

Secondary old-field succession in an ecosystem with restrictive soils: does time from abandonment matter?

E. Martínez-Duro, P. Ferrandis, A. Escudero, A.L. Luzuriaga & J.M. Herranz

Abstract

Question: Our knowledge of secondary old-field succession in Mediterranean environments is extremely poor and is non-existent for restrictive soil conditions. How these ecosystems, such as those on semi-arid gypsum outcrops, recover seems a priority for managing change and for ensuring conservation of specialized and endangered biota. We tested whether reinstallation of gypsum vegetation after cropland abandonment requires: (1) soil physical restructuring and (2) chemical readjustment to enable growth and survival of specialized gypsophilous vegetation, and more specifically how time from abandonment drives such environmental change.

Location: We sampled a complete set of old fields on gypsum soils (1–60 yr since abandonment) in Villarrubia de Santiago (Toledo, Spain).

Methods: Generalized linear models and model comparisons were used to analyse the effect of several environmental parameters on species abundance and richness. Ordination methods (canonical correspondence analyses and partial canonical correspondence analyses) were undertaken to evaluate compositional variation among the sampled fields.

Results: Secondary old-field succession on semi-arid Mediterranean gypsum soils was controlled by a complex set of factors acting relatively independently. Surprisingly, time since abandonment explains only a small proportion of compositional variation (3%). Conversely, soil chemical features independently from time since abandonment are important for explaining differences found in old-field composition.

Conclusions: Secondary succession on specialized Mediterranean soils does not follow the widely described “amelioration” process in which soil features and composition are closely related over time. Restrictive soil conditions control both structure and functioning of mature communities and also secondary succession.

Keywords: Chronosequence; Cropland abandonment; Gypsovag; Gypsophyte; Gypsum steppe.

Nomenclature: (Tutin et al. 1964–1993).

Abbreviations: CCA = Canonical Correspondence Analysis; pCCA = Partial Canonical Correspondence Analysis; GLM = Generalized Linear Model; TVE = Total Variation Explained; VIF = Variance Inflation Factor.

Introduction

Plant succession in arid and semi-arid regions is thought to be a very slow process (Carpenter et al. 1986; McAuliffe 1988). The time required to approach the so-called compositional equilibrium stage is considered to be in the order of hundreds of years (Agami et al. 1998; Dana & Mota 2006). Studies on secondary succession in arid and semi-arid environments are rather scarce (Wezel & Böcker 1999; Bolling & Walker 2000). Most of these have been based on chronosequence approaches but a few were diachronic studies (Escarré et al. 1983; Tautoni & Roche 1994).

It has been postulated that succession in arid and semi-arid ecosystems is mainly driven by external factors such as rainfall and temperature, and to a lesser extent by biological factors (Noy-Meir 1973; Aguiar & Sala 1999). However, patch dynamics based on some type of nutrient, water or light amelioration, secondary seed spatial redistribution and shifts of plant–plant relationships have been highlighted as crucial processes in these systems (Pugnaire et al. 1996; Aguiar & Sala 1997; Flores & Jurado 2003) but, to our knowledge, have not been broadened to time-scales adequate to address community replacement.

Martínez-Duro, E. (corresponding author, esmeralda.martinez@uclm.es) **Ferrandis, P.** (pablo.ferrandis@uclm.es) & **Herranz, J.M.** (jose.herranz@uclm.es) Unidad de Ecología y Botánica, ETS de Ingenieros Agrónomos, Universidad de Castilla-La Mancha, Albacete ES-02071, Spain
Escudero, A. (adrian.escudero@urjc.es), **Luzuriaga, A.L.** (arantzazu.lopezdeluzuriaga@urjc.es) Área de Biodiversidad y Conservación, ESCET, Universidad Rey Juan Carlos, Móstoles ES-28933, Spain.

Old-field succession is a special case of secondary succession on abandoned, usually arable, croplands. Abandonment of agricultural practices in Mediterranean semi-arid areas during recent decades is recognized as the most important regional global change driver and a key landscape shaper. Centuries of man-induced changes owing to agriculture have promoted severe changes in composition and cover of natural plant communities, which have been confined to isolated and small remnants on an adverse matrix (García-Ruiz et al. 1996; Bonet 2004).

Unfortunately, our knowledge on secondary old-field succession in semi-arid Mediterranean environments is extremely poor (Noy-Meir 1973; Margaris et al. 1996; Bonet 2004; Bonet & Pausas 2004) and non-existent for restrictive soil conditions. How these ecosystems, such as those on semi-arid gypsum outcrops, recover seems a priority for managing change and for ensuring conservation of their specialized and endangered biota. Factors controlling such change are not known. Secondary succession on Mediterranean old fields follows an “amelioration” process in which composition and structure of vegetation not only change with time since abandonment but closely track parallel changes in soil physico-chemical properties driven by vegetation itself (Debussche et al. 1996; Haase et al. 1996; Ne’eman & Izhaki 1996; Pugnaire & Luque 2001). Other local factors may marginally explain some community attributes of a developing plant community not necessarily linked to soil conditions, such as changes in the biotic environment owing to the development of the community. However, it is expected that such “endogenous” soil properties may be especially relevant for these specialized soils.

The very particular physical and chemical properties of gypsum soils strongly affect community patterns and vegetation composition (Meyer et al. 1992). Gypsum vegetation seems an exceptional vegetation model for testing the effect of soil constraints on old-field succession. Despite gypsum soils being extremely adverse habitats for plant life, they support a conspicuous specialist endemic group of plants (Parsons 1976; Guerra et al. 1995; Mota et al. 2003) and constitute one of the most endangered habitats in Europe (European-Community 1992). The ecology of gypsum plant communities has recently received a great deal of attention (Meyer 1986; Escudero et al. 1999, 2000; Guerrero-Campo et al. 1999a, b; Palacio et al. 2007; Pueyo & Alados 2007), but there is little information about the rate of reappearance of gypsophytes following

human disturbance or of the environmental factors influencing natural recovery and secondary succession.

It has been proposed that the chemically and physically restrictive conditions of gypsum soils determine gypsophily in plants (Escudero et al. 1999, 2000; Guerrero-Campo et al. 1999b; Pueyo et al. 2007). A corollary is that gypsum vegetation requires very restrictive chemical and physical conditions to occur beyond the existence of gypsum in the soil (Pueyo et al. 2007). The main feature of chemical composition in gypsum soils is the unbalanced ion concentration, with an excess of sulphur and calcium (Boukhris & Lossaint 1975) and a poor retention of ions such as phosphorous, potassium and nitrogen because of exchange with calcium in the soil complex (Guerrero-Campo et al. 1999b). Conversely, seed establishment (Meyer et al. 1992; Escudero et al. 1999) and root physical penetration (Verheyne & Boyadgiev 1997) are determined by the hard physical and biological soil gypsum crust. In addition, it has been suggested that gypsophily is controlled primarily by the capability to penetrate extremely hard physical crusts during emergence (Meyer 1986; Romao & Escudero 2005).

Thus, we hypothesize that reinstallation of gypsum vegetation after cropland abandonment requires, first, soil physical restructuring to meet emergence requirements and, second, chemical readjustment for growth and survival of these restrictive soil edaphisms. Historical cropland management would probably have drastically altered soil physical and chemical conditions from those required for establishment and growth of gypsophilous vegetation.

In order to test this hypothesis, we sampled a complete set of old fields on gypsum soils ranging from 1 yr to more than 60 yr since abandonment. Some methodological limitations of the chronosequence approach have been pointed out (Glenn-Lewin & van der Maarel 1992) otherwise some studies have re-established the robustness of this technique since they validated the predictions after resampling communities studied (Debussche et al. 1996; Foster & Tilman 2000). Thus, chronosequences may help to expand our scarce knowledge in the secondary dynamics of these stressful habitats.

The specific objectives of this work were to: (1) evaluate the importance of time since abandonment on the recovery of gypsum communities in old-fields, (2) define environmental attributes which drive secondary succession, and (3) determine species relationships to establish temporal patterns.

To achieve these goals, species richness, cover, evenness together with species composition were evaluated and the relative influence of different physical and chemical soil variables and some local variables, were investigated.

Methods

Study site and species

The study was undertaken in the surrounding of Villarrubia de Santiago, province of Toledo (Castilla-La Mancha region; central Spain; Fig. 1) on a rectangular area of 6.9 km \times 2.8 km (altitudinal range: 153 m). The very homogeneous climate in the area is semi-arid Mediterranean, with a typically drastic summer drought and an upper semiarid annual mean rainfall of ca. 400 mm. Mean temperature is 13.7°C with a mean minimum temperature in the coldest month of -0.2°C and a mean maximum temperature in the hottest month of 33°C . Soils are rich in massive calcium sulphate (average $>50\%$) which forms extremely hard gypsum crusts (Ferrandis et al. 2005).

The landscape consists of low hills and flat-bottomed valleys, usually cultivated, leading to the

fragmentation of plant communities on hills. Natural vegetation is rich in endemic strict gypsophytes, such as *Centaurea hyssopifolia*, *Gypsophila struthium*, *Gypsophila bermejoi*, *Helianthemum squamatum*, *Koeleria vallesiana* subsp. *castellana*, *Ononis tridentata*, *Odontites longiflora* var. *gypsophila*, *Teucrium pumilum*, *Thymus lacaitae* and *Reseda stricta*. Two plant communities are neatly distinguishable on gypsum outcrops: (1) a scrubland on slopes dominated by *G. struthium*, *C. hyssopifolia*, *T. lacaitae* and *H. squamatum*, and (2) a sparse dwarf scrubland dominated by *T. pumilum* and *Hernaria fruticosa* subsp. *fruticosa*, established on gypsum-crusts summits (Rivas-Martínez & Costa 1970).

Dry cereal croplands and olive groves are usually present in valleys. Rural exodus and European agrarian policy has caused changes in traditional land uses and lifestyle, resulting in field abandonment becoming prevalent in recent decades.

Sampling

Vegetation was surveyed following an old-field chronosequence approach. During spring and summer of 2004, we sampled 50 plots in abandoned croplands that had not been managed or used

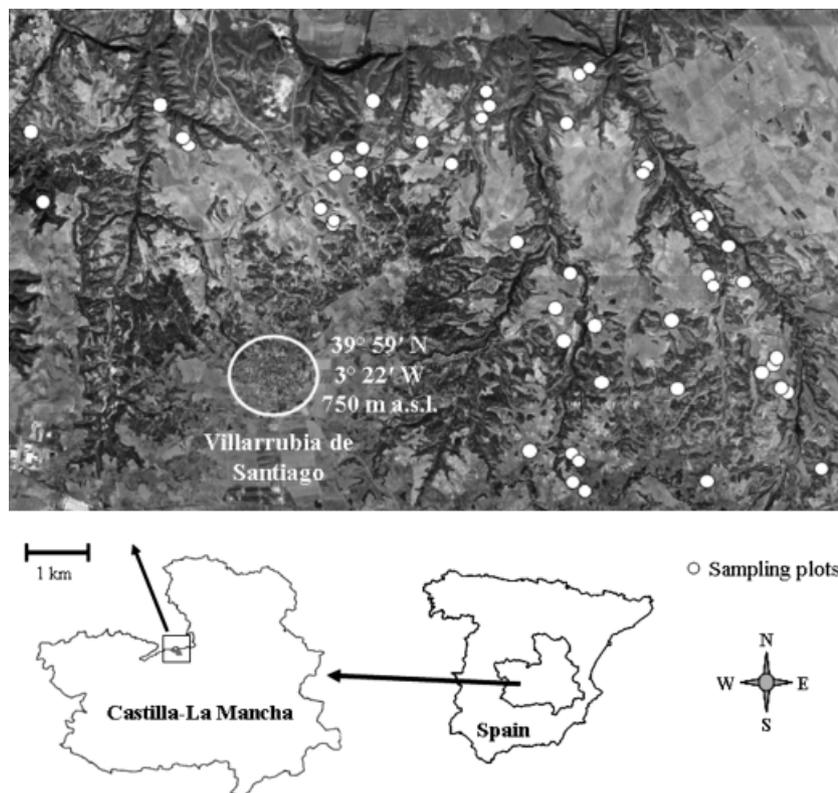


Fig. 1. Location of the study area in Spain and location of sampling plots in Villarrubia de Santiago (Toledo, Spain).

subsequent to abandonment. Nine “control” plots were randomly selected in remnants of gypsum vegetation that had never been cultivated. The remainders of plots were located on formerly cultivated sites that had last been cultivated 1–60 yr previously. This crucial information was collected by the staff of the wildlife conservation service in the area through direct consultation with landowners.

On each old-field, a 50 m² (5 m × 10 m) plot was delimited randomly avoiding community edges and field margins (>10 m). Vegetation sampling was undertaken following the “Point Quadrat” method (Groeneveld 1997). Within each plot four parallel 10-m linear transects separated by 1 m were established. Each transect comprised 100 contact points positioned at a regular 10-cm interval (i.e. 400 contact points per plot). On each point, each species contacting a vertical needle was recorded.

Plants living in gypsum habitats are classified as gypsophytes when they only occur on gypsum soils and as gypsovags when they are able to grow on gypsisols but achieve the optimum growth on non-gypsum soils (Meyer 1986). Plant species were ascribed to one of three functional groups: (1) annual gypsovags (including annual and biannual species), (2) perennial gypsovags and (3) gypsophytes. We calculated cover, richness and evenness per plot for each functional group.

We measured slope (%), orientation (rad) and altitude (m) in each plot (Table 1). Three soil samples (5 cm diameter) per plot were taken at a depth of 10 cm in order to determine soil chemical parameters. These soil samples were sent to the agrarian laboratory of the regional government to estimate the several soil chemical parameters: pH (in water 1:2.5), conductivity ($\mu\text{S cm}^{-1}$), C:N ratio, active limestone ($\text{g } 100 \text{ g}^{-1}$), sodium ($\text{mEq } 100 \text{ g}^{-1}$), potassium ($\text{mEq } 100 \text{ g}^{-1}$), calcium ($\text{mEq } 100 \text{ g}^{-1}$), total nitrogen ($\text{g } 100 \text{ g}^{-1}$), available phosphorous (mg kg^{-1}), sulphate ($\text{mEq } 100 \text{ g}^{-1}$), magnesium ($\text{mEq } 100 \text{ g}^{-1}$), organic matter ($\text{g } 100 \text{ g}^{-1}$) and organic carbon ($\text{g } 100 \text{ g}^{-1}$). Active limestone is the proportion of calcium carbonate (CaCO_3) extractable with a CO_2 water solution and can be taken up by plants. Soil texture was estimated per plot (Bouyoucos Soil Hydrometer Method, Bouyoucos 1936). In order to evaluate the effect of land use on vegetation dynamics, the crop type grown in each field prior to abandonment was recorded for each old field. Distance to the nearest active cropland was measured in order to evaluate its influence on the composition of the plant community as a weed source. Although seed source is related to the gypsophyte and gypsovag perennial dispersal strategy, any distance variable associated

Table 1. Fixed predictor variables used in the GLM and canonical correspondence analysis (CCA) models undertaken for the seven response variables (total richness, perennial gypsovag richness, annual gypsovag richness, gypsophyte richness, total cover, gypsophyte cover and total evenness). ^aOnly in general linear model (GLM). ^bonly in CCA.

Age model (1 predictor variable)	Time since abandonment (yr)
Soil chemical composition (11 predictor variables)	pH Conductivity ($\mu\text{S cm}^{-1}$) C:N ratio Active limestone ($\text{g } 100 \text{ g}^{-1}$) Sodium ($\text{mEq } 100 \text{ g}^{-1}$) Potassium ($\text{mEq } 100 \text{ g}^{-1}$) Calcium ($\text{mEq } 100 \text{ g}^{-1}$) Nitrogen ($\text{g } 100 \text{ g}^{-1}$) Phosphorous (mg kg^{-1}) Sulphate ($\text{mEq } 100 \text{ g}^{-1}$) Magnesium ($\text{mEq } 100 \text{ g}^{-1}$)
Geography (six predictor variables)	Slope (%) Orientation (rad) Latitude (m) Longitude (m) Altitude (m) Cropland distance (m)
Soil physical features [five (GLM) or seven (CCA) predictor variables]	Fine sand (%) Silt (%) Clay (%) Herbivory pressure (rabbit faeces m^{-2}) Agricultural practices (0,1,2,3) ^a Shallow ploughing (dummy) ^b Medium ploughing (dummy) ^b Deep ploughing (dummy) ^b

was not measured because of (1) the high fragmentation of the study site, where croplands are abundant and large, but natural remnants are scarce, small and isolated, and (2) the short-range dispersal of gypsophytes, whose most favourable environment is located in the vicinity of mother plant (Ellner & Schmid 1984; Escudero et al. 1999, 2000).

Numerical analysis

Vegetation patterns

Total richness, annual gypsovag richness, perennial gypsovag richness, gypsophyte richness, total cover, gypsophyte cover and total evenness were modelled by means of Generalized linear models (GLMs) using all the measured predictors (McCullagh & Nelder 1989). The GLMs allow handling of larger distribution types for the response variable than standard linear regressions. We applied a quasi-likelihood estimation of the regression coefficients for all these models. This allowed estimation of regression coefficients in data sets without fully

knowing the error distribution of the response variable and in cases when dispersion parameters were over or under-dispersed. This method gives an estimate of the dispersion parameter of the variance function which otherwise is set to a constant equal to one (MathSoft 1999). Significance of the regression coefficients were tested by means of a *t*-test (H_0 : coefficients are equal to 0).

Variance inflation factor (VIF) is a useful diagnostic tool for detecting nearly collinear constraints among predictors. Using a common rule where values over 10 indicate redundant constraints (ter Braak & Smilauer 1998), organic matter, organic carbon and coarse sand were eliminated. The remaining predictor variables were classified into four complementary groups in order to consider previous information in the modelling process (Table 1). The “Age” model included only the variable time since abandonment and the “Soil Chemical Composition” model grouped soil chemical predictor variables (11 variables). We built a third model called “Geography” (six variables) to assess the importance of location and to detect a possible subjacent gradient or any historical land use influence. Finally, the “Soil Physical Features” model (five variables) included variables related to soil physical structure (Table 1).

We built a saturated model hereafter called the COMPLETE model (23 variables), incorporating all the predictors for each functional group (Table 1). Comparisons between each of the above models with the COMPLETE model were feasible because they were nested. Model comparisons allowed one effect to be partialled out after adjusting the others. Change in deviance between each pair of nested models was assessed using an *F*-test. The fitted value of the model was expressed by means of the D^2 adjusted value, the equivalent to r^2 in least-squares models (Guisan & Zimmermann 2000). The construction of the final models through the evaluation of sub-models minimizes the risk inherent to stepwise procedures (Guisan & Zimmermann 2000). Nested model comparisons were focused on evaluating the effect of time since abandonment and the interaction with other environmental variables. The significant terms of the COMPLETE model were identified using a stepwise addition of variables to the null model (intercept only). At each step, one term is selected on the basis of the magnitude of the C_p statistic estimated for each term, until no additional terms improved the model. The change of deviance of the model by the inclusion of a term was tested against an *F* distribution. The final model was characterized by fitted D^2 . The variables selected after a forward selection procedure were used to build a simpler REDUCED model. All

these GLMs were built with R 2.4.1 statistical software (Free software, Boston, MA, US).

Constrained ordination for hypothesis testing

Ordination methods were used to evaluate compositional variation among the fields sampled. The major advantages of this technique over classical multivariate analysis of variance are that it is distribution-free and has no restrictive upper limit to the number of species included (Verdonchot & ter Braak 1994). The main matrix was built with the 50 plots (rows) and with the species that were present in more than 10% of the plots. Following Legendre & Anderson's (1999) recommendations, when axis length was above three standard deviation units, a Canonical Constrained Analysis (CCA) was performed to relate the main data matrices to other environmental variables, scaling on inter-species distances and biplot rescaling of the axes. Four constraining matrices for the species data sets were built, the same variable groups used in GLMs: “Age” matrix, “Soil Chemical Composition” matrix, “Geography” matrix and “Soil Physical Features” matrix (Table 1). The “Agriculture practices” matrix (categorical variable in GLM) was previously transformed to dummy variables: “none”, “shallow”, “medium” and “deep ploughing”. The “None ploughing” dummy variable was eliminated to avoid colinearity problems. A “Complete” matrix with all the variables was used as constraining matrix (27 variables) for a complete model.

Total variation explained (TVE) by each constraining matrix was calculated as the sum of all canonical extracted axes (Borcard et al. 1992). Monte Carlo permutation tests were performed to determine the accuracy of every relationship (999 randomizations) between the two data sets. The sum of all canonical eigenvalues was used to build the *F*-ratio statistic (Legendre & Anderson 1999). Only when $P < 0.01$ (adjusted for multiple comparisons by the Holm's method; Legendre & Legendre 1998) was the relationship between the two data sets considered significant. If the model was significant, a forward stepwise procedure was undertaken to select a reduced model including only significant variables. We incorporated explanatory variables one at a time and step by step in the order of their decreasing eigenvalues after partialling out the variation accounted for the already included variables. The process stopped when the new variable was not significant ($P > 0.05$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 999 randomizations.

Variance partitioning with CCA was performed to evaluate the relative importance of time since abandonment after adjusting the variability of other two more important data sets considered as covariables (Borcard et al. 1992). This procedure is called partial CCA. A series of nine partial CCAs were run for each of the constrained models after removing the singular effects of each of the other two matrices, and the combined effects of the other two matrices. The results of the latter gave us the “pure” effect (as a percentage of variation accounted for) of each predictor matrix after dividing the inertia from each canonical analysis by the inertia from the correspondence analysis and multiplying by 100. Once all of the appropriate analyses were computed it was possible to determine the total variation accounted for in the abundance matrix by all predictor matrices, the pure variation that each matrix contributed, and all of the possible combinations of

shared variation among the matrices (Borcard et al. 1992; Anderson & Gribble 1998). All these analyses were performed with the programme CANOCO for Windows v 4.0.

Results

Vegetation patterns

A total of 158 species were found in the 50 plots surveyed (18 gypsophytes and 140 gypsovags) (see the Supporting Information, Appendix S1). Time since abandonment affects most community attributes, except for perennial gypsovag richness and total evenness (Tables 2 and 3). Total species richness, annual gypsovag species richness and total cover decreased over time, whereas gypsophyte richness and cover increased over time. Total cover was determined only negatively by time since aban-

Table 2. Residual deviance and D^2 fitted values for the GLM models with the seven indices calculated in the 50 plots. Models were built with the link function = ‘identity’ and the variance function = ‘μ’. The reduced model only included the variables significantly selected in the forward stepwise selection procedure (see Table 3). Res. Dev. = Residual deviance; Fit. D^2 = D^2 fitted values.

Model	Res. Dev.	df	Fit. D^2	Model	Res. Dev.	df	Fit. D^2
Total richness				Total cover			
<i>Null</i>	3633.3	49		<i>Null</i>	10 215.3	49	
Age	2936.9	48	0.192	Age	8598.2	48	0.158
Geography	2742.2	43	0.159	Geography	7872.3	43	0.142
Soil chemical composition	2187.8	38	0.243	Soil chemical composition	7625.8	38	0.062
Soil physical features	3398.8	44	0.019	Soil physical features	9351.7	44	0.003
Complete	1200.1	26	0.401	Complete	4983.5	26	0.115
Reduced	1827.8	44	0.452	Reduced	8598.2	49	0.158
Perennial gypsovag richness				Gypsophyte cover			
<i>Null</i>	563.0	49		<i>Null</i>	1035.0	49	
Age	535.8	48	0.048	Age	720.6	48	0.304
Geography	514.2	43	0.017	Geography	868.4	43	0.066
Soil chemical composition	220.8	38	0.507	Soil chemical composition	533.6	38	0.352
Soil physical features	477.1	44	0.077	Soil physical features	836.2	44	0.120
Complete	170.2	26	0.451	Complete	349.3	26	0.388
Reduced	271.1	47	0.508	Reduced	489.9	44	0.485
Annual gypsovag richness				Total evenness			
<i>Null</i>	3713.4	49		<i>Null</i>	0.120	49	
Age	2625.4	48	0.293	Age	0.120	48	0.002
Geography	2614.9	43	0.216	Geography	0.110	43	-0.019
Soil chemical composition	2093.4	38	0.292	Soil chemical composition	0.097	38	-0.011
Soil physical features	3381.8	44	0.008	Soil physical features	0.113	44	-0.026
Complete	1252.2	26	0.388	Complete	0.073	26	-0.102
Reduced	2197.7	46	0.383				
Gypsophyte richness							
<i>Null</i>	497.7	49					
Age	358.4	48	0.280				
Geography	384.8	43	0.139				
Soil chemical composition	234.3	38	0.408				
Soil physical features	323.9	44	0.291				
Complete	111.8	26	0.592				
Reduced	216.4	44	0.527				

Table 3. Parameters and fitted values of the reduced generalized linear models built after the forward selection analysis for six response variables (the reduced model for total evenness was not significant). Act. lims. = Active limestone, Agr. pract. = agriculture practices, Coef. = regression coefficient for each variable, SE = standard error, $t = t$ statistic to test if the coefficient is different from zero, d.f. res = residual degrees of freedom, Res. Dev. = residual deviance, $F = F$ statistic to test the fit of the model after introducing each variable. Significance was considered at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). D^2 adjusted value is the equivalent to r^2 in these models.

	Coef. (SE)	t	df	Res. Dev.	D^2	F
Total richness						
<i>Null</i>						
Intercept			49	3633.3		
Act. limes.	411.3 (142.8)	2.879**				
Age	0.546 (0.165)	3.318**	48	2667.4	0.266	23.25***
Longitude	-0.123 (0.040)	-3.047**	47	2444.2	0.327	5.37*
Agr. pract.	-0.0008 (0.0003)	-2.651*	46	2293.2	0.369	3.64*
Nitrogen	-3.14 (1.28)	-2.442*	45	2044.4	0.437	5.99*
	77.18 (33.80)	2.284*	44	1827.8	0.497	5.21*
Perennial gypsovag richness						
<i>Null</i>						
Intercept			49	563.0		
Conductivity	26.11 (3.58)	7.291***				
Sulphates	-0.006 (0.002)	-3.983***	48	444.7	0.210	20.51***
	-0.348 (0.063)	-5.485***	47	271.1	0.518	30.08***
Annual gypsovag richness						
<i>Null</i>						
Intercept			49	3713.4		
Age	29.536 (4.203)	7.027***				
Act. lims.	-0.169 (0.043)	-3.912***	48	2625.4	0.293	22.77***
Agr. pract.	0.385 (0.173)	2.222*	47	2398.6	0.354	4.75**
	-2.765 (1.349)	-2.050*	46	2197.7	0.408	4.20**
Gypsophyte richness						
<i>Null</i>						
Intercept			49	497.7		
Age	150.40 (48.06)	3.130**				
Calcium	0.034 (0.010)	3.229**	48	358.4	0.280	28.34***
Longitude	0.008 (0.002)	3.769***	47	295.1	0.407	12.86***
Nitrogen	-0.0003 (0.0001)	-3.109**	46	255.4	0.487	8.07**
Slope	24.42 (11.55)	2.116*	45	236.4	0.525	3.87*
	0.105 (0.052)	2.020*	44	216.4	0.565	4.08*
Total cover						
<i>Null</i>						
Intercept			49	10215.3		
Age	82.59 (2.68)	30.801***				
	-0.165 (0.055)	-3.005**	48	8598.2	0.158	9.03**
Gypsophyte cover						
<i>Null</i>						
Intercept			49	1035.0		
Age	-0.850 (2.496)	-0.341				
Act. lims.	0.047 (0.015)	3.069**	48	720.6	0.304	28.24***
C:N ratio	-0.641 (0.154)	-4.160***	47	671.1	0.352	4.45*
Potassium	0.654 (0.196)	3.329**	46	594.2	0.426	6.91*
Nitrogen	19.57 (7.36)	2.658*	45	537.9	0.480	5.05*
	37.35 (17.98)	2.078*	44	489.8	0.527	4.32*

donment. The TVE by the “Age” model ranged from 15% to 30% and showed especially high values for gypsophyte cover (30%) and richness (28%).

The model for “Soil chemical composition” explained a high percentage of richness variability (24–50%), but in pairwise model comparisons only perennial gypsovag and gypsophyte richness were explained significantly by this model. Although this model exerted no influence on total cover it did explain the 35.2% of gypsophyte cover variability; however, when the influence of “Age” model in “Soil chemical composition” model was considered, no significant influence in cover was found (Tables 2 and 4). Nitrogen positively affected total and gypsophyte richness as well as gypsophyte cover (Table 3). Active limestone positively influenced total rich-

ness and annual gypsovag richness, but negatively influenced gypsophyte cover. Perennial gypsovag richness was negatively influenced by conductivity and sulphate concentration. The reduced model with these two factors explained 51.8% of the variance. The calcium content and the C:N ratio, significantly explained gypsophyte richness and cover, respectively (Table 3).

The model for “Geography” and for “Soil physical features” were unimportant for explaining variance of diversity indices; furthermore, these variables were not significant in pairwise model comparisons (Tables 2 and 4). The reduced models showed that agricultural practices negatively affected total and annual gypsovag richness, and slope positively influenced gypsophyte richness (Table 3).

Table 4. Pairwise comparison of nested generalized Linear Models (GLMs) for richness and cover. Change in deviance for each comparison was tested by means of an *F*-test. The saturated model with all the variables (AGCP) was compared with the combination of the nested models and then the nested models were compared with individual components (A = age, G = geography, C = soil chemical composition, and P = soil physical features). ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$. df.: difference in degrees of freedom. *F*: *F*-ratio statistic. Res. Dev.: residual deviance. Letters in bold represent the model analysed in each case.

	<i>df</i>	Res. Dev.	<i>F</i>	<i>df</i>	Res. Dev.	<i>F</i>	<i>df</i>	Res. Dev.	<i>F</i>
Total richness			Perennial gypsosag richness			Annual gypsosag richness			
AG – A	6	538.63	1.572	6	49.88	0.718	6	519.88	1.728
AG – G	1	343.99	6.024*	1	28.19	2.437	1	509.37	10.161**
AGCP – CP	7	878.17	2.718*	7	25.27	0.551	7	765.34	2.270
AC – A	11	912.29	1.516	11	315.20	4.805***	11	863.64	1.649
AC – C	1	163.25	2.984	1	0.16	0.026	1	331.71	6.967*
AGCP – GP	12	1374.00	2.481*	12	261.16	3.324**	12	1127.80	1.951
AP – A	5	326.22	1.075	5	59.88	1.082	5	344.92	1.301
AP – P	1	788.20	12.983***	1	1.10	0.099	1	1101.30	20.767***
AGCP – GC	6	512.75	1.851	6	34.47	0.878	6	355.74	1.231
Gypsophyte richness			Total cover			Gypsophyte cover			
AG – A	6	60.60	1.425	6	1273.10	1.217	6	70.54	0.759
AG – G	1	87.08	12.284***	1	547.20	3.138	1	218.33	14.105***
AGCP – CP	7	81.25	2.700*	7	1834.10	1.367	7	151.93	1.616
AC – A	11	149.44	2.406*	11	1798.70	0.900	11	259.89	1.897
AC – C	1	25.40	4.498*	1	826.30	4.496*	1	72.88	5.852*
AGCP – GP	12	134.93	2.615*	12	2145.10	0.933	12	374.02	2.320*
AP – A	5	50.92	1.424	5	239.60	0.247	5	37.23	0.469
AP – P	1	16.49	2.307	1	993.10	5.109*	1	152.79	9.614**
AGCP – GC	6	40.01	1.551	6	782.60	0.681	6	125.13	1.552

Table 5. Canonical correspondence analysis (CCA) models using species count data as the main matrix and data sets based on age, geography, soil chemical composition, soil physical features data and a complete with all variables as constraining matrixes (same as in generalized linear models models). λ_1 , λ_2 , λ_3 are the eigenvalues of the corresponding extracted axes. Σ cons is the sum of all constrained axes. TVE is the variation explained by the constraining data set. *P* is the significance level of the model (999 randomizations; $P < 0.01$ following Holm's method).

Constraining matrix	λ_1	λ_2	λ_3	Σ cons	TVE	<i>F</i> -ratio	<i>P</i>
AGE (1 var)	0.187	0.415	0.298	0.187	4.29%	2.158	0.0010
Geography (6 var)	0.222	0.207	0.123	0.751	17.24%	1.493	0.0010
Soil chemical composition (11 var)	0.262	0.213	0.166	1.266	29.06%	1.415	0.0010
Soil physical features (7 var)	0.227	0.154	0.120	0.841	19.31%	1.435	0.0030
Complete (25 var)	0.341	0.282	0.246	2.650	60.84%	1.491	0.0010

Pairwise model comparisons demonstrated that the “Age” model alone was able to explain a large proportion of variability with little overlap with other models evaluated, although those models included many more variables (Table 4). Perennial gypsosag richness was primarily determined by soil chemical composition, which coincided with the results obtained in the reduced models. Both time since abandonment and soil chemical composition significantly explained gypsophyte richness.

Constrained ordination for hypothesis testing

Canonical Constrained Analyses were conducted in order to determine which fraction of the

total variation of the species data matrix was explained by each data set (Table 5). All the constraining matrixes explained significant fractions of variation ranging from 4.3% of the variation explained by the time of abandonment to the 29.1% explained by the soil chemical composition. The complete constraining matrix (25 variables) explained more than 60% of variation in species composition.

In the “Geography” model only latitude and cropland distance were selected by stepwise forward selection (Table 6). Magnesium, active limestone and phosphorous were significant in the case of soil chemical composition and only shallow ploughing was selected in the “soil physical features” model. In

Table 6. Results of the stepwise canonical correspondence analysis (CCA) forward selection for the significant CCA models (see Table 5). The 'Age' model did not need to be reduced. The 'Complete' model was also reduced. Only significant selected variables are represented. λ is the additional variance that each variable explains at the time it is included in the reduced model. Drop TVE expresses the difference between TVE of a model including all the variables and the TVE of the reduced model. F is the F -ratio statistic and P is the significance level of the reduced model (999 randomizations). Constraining matrices are indicated in the first row. Cro.dis. = Cropland distance; Magne. = magnesium, Ac.lims. = active limestone, Phosp. = phosphorous, Sha.plo. = shallow ploughing, Ab.age = abandonment age, Med.plo. = medium ploughing, Fin.san. = fine sand, Potass. = potassium.

<i>Geography (six variables)</i>				<i>Soil chemical composition (11 variables)</i>				<i>Soil physical features (seven variables)</i>			
	λ	F	P		λ	F	P		λ	F	P
Latitude	0.19	2.14	0.001	Magne.	0.20	2.34	0.003	Sha.plo.	0.14	1.57	0.045
Cro.dis.	0.17	1.99	0.008	Ac.lims.	0.18	2.08	0.004				
				Phosp.	0.13	1.59	0.015				
Reduced model				Reduced model				Reduced model			
TVE		8.15		TVE		11.73		TVE		3.17	
Drop TVE		9.09		Drop TVE		17.33		Drop TVE		16.14	
F		2.039		F		2.039		F		1.565	
P		0.001		P		0.001		P		0.037	
<i>Complete (25 var)</i>											
Magne.	0.20	2.34	0.006	Sulphate	0.16	1.90	0.003	Med.plo.	0.12	1.59	0.008
Altitude	0.18	2.08	0.002	Cro.dis.	0.15	1.86	0.014	Fin.san.	0.12	1.50	0.033
Ab.age	0.16	1.99	0.002	Phosp.	0.13	1.69	0.008	Potass.	0.11	1.48	0.036
				Reduced model							
				TVE		30.49					
				Drop TVE		30.35					
				F		1.950					
				P		0.0010					

the saturated matrix, nine out of 25 variables were selected to build the reduced model (30.5% of variance explained; Table 6).

The biplots of the reduced model (nine variables) showed that old plots were rich in phosphorous and sulphates and poor in magnesium and potassium content, and that they were located far from new croplands (Fig. 2b). In summary, although time since abandonment only explained 4.3% of species compositional variability, our results showed that gypsophyte species tended to appear in older plots. *Reseda stricta* and *Reseda suffruticosa* were exceptions, which were found in early succession plots, whereas *Sedum gypsicola*, *T. pumilum*, *T. lacaitae* and *H. fruticosa* appeared later. It is notable that some perennial species established very early in succession, such as *Matthiola fruticulosa* and *Euphorbia nicaeensis* (Fig. 2a).

Age, geography and soil chemical composition variables explained a total of 22.5% of the variation in species composition. Only the three environmental variable models that explained a higher percentage of variability were used. Partial CCAs showed that the overlap between models was low (1.4%) because the largest amount of this explained variation was explained by "pure" (non-shared)

models: 10.5% by soil chemical composition variables, 7.2% by geography variables and 3.4% by time since abandonment (Fig. 3).

Discussion

Community composition recovery

The chronosequence showed that old-field succession on semi-arid Mediterranean gypsum soils was controlled by a complex set of factors: time since abandonment, soil chemical conditions and other topographic and spatial components such as distance to the nearest cropland. These factors together significantly explained a relevant fraction of the community composition (22%) with almost no overlap among them. However we unexpectedly found that time from abandonment only explained a small but significant proportion of compositional variation (3.4%; Fig. 3). In most studies on plant secondary succession, time since abandonment strongly affects vegetation composition and structure (Ne'eman & Izhaki 1996; Bonet & Pausas 2004; Lesschen 2008). It is further expected that soil features and time since abandonment should be tightly

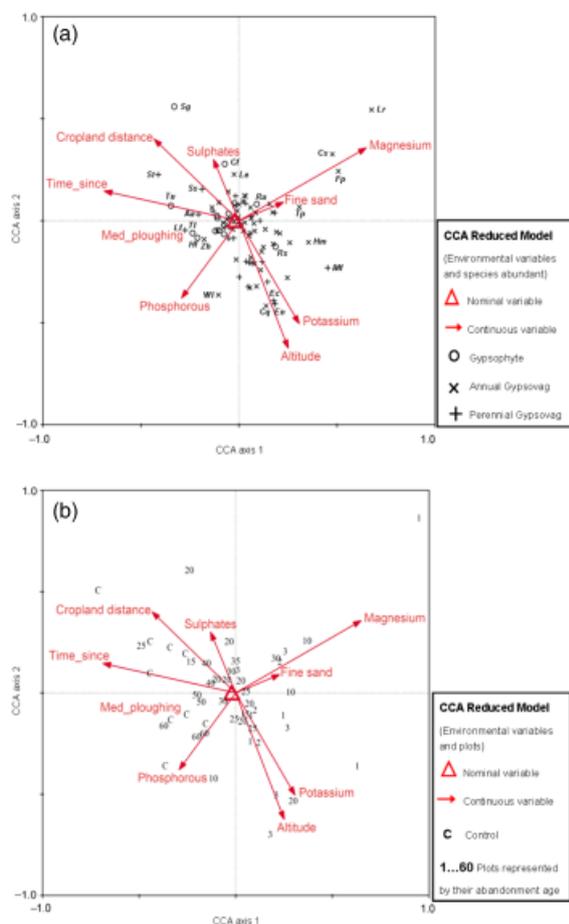


Fig 2. Biplot of the constrained axes of the reduced model for canonical correspondence analysis (CCA) using as the main matrix species abundance and as the constraining matrix the environmental variables selected in the forward selection process: (a) Species abundance and environmental variables; (b) Plots and environmental variables. Aa = *Asphodelus albus*; Cf = *Campanula fastigiata*; Cq = *Centaurium quadrifolium*; Cs = *Coronilla scorpioides*; Ec = *Eryngium campestre*; En = *Euphorbia nicaeensis*; Fp = *Filago pyramidata*; Hf = *Herniaria fruticosa*; Hm = *Hordeum murinum*; Le = *Limonium echioides*; Lf = *Lithodora fruticosa*; Lr = *Lolium rigidum*; Mf = *Matthiola fruticulosa*; Rs = *Reseda stricta*; Ru = *Reseda suffruticosa*; Sg = *Sedum gypsicola*; Ss = *Sedum sediforme*; St = *Stipa tenacissima*; Tl = *Thymus lacaitae*; Tp = *Trigonella polycerata*; Tu = *Teucrium pumilum*; Wl = *Wangenheimia lima*; Zh = *Ziziphora hispanica*; Med_ploughing = medium ploughing; Time_since = time since abandonment.

related such that their effects on composition overlap conspicuously. As a consequence we may expect that as secondary succession advances, soil conditions would undergo a parallel amelioration process (Martínez-Fernández et al. 1995; Ruecker et al. 1998; Dunjó et al. 2003; Bonet 2004).

However, we found some significant effects of time from cultivation on community attributes. The

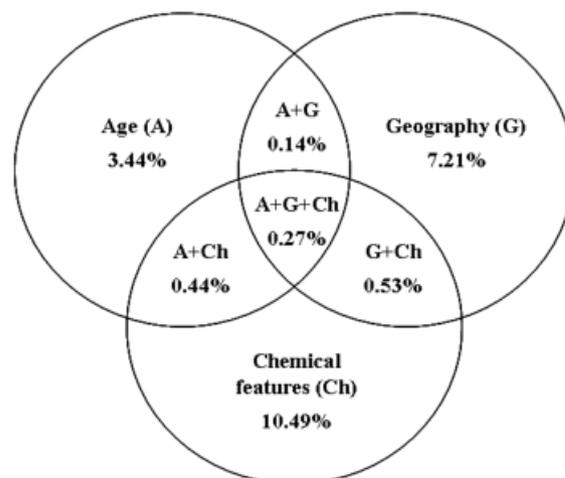


Fig. 3. Result of the variance partitioning analysis. Percentage of explained variation in species community structure accounted for by age, geography and soil chemical composition variables, and the shared variation among these components.

highest values for richness and cover were detected immediately after abandonment. Richness and cover decreased with time, from a rich grassland dominated by annual gypsovag species to a shrubland dominated by perennial gypsovag and gypsophyte specialists. This pattern of vegetation change is closely comparable with the one described for abandoned vineyards in dry Mediterranean areas (Ne'eman & Izhaki 1996), in which annual plants are replaced by perennial grasses and shrubs. However, for this semi-arid system plant cover was not dependent on age of abandonment as reported for other dry Mediterranean ecosystems (Bonet & Pausas 2004; Dana & Mota 2006). Cover, a recognized surrogate of primary productivity, may vary little over time and remain near 40% in these semi-arid environments (Bonet & Pausas 2004; Dana & Mota 2006). Our unexpected result is probably related to the fact that gypsum soils are extremely poor and recently abandoned crop fields which have been managed for long periods could maintain relatively higher levels of primary productivity for the first stages of secondary succession. Species richness usually increases with field age in old-field succession in tropical and temperate ecosystems (Bazzaz 1975; Bornkamm 1981; Tilman 1988). However, a decrease in species richness from intermediate to later stages is a general trend in Mediterranean old fields (Debussche et al. 1996; Bonet 2004). In this study, maximum species richness was reached immediately after abandonment, which was probably related to higher productivity

after abandonment and to the annual gypsovag assembly of soil seed banks (Bonet 2004). Seed bank composition and density can play a crucial role in above-ground vegetation dynamics immediately after abandonment (Baskin & Baskin 1998; Luzuriaga et al. 2005).

Succession process and mechanisms

Recovery of community structure and composition seems relatively rapid, in that composition and total cover of control plots did not differ from that of plots 50-60 yr after abandonment. An apparent feature of the studied succession was an increasing representation of specialized gypsophyte species, as suggested by the separation of annual gypsovags from perennial gypsophytes on the time environmental axis on Fig. 2a. However, some true gypsophytes were detected at early stages of the succession. Their presence is unlikely to rely on dispersal, which is very inefficient in most gypsophytes (i.e. mixospermy; see Escudero et al. 2000), and most likely relies on a dense soil seed bank (Caballero et al. 2008). Anchoring by mucilage is a common dispersal mechanism of desert and Mediterranean plants (Gutterman 1993): long-range dispersal represents a low benefit as an adaptive trait in these species because the most favourable environment is usually located in the vicinity of mother plants (Ellner & Schmid 1984). In the case of gypsophytes, the scarcity and unpredictable distribution of gypsum outcrops make the dispersal process even more risky (Escudero et al. 1999, 2000). This limited dispersal pattern may help explain why most gypsophytes are narrow endemics restricted to very local gypsum outcrops.

The most relevant set of predictors for species composition is the soil chemical data set (Fig. 3) independent of time since abandonment. Experimental approaches showed that nutritional levels, especially nitrogen, in dry soil played a decisive role on composition and community structure (Tilman 1988; Pausas 1994; Pugnaire et al. 1996). We found a positive correlation between nitrogen content and total richness and gypsophyte richness and gypsophyte cover. It has also been suggested that organic carbon plays an important role in semi-arid successional stages (Carreira et al. 1994; Bonet 2004). In our case, this type of response is related to the amount of active limestone and not to the organic carbon, which influenced positively total and annual gypsovag richness, but negatively influenced gypsophyte cover. This is an expected result as gypsovags are able to grow on a wide range of calcium con-

centrations in soils (Palacio et al. 2007). However, perennial gypsovag richness was strongly negatively correlated to salt (conductivity) and gypsum (sulphates) concentration in soil. This result suggests that re-establishment of true perennial specialists is not a question of time, but mainly of soil chemical heterogeneity. High salt and gypsum concentrations were associated with fewer perennial gypsovag species (Escudero et al. 1999; Romao & Escudero 2005; Dana & Mota 2006; Pueyo & Alados 2007). Unbalanced ion concentration can prevent non-gypsophile vegetation from establishing on these substrates (Pueyo et al. 2007). High contents of gypsum and phosphorous and low contents of magnesium and potassium were characteristic of control plots and related to gypsophyte species composition.

Other studies showed that previous land uses were the key to understanding the variability of plant composition and richness in semi-arid old fields, and they suggest that different disturbance regimes should be considered in order to understand the mechanisms driving old-field succession (Bonet & Pausas 2007) and affecting vegetation dynamics (Bonet 2004). However, in our study, composition was not affected by land-use intensity. Only high-intensity agricultural practices before abandonment reduced the number of annual gypsovags, probably owing to impoverishment of the soil seed bank (Ball 1992; Reiné et al. 2004).

Topography is a key factor determining plant patterns on gypsum hills (Machín & Navas 1998; Escudero et al. 1999; Pueyo et al. 2007). Topographical position on gypsum hills promotes differences in rigours of gypsum soil conditions which, in turn, leads to changes in the gypsophile plant communities (Pueyo et al. 2007). Slope appeared to be an important factor in gypsophyte composition, while altitude and distance to cropland affected vegetation composition. These factors were related to the process of field abandonment. Fields characterized by difficult conditions for farming were the first to be abandoned. A high correlation is therefore expected between altitude or slope and age of abandonment (Bonet 2004). Remnant crops in the vicinity were rich in ruderal and weed gypsovags, which may have dispersed as seed sources into surrounding plots.

Individual responses along succession

Gypsophyte species abundance showed contrasting responses. For example *R. stricta* and *R. suffruticosa* appeared early in the secondary

succession, although *R. suffruticosa* needed soils richer in sulphates. They behaved like annual gypsovags and were more abundant on plots with less restrictive soil conditions. In contrast, the gypsophytes *T. pumilum* and *S. gypsicola* competed better on genuine gypsum soils with well-developed physical surface soil crusts; thus they needed more time to reappear in the secondary succession. These dynamics have been reported in other studies related to different topographical habitat preferences (Pueyo et al. 2007).

Conclusions

Our results suggest that old-field succession in specialized habitats such as gypsum outcrops constitutes a new dynamic model for Mediterranean ecosystems. This model contrasts markedly with the amelioration mechanism that describes many old-field successions (Debussche et al. 1996; Haase et al. 1996; Ne'eman & Izhaki 1996; Pugnaire & Luque 2001; Bonet 2004). Time since abandonment was only a minor predictor of the composition and other attributes of the plant community in secondary succession. Furthermore, time since abandonment was independent of other predictors. This was especially significant in the case of soil chemical composition. Heterogeneity of other predictors was relevant in explaining vegetation composition and structure independent of time since abandonment. The most conspicuous differences along succession in these restrictive habitats were related to the global performance of the specialized gypsophytes and generalist gypsovags. Romao & Escudero (2005) experimentally re-confirmed that gypsum edaphic specialists based their establishment strategy largely on the ability to overcome the extremely hard gypsum surface crusts during emergence (Meyer 1986). Recovery of biological soil crusts is very slow (Martínez et al. 2006) and directly related to the hardness of the physical crust (Tarazona et al. 1980), but the physical gypsum crust is conformed within a few years of abandonment. Once the gypsum crust is conformed, gypsovags only can occur in gypsum islands under the canopy of genuine gypsophytes (Romao & Escudero 2005). Even more in mature gypsum communities the presence of biological crusts probably affects dispersal and emergence of most plants in the community (Escudero et al. 2007). As a consequence, annual gypsovags may dominate before the soil physical crust is reconstructed but gradually become rarer as succession advances.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. List of species detected in the vegetation samples. F.g. = functional groups; aG: annual gypsovags (annual and biannual species); pG = perennial gypsovags; Gy = gypsophytes; % plots = percentage of plots where the species was present ($n = 50$); % counts = percentage of total counts per species in plots overall ($n = 20\,000$).

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