatic conditions in a region can be subjected to the selective pressures of landscape-level disturbance regime and then to local-level biotic interactions (Woodward & Diament 1991; Díaz et al. 1998a, b). The regional pool on which successive filters act is determined by biogeographical and historical factors, operating at broad spatial and temporal scales.

Global change is expected to alter all three filters. Changes are expected in mean and extreme temperatures and rainfall (Houghton et al. 1996), in land-use patterns (Vitousek et al. 1997), and in vegetation flammability (Gardner et al. 1996; Pausas 1999). Interactions between plant species (e.g. invasions, Chapin et al. 1998), between plants and above-ground herbivores (Lindroth 1996), and between plants and below-ground microbiota (Côuteaux et al. 1996; Klironomos et al. 1996; Yeates et al. 1997) are also expected to suffer alterations. In general, it is believed that ecosystem effects of changes in land use will be more dramatic than those changes brought about by climate alone, and will strongly interact with them (Vitousek et al. 1997). The effects of land use, therefore, have to be fully considered – conceptually and methodologically – in global change studies. Díaz & Cabido (1997) and Díaz et al. (1998, 1999) have suggested that a common methodology could be applied to the analysis of community responses to both climate and disturbance, but that remained untested until now.

On the other hand, the idea that local dominant genotypes – those who have survived the climatic and disturbance filters – exert strong effects on community structure and ecosystem function has recently gained growing acceptance (Hobbie 1992; Wilson & Agnew 1992; Schulze & Mooney 1994; Mooney et al. 1996; Chapin et al. 1998). Interestingly, this duality has been captured in the concept of plant functional types proposed by Walker (1992) and Gitay & Noble (1997) in the context of global change research. According to these authors, plant functional types are sets of plants exhibiting similar responses to environmental conditions and having similar effects on dominant ecosystem processes.

Data-based approaches to the description of ecosystem structure

The main reason for describing vegetation in terms of functional traits rather than floristic composition has often been an operational one, namely the possibility of comparing taxonomically distinct floras (e.g. Orlóci & Stofella 1986; Lausi et al. 1989), and/or of summarizing the overwhelming biodiversity of natural systems (Grime et al. 1997; Gitay & Noble 1997; McIntyre et al. 1999a). Another powerful reason, only recently stressed, is that dominant plant traits are known to strongly influence ecosystem function (see above). This is highly relevant to ecological theory (Sala et al. 1996; Grime et al. 1997; Lavorel et al. 1997; Chapin et al. 1998), as well as having important practical implications, for example in ecosystem service assessment (Costanza et al. 1997) or predictive modeling (Lavorel et al. 1997; Campbell et al. 1999).

Plant functional trait responses to filtering factors – an overview of case studies in central-western Argentina

Data sets

In order to analyse plant trait responses to climate, we selected a climatic gradient in central-western Argentina (ca. 31° 25' - 32° S, 64° 10' - 69° W) for study, with a difference in annual rainfall 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 its extreme points. It stretches from the subhumid high plateaus of the Córdoba mountains to western semi-arid to arid plains and foothills of the Andes. Dry and relatively cold winters and rainfall heavily concentrated in the warm season are characteristic of the climate over the whole region. Vegetation types ranged from montane grassland at one extreme of the gradient to open xerophytic and halophytic shrublands at the other extreme. We compiled published floristic information from 63 sites along the gradient (Table 1; see Díaz & Cabido 1997 for details on sites and methods).

In order to analyse plant functional trait responses to land-use regime, we focused on three sectors along the aforementioned climatic gradient. These were xerophytic woodlands (representing an intermediate situation), xerophytic open shrubland (representing the drier extreme) and upper-belt montane grasslands (representing the colder and wetter extreme). The three sectors showed contrasting climatic conditions, land-use regimes (Table 1), and disturbance histories (Morello 1958; Morello & Saravia Toledo 1959; Bucher 1987; Díaz et al. 1987, 1994). The disturbance situations chosen for study varied according to the usual land-use practices in each sector. In the case of xerophytic woodlands, we selected three situations under different intensities of a combination of logging and grazing, and two situations with different ages of abandonment after clearing and cultivation. In the case of xerophytic open shrublands, we selected two situations under different logging and grazing regimes. In the case of montane grasslands, we selected four situations under different grazing regimes, and three situations with different ages of abandonment after cultivation. Table 1 summarizes the range of situations and number of sites considered. See Cabido et al. (1994), Araníbar (1997), and Díaz et al. (1994) for further details on environmental conditions and sampling methods used in xerophytic woodlands, xerophytic open shrublands, and montane grasslands, respectively.

For analysis of functional trait responses to climatic factors, we selected the 100 most abundant species along the whole gradient (see Díaz & Cabido 1997 for details on species selection). For analysis of responses to land use, we selected all the species which were present in at least 10 % of the original samples. This resulted in the consideration of 60 species in the case of xerophytic woodlands, 49 in the case of xerophytic open shrublands, and 64 in the case of montane grasslands. The total number of species considered was 191, representing 44 families (complete list available upon request.). We selected 24 traits measurable at the individual plant level (App. 1). They were all simple to measure in the field or with very basic laboratory facilities. We measured most traits on field material. Information from herbaria, floras, and experts was also utilized. The scales of measurement of plant traits were originally continuous or categorical, but they were all transformed into categorical scales for analysis (see Díaz & Cabido 1997 for trait choice and measurement details). Those 24 traits were measured at the species level, i.e., the traits of each species were measured in only one site, where the species was most abundant. In the case of montane grasslands, a smaller set of traits (App. 1) were measured at the population (or 'morph' *sensu* Dirzo 1984) level, i.e., the traits of each species were measured in all the sites in which

Table 1. Summary of climatic and disturbance conditions in sites sampled along a regional gradient in central-western Argentina. Meteorological data are from the Argentine Meteorological Services, Argentine Railways, and Palacios & Zamar (1986). Original samples from Cabido et al. (1990-1994), Acosta et al. (1992), Díaz et al. (1992, 1994), and Araníbar (1996). MG = montane grassland; MW = montane woodland; XW = xerophytic woodland; XS = xerophytic open shrubland; HS = halophytic open shrubland.

Type	Disturbance regime	No. sites	Alt. (m)	Mean temp. (° C)	Mean min. temp. (° C)	Mean max. temp. (° C)	No. frost-free months	Annual rainfall (mm)	No. dry months
MG	Undisturbed	5	2155	8.1	3.9	12.9	0	911.5	1
MG	Undisturbed (>5 yr without grazing)	12 *	1850	8.9	5.2	15.8	0	840.4	1
MG	1 yr without grazing	12	1850	8.9	5.2	15.8	0	840.4	1
MG	Moderate grazing	15	1850	8.9	5.2	15.8	0	840.4	1
MG	Heavy grazing	11	1850	8.9	5.2	15.8	0	840.4	1
MG	1 yr abandonment following cultivation	8	1850	8.9	5.2	15.8	0	840.4	1
MG	3 - 5 yr abandonment following cultivation	11	1850	8.9	5.2	15.8	0	840.4	1
MG	25 yr abandonment following cultivation	8	1850	8.9	5.2	15.8	0	840.4	1
MG	Undisturbed	5	1450	11.4	6.8	18.5	2	887.3	2
MG	Undisturbed	5	1000	13.1	8.8	21.6	4	996.0	2
MW	Undisturbed	3	900	13.1	9.4	21.9	5	996.0	2
MW	Undisturbed	5	750	15.6	9.2	23.8	5	826.4	4
MW	Undisturbed	5	600	17.5	10.7	24.5	6	662.0	4
XW	Undisturbed (no logging or grazing for >25 yr)	5	350	19.6	12.2	26.8	8	520.0	6
XW	Selective logging + moderate grazing	5	350	19.6	12.2	26.8	8	520.0	6
XW	Total removal of the upper canopy + heavy grazing	5	350	19.6	12.2	26.8	8	520.0	6
XW	15 yr abandonment following cultivation	4	350	19.6	12.2	26.8	8	520.0	6
XW	3 yr abandonment following cultivation	3	350	19.6	12.2	26.8	8	520.0	6
XW	Undisturbed	5	368	19.6	12.4	25.2	8	520.0	7
XW	Undisturbed	5	652	18.3	12.4	25.2	7	381.0	7
XS	Undisturbed	5	500	18.2	12.5	25.5	6	260.0	9
XS	Undisturbed	5	641	18.0	10.4	25.7	6	85.0	12
XS	Undisturbed (27 yr without grazing or logging)	10 **	900	16.0	7.1	24.7	6 - 7	180.0	12
XS	Heavy logging + grazing	10	900	16.0	7.1	24.7	6 - 7	180.0	12
HS	Undisturbed	5	350 - 400	18.2 - 19.6	12.4 - 12.5	25.2 - 25.5	6 - 8	260.0 - 520.0	7-9

*Only five considered for climate analysis; **Not included in the climate analysis (Fig. 1).

the species was present, and each population was treated as a separate entity for analysis, following the approach of Díaz et al. (1992, 1994).

In order to identify the predominant plant traits along the climatic gradients, we used a non-hierarchical, low-tech, data-driven multivariate approach, as described in Díaz et al. (1992) and Díaz & Cabido (1997). In the analysis of both climatic and disturbance factors, we built a species ↔ sites matrix (obtained from the vegetation surveys mentioned above) and multiplied it by the traits ↔ species matrix. The result was a traits ↔ sites matrix, which was subjected to Detrended Correspondence Analysis (DCA; Gauch 1981). All original matrices are available upon request.

Plant functional trait responses to climatic factors

In previous work, Díaz & Cabido (1997) have documented differences in ecosystem structure at different sites along a steep regional climatic gradient (Fig. 1). The main trend of variation separated high-mountain grasslands, dominated by traits related with high investment in photosynthesis and growth, short life span and strong seasonal green biomass peaks, from xerophytic and halophytic open shrublands, dominated by plants with low investment in photosynthetic area, preferential allocation to defence and storage, high degree of ramification at the ground level, and usually succulent, evergreen leaves or photosynthetic stems, protected by epidermal coats. At intermediate positions on the ordination plane, woodlands were characterized by large-sized, deep-rooted, mostly deciduous woody plants, coexisting with smaller, shorter-leafed, shallow-rooted grasses, forbs and epiphytes.

Díaz et al. (1998a, b) provided evidence of the strong filtering effect of climatic factors along the same gradient on vegetative plan traits, such as specific leaf area, life history, carbon allocation to support and storage tissue, and height. Regeneration traits were filtered to a lesser degree, with pollination mode and seed size being the traits filtered more often. Filtering effect was strongest in high-altitude grasslands, and was also considerable in open xerophytic shrublands. This was attributed to the low minimum and mean temperatures and the high occurrence of frost which characterize mountain climate, and to the almost permanent water deficit which is typical of xerophytic shrublands (Table 1). Woodlands showed the highest diversity of categories of plant traits. Therefore they were suggested as the sectors along the gradient in which the filtering effect of climate was the weakest. In those sectors frosts are rare and confined to a short period during the annual cycle, and

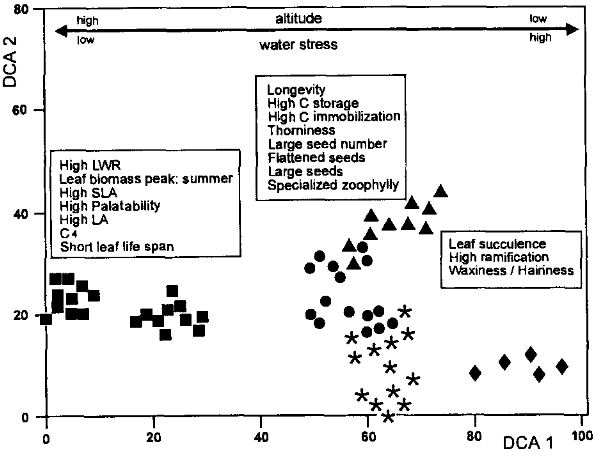

Fig. 1. DCA-ordination of sites along a climatic gradient, considering 24 plant traits (App. 1). See Table 1 for climatic conditions at different sites. ■ = montane grasslands, ✳ = montane woodlands; ● = xerophytic woodlands and woodland-shrublands; ▲ = open xerophytic shrublands; ◆ = halophytic vegetation on poorly-drained soils. Plant traits associated with different sectors of the ordination plane are displayed in boxes (adapted from Díaz & Cabido 1997).

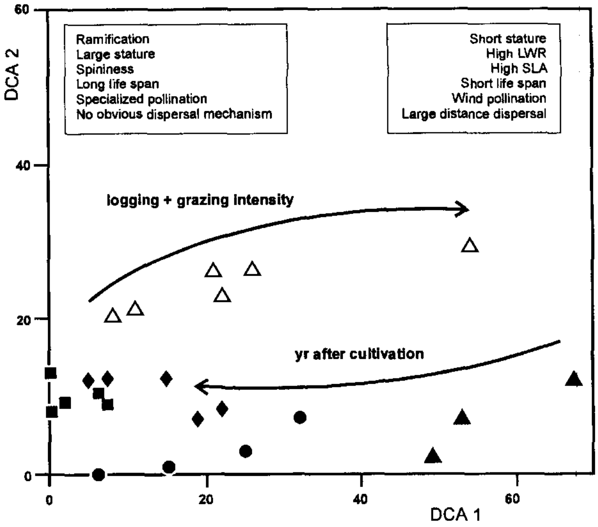

Fig. 2. DCA-ordination of xerophytic woodland sites under different land-use regimes, considering 24 plant traits (App. 1). ■ = no logging or grazing for > 25 yr; ◆ = selective logging + moderate grazing by cattle and goats; Δ = heavy logging + grazing by cattle and goats; ▲ = 2 yr after cultivation; ● = > 15 yr after cultivation. Plant traits associated with different sectors of the ordination plane are displayed in boxes.

water deficit is largely ameliorated during the rainy season (late spring to early autumn) (Table 1). This probably allows the survival of a relatively wide variety of plant functional types.

Plant functional trait responses to land use

The sites considered by Díaz & Cabido (1997) were as little disturbed as possible, since sampling was specifically designed to study the effects of climate. In order to analyse how disturbance operates on local plant assemblages, within the envelope of local climatic conditions at different positions along the climatic gradient, we considered three sectors: xerophytic woodlands, xerophytic open shrublands, and high-altitude montane grasslands.

In the case of xerophytic woodlands, there was a good discrimination of sites under different land-use regimes (Fig. 2). The main trend of variation separated sites not disturbed at present (including those cultivated and abandoned for > 15 yr), with predominance of woody, long-lived, spiny plants, highly ramified at the ground level, and with specialized animal pollination and no obvious dispersal mechanisms, from sites under severe disturbance (recent abandonment after cultivation and, to a lesser extent, heavy logging + grazing), in which short life span, high leaf weight ratio, high specific leaf area, wind pollination and long-distance seed dispersal (wind or highly-mobile animals) were the most predominant traits. Although shifts in functional trait composition were maximal in the case of post-cultivation abandonment, different intensities of logging + grazing were also well discriminated.

In contrast, in the cases of xerophytic open shrublands (Fig. 3) and montane grasslands (Fig. 4), the analysis performed provided no clear discrimination of sites under different disturbance regimes. Among xerophytic open shrublands, there was no discernible difference in ecosystem structure between heavily logged and grazed sites and sites undisturbed for 27 yr (Fig. 3). In the case of montane grasslands (Fig. 4), although sites recently abandoned following cultivation were separated along DCA-axis 2, trends along DCA-axis 1 were not clearly defined. The reason for this lack of clear differences in ecosystem structure among sites under different land-use regimes is that they tended to show a similar set of dominant species. In the case of montane grasslands, recently abandoned sites showed some exclusive species, of which ca. 22 % were exotic (Díaz et al. 1994), but they tended to disappear quickly.

All these results suggest that there is more room for operation of disturbance filters in those situations like xerophytic woodlands, in which climatic filters are not particularly severe. In the case of areas with strong filtering climatic effect (xerophytic open shrublands and high-mountain grasslands), the available pool is much poorer, and therefore disturbance is likely to have

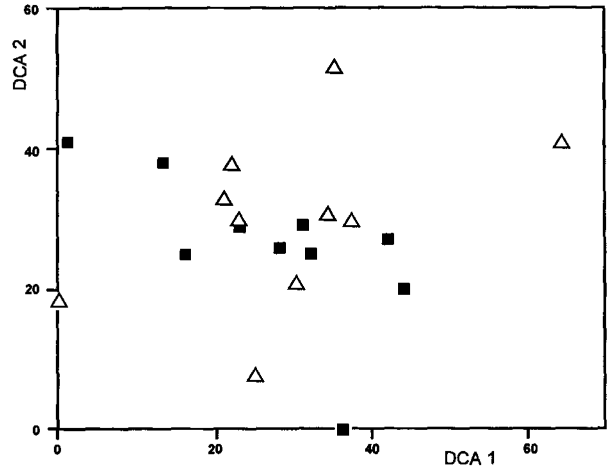

Fig. 3. DCA-ordination of xerophytic open shrublands under different land-use regimes, considering 24 plant traits (App. 1). Δ = heavy logging + grazing by cattle and goats; ■ = no logging or grazing for 27 yr.

less strong effects. It should be stressed, however, that this refers to the pool of functional types, or combinations of traits, since species richness was lower in shrublands (49) but higher in montane grasslands (64), as compared to xerophytic woodlands.

Very often, however, the lack of strong species turnover may mask structural differences. In order to explore that possibility, Díaz et al. (1992, 1994) analysed the same montane-grassland sites measuring the traits of each dominant population at different sites under different land-use regimes (App. 1). In that case, the differences between sites in terms of predominant plant traits were very clear (Fig. 5). There was a good discrimination both among post-cultivation and among grazing situations. Also in this case the maximal shifts in ecosystem structure were observed among post-cultivation situations, where the strongest species turnover was observed (Díaz et al. 1994), but sites under different grazing regimes were also well discriminated, with differences among them being mostly the result of shifts in relative abundance or in morphological traits of a common set of dominant species which showed contrasting morphological features under different grazing regimes (Díaz et al. 1992, 1994).

The general protocol described above provides a good description of ecosystem structure at different scales, from plots to regions. However, precision of measurement (on various local populations or morphs under different conditions vs. on only one local undisturbed population, at the peak of the species' regional distribution) is an extremely important consideration, especially when vegetation responses do not involve strong species turnover.

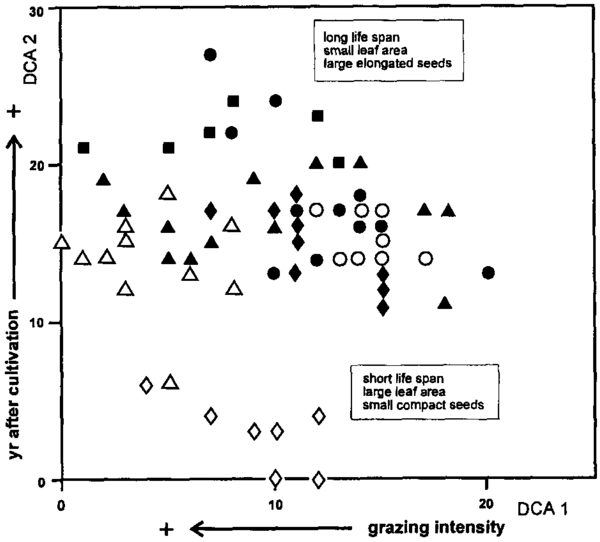

Fig. 4. DCA-ordination of high-mountain grassland sites under different land-use regimes, considering 24 plant traits (App. 1). ● = > 5 yr without grazing; ○ = 1 yr without grazing; ▲ = moderate grazing by cattle and sheep; Δ = heavy grazing by cattle and sheep; ■ = 25 yr of abandonment following cultivation; ◆ = 3 - 5 yr; ◇ = 1 yr. Plant traits associated with different sectors of the ordination plane are displayed in boxes.

Plant traits and ecosystem structure and processes

Two reasons for the use of trait-based approaches to the study of vegetation responses to climate and disturbance were mentioned above: operational reasons and the improvement of our level of understanding of the links between vegetation structure and ecosystem processes. Arguably, measuring traits at the species level may represent some operational advantages in some cases, but certainly measuring traits in different local populations of the same species under different disturbance regimes is operationally more complicated than a traditional floristic study. However, it provides an insight into ecosystem processes which could hardly be allowed by an approach based on species composition only. In the case of montane grasslands, for example, a floristic study would be unable to detect strong differences between plots under different grazing intensities, since the dominant species are mostly the same (Cabido et al. 1996). However, there are important differences in productivity (Pucheta et al. 1998), forage nutrient content, below-ground production patterns (Pucheta et al. 1999), and insect guild diversity and composition (Molina et al. 1998a, b). It is in linking ecosystem structure with ecosystem processes where the plant functional trait approach provides its greatest contribution. Because of the connections between dominant

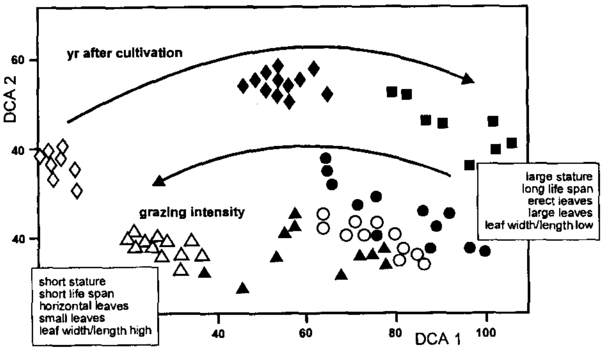

Fig. 5. DCA-ordination of high-mountain grassland sites under different land-use regimes, considering 12 plant traits (App. 1), measured in different populations of the same set of species in different sites. ● = > 5 yr without grazing; ○ = 1 yr without grazing; ▲ = moderate grazing by cattle and sheep; Δ = heavy grazing by cattle and sheep; ■ = 25 yr of abandonment following cultivation; ◆ = 3 - 5 yr; ◇ = 1 yr. Plant traits associated with different sectors of the ordination plane are displayed in boxes (adapted from Díaz et al. 1994).

plant traits and ecosystem functioning, the protocol 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 (see Díaz & Cabido 1997 and references therein for further details). Also, given a certain scenario of future climatic or land-use conditions, and assuming consistent trait-environment linkages, present distribution of dominant plant traits may be used as a proxy for changes in time. In this sense, the analysis of present ecosystem structure is a useful empirical input to modeling efforts at the regional scale (e.g. Campbell et al. 1999).

An often overlooked dimension: disturbance history

Considering the model of filters proposed by Woodward & Diament (1991), one could assume that a disturbance that has a long evolutionary history in an area, and suffers only slight modifications, will simply prompt an adjustment of dominant populations in terms of phenological plasticity, shifts of genotype frequency within heterogeneous populations of the same species, or shifts in relative abundance in the vegetation. On the other hand, if the disturbance sieve is drastically modified, some species or even functional types will be filtered out, and some others, which had been arriving to a site but never thriving, would be able to establish. It could be assumed that the richer the assemblage that can survive the climate filter, the stronger the change in vegetation composition if the disturbance filter is substantially changed. Therefore a similar disturbance would not always produce similar responses in different ecosystems under similar climatic conditions.

Despite the fact that it is still often overlooked, disturbance history has been stressed by several authors as a key element in the interpretation of vegetation responses to land use (Naveh & Whittaker 1979; Denslow 1985; Milchunas et al. 1988; Montalvo et al. 1993; Díaz et al. 1994; Lavorel et al. 1997; Lavorel et al. 1999; McIntyre et al. 1999a). In a study based on a world-wide 236-site data set, Milchunas & Lauenroth (1993) found that evolutionary history of grazing was a more explanatory variable of composition and productivity change of plant communities than grazing intensity. As a major determinant of whether a land-use regime produces changes which take the form of species turnover or changes in the traits of a common set of dominants, and of whether invasion by exotics is likely or not, disturbance history should be incorporated in wide comparative frameworks of responses of vegetation to disturbance such as the one proposed by GCTE Task 2.2.1 (McIntyre et al. 1999b).

Particularly in relation to the study cases presented, cultivation, logging and grazing show an increasingly long evolutionary history in central-western Argentina. The magnitude of species turnover, the architectural shifts in response to them, the predominant traits (e.g., grazing-tolerant herbaceous species, spiny woody vegetation with endozoochorous seeds), and the low invasion by exotics closely match the predictions of models in which disturbance history (as well as climate) is considered one of the main drivers of plant responses to present disturbances (e.g. Milchunas et al. 1988). It may be argued that cultivation, logging, and grazing differ in nature and inherent intensity, as well as in their history in a particular area. However, as pointed out by Díaz et al. (1994), grazing has the potential to produce major shifts in species composition in some areas. The fact that in the cases studied it mainly affected relative abundances and morphological traits without major shifts in floristic composition is in accordance with the palaeontological, archaeological and historical evidence that suggests that at least some regions of South America, including the study area, have long evolutionary history of grazing (see Morello & Saravia Toledo 1959; Bucher 1987; Díaz et al. 1987, 1994 for details and references).

Disturbance history models can be very useful to understand differential responses of different vegetation types to similar disturbances observed in different regions and – perhaps more interestingly – within a region. Discussions of the role of disturbance history in differential responses to land use within similar geographical regions can be found, for example, in

Diaz et al. (1994) for montane and pampean grasslands in Argentina, and in Lavorel et al. (1999) for grasslands in Portugal, Spain, and Israel. The main difficulties to be overcome when testing disturbance history hypotheses within a comparative framework are often the lack of reliable historical information and standard measurements of the magnitude and nature of vegetation change.

Concluding remarks

On the basis of previous and new findings in central-western Argentina, this article suggests that the same general approach can be applied to the analysis of responses to climatic and land-use factors over a wide range of spatial scales, with only modifying the precision with which the traits are measured. Since it is based on easily measured traits, it allows the consideration of large numbers of species with minimum technological and monetary investment, and it is therefore a promising tool in inter-regional or intercontinental comparisons. Also, climatic factors and disturbance can affect diversity of traits, ecosystem structure, and therefore ecosystem function, sometimes without substantial changes in species richness and/or composition. These changes can be detected by functional trait analysis much more easily than by using approaches based on floristic information only.

Climate and disturbance regime appear to act in an interactive way as filters imposed on the regional genotypic pool. The magnitude of vegetation response to disturbance seems to depend on the severity of climatic filtering effects, being less dramatic in those areas where only a very limited assemblage of genotypes/functional types are viable as a result of climatic constraints. Disturbance history, as well as frequency and intensity, appears as a third important driver in determining vegetation response to land use. It may determine whether vegetation response takes the form of species turnover, or shifts in abundance and/or morpho-functional traits. This determines the precision of trait measurements needed to evaluate changes at the level of ecosystem structure. This suggests that climate (means, extremes, and seasonal distribution) and disturbance (frequency, intensity, and history) should be essential axes of variation to be incorporated in global comparative frameworks of the effects of land use on vegetation structure (McIntyre et al. 1999b), and into rule-based predictive models of ecosystem dynamics (Campbell et al. 1999).

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For App. 1, see next page.

App 1. Traits recorded on the most abundant species along climatic and land-use gradients in central-western Argentina. See Díaz et al. (1992, 1994) and Díaz & Cabido (1997) for details on selection criteria and measurement.

Traits and classes in matrix

Photosynthetic metabolism[1]
CAM = 1; C_4 = 2; C_3 = 3
Leaf area (LA) or size (length)[1, 2]
aphyllous = 0; > 0 - 0.1 cm^2 = 1; > 0.1 - 1 = 2; > 1 - 9 = 3; > 9 = 4
Specific leaf area (SLA)[1]
aphyllous = 0; > 0 - < 10 $cm^2.gr^{-1}$ = 1; 10 - < 100 = 2; 100 - ≤ 500 = 3; > 500 = 4
Leaf weight ratio (LWR)[1]
LWR< 1 = 0; L ≅ 1 = 1; LWR> 1= 2
Deciduousness[1]
aphyllous or evergreen = 0; deciduous = 1
Leaf succulence[1]
non-succulent = 0; slightly succulent =1; highly succulent = 2
Leaf shape (weigth/length ratio)[2]
h:w > 1 = 0; h:w ≅ 1 = 1; h:w < 1 = 2
Leaf angle[2]
< 90° = 1; ≥ 90 = 2
Size[1, 2]
≤ 20 cm = 1; 20 - 60 = 2; - 100 = 3; - 300 = 4; - 600 = 5, ≥ 600 = 6
Height/width[1, 2]
h:w > 1 = 0; h:w ≅ 1 = 1; h:w < 1 = 2
Life span[1, 2]
annual = 1; biennial = 2; 3 - 10 yr = 3; 11 - 50 = 4; > 50 = 5
General plant form[2]
prostrate = 1; rosette = 2; erect = 3; tussock = 4
Position of dormant buds[2]
annual = 0; geophyte = 1; hemicryptophyte = 2; phanerophyte = 3
Carbohydrate storage in thickened roots and stems, bulbs, rhizomes, etc.[1, 2]
no specialized storage organs = 0; specialized storage organs = 1
Carbon immobilization in support tissue (xylem, bark, etc.)[1]
herbaceous monocots = 0; herbaceous dicots = 1; semi-woody dicots = 2; woody dicots with trunk and bark = 3
Ramification (number of stems at the ground level)[1]
non-woody species = 0; 1 single trunk = 1; 2 - 10 = 2; > 10 = 3
Drought avoidance (deep taproot, highly succulent stem)[1]
no drought-avoiding organs = 0; taproot or highly succulent stem = 1
Waxiness/Hairiness[1, 2]
hairs, waxes and/or cutines absent = 0; present = 1
Thorniness[1, 2]
no thorns = 0; slightly thorny = 1; very thorny (e.g. *Cactaceae*) = 2
Vegetative spread (capacity to produce expanding clones)[1]
no evident clonal expansion = 0; evident clonal patches = 1
Palatability for ungulates[1, 2]
unpalatable = 0; low palatability, or palatable only at juvenile stages = 1; moderately palatable = 2; highly palatable = 3
Shoot phenology (seasonality of max. photosynthetic tissue production)[1]
no evident peak = 1; winter, autumn, early spring = 2; late spring, spring, spring-summer, late summer-early autumn = 3; late spring-summer, summer = 4
Seed size (maximum length)[1]
< 2 mm = 1; 2 - < 4 = 2; 4 - 10 = 3; > 10 = 4
Seed shape (variance of seed length, width and depth)[1]
< 0.15 = 1; 0.15 - > 1 = 2; 1 - 5 = 3; > 5 = 4
Seed number per plant[1]
< 100 seeds = 1; 100 - 999 = 2; 1000 - 5000 = 3; > 5000 = 4
Seed dispersal in space[1]
no obvious dispersal agent = 0; animals with relatively low mobility (ants, rodents) = 1; highly mobile animals (large mammals, bats, birds) = 2; wind = 3
Pollination mode[1]
anemophyllous = 0; unspecialized zoophyllous = 1; specialized zoophyllous = 2
Reproductive phenology (seasonality of maximum flower and fruit production)[1]
no evident peak = 1; winter, autumn, early spring = 1; late spring, spring, spring-summer, late summer-early autumn = 3; late spring-summer, summer = 4

[1] Climate gradient; species level; 100 species (Díaz & Cabido 1997);
[2] Different land-use situations in montane grasslands; population- or morph level; 78 species (Díaz et al. 1992, 1994).