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Trends and fluctuations in species abundance and richness in Mediterranean annual pastures

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Abstract. Floristic data collected from permanent plots during 14 consecutive years are used to model the frequency of the 62 most abundant species in relation to post-ploughing succession, topography and rainfall in annual Mediterranean grasslands located in a *Quercus rotundifolia* dehesa. The interannual dynamics of species richness are also analysed. From 1980 to 1993, presence/absence data of grassland species were noted in five 20 cm × 20 cm permanent quadrats placed at random in 1980 in 14 permanent plots on a south-facing slope along the topographic gradient. Weekly autumn rainfall data over the 14 years were analysed using a profile attributes index and Hybrid Multidimensional Scaling to arrange the years according to their autumn rainfall pattern. Generalized Linear Models were used to fit the species richness and species frequency according to topographic position, age since the last ploughing episode, total rainfall in the growing season and autumn rainfall pattern using a forward stepwise procedure. The richness model includes all of these variables, and reveals a relatively high goodness-of-fit (71%). The fact that the meteorological factors play a key role in modelling richness forces us to include them if we wish to use richness as an indicator of the degree of disturbance in these highly fluctuating annual pastures. Models of species dynamics show that although roughly 33 % of the species have a successional behaviour, the majority are more dependent on temporal heterogeneity associated with rainfall or spatial heterogeneity linked to the topographic gradient.

Keywords: Autumn rainfall distribution; Generalized Linear Models; Post-ploughing succession; Topography.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Dehesas and Montados on the Iberian peninsula are agro-sylvo-pastoral systems composed of cleared oak woodlands with an annual grassland understorey. They are very well adapted to the shallow acidic soils and seasonal droughts of the Mediterranean climate. These systems are ecologically remarkable, especially due to their maintenance of a high biological diversity and their cultural heritage (Marañon 1988).

The grasslands feature a high species richness: 130 species/0.1 ha (Marañon 1985) and 30 species/400 cm^2 (Pineda et al. 1981), probably as a result of their high level of spatial and temporal heterogeneity, grazing practice and human action involved in their maintenance, including brush cutting, sylviculture, stock shifting (local or long-distance transhumance or droving) and livestock management at farms.

Two of the most important aspects that structure these grasslands are slope-valley systems and trees, both of which influence water and nutrient availability and thus have a bearing on their floristic richness (Peco et al. 1983a; Marañon 1986**)**. Grazing is another important feature in these systems, traditionally subjected to rough grazing by livestock (cattle and sheep) and wild herbivores (rabbits, deer, bucks). Their effects on floristic composition have been described in terms of both defoliation (Noy-Meir et al. 1989; Montalvo et al. 1991) and as seed consumers and/or dispersers (Malo & Suárez 1995a, b; Ortega et al. 1997). Finally, another key element that should be mentioned is regular ploughing, done traditionally to prevent invasion by shrubs, which causes a continuous rejuvenation of the grasslands and a mosaic of plots with different successional ages. Analysis of their successional dynamics has revealed an increase in species richness of these semi-natural grasslands as succession advances under constant intermediate grazing pressure (Pineda et al. 1981; Peco et al. 1983b).

The value of species richness as an indicator of the degree of disturbance (e.g. ploughing, fertilization, cessation of grazing) or recovery in semi-natural grasslands has been under debate recently (see van Andel, this issue). Parameters that typify the community, such as its species richness or floristic composition, are not only influenced by the degree of disturbance the communities have been subjected to, but also by less predictable environmental factors such as fluctuations in meteorological conditions. We must therefore ascertain how these types of fluctuations affect the above parameters in order to determine the extent to which they might be suitable indicators of the state of recovery of these ecosystems.

Rainfall fluctuations are common in mediterranean-type climates, (Noy Meir 1973). Extreme fluctuations in environmental conditions have been cited as one of the possible causes of the high diversity in annual pastures as they permit the coexistence of numerous species with differing requirements (Grubb 1977; Namba 1984; Shmida & Ellner 1984; Rice & Menke 1985; Ellner 1987). Some authors have even found competitive reversals linked to these fluctuations (Rabotnov 1974; Armstrong & McGehee 1980; Rice & Menke 1985).

The adult individuals of these annual species die in spring or summer, while the grassland regenerates every autumn from the seed banks. This leads to hypotheses about the importance of meteorological factors, especially at the point of regeneration, for the floristic composition of these grasslands (Heady 1958; Murphy 1970; Austin et al. 1981; van der Maarel 1981). The seed banks of these communities (Ortega et al. 1997) feature a high proportion of transient seeds, although a large percentage of species have a persistent (20%) or mixed bank (25%, transient with a fraction of the persistent seeds).

We began our analysis of the dynamics of these grasslands in 1980 on permanent plots established along the topographic gradient on slopes with similar lithology, orientation and slope, but different successional ages since the last ploughing episode. The analysis of the frequency of each species on the slopes revealed a successional trend that is masked by a fluctuation linked to the total rainfall. While wet years produce a change in the floristic composition in the same direction as succession, dry years produce a reversal (Peco et al. 1983a, b).

Peco (1989), monitoring the trajectories in the ordination of the permanent plots to describe vegetation dynamics (Austin 1977; van der Maarel & Werger 1978; Austin et al. 1981; Cramer & Hytteborn 1987), produced the first approach to a model for the dynamics of this type of pasture using data from eight consecutive sampling years and five different slopes. The proposed model included the age of the plot since the last ploughing episode, total annual rainfall and November rainfall as explanatory variables**.** These variables reflected the post-ploughing successional trend in the floristic composition and structure of the communities, as well as the fluctuations in these dynamics enforced by water availability during the growing season and particularly in the germination and seedling establishment periods.

The objective of this paper is, after 14 years of sampling, to estimate the influence of successional, topographic and climatic factors (total annual rainfall and autumn rainfall pattern) on species richness and modelling the dynamics of individual species, impossible to tackle previously because of a lack of a sufficiently long-term data set. We also propose to ascertain the interannual behaviour of the richness and its potential for modelling and prediction with a view to its use as an indicator of the degree of ecological recovery of these systems.

Material and Methods

Study area

The study area is an undulating *Quercus rotundifolia* dehesa 15 km north of Madrid (Spain) on a sandy substratum derived from the tertiary erosion of the Guadarrama massif. The area is ploughed regularly to prevent invasion by shrubs (e.g. *Cistus ladanifer, Santolina rosmarinifolia*), giving rise to a grassland dominated by therophytes. The mean annual rainfall is ca. 450 mm with large interannual fluctuations in both total rainfall and its distribution over the year (Peco 1989). The rainfall distribution is typically Mediterranean, with 3 or 4 months of dry summer after which most of the grassland species germinate (Ortega et al. 1997).

Sampling and data analysis

In 1980, a south-facing 15% slope ploughed 5 yr before was used to establish 14 permanent plots, 2m×4m, along the topographic gradient from the high slope zones where erosion predominates to the low zones where the accumulation of water and matter predominates (Peco et al. 1983a). The frequency of pasture species was recorded in spring over 14 consecutive years (1980-1993) using presence/absence data in five 20 cm × 20 cm permanent quadrats, placed at random in 1980 within each plot. 118 species were noted over the period.

The plots were classified into three topographic sectors: upper slope zones (four plots), intermediate zones (six plots) and lower zones (four plots). The average frequency of each species in each of them was calculated for the 14 consecutive years. Richness was also calculated for these topographic sectors, in this case using the data from four plots for each sector. In the case of the intermediate sector (six plots), the data from the first and last plots were deleted.

The climatic analysis focused on total annual precipitation and autumn rainfall pattern, presumably linked to the floristic composition. We analysed the weekly rainfall data from the autumn prior to the vegetation sampling of each year using a profile attributes index (Faith et al. 1985). These attributes had individual classes that were explicitly arranged along some dimension (e.g. rainfall records). Hybrid Multidimensional Scaling (Faith et al. 1987) of this similarity matrix enabled us to ordinate the different years according to their autumn rainfall distribution. The computer software package PATN (Belbin 1987) was used to perform the analysis.

Generalized Linear Models (GLM, McCullagh & Nelder 1989) were used in the modelling process to express species richness and species dynamics as a function of succession, topography and rainfall. These models are structurally similar to the classic regression models but are free of the constraint of assuming a normal error distribution, and allow a greater range of relationships between the response and the explanatory variables, as well as the use of continuous and categoric variables. Such models have been suggested for the analysis of species response in relation to environmental factors (Austin & Cunningham 1981; Austin et al. 1984; 1990) and richness (Margules et al. 1987). Annual species richness and average frequency in these sectors for each species and each year were also used as response variables. The explanatory variables were years since last ploughing (from 5 to 18), coordinate on axis 1 of the Hybrid Multidimensional Scaling, performed with autumn rainfall data, total growing season rainfall (from September to the sampling date in spring) and slope zone used as a factor variable with three classes.

To model the species dynamics we assumed normal error distribution, while for species richness we assumed a Poisson error distribution (Vincent & Harworth 1983; Nicholls 1991). We applied an F-test on the change in deviation to the former model, while in the latter this change was assumed to be χ^2 distributed (McCullagh & Nelder 1989). The models were fitted using a forward stepwise selection procedure (Draper & Smith 1966).

Results

Rainfall patterns

The Hybrid Multidimensional Scaling of the weekly autumn rainfall data enabled us to ordinate the years along a goodness-of-fit gradient in the autumn rainfall distribution (Fig. 1, axis 1): from years with low autumn rainfall or late rains (negative end of the axis), years with early rains and clear drought periods afterwards, to years with early rains in which the precipitation had a more uniform distribution through the autumn (positive end). The coordinate value for the sampling years on axis 1 was used afterwards as a response variable to express autumn rainfall distribution.

Total autumn and growing season rainfall fluctuated considerably around the mean (129.6 and 336.5 respectively) over the 14 sampling years (Fig. 1).

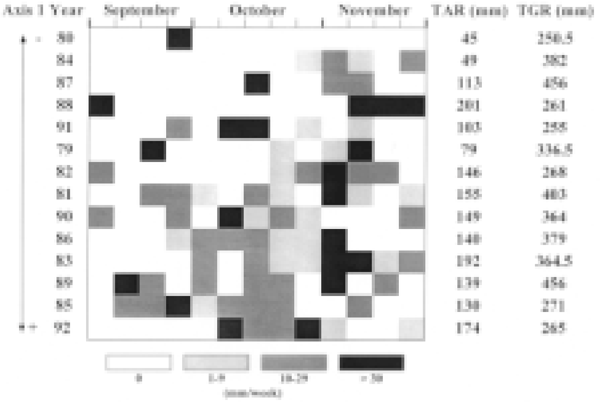

Fig. 1. Weekly distribution of rainfall during the autumn prior to each sampling campaign. Years are ordinated on the basis of axis 1 of Hybrid Multidimensional Scaling. TAR: total autumn rainfall of each year. TGR: total rainfall of the growing season (from the autumn to the spring sampling date).

Richness model

The richness data were assumed to be drawn from a Poisson distribution and the most appropriate link function for such a distribution is the natural logarithm. The forward stepwise fitting procedure is summarised in Table 1. Firstly, the topographic sector, succession, autumn rainfall pattern (Hybrid Multidimensional Scaling) and total rainfall in the growing season were fitted individually. Secondly, the variable accounting for the greatest significant change in the deviation was selected. The remaining variables were then added individually to the model to test their possible effect on the response variable. The chosen model ($R^2 = 0.71$, $p < 0.005$) included the spatial heterogeneity (topographic sector), successional trend (years since last ploughing episode) and interannual fluctuations in water availability (total growing season rainfall and autumn rainfall distribution). Richness has a positive relationship with years since last ploughing, total growing season rainfall and autumn rainfall distribution (positive end of Axis 1), and it is higher in the lower slope zones (Fig. 2).

Modelling species dynamics

By using a similar procedure and the same explanatory variables we modelled species abundances. In this case, a normal error distribution was assumed. We only used the data for the 62 species that were found in more than five sampling campaigns. The 56 remaining species were not modelled because their low frequency might have caused errors in the estimation of their abundance in the respective years.

The models chosen for each species are shown in

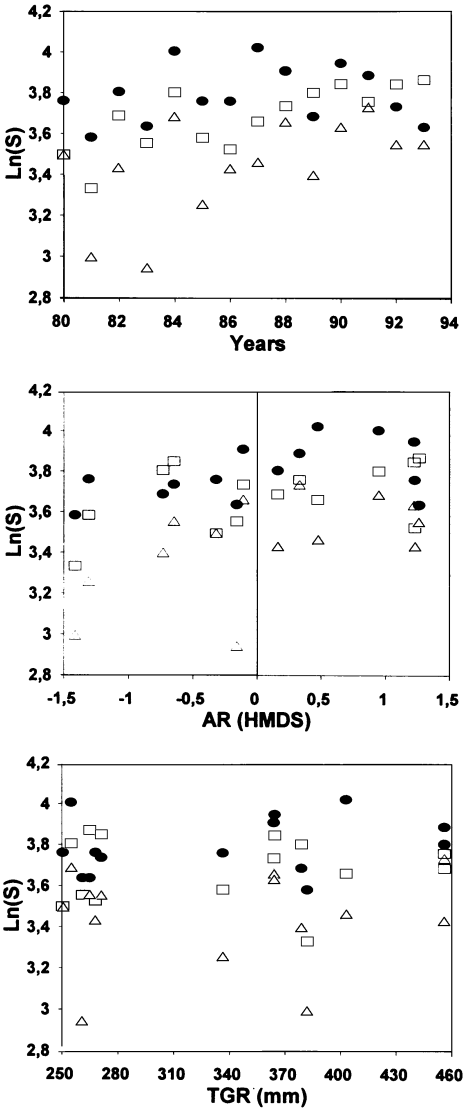

Fig. 2. Relationship between richness and three explanatory variables of the model. Years since last ploughing: variable used to measure succession, AR: axis 1 coordinate of the HMS performed with autumn rainfall data, TGR: total rainfall during the growing season. Data have been split according to topographic position: Filled circles: lower; empty squares: intermediate, and empty triangles: upper zones.

Table 1. Forward stepwise selection procedure used to model species richness. S: years since last ploughing episode, T: topographic position (upper, intermediate or lower slope zones), AR: autumn rainfall pattern (HMS axis I of weekly autumn rainfall data) and TGR: total rainfall in growing season from September of the previous year to the sampling date in spring. Arrow shows model chosen in each step. Each model is tested (χ^2 test) in relation to previously selected model. *** (p <0.005), ** (p <0.01), * (p <0.05).

Model	Deviance	d.f.	ΔD	Δd.f.	*P*
Null	75.338	41			
→ T	45.001	39	30.337	2	***
S	65.106	40	10.232	1	***
AR	64.779	40	10.559	1	***
TGR	64.923	40	10.415	1	***
T + S	34.769	38	10.232	1	***
→ T + AR	34.442	38	10.559	1	***
T + TGR	34.593	38	10.408	1	***
T + AR + S	29.618	37	4.824	1	*
→ T + AR + TGR	27.983	37	6.459	1	*
→ T + AR + TGR + S	21.819	36	6.164	1	*

Table 2. Species are classified into three categories on the basis of the explanatory variables used in the models. Successional species are those modelled on the basis of years since last ploughing and topographic position, with the exception of *Bromus tectorum* and *Lophochloa cristata* which were modelled only with the successional component. Fluctuating species are those which need the inclusion of the rainfall-related variables in the model. The species *Trifolium glomeratum*, *Vulpia membranacea*, *V. muralis*, *V. myuros* and *V. unilateralis* could only be modelled with these variables. Spatially-dependent species are those modelled only on the basis of the topographic variable (*Capsella bursa-pastoris*, *Carduus pycnocephalus*, *Crepis capillaris*, *Filago pyramidata*, *Geranium rotundifolium*, *Holcus setiglumis*, *Hypochoeris glabra*, *Myosotis ramosissima*, *Trifolium campestre* and *Vicia lathyroides*). The order in which each factor was included in the regression, also expressed in Table 2, provides an idea of their relative importance on an ordinal scale. Fig. 3 illustrates the frequency distribution pattern of some representative species from each group in the 14 samples.

Discussion

Modelling richness

The richness of Mediterranean annual grasslands can be modelled with a relatively high goodness-of-fit (71%) using information related to the spatial heterogeneity (topographic sector), the interannual fluctuations in water availability (both total rainfall during the growing season and its distribution during autumn, when most germinations and seedling establishments occur) and the successional trend (years since last ploughing).

The influence of spatial heterogeneity is manifested in an increase in richness in the low parts of the topographic gradient (a higher availability of water and nutrients). This seems to contradict the widely accepted model that species richness is a unimodal function of productivity, in the sense that the most productive habi-

Table 2. Factors or variables included in models of species chosen after a stepwise selection process. Order of inclusion in the model is also indicated (1, 2, 3): S: years since last ploughing episode, T: topographic position (upper, intermediate or lower slope zones), AR: autumn rainfall pattern and TGR: total rainfall in the growing season from September of the previous year to the sampling date in spring. The table indicates the value of R^2 (goodness-of-fit of the model to the data), the *F* value with respect to the corresponding null hypothesis, and the level of significance of each model: *** (p <0.001), ** (p <0.01), * (p <0.05).

Successional species	S	T	AR	TGR	R^2	F	*P*
Anthriscus caucalis	2	1			0.38	7.67	***
Asterolinon linum-stellatum	1	2			0.38	7.87	***
Biserrula pelecinus	2	1			0.67	25.82	***
Brassica barrelieri	2	1			0.61	20.29	***
Bromus hordeaceus	2	1			0.65	23.85	***
Bromus tectorum	1				0.43	30.30	***
Centaurea melitensis	2	1			0.57	16.63	***
Cerastium semidecandrum	2	1			0.62	20.57	***
Corynephorus fasciculatus	2	1			0.37	7.62	***
Evax carpetana	2	1			0.34	6.56	**
Galium parisiense	2	1			0.42	9.30	***
Geranium molle	2	1			0.41	8.99	***
Hordeum murinum ssp. *leporinum*	2	1			0.44	10.09	***
Lophochloa cristata	1				0.16	7.54	**
Neatostema apulum	1	2			0.31	5.73	**
Polycarpon tetraphyllum	2	1			0.58	17.22	***
Pterocephalus diandrus	2	1			0.31	5.68	**
Rumex acetosella	2	1			0.51	13.46	***
Scandix australis	1	2			0.45	10.53	***
Scolymus hispanicus	1	2			0.30	5.50	**
Taeniatherum caput-medusae	1	2			0.83	61.54	***
Trifolium striatum	2	1			0.27	4.72	**
Trifolium tomentosum	2	1			0.35	6.95	***
Fluctuating species							
Aphanes microcarpa	2		1		0.42	14.01	***
Andryala integrifolia		2	3	1	0.52	9.96	***
Arenaria leptoclados	2	1		3	0.70	21.65	***
Asteriscus aquaticus	1	2	3		0.51	9.53	***
Bromus madritensis		1	2		0.27	4.62	**
Crassula tillaea	2	1		3	0.33	4.55	**
Echium vulgare	1		2		0.27	7.33	**
Erodium cicutarium	1	2	3		0.46	7.81	***
Fluctuating species (cont.)	S	T	AR	TGR	R^2	F	*P*
Herniaria hirsuta	1	2	3		0.56	11.84	***
Lathyrus angulatus		1	2		0’36	7.04	***
Leontodon taraxacoides	3	1	2		0.43	7.02	***
Logfia minima		1		2	0.67	25.57	***
Medicago minima		1		2	0.49	12.04	***
Ranunculus parviflorus		1		2	0.52	13.51	***
Sagina apetala	2		3	1	0.45	35.01	***
Spergularia purpurea		2	1		0.53	14.18	***
Trifolium arvense	3	1		2	0.72	23.47	***
Trifolium cernuum		1		2	0.35	6.96	***
Trifolium glomeratum				1	0.14	6.63	*
Trifolium suffocatum	2	1	3		0.57	12.53	***
Tuberaria guttata	3	1		2	0.72	24.05	***
Veronica arvensis	3	1		2	0.66	17.94	***
Viola kitaibeliana		1		2	0.57	16.90	***
Vulpia ciliata		1		2	0.32	6.01	**
Vulpia membranacea			2	1	0.21	5.18	**
Vulpia muralis				1	0.13	5.96	*
Vulpia myuros			1		0.21	10.40	**
Vulpia unilateralis			1		0.21	10.92	**
Spatially dependent species							
Capsella bursa-pastoris		1			0.29	7.99	**
Crepis capillaris		1			0.26	6.97	**
Filago pyramidata		1			0.27	7.32	**
Geranium rotundifolium		1			0.37	11.33	***
Holcus setiglumis		1			0.28	7.69	**
Hypochoeris glabra		1			0.27	7.22	**
Myosotis ramosissima		1			0.26	6.91	**
Tolpis barbata		1			0.25	6.47	**
Trifolium campestre		1			0.17	4.09	*
Vicia lathyroides		1			0.26	7.05	**
Carduus pycnocephalus		1			0.69	44.27	***

tats should have a decline in richness due to the competitive displacement by the most dominant species (Tilman & Pacala 1993). This contradiction is only apparent, however, given that these extremely poor sandy soils only permit lower production rates than those described in these models: the productivity peaks in these grasslands are never more than 300 g/m^2 (Casado et al. 1985).

The effect of meteorological fluctuations depends on the total rainfall during the growing season (the more water available, the greater the species richness), and the goodness of the autumn rain distribution (the less drought periods between rain episodes, the greater the richness). The effect of total rainfall during the growing season on richness in Mediterranean annual pastures has also been confirmed by other phenomenological studies (Peco et al. 1983b; Figueroa & Davy 1991), on the basis of field observations linked to rainfall data. Its effect on the community's floristic composition has also been confirmed for grasslands with many annual species although not specifically for richness. Many authors (Talbot et al. 1939; Watt 1947; Bentley & Talbot 1948; Heady 1956, 1958, 1961; Rossiter 1966; Austin et al. 1981 and Peco 1989) used a phenomenological approach and van der Maarel (1981) an experimental one. Some of these authors also provide evidence or hypotheses about the effect of the timing of autumn rains on species composition. In the present case, the data confirm a positive relationship between the goodness of autumn rainfall distribution and richness. The fact that highly unpredictable environment factors such as meteorological fluctuations play such an important role in the modelling of these communities' richness forces us to include them if we wish to use richness as an indicator of the degree of disturbance in these systems.

The positive relationship between the richness of these grasslands and their age since the last ploughing is confirmed once more (Pineda et al. 1981). This trend is restricted by the fact that these grasslands are rough-grazed, and if grazing stops, the trend should be reversed (Montalvo et al. 1991).

The inclusion of all these factors in a model to predict richness thus makes it a more powerful tool for evaluating the post-ploughing recovery of these systems where spa-

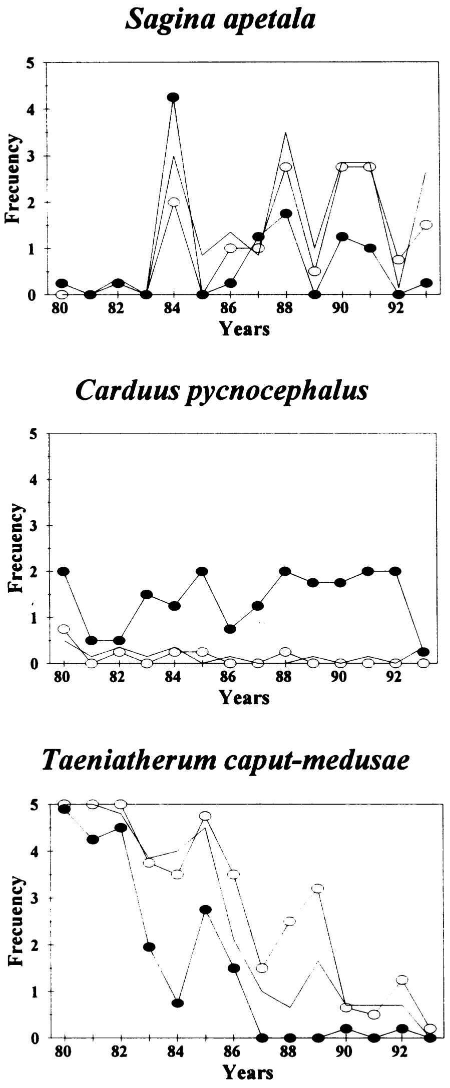

Fig. 3. Frequency distribution pattern of representative species of each group. *Sagina apetala* (fluctuating species), *Carduus pycnocephalus* (spatially-dependent species), *Taeniatherum caput-medusae* (successional species). Annual frequency in each topographic position is represented. Filled circles: lower zones, no symbol: intermediate zones, empty circles: upper zones.

tial and temporal heterogeneity influences the vegetation dynamics. It should also be noted that this modelling was possible in spite of the large number of rare species (47%), whose role in these systems is yet to be established clearly. We may assume that they are species with persistent or semi-persistent seed banks that enable them to remain in the system for most of the time, in spite of their rarity, thanks to the 'good years' when they can generate a new seed input. In fact, seed bank data available for 20 of such species reveals the existence of persistent or semi-persistent seed banks (Ortega et al. 1997). One exception is *Heliotropium europaeum*, which has a transient winter seed bank. Its rarity might be due to the spring sampling date, when in fact this is a C4 species with a peak abundance in summer. It should be borne in mind, however, that the information available to date on persistence in the bank by species from these communities only covers 44 species (37% of those found in this study), which seriously restricts our conclusions in this respect.

Modelling species dynamics

Modelling the dynamics of the most abundant species has highlighted the differences between species in the relative importance of the explanatory variables used in each case.

34% of the species show a successional type of dynamic behaviour, i.e., their interannual abundance can be explained by the time elapsed since the last ploughing episode. Some species, for instance *Bromus tectorum* depend exclusively on this time variable. Mack & Pyke (1983) mention possible reasons why this species is less sensitive to meteorological fluctuations: its successive rounds of germination from autumn until spring, regardless of the rainfall. The rest of the species in this group also require the topographic factor, which seems to back the hypothesis that spatial heterogeneity might mediate in the interannual dynamics (Grubb 1987; Palmer 1994). The interannual dynamics of many species (17%) can in fact be explained solely in terms of the topographic position. Such species are probably ones that use spatial refuges to get through the unfavourable years. This strategy can be an alternative mechanism to dispersal in time –via a persistent seed bank- to avoid extinction (see Ehrlén & van Groenendael, this issue). In our system, competition for light is likely to be unimportant because of the low productivity (300g m^{-2}/ yr^{-1}), but water availability during the autumn has been identified as a limiting factor, being the cause of different seedling mortality among species (Espigares & Peco 1995).

Another large group consists of fluctuating species (45%) which require meteorological aspects to be modelled. Some time ago several authors pointed out the relationship between certain species, the amount of total rainfall and its autumn distribution. Talbot & Biswell (1942) distinguished between 'clover years' associated with late autumn rains, and 'filaree years', associated with early autumn rains. Beatley (1969) linked the germination and survival of annual species in the Nevada desert, the amount of annual rainfall and the timing of arrival of the autumn rains. This dependence was also detected in many species in Öland (Sweden) limestone grasslands (Rusch & van der Maarel 1992). Moreover, Figueroa & Davy's (1991) analysis of the frequency of 99 therophyte species in dehesas of SW Spain through

11 sampling campaigns found a 28 % correlation of species with annual rainfall but only a few with autumn rain in particular, perhaps because they only used the total accumulated precipitation without taking its distribution into account, which we found to have a manifest importance.

Permanent plot data can also be used to corroborate predictions made in experimental studies (Bakker et al. 1996; Herben 1996). Rice & Menke (1985) found competitive reversals between two filaree species by manipulating the arrival time of autumn rains. Our results indicate that *Erodium cicutarium* can be modelled on the basis of the autumn rainfall pattern, confirming the experimental variation trend of this taxon.

The results in the present study also corroborate our previous experimental work on the timing of autumn rains and the effect of a prolonged post-germination drought:

(1) The fluctuating species *Aphanes microcarpa*, *Herniaria hirsuta* and *Sagina apetala* yielded significant differences in percentages of germination between simulated conditions of autumn drought and uniform rainfall distribution. More individuals of these species appear to germinate if there are no prolonged autumn drought periods. Also, *Aphanes microcarpa*, *Arenaria leptoclados*, *Sagina apetala*, *Spergularia purpurea*, *Trifolium arvense*, *T. glomeratum*, *T. suffocatum*, *Veronica arvensis*, *Vulpia ciliata*, *V. membranacea*, *V. muralis*, and *V. myuros*, have a higher mortality under autumn drought conditions (Espigares & Peco 1995).

(2) *Bromus madritensis*, *Crassula tillaea*, *Sagina apetala* and *Trifolium suffocatum*, again species with a fluctuating behaviour in this study, have significant differences in percentages of germination between treatments simulating different timings of the arrival of the first autumn rain (Espigares & Peco 1993).

Seedling mortality has also been analysed (Peco & Espigares 1994) in terms of density and emergence timing with respect to the timing of the first autumn rain. The potential competition between seedlings has a scarcely noticeable effect on the germination and survival of seedlings, although there is evidence that the seedlings that emerge first have a better chance of survival (Espigares & Peco, in prep.).

We therefore support the hypothesis that through their effect on seedling germination and survival, the autumn meteorological conditions, along with the fact that these species have both persistent and semi-persistent seed banks (Ortega et al. 1997), can facilitate alternations in the reproductive success of the species and their coexistence, thus partially explaining the high species richness in these grasslands.

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