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Prediction of plant cover from seed bank analysis in a semi-arid plant community on gypsum

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Abstract

Question: Does the seed bank filter annual plant composition and determine cover at the species level?

Location: 510 m a.s.l., central Spain.

Methods: Seven transects and 136 quadrats were established in a semi-arid gypsum system. Seed bank samples were collected in each quadrat in September. The community was sampled the following April. For each quadrat we measured slope, microslope, landform, elevation, perennial cover and crust cover. Seed bank was estimated using the direct emergence method in glasshouse. Relationship among seed bank and annual community was assessed by Mantel correlations. Above-ground cover for the five most abundant species was modelled with GLMs.

Results: Seed bank density was the best predictor for annual community cover; perennial cover and landform were also included in the model. Species composition between September seed bank and April annual community cover was also highly related according to the Mantel test. This relationship was constant, even when the effect due to other abiotic (landform, microslope) or biotic (perennial cover, crust cover) parameters were partialled out. Microslope, elevation and seed bank density were the best parameters to predict spring cover of the five most abundant species.

Conclusions: Above-ground and below-ground community compartments are strongly related in terms of abundance and species composition. This relationship is filtered by several environmental factors (e.g. perennial cover, landform, microslope) that exert a strong control at community and individual levels. Our results support the hypothesis that annual community performance is affected by seed bank pattern.

Keywords: Annual; Central Spain; Community structure; Filter; Mantel test; Seed bank pattern.

Nomenclature: Tutin et al. (1964-1980) and Castroviejo et al. (1986-2005), except for *Chaenorhinum reyesii* (C. Vicioso & Pau) Benedí.

Abbreviation: GLM = General linearized model.

Introduction

The potential to influence above-ground vegetation is one of the most relevant functions of soil seed banks (Fenner 1985). Several observations support this assessment. 1. Experiments based on soil sterilization treatments have shown that the lack of local seed banks may have an enormous impact on community response (Kalamees & Zobel 2002; Luzuriaga et al. 2005). 2. Seed bank addition experiments have found large differences in community structure related to sowing densities (Goldberg et al. 2001; Lortie & Turkington 2003). 3. Agronomic studies have proven that weed seed bank density in cultivated fields is a good predictor of infestation rates (Wilson et al. 1985; Debaeke 1988).

This all sustains the hypothesis that propagule limitation affects community structure and dynamics (Aguiar & Sala 1997; Clark et al. 1999a). Nevertheless, emergence and recruitment is a complex process, probably controlled by many environmental factors (Baskin & Baskin 1998; Gutiérrez & Meserve 2003; Laskurain et al. 2004) beside seed availability. Specifically, few studies have assessed the relationship between seed bank and above-ground vegetation within a quantitative and small-scale point to point spatial pattern framework (Henderson et al. 1988; Jutila 1998; Marañón 1998). Our aim is to explore the seed bank - annual community cover relationship following a small-scale approach and partialling out the effect of some environmental factors on seed bank-annual community cover relationship.

The seed bank is a key element in community dynamics (Fenner 1985; Kemp 1989). Under the extreme and mostly unpredictable conditions of arid environments, seed banks enable local populations to withstand conditions that are fatal to established individuals of the species. Moreover, seed banks may capitalize population growth from favourable periods, diminishing the detrimental demographic effects of adverse environmental conditions, thus promoting species coexistence (Chesson 2000). This process, termed ‘storage effect’

(Chesson 1994), is relevant for short-lived species, especially annuals. So, effects of seed bank on standing vegetation can well be studied in semi-arid annual communities. Moreover, a wealth of empirical and theoretical research concerning seed banks has taken place in these habitats (Bertiller et al. 1992; Cabin 1996; Clauss & Venable 2000; Flores & Jurado 2003; Lortie & Turkington 2003).

We have chosen a semi-arid annual community on gypsum to evaluate the relationship between seed bank structure and composition and the corresponding annual community (see also Caballero et al. 2003). This type of community has many very rare and specialized plants and it is of global conservation interest (Anon. 1992).

We pose some questions to improve our knowledge of the relationship between seed bank and above-ground vegetation. In community terms, we want to answer the following questions: 1. Is the cover of annual plant community in April related to the seed bank density in the previous September? 2. Can seed bank composition be used to predict annual community performance in terms of composition and abundance? 3. To what extent is that relationship independent of other biotic or abiotic factors (namely landform, microslope, perennial cover or crust cover)? We also wanted to evaluate the response at the species level, so we asked 4. Whether or not the seed density in September is an adequate predictor of the April cover for the five most abundant species.

Methods

Study site

The study was carried out at Espartinas, a site close to Ciempozuelos, ca. 40 km south of Madrid, in central Spain (40°11' N, 3° 36' W, 570 m a.s.l.). The climate is upper semi-arid mesomediterranean (Rivas-Martínez & Loidi 1997), with an annual rainfall of 415 mm, but with almost no rainfall in summer. Mean daily maximum and minimum temperatures in January are 9.6 °C and 0.6 °C, and 32.7 °C and 15.4 °C in July. The soils are classified as Calcic Gypsisols, developed over parental gypsum rocks (Monturiol & Alcalá del Olmo 1990).

Gypsum outcrops have a characteristic geomorphology, with a flat crest, a steep slope and a mostly flat piedmont. Soil characteristics show marked differences through this spatial context (Rubio & Escudero 2000). A sparse shrub community dominated by genuine gypsophytes (*Gypsophylo struthii-Centaureetum hyssopifoliae*) covers this slope system, excluding the lower piedmont. Shrubs are interspersed with annual species, which are our topic of research.

Sampling design

Sampling was performed in September 2001, just after all seeds had been shed and prior to autumn emergence. This seed bank includes transient and persistent seed bank. We established seven south exposed transects, running from the top of the ridge to the bottom, parallel to the maximum slope, because in a previous research (Rubio & Escudero 2000) we found soil components to be spatially structured following such a pattern. Transects were established parallel to each other and > 15 m apart. Number of plots per transect ranged from 14 to 27 depending on the length of the slope. A second seed bank sampling was done in April in the same quadrats. This second sampling aimed to estimate permanent seed bank.

Quadrats (0.5 m × 0.5 m) were spaced every 2.5 m. The corners of each quadrat were marked to allow relocation. Five soil cores were taken from the centre of each quadrat and merged. Soil cores were 3 cm deep and 1.85 cm diameter since, according to Childs & Goodall (1973), the first 2 cm accumulate most of the seed bank in arid environments. Several parameters were measured in each quadrat, i.e. estimated cover of perennial plants and of lichenic crust, microslope (slope of the quadrat measured on the ground in the centre of each quadrat), macroslope (considered as the slope between a quadrat and the previous one), both measured with a Suunto PM-5 clinometer and elevation (m) with respect to the first quadrat in each transect. The total number of quadrats was 136 and the total area cored was 0.1827 m^2. Annual community cover and composition were sampled in the same quadrats in the last week of April 2002 when it reached its phenological optimum, but avoiding the soil core zones. Percentage cover of each species was estimated visually using a marked quadrat. After that, soil samples were taken following the previously mentioned procedure to estimate spring seed bank.

The viable seed bank was studied by monitoring seedling emergence (ter Heerdt et al. 1996). Soil samples were kept at 4 °C for two months. Thereafter, they were washed and sieved through a 0.5 cm mesh to retain the coarse fraction. The resulting material was sieved again through a 0.2 mm mesh, to reduce the fine material volume and produce scarification of the seeds, so favouring germination (Thompson et al. 1997).

The resulting soil samples were placed in 0.1 m × 0.1 m plastic trays in a greenhouse. To improve the water carrying capacity of soil samples a sterile substratum of vermiculite and peat (2:1) was added and thoroughly mixed with the sampled soil until a 1 cm depth was reached. Ten trays were filled only with the sterile mixture and located in the greenhouse to detect contamination. As soon as a seedling emerged, it was identified and removed. When identification at the species level was not feasible, seedlings were transplanted into individual pots and allowed to grow until identification was possible. After five months, the soil in the cells was regularly crumbled to enhance emergence and emergence monitored for another three months. Finally, the cells were watered with a gibberellic acid (GA_3) solution (1000 ppm) to complete the data set (seeds with endogenous dormancy) and emergence monitored for a further two months (Hartmann & Kester 1999). For this study only the annual species of the seed bank were considered.

Numerical analysis

Spatial pattern for seed density and emerged plants density was checked with Morisita's index (Morisita 1959). To determine which factors affected annual plant cover per quadrat (square root transformed to meet normality assumptions) we conducted a multiple regression approach. Three dummy variables were considered to deal with landform position (piedmont, slope and crest; given a value of 0 or 1). These, together with six continuous variables (seed bank density, microslope, macroslope, crust cover, perennial species richness and perennial plant cover), were considered in a forward stepwise procedure. Parameters were included in the model when $P < 0.05$ and dropped when $P > 0.1$.

A Mantel test was performed to measure the relationship between seed bank and annual cover in terms of abundance and composition. The Mantel test is a procedure to compare two similarity matrices computed for the same objects (Legendre & Legendre 1998). As individual seed counts and species cover values were not normally distributed, original values were transformed into ranks. Consequently, the results can be interpreted as a non-parametric Spearman correlation among similarity indices. Mantel statistical significance was tested using a randomization approach with 9999 permutations. To check if the relationship between both matrices was the result of an indirect and common dependence from underlying environmental parameters, several partial Mantel tests were conducted with four *a priori* explaining environmental matrices (landform, microslope, perennial cover, crust cover). This technique is similar to a partial correlation, being able to detect the correlation between two matrices of interest when the effect of a third matrix is kept constant. Mantel tests were performed with Passage freeware program (Rosenberg 2001).

We built models to predict spring cover for the five most abundant species based on their seed bank density and a set of environmental parameters. The species were three 'gypsovag' species, appearing on gypsum soils, but also on other types of widely distributed soils (*Asterolinon linum-stellatum*, *Campanula erinus* and *Vulpia unilateralis*) and two strict gypsophiles (*Campanula fastigiata* and *Chaenorhinum reyesii*). As cover for individual species could not be fitted to a normal distribution, we used General Linearized Models. We chose GLMs instead of linear regressions because of their capability to handle a larger class of distributions for the response variable (McCullagh & Nelder 1989). In our case, the selected distribution was a binomial model through a quasi likelihood approach, with logit as the link function and variance set as $\mu * (1 - \mu)$. The quasi likelihood approach permits to estimate the dispersion parameter in under and overdispersed regression models. All parameters used in the previous analyses, except total autumn seed bank, which was substituted by each species autumn seed bank, were considered in a forward stepwise procedure. Only variables explaining a significant amount of deviance were included in the statistical model. The change in the deviance was tested by the *F*-ratio test. Analyses were conducted with S-Plus 2000.

Results

Diversity and richness

A total of 2114 seedlings and at least 45 species of annual plants emerged in the greenhouse from the September seed bank (Table 1). Mean September seed bank density was 11 570 seeds per m^2. As a baseline for comparison, the April seed bank was smaller, comprising 23 species and 3736 seeds per m^2. Additionally, a relevant perennial seed bank was detected (September: 1489 seeds per m^2, 12 species; April: 328 seeds per m^2, six species). For a more detailed analysis on seed bank seasonal changes see Caballero et al. (in press). Above-ground April annual community cover was 6.5%, including 43 species and perennial species cover was 14.9%. September annual seed bank density and April annual cover exhibited clumped patterns (seed bank, $I_m = 2.9181$; annual cover, $I_m = 1.7854$). A point-to-point non-parametric Kendall correlation between the number of species in the September seed bank and in the annual plant community showed that parameters were highly correlated ($r = 0.362$; $P < 0.0001$), although species number was significantly higher in above-ground annual community (Wilcoxon $Z = -2.544$; $P = 0.01$).

Table 1. Species seed bank density and cover, ranked by seed bank frequency.

		Seed bank (September)		**Seed bank (April)**		**Above-ground cover**	
Species	Family	Freq. (%)	Density (seeds/m^2)	Freq. (%)	Density (seeds/m^2)	Freq. (%)	Mean cover when present (%)
Asterolinon linum-stellatum	*Primulaceae*	53	2134	18	197	76	1.2
Vulpia unilateralis	*Poaceae*	41	1751	21	208	56	0.7
Campanula erinus	*Campanulaceae*	38	2292	25	1182	38	0.8
Campanula fastigiata	*Campanulaceae*	35	1143	33	695	21	0.7
Chaenorhinum reyesii	*Scrophulariaceae*	34	624	7	98	32	0.7
Galium spec. (incl. *G. parisiense*)	*Rubiaceae*	27	558	1	5	67	0.7
Centaurium triphyllum	*Gentianaceae*	24	640	32	837	3	1.2
Filago pyramidata	*Asteraceae*	21	306	4	49	59	0.7
Plantago afra	*Plantaginaceae*	12	126	2	16	56	0.8
Parentucellia latifolia	*Scrophulariaceae*	11	284	14	213	1	0.5
Herniaria cinerea	*Caryophyllaceae*	7	164	4	65	8	0.8
Reseda stricta	*Resedaceae*	7	109	4	38	32	0.9
Vulpia ciliata	*Poaceae*	7	148	3	43	9	0.7
Euphorbia sulcata	*Euphorbiaceae*	6	44	1	5	38	0.7
Trisetum loeflingianum	*Poaceae*	6	66	1	5	26	0.7
Helianthemum salicifolium	*Cistaceae*	5	38	4	27	34	1.1
Neatostema apulum	*Boraginaceae*	5	38			59	0.8
Cerastium pumilum	*Caryophyllaceae*	3	60			1	0.5
Desmazeria rigida	*Poaceae*	3	49			7	0.6
Linaria glauca	*Scrophulariaceae*	3	27	1	5	10	0.7
Plantago coronopus	*Plantaginaceae*	3	22			0	
Stellaria media	*Caryophyllaceae*	3	27			0	
Bromus madritensis	*Poaceae*	2	16			0	
Centaurea melitensis	*Asteraceae*	2	16			23	2.8
Erophila verna	*Brassicaceae*	2	22	1			**5** 0
Medicago minima	*Fabaceae*	2	16			15	0.7
Sagina apetala	*Caryophyllaceae*	2	33			1	2.0
Valerianella coronata	*Valerianaceae*	2	55			10	0.7
Arabis auriculata	*Brassicaceae*	1	5			0	
Blackstonia perfoliata	*Gentianaceae*	1	5			0	
Cerastium glomeratum	*Caryophyllaceae*	1	5			0	
Cirsium spec.	*Asteraceae*	1	5			0	
Crepis capillaris	*Asteraceae*	1	11			13	0.7
Erodium cicutarium	*Geraniaceae*	1	11			73	2.1
Erodium malacoides	*Geraniaceae*	1	11			17	0.9
Euphorbia falcata	*Euphorbiaceae*	1	5			10	0.7
Heliotropium supinum	*Boraginaceae*	1	5			0	
Hymenolobus procumbens	*Brassicaceae*	1	16			0	
Leontodon taraxacoides	*Asteraceae*	1	5	1	5	22	0.9
Polygala monspeliaca	*Polygalaceae*	1	11			10	0.8
Polypogon maritimus	*Poaceae*	1	5	1	5	1	0.5
Scabiosa stellata	*Dipsacaceae*	1	5			1	2.0
Scleranthus verticillatus	*Caryophyllaceae*	1	5			1	0.5
Sherardia arvensis	*Rubiaceae*	1	16	1	5		
Hedypnois cretica	*Asteraceae*			1	5		
Adonis microcarpa	*Ranunculaceae*				0	2	0.8
Alyssum minus	*Brassicaceae*				0	2	0.8
Asteriscus aquaticus	*Asteraceae*				0	1	1.0
Centranthus calcitrapae	*Valerianaceae*				0	2	0.8
Clypeola jonthlaspi	*Brassicaceae*				0	3	0.7
Crucianella patula	*Rubiaceae*			0	0	3	0.7
Echinaria capitata	*Poaceae*			0	0	2	0.8
Hippocrepis ciliata	*Fabaceae*			0	0	7	0.6
Odontites viscosa	*Scrophulariaceae*			1	11	29	0.8
Veronica arvensis	*Scrophulariaceae*			0	0	1	0.5

Seed bank density vs annual cover

Seed bank density and annual cover were highly correlated ($r = 0.479$; $P < 0.0001$). The linear model for the annual plant cover was significant ($P < 0.001$), seed bank density was the first parameter included in the model with a positive effect ($r = 0.586$; $P < 0.0001$), followed by perennial cover with a negative effect ($r = -0.207$; $P = 0.002$) and piedmont landform with a positive effect ($r = 0.190$; $P = 0.006$).

Seed bank vs annual plant composition

The Mantel test showed a significant correlation between seed bank and above-ground annual community composition (r_m= 0.399; $P < 0.0001$). This correlation was maintained when the effect of different environmental parameters was controlled with a partial Mantel test (landform: $r_m = 0.396$; $P < 0.0001$, microslope: $r_m = 0.3968$; $P < 0.0001$, perennial cover: $r_m = 0.3968$; $P < 0.0001$ and crust cover: $r_m = 0.3968$; $P < 0.0001$). From the constraining matrices, only landform exerted a significant effect on any of the two matrices of interest (seed bank vs landform: $r_m = 0.135$; $P = 0.0003$). This strong relationship between the transient component (September) of the local seed bank and annual community performance was also detected in the permanent seed bank (April) ($r_m = 0.34$; $P < 0.0001$).

Individual species

We were able to build significant models for the five most common species (Table 2). Microslope was included in four of the models. It was the main parameter for *Asterolinon linum-stellatum*, *Chaenorhinum reyesii* and *Vulpia unilateralis* and the second for *Campanula fastigiata*, always with negative coefficients. Elevation was included in three models (*C. fastigiata*, *C. erinus* and *Vulpia*), also with negative coefficients. Seed density of the target species was included in three of the models (*C. erinus*, *C. fastigiata* and *Chaenorhinum*), in all cases it had a positive effect on cover. Landform crest (*Asterolinon*), slope (*C. fastigiata*) and perennial cover (*Chaenorhinum*) were included only once.

Discussion

Is annual cover related to seed bank density?

Annual community cover was highly correlated with autumn seed bank density, supporting the expected hypothesis that seed bank is a good predictor of annual community performance. This result agrees with manipulative experiments involving additional sowing, which have reported rises in standing population density as response to increased seed density (Zobel et al. 2000; Lortie & Turkington 2003). However, this relationship might not be straightforward, as the proportion of seeds emerging decreased as seed bank density increased (Goldberg & Estabrook 1998; Lortie & Turkington 2003), a fact that would reduce correlation between both compartments.

Aggregation phenomena have been widely described in arid and semi-arid environments, both for the abiotic (Rubio & Escudero 2000) and biotic (Guo 1998; Maestre et al. 2003) components of the system. Therefore, our observed clumped pattern for annual cover and seed bank supports this general rule (Aguiar & Sala 1997; Lortie & Turkington 2002). Seed bank clumping has been widely mentioned as a result of higher seed rain beneath adult plants (Clark et al. 1999b; Olano et al. 2002), a fact which would explain the relationship between seed banks and standing vegetation. Nevertheless, secondary dispersal and accumulation in favoured microsites, such as perennial patches or concave areas, has been demonstrated to play a relevant role structuring seed bank in these barren and steep environments (Kemp 1989; Caballero et al. 2003). This correlation would

Table 2. GLM models for above-ground cover for the five species with highest abundance in the seed bank. The parameters considered for the model were seed bank of the target species, macroslope, microslope, crust cover, perennial cover and landform (piedmont, slope and crest). Deviance is an estimate of total variation unexplained by the model.

Species	Model	Coefficient	Deviance	d.f.	Change in deviance	*F*	*P*
Asterolinon linum-stellatum	Null model		11.56	135			
	+ Microslope	– 0.0541 + 0.013	10.68	134	0.983	13.89	0.0002
	+ Landform crest	– 0.7928 + 0.295	10.37	133	0.303	8.65	0.003
Campanula erinus	Null model		6.73	135			
	+ Seed bank	0.0210+0.009	6.37	134	0.359	6.07	0.014
	+ Elevation	– 0.0006 + 0.000	6.06	133	0.305	5.14	0.024
Chaenorhinum reyesii	Null		5.18	135			
	+ Microslope	– 0.0524 + 0.017	4.14	134	1.038	34.46	<0.0001
	+ Seed bank	0.1027 + 0.034	3.91	133	0.226	7.53	0.006
	+ Perennial cover	– 0.0342 + 0.015	3.78	132	0.137	4.57	0.034
Campanula fastigiata	Null model		4.22	135			
	+ Elevation	– 0.0011 + 0.000	3.25	134	0.253	10.13	0.001
	+ Microslope	– 0.0681 + 0.020	3.13	133	0.963	38.82	<0.0001
	+ Seed bank	0.0651 + 0.023	2.87	132	0.118	4.73	0.031
	+ Slope	– 0.0007 + 0.000	2.80	131	0.256	10.21	0.001
Vulpia unilateralis	Null model		4.70	135			
	+ Microslope	– 0.0435 + 0.008	4.05	134	0.655	29.00	<0.0001
	+ Elevation	– 0.0004 + 0.000	3.86	133	0.184	8.19	0.004

only be consistent if these microsites were suitable for emergence and survival (Aguiar & Sala 1997), otherwise there would be a mismatch between seed bank densities and emergences.

Seed bank density was a powerful predictor of the cover of annual plants in the following year, even after a set of environmental factors was partialled out. Although perennial cover and landform piedmont were also related with annual community cover, their effect was minor compared to seed bank density. The positive effect of piedmont on annual cover can be attributed to the better soil conditions found in this landform (Guerrero-Campo et al. 1999; Rubio & Escudero 2000). In fact, higher productivity and emergence for perennial species in the piedmont have already been reported in this habitat (Escudero et al. 1999, 2000). The negative effect of perennial cover on annual cover seems to contradict most research conducted in arid and semi-arid environments, where facilitation of perennial plants on annual communities has been widely reported (Callaway 1995; Moro et al. 1997; Facelli & Temby 2002; Pugnaire et al. 2004). This effect can be interpreted as a consequence of competition, as a lower proportion of the seed bank emerges under shrubs, rather than to lower seed availability (Lortie & Turkington 2003).

Is there a relationship in terms of abundance and composition?

In dense communities, such as grasslands or forests, the recruitment potential represented in the seed bank is generally only expressed in a narrow subset of microsites (Eriksson & Ehrlén 1992; Davies & Waite 1998; Moles & Drake 1999). In all these communities, seed bank usually has a very different composition from standing vegetation (Olmsted & Curtis 1947; Jankowska-Blaszczuk & Grubb 1997). But, how close is this relationship in sparse communities such as annual communities from arid or semi-arid environments?

Seed bank and annual community were correlated in terms of abundance and composition, thus seed bank predicted above-ground vegetation. Using a similar approach, Jutila (1998) found a highly significant point-to-point resemblance between a grassland seashore community and its seed bank. Nevertheless, environmental control on seed bank expression has also been emphasized. Gutiérrez & Meserve (2003) found profound changes in seed bank emergence and resulting above-ground cover in annual communities in arid central Chile, depending on annual rainfall. Similarly, Pugnaire & Lázaro (2000), in a study in SW Spain, found that environmental conditions related to shrub age were crucial to filter seed bank expression. We consider that relationships between seed bank and above-ground vegetation are the rule in semi-arid communities, despite environmental filters.

We found that controlling for environmental factors did not change the seed bank - annual community relationship. Although our environmental parameters (landform, microslope, perennial cover and crust cover) have already been reported as relevant for both seed bank and annual community composition (Meyer et al. 1992; Pugnaire & Lázaro 2000; Caballero et al. 2003; Romão 2003). This discrepancy may be related to the humid conditions of the studied year. Accordingly to Clauss & Venable (2000), higher germination rates are expected in good years and therefore a higher correlation among seed bank and emergence should occur. In any case, our results show that, at least at the spatial and temporal scale studied, the pre-existing seed bank exerts a control on above-ground vegetation.

Despite drastic changes in seed bank density between transient (September) and permanent (April) seed banks, a significant relationship between the permanent seed bank and the April annual community is maintained. This temporal inertia supports the existence of a storage effect (Chesson 1994). Seed banks in these communities not only shape above-ground vegetation, but also contribute to longer-term stability and maintenance of diversity. In fact, this is a function that has repeatedly been considered as one of the main roles for seed banks (Fenner 1985).

Does seed bank play a role for individual species?

Specific responses were mostly consistent with the observed patterns for the whole community. Three of the five models for above-ground cover included the seed bank density of each individual species, including the two gypsophytes (*C. fastigiata* and *C. rubrifolium*), but only one of the three gypsovags (*C. erinus*). The seed bank effect was remarkably robust since as it occurs with most seed bank research, seed bank sampling is based only on a tiny fraction of the surface compared with above-ground vegetation cover estimates (0.5% of the whole quadrat). Furthermore, and as expected, the physical environment also explained a relevant fraction of the total variation of cover at the species level. Thus, individual species cover was higher in quadrats with smaller microslope (four of five species) and mainly at the lower parts of the slope system (three of five species). This relationship seems to be related to more favourable hydric conditions and soil properties at the microsite scale. Remarkably interesting is the negative effect of perennial cover on *C. rubrifolium*, which matches with its preference for bare areas with well developed soil biological crusts.

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