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Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain

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Abstract

We analyse changes in plant cover and species richness along a 60-year chronosequence in semi-arid Mediterranean old-fields of southeastern Spain. The objectives were: (i) to study patterns of species richness along the abandonment gradient in semi-arid conditions (e.g., to test the "humped-back model" in our system); (ii) to test whether different broad life forms (annuals, forbs, grasses and woody species) showed different patterns along the abandonment gradient, and (iii) to examine to what extent plants with different dispersal strategies dominate at different stages of succession. The explained variance of the regression relating species richness to years since abandonment is improved when considering different life forms. The results suggest that cover and richness of different functional groups show a non-linear unimodal (often positive-skewed) pattern along the gradient (age since abandonment). Maximum total richness is found at young stages of abandonment ($<$ 20 years), when most life forms and dispersal strategies coexist. Annuals and perennial forbs reached their maximum richness during the first 10 years of abandonment. About 45% of total woody species richness is reached at this time as a consequence of early colonization of zoochorous shrubs. While the results showed a tendency towards a life-form replacement sequence, the pattern is not so clear when looking at the different dispersal strategies. The results complement previous results in Mediterranean conditions and emphasise the importance of considering different functional types when studying successional patterns.

Introduction

Mediterranean landscapes of Europe are suffering from the rural exodus caused by the socioeconomic changes of the last decades. These changes in traditional land-uses and lifestyles have resulted in the abandonment of large areas of farm-land (Lepart and Debussche 1992; Lasanta and García-Ruiz 1996). The resulting build-up of early successional vegetation has strong implications on water balances (Bellot et al. 2001) and fire regimes (Rego 1992; Pausas and Vallejo 1999; Pausas in press).

Secondary succession in Mediterranean ecosystems has been studied extensively in mesic conditions (Houssard et al. 1980; Escarré et al. 1983; Peco et al. 1991; Lavorel et al. 1994; Tatoni and Roche 1994; Tatoni et al. 1994; Montalvo et al. 1995; Debussche et al. 1996; Ne'eman and Izhaki 1996; Bonet 1997), but few studies have been made in semi-arid environments (e.g., Noy-Meir 1973; Martínez-Fernández 1995; Margaris et al. 1996; Bonet et al. 2001; Bonet, 2004). In dry environmental conditions, vegetation cover tends to be low and sparse (Schlesinger et al. 1990), and interspecific interactions such as competition or facilitation may be different from those in more mesic Mediterranean conditions (e.g., Pugnaire and Luque 2001; Maestre et al. 2003). Under arid conditions, two vegetation parameters are particularly relevant: plant cover (as a factor for soil protection and for enhancing ecosystem processes) and richness (a measure of biodiversity). In the present work, we attempt to study these two parameters during a 60-year chronosequence in semi-arid old-fields of the southeastern Iberian Peninsula.

During the early stages of succession, the gradual colonisation and increase in spatial heterogeneity should lead to an increase in species richness. Subsequently, species richness may drop as a result of competitive interactions (Bazzaz 1975; Huston 1979; Tilman 1982; Peet and Christensen 1988). Thus, the so-called "humped-back model" (unimodal response curve) of species richness proposed for nutrient and productive gradients (Grime 1973; Wheeler and Giller 1982; Tilman 1982; Wisheu and Keddy 1989; see the review by Pausas and Austin 2001) and disturbance frequency gradients (Connell 1978; Lubchenco 1978; Huston 1979; Wilson and Keddy 1988) could also be applied to the time since abandonment (e.g., Peet 1978), although the underlying factors may be different in each of these cases.

However, some successional studies in Mediterranean climates have found a decreasing (Debussche et al. 1996) or fluctuating pattern (Houssard et al. 1980) of species richness after abandonment, and Noy-Meir (1973) found little changes in diversity through time in arid conditions. Furthermore, several studies suggested that after perturbation, the pattern of richness should be different in different environmental conditions (Auclair and Goff 1971; Peet 1978; Huston 1994). These researchers suggested that under mesic conditions species richness will show a peak at early stages of succession, while on sites under stressful conditions (e.g., xeric sites) a steady increase in diversity is expected.

Because species of the same functional type share many characteristics, competitive interactions among species of the same functional types may be stronger than between species of different functional types, and so, patterns of species richness along gradients may be more interpretable by considering the species richness of the different functional types (Peet 1978; Pausas 1994; Pausas and Austin 2001). In this work we consider two functional classifications of species, one based on life form and the other on dispersal strategy. Life forms are well-known broad functional types related to longevity and resource acquisition (e.g., Wright 1992; Lavorel et al. 1997). If succession from abandonment is determined by the ability of plant arrival (colonisation capacity; van der Valk 1992; Willson 1993), then, plants with different dispersal strategies should have differential dominance along succession (i.e., the 'relay floristics' model; Egler 1954; Myster 1993). The dispersal mechanism adopted by species is a key trait influencing the structure of communities (Brown 1992).

Our aims were: 1) to analyse the changes in plant cover and species richness along a land abandonment gradient in a semi-arid ecosystem; 2) to test whether different broad life forms (annuals, forbs, grasses and woody species) showed different patterns along the temporal gradient; 3) to test to what extent plants with different dispersal strategies dominate at different stages of land abandonment.

To answer these questions, we used the time since abandonment as an indicator of the successional gradient. For practical reasons, many of the Mediterranean secondary succession studies in old-fields have used a chronosequence approach instead of diachronic studies (Escarré et al. 1983; Tatoni and Roche 1994; Bonet 1997). Despite the existence of several methodological problems using chronosequencing (Lepart and Escarré 1983; Glenn-Lewin and van der Maarel 1992), most of the predictions made with some of these synchronic studies or space-for-time substitutions (*sensu* Pickett 1989) have been validated by revisiting and re-sampling the studied communities (Debussche et al. 1996; Foster and Tilman 2000).

Methods

Study area

The study was conducted at the Ventós-Agost Catchment Experimental Station (University of Alacant), in the Municipality of Agost, Alacant Province, SE Spain (38° 28'N, 0° 37'W, 10-840 m a.s.l.). The catchment area (approx. 1537 ha) is characterised by a semi-arid Mediterranean climate, with a very high interannual variability. Mean annual temperature is 18.2 ºC and annual rainfall is 302.1 mm, most of which falls in autumn (Agost Meteorological Station, 1961-1990 period). Soils have developed over marls and calcareous bedrock, and slopes vary between 25-30%, and are mainly south-facing. Other soil characteristics are summarised in Bellot et al. (1999).

The present vegetation mosaic of the overall area is dominated by *Stipa tenacissima* L. steppes, resulting from the disturbance of shrublands (Rivas-Martínez 1987), but probably also resulting from abandoned *Stipa* plantations in non-arable lands (Barber et al. 1997). Other important communities are dry grassland formations of *Brachypodium retusum* Pers. Beauv. with dwarf scrubs, and scattered shrublands with *Quercus coccifera* L.

The lower part of the catchment is occupied by traditional agriculture terraces currently abandoned and surrounded by steppes and the described vegetation mosaic. Field abandonment ranged from 1 to 60 years following the last cultivation, but the main land abandonment process was experienced during the period 1946-1956 (Bonet et al. 2001). Abandoned fields on terraces were mainly composed of tree crops, such as almond (*Prunus dulcis* (Miller) D.A. Webb), olive (*Olea europaea* L.) and carob trees (*Ceratonia siliqua* L.). Traditional agricultural practices such as tilling and irrigation regimes were quite homogeneous for all these tree crop stands before abandonment, but there were also some scattered cereals and horticulture abandoned crops in the area. The great species composition variability associated with different management and land uses of the fields (Bonet, in press) justifies the use of life forms rather than species in the trend analysis along the analysed gradient.

Sampling

Vegetation was sampled through a chronosequence of old-fields. During spring 1999 and 2000, we sampled 96 plots of abandoned croplands on field terraces. The abandonment is defined here as the cessation of ploughing and sowing, but other uses and activities such as grazing could still be present in the fields (Bonet, 2004).

We first estimated the period of abandonment by using a sequence of aerial photographs (1946, 1956, 1974, 1980, and 1995). Then we consulted the Agost Municipal Archives and held personal interviews with landowners and managers in order to determine the age of abandonment more precisely.

On each old-field terrace, a 10 × 10 m (100 m^2) plot was delineated avoiding edges and field margins (i.e., with at least a 2 m-wide buffer zone). For the whole 10 × 10 m-plot a complete species list was recorded and total species richness was calculated. In each of these plots, 20 quadrats of 1 × 1 m were marked off in a systematic sampling procedure along four transects (5 quadrats per transect). Each transect was separated from its neighbour by 2 m, and the distance between quadrats in each transect was 1 m. The species cover (%) was visually estimated in each quadrat and then an average cover was calculated for all the quadrats in a plot (total sampled area was 20 m^2).

Data analysis

Species were grouped by life forms (annuals or biennials, perennial forbs, perennial grasses and woody species) and by their main dispersal strategy (anemochory, barochory, ectozoochory, endozoochory, and mirmecochory) (see Appendix). The main dispersal mode of each species was based on field observations and following Molinier and Müller (1938), van der Pijl (1972) and Bonet (1997); secondary dispersal strategies were not considered in this study. Cover and richness were computed for all species as well as for each life form and each dispersal mode. Cover was calculated on each old-field from the sampled quadrats, and richness was determined by the number of species in the whole 10 m × 10 m plot.

Cover and richness patterns (total, for the different life forms and for the different dispersal strategies) were related to years since abandonment by least square regressions using SPSS (v. 11.0) statistical software. Three different types of regression equations were tested (Linear, Gaussian and Lognormal) and the most significant was chosen. In most cases the most significant was the non-linear lognormal regression because it allowed us to detect skewed unimodal patterns (Draper and Smith 1981; Scales 1985; Sokal and Rohlf 1995). The goodness of fit was evaluated using the F-test. Parameters were tested by a t-test and their standard errors were used as a gauge of the accuracy of the fitted curve. We also searched for parameter dependencies in order to avoid over-parameterisation of the regression equations.

Results

A total of 222 species were recorded in the whole study area (see Appendix). Total plant cover ranged from 45.5 to 100% (Table 1), and this variation was not related to age since abandonment ($p = 0.4189$ for the lognormal model). Some recently abandoned plots had close to 100% cover. Species richness per plot (100 m^2) ranged from 4 to 34, and there was a sig-

Table 1. Summary of cover (%) and species richness (per 100 m^2) in all old-fields for the different life forms and dispersal types considered.

	Cover (%)				Species richness			
	mean	sd	min	max	Mean	sd	min	max
Life form								
Annuals	22.18	29.64	0.00	100	4.40	4.33	0	17
Grasses	27.54	22.58	0.00	75.76	2.43	1.65	0	8
Forbs	23.46	20.88	0.00	82.61	6.33	3.31	0	16
Woodies	26.45	25.73	0.00	93.68	6.97	5.54	0	21
Dispersal								
Anemochorous	45.40	21.03	1.00	93.10	7.86	3.56	1	18
Mirmecochorous	1.35	3.88	0.00	22.50	0.40	0.59	0	2
Barochorous	37.35	22.80	3.75	90.20	9.13	4.20	2	19
Ectozoochorous	11.92	16.80	0.00	61.11	1.94	1.62	0	6
Endozoochorous	53.58	8.67	0.00	59.20	0.80	0.99	0	4
Total	96.90	9.72	45.50	100	19.76	6.41	4	34

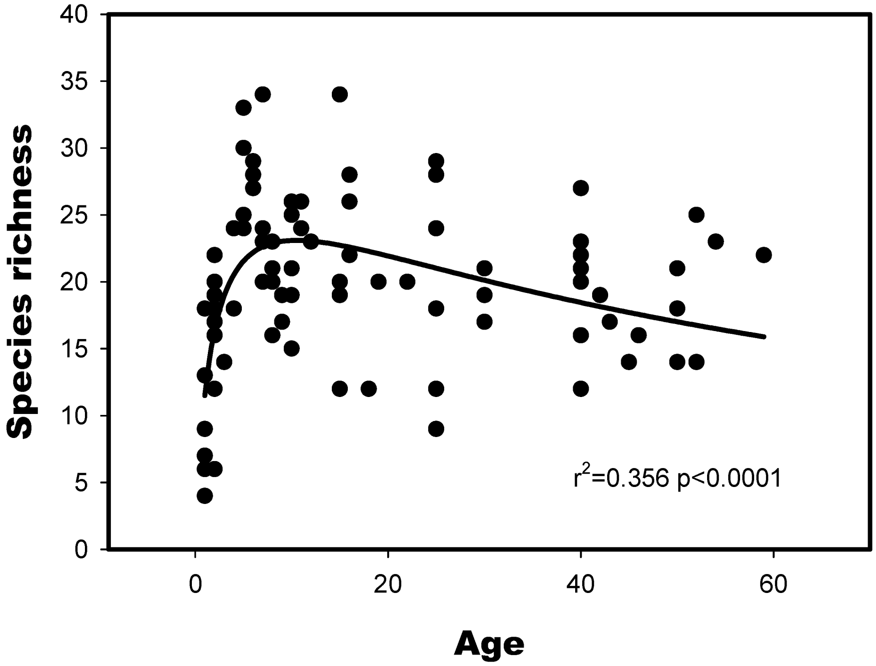

Figure 1. Total species richness (on 100 m^2-plots) along the successional gradient. Fitted line is the significant non-linear regression (see Table 2 for more details).

nificant non-linear relationship with age ($R^2 = 0.36$, $p < 0.0001$; Figure 1).

Life forms

Of the 222 species, the most represented life form was annual species (36%). Forbs and woody species were 29 and 27% respectively, and grasses were represented by 8% of the species. At plot scale (i.e., 10 × 10 m), woody species were the most abundant species (mean woody species richness = 7 / 100 m^2), followed by forbs (6.3), annuals (4.4) and then grasses (1.7) (Table 1). Mean cover of the different life forms ranged from 22% (annuals) to 26% (woody species). However, both species richness and cover showed great variation (Table 1), which can be explained by plot age (time since abandonment; Figure 1, Figure 2, Figure 3; Table 2).

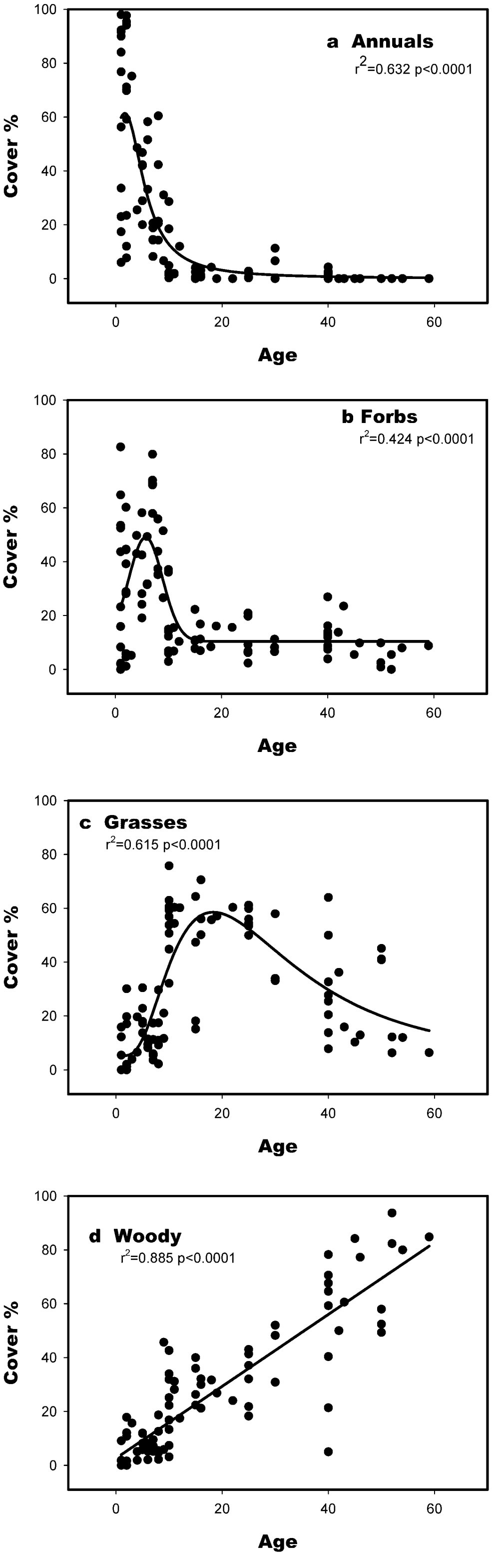

Figure 2. Plant cover (%) of different life forms along successional gradient. Fitted lines are the significant non-linear and linear regressions (see Table 2 for more details).

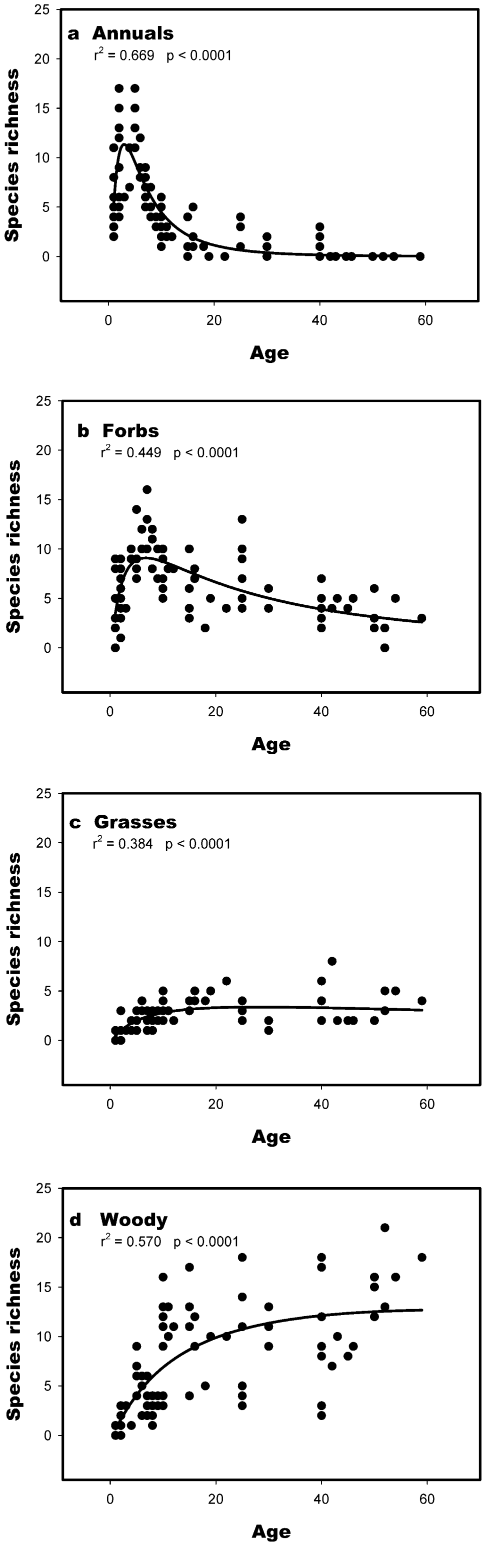

Figure 3. Species richness (on 100 m^2-plots) of different life forms along successional gradient. Fitted lines are the significant non-linear regressions (see Table 2 for more details).

Table 2. Summary of the lognormal regression equations developed for richness and for cover in relation to time since abandonment for all species (total) and for the different life forms and dispersal strategies (see Figure 1 to 5). a, b, x_0 and y_0 are the regression parameters of the equation $y = a \exp[-0.5 (\ln(x/x_0)/b)^2] + y_0$. Cover of woody plants linear regression is $y = y_0 + a x$. Only significant regressions are included (parameter mean ± standard error).

	a	X_0	b	Y_0	R^2	p
Life forms						
Cover						
Annuals	64.93 ± 4.51	1.55 ± 0.25	1.06 ± 0.14	–	0.632	< 0.0001
Forbs	38.66 ± 4.96	5.71 ± 0.37	3.17 ± 0.44	10.40 ± 2.54	0.424	< 0.0001
Grasses	53.31 ± 4.42	18.32 ± 0.75	0.63 ± 0.05	5.22 ± 0.90	0.615	< 0.0001
Woodies	1.34 ± 0.07	–	–	2.59 ± 1.73	0.885	< 0.0001
Richness						
Total	23.10 ± 0.8	10.52 ± 1.17	1.99 ± 0.17	–	0.356	< 0.0001
Annuals	11.34 ± 0.73	2.97 ± 0.16	0.89 ± 0.06	–	0.669	< 0.0001
Forbs	9.10 ± 0.42	6.74 ± 0.58	1.37 ± 0.09	–	0.448	< 0.0001
Grasses	3.38 ± 0.20	28.12 ± 8.40	1.68 ± 0.31	–	0.384	< 0.0001
Woodies	12.72 ± 1.60	68.65 ± 46.7	1.74 ± 0.44	–	0.571	< 0.0001
Dispersal mode						
Cover						
Anemochory	55.29 ± 2.94	10.38 ± 1.57	1.84 ± 0.22	–	0.203	< 0.0001
Ectozoochory	26.83 ± 3.31	1.20 ± 0.27	2.26 ± 0.53	–	0.320	< 0.0001
Richness						
Anemochory	6.56 ± 0.73	6.0 ± 0.52	0.68 ± 0.11	5.32 ± 0.53	0.488	< 0.0001
Barochory	12.05 ± 1.02	65.05 ± 57.16	2.80 ± 0.69	–	0.412	< 0.0001
Ectozoochory	3.49 ± 0.27	3.11 ± 0.39	1.30 ± 0.14	–	0.423	< 0.0001

The cover of each life form showed a significant and different pattern along the abandonment age gradient, and there was a clear tendency in the order of cover dominance of the different life forms (Figure 2, Table 2). The explained variance of the regressions ranged from 0.42 (forbs) to 0.89 (woody species). Annuals, forbs and grasses showed a skewed pattern while woody species showed a linear tendency. Annuals were the first species covering the old-fields and reached up to 100% of the soil in the first years. However, they were almost absent ca. 12 years after abandonment. Perennial forbs also reached their maximum during the first 10 years, while perennial grasses peaked at 10-25 years after abandonment. Woody species showed a significant monotonic increase throughout the time window studied (60 years).

Species richness also showed different patterns for the different life forms (Figure 3, Table 2), and the order along the age gradient was similar to cover; the main difference was that there were few species of perennial grasses. The explained variance in the lognormal regressions was higher in all cases than the explained variance for total species richness (0.36), and ranged from 0.38 (grasses) to 0.67 (annuals).

The number of life forms decreased with abandonment age, from 4 co-occurring during the first 20 years, to 2 life forms, and finally (at ~ 60 years) the vegetation was practically dominated by one life form (woody species), although one grass species (*Brachypodium retusum*) persisted (with low cover) on the 60-year-old plots.

Dispersal strategy

Of all the species recorded in the study area, most were dispersed by gravity (43%) or by wind (42%); a few were considered ectozoochorous (9%), endozoochorous (3%) and mirmecochorous (3%) species. A similar ranking was observed for mean species richness at the plot level (Table 1). Mean plant cover was highest for endozochory (54%) and anemochory (45%), intermediate for barochory (37%) and relatively low for ectozoochory (12%) and mirmecochory (1%). In all cases, the variability of these values was very large (Table 1). The cover pattern for each dispersal strategy along the time gradient since abandon-

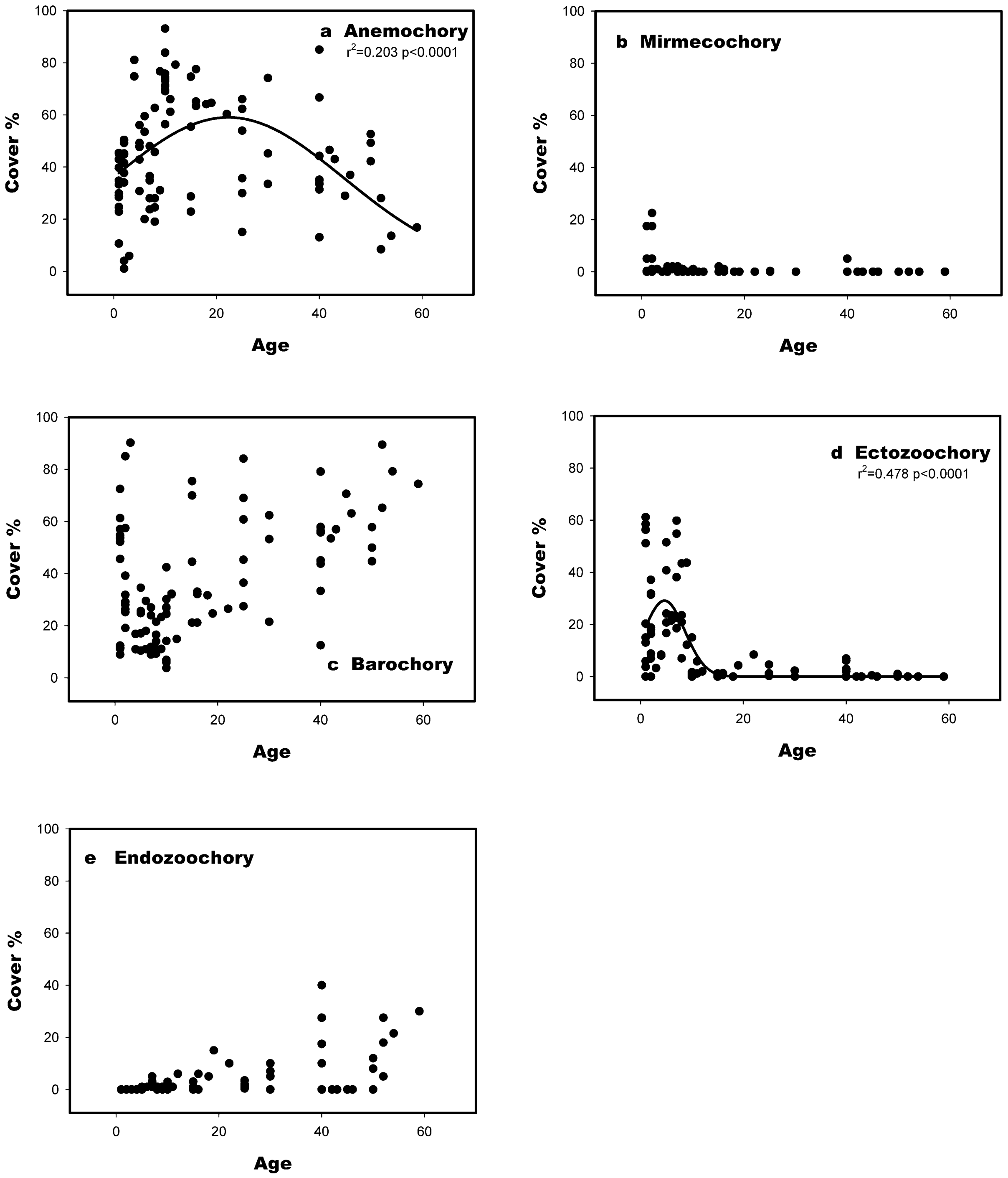

Figure 4. Cover (%) of plant species with different dispersal strategy along successional gradient. Fitted lines are the significant non-linear regressions (see Table 2 for more details).

ment was only significant for anemochorous and ectozoochorous species (Figure 4; Table 2). Ectozoochorous species only appeared at early stages of succession (<15 years after abandonment). Anemochorous species peaked at approximately intermediate stages, and barochory occurred at all stages without

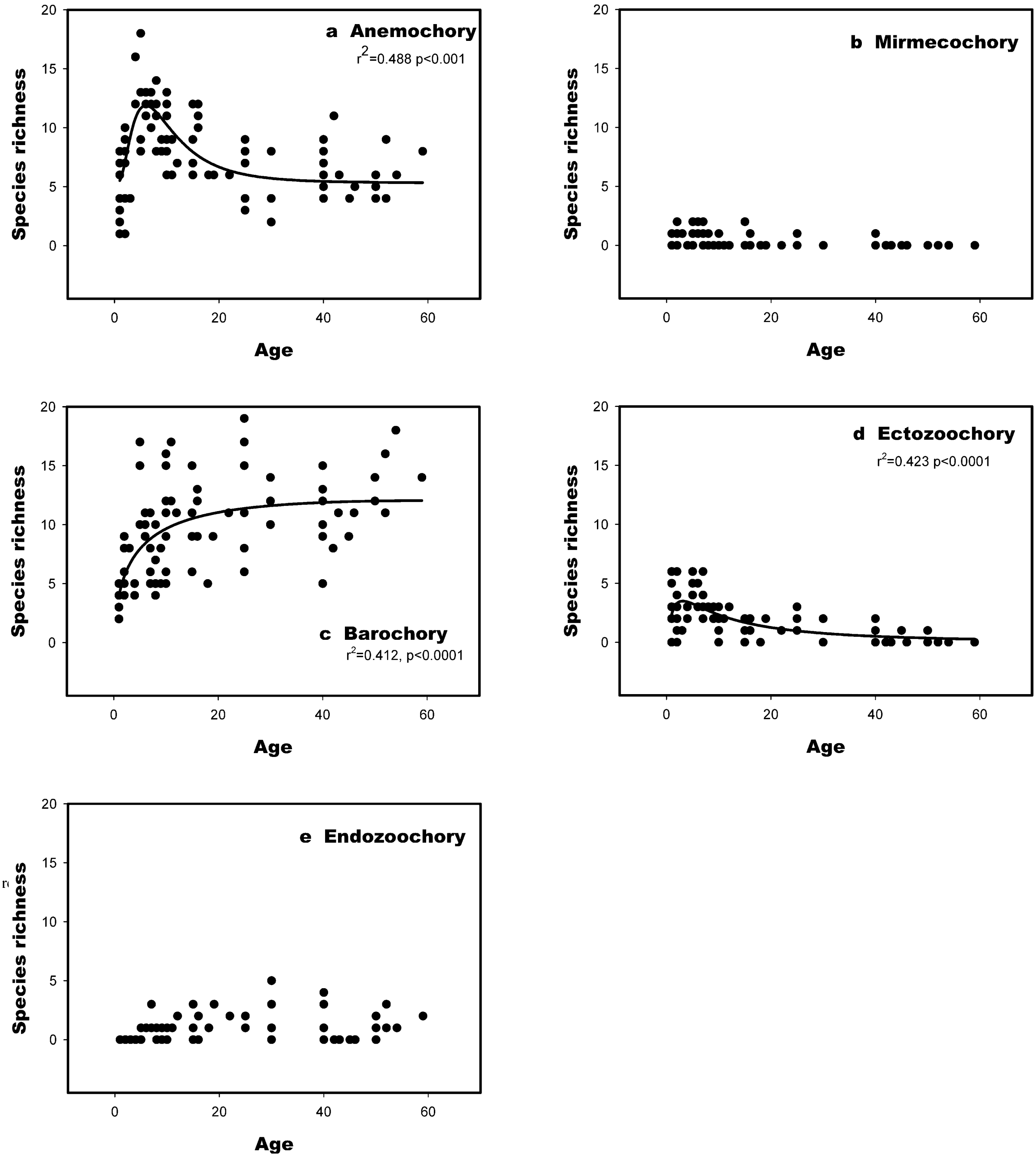

Figure 5. Richness (on 100 m^2-plots) of plant species with different dispersal strategy along successional gradient. Fitted lines are the significant non-linear regressions (see Table 2 for more details).

any clear pattern. Endozoochory showed no statistical pattern either but tended to increase with time.

Species richness of the different dispersal strategies showed different patterns along the abandonment age gradient (Figure 5, Table 2). Anemochory and ectozoochory species richness peaked at the early stages of the analysed period ($<$ 15 years). Barochory species richness increased during the first 20 years and then was maintained. Mirmecochory and endozoochory did not show any clear pattern. The number of dispersal types did not show a clear trend along the land abandonment gradient.

Discussion

Our results suggest that total plant cover in semi-arid Mediterranean systems is not dependent on abandonment age, and high cover values can be found at any time following abandonment. The results also suggest that, even in semi-arid conditions (annual rainfall ca. 300 mm), total species richness shows a peak at early stages of the chronosequence (Fig 1). The early peak pattern in richness appears to be in conflict with the decreasing pattern of species richness found by Debussche et al. (1996) in mesic Mediterranean conditions. However, their study did not include old-fields younger than ca. 20 years, and so they were not able to detect the pattern at early abandonment stages. In this sense, our results complement those by Debussche et al. (1996). In fact, the original work by Escarré et al. (1983) showed a peak in richness at early stages (<20 years). This pattern may be attributable to the importance of immigration processes during the early stages of succession and the dominance of extinction processes after ca. 15 years since abandonment. The peak in richness described by Tatoni and Roche (1994) for an abandonment gradient on terraces in Provence (Mediterranean southern France) showed maximum values at intermediate stages on an ordination gradient, but without any reference to age since abandonment.

A comparison of the trends in species richness indicates that the richness peak is the result of the coexistence of annual and biennial species with perennial forbs, some grasses, and woody plants during the first decades of the chronosequence (Figure 2, Figure 3). Although all four life forms coexist, there is a tendency towards life-form replacement, as shown by the displacement of the peak (annuals, forbs, grasses, and woody species, consecutively) when looking at the different life forms (Figure 2). Annuals and forbs showed more markedly unimodal responses than perennial grasses and woody species, indicating that the transition between life forms is more abrupt between pioneers and the rest, as pointed out by Brown (1992) when comparing different succession case studies. Seed bank composition plays an important role in the peak of annuals and forbs at early stages of abandonment because many of these species are ruderals or weeds present as seeds in the agricultural fallows (Baskin and Baskin 1998).

The main difference observed between this pattern and the classic replacement patterns suggested for mesic Mediterranean ecosystems (Houssard et al. 1980; Escarré et al. 1983) has to do with the time lag in which these changes occur. In our case, about 45% of total woody species richness is reached 10 years after abandonment (Figure 3), while in mesic Mediterranean conditions (southern France), woody species reached less than 20% of total richness at this time (Escarré et al. 1983). This pattern could be partially attributed to an early colonisation of some shrub species (e.g., *Rhamnus lycioides*) through the facilitation of bird-dispersed seeds by cultivated trees acting as perches (McDonell and Stiles 1983; Ne'eman and Izhaki 1996; Verdú and García-Fayos 1996, 1998). In fact, most (ca. 90%) of the endozoochorous species were woody, and they were present throughout the entire chronosequence without showing any period of dominance; this pattern is similar to the one reported in Near-East vineyards (Ne'eman and Izhaki 1996). It is interesting that woody species seem to appear earlier in dry than in mesic conditions. This may be attributable to the lower competition for woody species seedlings in drier conditions (higher site availability) than in mesic ones where a thick herbaceous layer is common (Keeley et al. 1981; Davis et al. 1998; Vilà and Sardans 1999). Moreover, some old-field chronosequences in non-Mediterranean conditions (e.g., east-central Minnesota, USA, Lawson et al. 1999;) did not show any successional trend in the abundance of woody species.

The high species richness at early stages of the chronosequence could also be inferred from coexistence of different dispersal types (Hovestadt et al. 2000). The recently abandoned fields had more anemochorous and ectozoochorous species than the earlier abandoned (older) fields, supporting the shift in dominance due to differences in dispersal mode as predicted by the 'relay floristics' model (Egler 1954; Myster 1993). However, barochory, endozoochory and mirmecochory were also present at the beginning of the chronosequence.

Several authors have found that wind is a more important dispersal vector in early successional stages, while dispersal by animals becomes important only at later successional stages (Houssard et al. 1980; Hodgson and Grime 1990). Our results in anemochory trends are consistent with these observations. However, when analysing animal-dispersed species in our study, we found that ectozoochorous species are mainly associated with young stages of the chronosequence. Endozoochorus (bird-dispersed) species are also present at early stages, but did not show a clear trend along the abandonment time gradient. Previous observations in other Mediterranean old-fields (Debussche et al. 1982; Verdú and García-Fayos 1998), indicated that bird-dispersed species were important at early stages.

The results also support the idea that patterns related to plant species interactions are more interpretable when the species are segregated into different functional groups (Pausas and Austin 2001). For example, both cover and richness showed differential patterns and improved prediction (higher explained variance) when species were separated by life form. Although life forms are crude functional types, they have been suggested as a first approximation for classifying species by function (Lavorel et al. 1997). The increase in predictability achieved by subdividing total species richness into different plant types has also been observed in different ecosystems (Nilsson et al. 1989; Moore and Keddy 1989; Pausas 1994; Pausas and Carreras 1995; Austin et al. 1996; Leathwick et al. 1998; Pausas et al. 1999). Functional classifications like life forms can be useful tools for prediction and for inter-regional comparisons (Pausas and Lavorel 2003) of richness and cover trends along successional gradients.

Although we found clear patterns of richness and cover in relation to abandonment age, the models could be improved by considering the different conditions of the old-fields. Small differences in environmental conditions (e.g., altitude, soil type), type and tree-density of the old crops (e.g., Ne'eman and Izhaki 1996; Bonet 2004), and different disturbance regimes (mainly grazing), should be considered for a better understanding of the mechanisms driving patterns through abandonment age and succession (Bonet, 2004).

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Appendix

Table A1. Complete list of the species found on the plots. Raunkiaer's life form: Ch = chamephyte; H = hemicryptophyte; P = phanerophyte; Th = therophyte. Considered life forms: A = annual or biennial; F = perennial forb; G = perennial grass; W = woody (d = dwarf scrub, s = shrub, t = tree). Main dispersal strategy: a = anemochory; b = barochory; e = ectozoochory; n = endozoochory; m = mirmecochory. Nomenclature follows Mateo and Crespo (1998).

Species name	Raunkiaer's life form	Life form	Dispersal strategy
Aegilops geniculata	Th	A	a
Aizoon hispanicum	Th	A	b
Ajuga chamaepitys	Th	A	b
Ajuga iva	Ch	F	b
Allium ampeloprassum	G	F	b
Amaranthus blitoides	Th	A	e
Amaranthus muricatus	Th	A	b
Anacyclus clavatus	Th	A	a
Anacyclus valentinus	Th	A	a
Anagallis arvensis	Th	A	e
Anthyllis cytisoides	P	Wd	b
Anthyllis terniflora	P	Wd	b
Argyrolobium zannoni	Ch	F	b
Aristolochia pistolochia	G	F	b
Artemisia barrelieri	P	Wd	a
Artemisia herba-alba	P	Wd	a
Asparagus horridus	Ch	Wd	n
Asperula aristata ssp. scabra	H	F	a
Asphodelus fistulosus	G	F	b
Asphodelus ramosus	G	F	b
Aster squamatus	Th	A	a
Astragalus hispanicus	Ch	F	b
Atractylis cancellata	Th	A	a
Atractylis humilis	Ch	F	a
Avena barbata	Th	A	a
Avenula bromoides	H	G	a
Ballota hirsuta	H	F	e
Beta vulgaris ssp martitima	Th	A	b
Brachypodium distachyon	H	G	a
Brachypodium phoenicoides	H	G	b
Brachypodium retusum	H	F	a
Brassica fruticulosa	Th	A	b
Bromus diandrus	Th	A	a
Bromus madritensis	Th	A	a
Bromus rigidus	Th	A	e
Bromus rubens	Th	A	a
Bupleurum fruticescens	P	Wd	b
Calendula arvensis	Th	A	e

Table A1. Continued.

Species name	Raunkiaer's life form	Life form	Dispersal strategy
Cardaria draba	Th	A	b
Carduus bourgeanus	Th	A	a
Carduus tenuifolius	Th	A	a
Carex halleriana	H	G	a
Carrichtera annua	Th	A	e
Carthamus lanatus	Th	A	a
Centaurea aspera ssp stenophylla	Ch	F	a
Centaurea calcitrapa	H	F	a
Centaurea melitensis	H	F	a
Chenopodium album	Th	A	b
Chenopodium murale	Th	A	b
Chenopodium vulvaria	Th	A	e
Chrozophora tinctoria	Th	A	b
Cichorium intybus	Th	A	a
Cirsium arvense	Th	A	a
Cirsum vulgare	H	F	a
Cistus albidus	P	Wd	b
Cistus clusii	P	Wd	b
Convolvulus althaeoides	H	F	b
Convolvulus arvensis	Th	A	b
Convolvulus lanuginosus	Ch	F	b
Conyza canadensis	Th	A	a
Coronilla minima ssp. lotoides	Ch	Wd	b
Crepis vesicaria	H	F	a
Cuscuta epithymum	Th	F	b
Cynodon dactylon	H	G	a
Cynoglossum ternifolium	H	F	b
Dactylis glomerata ssp hispanica	H	G	a
Daucus carota	H	F	e
Descurainia sophia	Th	A	b
Diplotaxis erucoides	Th	A	b
Dittrichia viscosa	P	Wd	a
Dorycnium pentaphyllum	Ch	Wd	b
Echium creticum ssp. coyncianum	H	F	b
Ephedra fragilis	P	Ws	n
Erica multiflora	P	Ws	b
Erodium cicutarium	H	F	e
Erodium malacoides	H	F	e
Eruca vesicaria	Th	A	b
Eryngium campestre	H	F	e
Euphorbia exigua	Th	A	m
Euphorbia falcata	Th	A	m
Euphorbia helioscopia	Th	A	m
Euphorbia lagascae	Th	A	m
Euphorbia mariolensis	Th	A	m
Euphorbia segetalis	Th	A	m
Euphorbia serrata	Ch	F	m
Fagonia cretica	Ch	F	b
Festuca capillifolia	H	G	a
Festuca valentina	H	G	a
Filago pyramidata	Th	A	a
Foeniculum vulgare ssp. piperitum	H	F	a

Table A1. Continued.

Species name	Raunkiaer's life form	Life form	Dispersal strategy
Fumana ericoides	Ch	Wd	b
Fumana hispidula	Ch	Wd	b
Fumana laevis	Ch	Wd	b
Fumana thymifolia	Ch	Wd	b
Fumaria parviflora	H	F	b
Galactites tomentosa	Th	A	a
Galium fruticescens	Th	A	b
Galium verrucosum	Th	A	b
Genista scorpius	P	Wd	b
Globularia alypum	P	Wd	a
Halogeton sativus	Th	A	b
Hammada articulata	P	Wd	b
Haplophyllum linifolium	Ch	Wd	b
Helianthemum cinereum ssp. rotundifolium	Ch	Wd	b
Helianthemum syriacum	Ch	Wd	b
Helianthemum violaceum	Ch	Wd	b
Helianthemun hirtum	Ch	Wd	b
Helianthemun squamatum	Ch	Wd	b
Helichrysum decumbens	Ch	F	a
Helichrysum stoechas	Ch	Wd	a
Helictotrichon filifolium	H	G	a
Hippocrepis ciliata	Ch	F	e
Hordeum murinum ssp. leporinum	Th	A	a
Hyparrhenia hirta	H	G	a
Hyparrhenia sinaica	H	G	a
Hypericum perforatum	H	F	b
Iberis hegelmairei	Th	A	a
Juniperus oxycedrus	P	Ws	n
Kochia scoparia	Th	A	b
Koeleria vallesiana	H	G	a
Lamarckia aurea	Th	A	a
Lavandula latifolia	P	Wd	b
Lavatera arborea	P	Wd	b
Lavatera cretica	Th	A	b
Leontodon logirostris	H	F	a
Leuzea confiera	H	F	a
Linum narbonense	Ch	F	b
Linum strictum	Th	A	b
Linum suffruticosum	H	F	b
Lithodora fruticosa	Ch	Wd	b
Lolium rigidum	Th	A	a
Lophocloa cristata	Th	A	a
Lygeum spartum	H	G	a
Malcolmia africana	Th	A	b
Malva hispanica	Th	A	b
Malva neglecta	Th	A	b
Malva parviflora	Th	A	b
Marrubium vulgare	Ch	F	b
Matthiola fruticulosa	Ch	F	b
Medicago arabica	Th	A	e
Medicago littoralis	Th	A	e
Medicago sativa	Th	A	b
Melilotus sulcata	Th	A	e
Mercurialis tomentosa	Ch	Wd	b

Table A1. Continued.

Species name	Raunkiaer's life form	Life form	Dispersal strategy
Misopates orontium	Th	A	a
Moricandia arvensis	Th	A	b
Muscari neglectum	G	F	b
Onobrychis stenorhiza	Ch	Wd	b
Ononis fruticosa	P	Wd	b
Ononis minutissima	Ch	Wd	b
Ononis sicula	Th	A	b
Onopordum macracanthus	H	F	a
Ophrys apifera	G	F	a
Ophrys fusca	G	F	a
Orobanche sp	G	F	a
Pallenis spinosa	H	F	a
Papaver rhoeas	Th	A	a
Paronychia argentea	Ch	Wd	a
Phagnalon rupestre	Ch	Wd	a
Phagnalon saxatile	Ch	F	a
Phlomis lychnitis	Ch	Wd	a
Pinus halepensis	P	Wt	a
Piptaterum miliaceum	H	G	a
Pistacia lentiscus	P	Ws	n
Plantago afra	Th	A	a
Plantago albicans	Ch	F	e
Plantago coronopus	Th	A	a
Plantago lagopus	Th	A	a
Plantago sempervirens	H	F	a
Poa annua	Th	A	a
Polygala rupestris	H	F	b
Potentilla reptans	H	F	b
Psoralea bituminosa	Ch	Wd	e
Quercus coccifera	P	Ws	n
Rapistrum rugosum	Th	A	b
Reichardia intermedia	Th	A	a
Reichardia tingitana	Th	A	a
Reseda lutea	H	F	a
Reseda phyteuma	Ch	F	a
Reseda undata	H	F	a
Rhamnus lycioides	P	Ws	n
Rosmarinus officinalis	P	Wd	b
Rubia peregrina	H	F	n
Ruta angustifolia	H	F	a
Salsola genistoides	P	Ws	a
Salvia verbenaca	Ch	Wd	b
Sanguisorba minor	H	F	e
Santolina chamaecyparissus ssp. squarrosa	P	Wd	a
Scabiosa atropurpurea	H	F	e
Schismus barbatus	Th	A	a
Scirpus holoschoenus	H	G	a
Scorpiurus sulcatus	Ch	F	e
Scorzonera angustifolia	Th	A	a
Scorzonera laciniata	H	F	a
Sedum sediforme	Ch	F	b
Senecio malacitanus	Ch	F	a
Senecio vulgaris	Th	A	a
Sideritis angustifolia	Ch	Wd	a
Sideritis leucantha	Ch	Wd	b

Table A1. Continued.

Species name	Raunkiaer's life form	Life form	Dispersal strategy
Silene mellifera	Ch	F	b
Silene vulgaris	H	F	b
Sisymbrium irio	Th	A	b
Sonchus asper	Th	A	a
Sonchus oleraceus	Th	A	a
Sonchus tenerrimus	Th	A	a
Staehelina dubia	Ch	Wd	a
Stipa capensis	Th	A	a
Stipa offneri	H	G	a
Stipa parviflora	H	G	a
Stipa tenacissima	H	G	a
Teucrium capitatum	Ch	Wd	b
Teucrium carolipauli	Ch	Wd	b
Teucrium homotrichum	Ch	Wd	b
Teucrium pseudochamaepitys	Ch	Wd	b
Thymelaea argentata	Ch	Wd	b
Thymelaea hirsuta	P	Wd	b
Thymus moroderi	Ch	Wd	b
Thymus vulgaris	Ch	Wd	b
Ulex parviflorus	P	Wd	b
Vicia peregrina	H	F	b
Vitis vinifera	P	Wd	n
Vulpia ciliata	Th	A	a

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