



# Species traits weakly involved in plant responses to landscape properties in Mediterranean grasslands

Guillem Bagaria, Joan Pino, Ferran Rodà & Moisès Guardiola

## Keywords

Grassland vegetation; Habitat loss; Land-use; Landscape structure; Phylogenetic signal; Plant traits; RLQ analysis; Three-table ordination

## Nomenclature

Bolòs et al. (2005)

Received 29 November 2010

Accepted 12 October 2011

Co-ordinating Editor: Amy Symstad

**Bagaria, G.** (corresponding author, g.bagaria@creaf.uab.cat), **Pino, J.** (joan.pino@uab.cat), **Rodà, F.** (ferran.roda@uab.cat) & **Guardiola, M.** (m.guardiola@creaf.uab.cat): Centre for Ecological Research and Forestry Applications (CREAF) and Unit of Ecology, Department of Animal and Plant Biology and Ecology, Universitat Autònoma de Barcelona, ES-08193, Bellaterra (Barcelona), Spain

## Abstract

**Questions:** What is the role of landscape structure and dynamics, compared with climatic and geographic factors, in determining species frequencies of grassland plant specialists under habitat loss? Do species traits mediate the relationship between plant community composition and environmental variables?

**Location:** The Mediterranean mountain grasslands of southern Catalonia (NE Iberian Peninsula), over an area of 100 × 20 km.

**Methods:** Using redundancy analysis (RDA), we explored the association between frequency of broad plant specialists and both present and past habitat patterns in the landscape (i.e. habitat amount and reduction over the period 1956–2003), after accounting for the effect of geographical location and climate in 29 grassland patches. Then, we constructed a database of biological and ecological plant traits potentially related to population persistence, in order to assess the role of these traits in explaining the found association between species composition and environmental variables. We used a single, three-table ordination analysis (RLQ) of the species frequencies, environmental variables and species traits to relate species traits to environmental variables, after allowing for phylogenetic dependence of traits.

**Results:** The main environmental gradient explaining species frequencies was climatic and geographic. Habitat amount in the current landscape significantly affected species frequencies, while habitat amount in the past landscape did not. A weak but significant association of species traits with environmental variables was detected. Taking into account the phylogenetic signal in plant traits did not change the results.

**Conclusions:** Plant species in Mediterranean grasslands seem to respond quickly to landscape change, since no effect of past landscape structure was observed on current species frequencies. Moreover, plant traits did not play a major role in mediating species response to environmental variation in these grasslands. Our findings differ from those obtained in northern and central European grasslands, probably due to differences in methodology but also to the smaller contrast in environmental conditions between grasslands and the adjacent forests and scrub in Mediterranean landscapes.

## Introduction

Global land-use changes over the last century have had a large negative impact on Earth's biodiversity through habitat loss and fragmentation (Millennium Ecosystem Assessment 2005), and these changes are expected to remain as the main extinction cause throughout the 21st century (Sala et al. 2000). Plant species might decline or even dis-

appear locally during or after land-cover changes, leading to smaller and more isolated habitat patches, especially if populations are small and the new habitat is not suitable for establishment and growth (Maina & Howe 2000; Lindborg & Eriksson 2004; Lindborg et al. 2005).

Habitat specialists are largely confined to remnant habitat fragments and hence are the species more affected by habitat loss and isolation (Dupré & Ehrlén 2002; Adriaens

et al. 2006; Pino et al. 2009). Furthermore, processes compromising the survival of small populations might result in non-random extinctions depending on species traits related with life-history and plant performance (Stöcklin & Fischer 1999; Grime 2002). Recent studies in grasslands and forests have identified several biological traits mediating species responses to landscape structure and dynamics. Plant height, specific leaf area, vegetative spread, flowering period and seed mass vary across successional gradients in abandoned grasslands, with contrasting results among studies (Kahmen & Poschlod 2004; Lindborg & Eriksson 2005). Plant and seed bank longevities, seed mass and dispersal type play an important role in explaining the effect of grassland area and connectivity on species composition (Bruun 2000; Lindborg 2007). Plant longevity, seed number and dispersal type also explain species' responses to habitat area and isolation in forests (Dupré & Ehrlén 2002). In the only study of this kind conducted in a Mediterranean area, Chust et al. (2006) found that life form and dispersal type were related to landscape composition in scrubland but not in grassland. However, these studies did not take into account phylogenetic relatedness among species, and Tremlová & Münzbergová (2007) recommended conducting the analyses with and without phylogenetic correction, as the conclusions of trait responses to environment can sometimes be altered.

The extent of European grasslands, which harbour a high number of endangered plant species (WallisDeVries et al. 2002), was substantially reduced following rural depopulation over the second half of the twentieth century; most of these grasslands were transformed to arable fields or forests (Eriksson et al. 2002; Adriaens et al. 2006; Helm et al. 2006). The Mediterranean basin is not an exception to this trend (Debussche et al. 1999) and, due to the high biodiversity found in these ecosystems, an important species pool is becoming endangered (Myers et al. 2000). Despite this, little is known about the role of species traits on plant persistence in these grasslands (e.g. Chust et al. 2006), unlike the thoroughly studied case of temperate and boreal European grasslands (e.g. Bruun 2000; Kahmen & Poschlod 2004; Adriaens et al. 2006; Lindborg 2007). Following those studies, we would expect plants with vegetative spread to be more frequent in reduced, small and isolated grasslands due to the maintenance of remnant populations that could persist for many years (Lindborg 2007). In contrast, large-seeded species and plants without any specific seed dispersal mechanism should be less frequent in these reduced, small and isolated grasslands, as they generally have limited dispersal ability (Willson 1993; Dorp et al. 1996). However, results could differ in Mediterranean grasslands, where woody species are much more abundant than in other European grasslands and few strict habitat specialists exist.

The aim of this study is thus to investigate plant community composition and species traits in response to landscape changes, specifically habitat loss and fragmentation experienced by semi-natural Mediterranean communities in the last few decades. Our main objectives were: (1) to determine the role of habitat spatio-temporal patterns at the landscape level (i.e. habitat amount and dynamics) in the distribution of grassland specialists in comparison with climatic and geographic factors; and (2) to investigate whether species traits mediate the relationship between species distribution and environmental variables.

We recorded plant frequencies in grassland patches with contrasting size and dynamics in the mountain ranges of southern Catalonia (NE Iberian Peninsula). Then, we selected broad habitat specialists and constructed a database of biological and ecological traits for these species. We used a three-table ordination analysis (RLQ) to relate plant traits to environmental variables through species frequencies (Dolédec et al. 1996), taking into account the phylogenetic signal (Pavoine et al. 2011). The approaches used by previous studies with similar purposes were less comprehensive, either defining a priori functional groups (Bruun 2000; McIntyre & Lavorel 2001; Verheyen et al. 2003; Kolb & Diekmann 2005; Adriaens et al. 2006), using the proportions or medians of traits at each plot (McIntyre & Lavorel 2001; Lindborg 2007), or analysing traits one by one (Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Chust et al. 2006). Our approach overcomes these limitations through simultaneous consideration of all plant traits over all sampled plots, while taking into account species composition and phylogeny.

## Methods

### Study area

We conducted the study in mountain ranges of southern Catalonia (NE Iberian Peninsula) aligned along a NE–SW axis between Prades and Ports massifs (40°39' – 41°23'N, 0°10' – 1°10'E). We focused our study on semi-natural Mediterranean mountain grasslands, rich in dwarf shrubs and corresponding to the *Aphyllanthes* grasslands of the CORINE habitats classification (Moss et al. 1990). These grasslands are, on average, equally dominated by hemi-cryptophytes and chamaephytes of less than 50 cm in height, and exhibit vegetation cover between 50% and 80%. In the study area, many of these grasslands are currently subject to woody encroachment due to grazing cessation. Also, they are concentrated in calcareous plateaux between 800 and 1400 m a.s.l., with mean annual temperature between 10 and 13 °C, mean annual precipitation between 650 and 1050 mm, and marked summer drought (Digital Climatic Atlas of Catalonia; [www.opengis.uab.cat/acdc](http://www.opengis.uab.cat/acdc)).

## Study patch selection

We digitized all grassland patches of the study area by on-screen photo-interpretation of historical (1956) and recent (2003) orthophotomaps using ArcGIS (version 9.2; Environmental Systems Research Institute, Redlands, CA, USA). We obtained historical aerial photographs from archives of the Spanish Army. Scale of the original photos was ca. 1:30 000, and pixel size of the resulting orthophotomaps was 1 m. The Cartographic Institute of Catalonia ([www.icc.cat](http://www.icc.cat)) produced present-day (2003) orthophotomaps, with a scale of 1:5000 and a pixel size of 0.5 m. Thus, there is a time period of 47 yr between current and historical landscape information. We used fieldwork to select 29 of the above patches that: (1) represented a range in current patch area (from 0.1 to 26.8 ha) and in patch area reduction in recent decades (from 0 to 99.8%); (2) were grassland both in 1956 and 2003, thus excluding grasslands in 2003 resulting from abandonment of cultivated fields in 1956; (3) showed no signs of recent burning; and (4) whenever possible, were at least 1-km apart from each other to increase data independence and reduce overlap between the surrounding landscapes. Sample patches were distributed over an area of 100 × 20 km, and were surrounded by forest and dense scrubland.

## Plant species composition

In each sample patch, we laid out 25 randomly distributed 0.5 m × 0.5 m plots during spring 2007 and recorded to subspecies level the presence of all vascular plants with any aerial part within the plot boundaries. For analysis we selected grassland specialist taxa in a broad sense, i.e. those that, according to the literature (Rivas-Martínez et al. 2001; Bolòs et al. 2005), mostly grow in grasslands and dwarf scrublands, as few plant species are specialists of this habitat in the strict sense. We excluded specialist taxa that were present in less than 3% of all sampled plots (pooled over all patches) from statistical analyses.

## Phylogeny

To account for phylogenetic effects on plant traits, we constructed a phylogenetic tree using the last update (Jul 2010) in the topology of the new Angiosperm Phylogeny Group classification (APG III Group 2009) and other phylogenies from groups lacking good resolution. We used the *bladj* algorithm with a set of 20 dated nodes (mostly from Hedges & Kumar 2009) to estimate tree branch lengths. Tree construction and dating were performed with the program Phylocom (version 4; Webb et al. 2008). See App. S1 for detailed information and sources.

## Species traits

For the species encountered in the field sampling, we used literature, databases, unpublished studies, personal observations and communications from other plant researchers to compile a database of 13 biological and ecological traits related to plant and population persistence (App. S2): seed size (maximum length without appendages, mm), dispersal type (anemochorous, wind-dispersed; zoochorous, animal-dispersed; barochorous, without any specific dispersal mechanism), corolla type (anemophilous; open entomophilous corolla; tubular; zygomorphic entomophilous), flower or pseudanthium (flower heads of Asteraceae, Globulariaceae, etc.), size (maximum length, mm), resprouting ability after fire (yes; no), life form (annual; herbaceous perennial; woody), mean plant height (small, <25 cm; intermediate, 25–50 cm; tall, >50 cm), vegetative spread (yes; no), leaf anatomy (aphyllous; succulent; mesomorphic, wrinkled once dry; scleromorphic, rigid once dry), leaf area (or leaflet in compound leaves, cm<sup>2</sup>), spinescence (yes; no), phytogeography (strictly Mediterranean, species distributed almost only in the area of Mediterranean climate; broadly Mediterranean, species distributed in the Mediterranean climate and in colder and wetter areas; other, mostly pluri-regional species [based on Bolòs et al. (2005)]), and mammalian herbivore preference (preferred; indifferent; rejected). The above list was based on the traits suggested by Weiher et al. (1999) and Westoby et al. (2002) but extended with traits used in more recent studies (e.g. Kolb & Diekmann 2005; Adriaens et al. 2006) or considered by us to be important in the study area for resistance to herbivores (spinescence) or for pollination (flower size). Phytogeography was included because it is closely related to climate tolerances, with strictly Mediterranean species preferring dry and warm sites and broadly Mediterranean ones also being abundant in colder and wetter sites. These traits were obtained for 49 species. The remaining 13 species were not used in analyses because information on all of their traits was not available, and our analysis method does not allow missing values. Almost half of these 49 species were woody (24 species; 49%), 22 (45%) were herbaceous perennials and only three (6%) were annuals.

## Environmental variables

Besides past and current patch areas and their change over time, we obtained from the orthophotomaps of 1956 and 2003 three additional variables related to habitat amount and connectivity: percentage of past and current grassland area in the landscape surrounding each patch (1-km buffer around the patch perimeter, including the patch itself), and percentage of grassland area reduction in this

landscape. We consider this buffer distance to be sufficient for taking into account dispersal events in our abrupt landscape, as it was also used in similar studies in flat areas (Lindborg & Eriksson 2004). In addition, we also considered four geographic and climatic variables for the analyses: longitude (UTMx), latitude (UTMy), mean annual temperature and mean annual precipitation (App. S3). Both climatic variables were obtained from the Digital Climatic Atlas of Catalonia ([www.opengis.uab.cat/acdc](http://www.opengis.uab.cat/acdc)). We did not include other environmental variables due to high correlations to the previous ones (e.g. altitude, correlated with temperature and precipitation; mean summer precipitation, correlated to annual precipitation) or lack of information (e.g. grazing pressure, time since pasture abandonment). The correlation matrix between environmental variables is given in App. S8.

### Statistical analyses

The relationship between environmental variables and species traits or trait combinations can be assessed through the simultaneous analysis of three data tables (Dolédec et al. 1996): a species abundance  $\times$  site table is used as the link between an environment  $\times$  site table and a trait  $\times$  species table to investigate the so-called 'fourth-corner' table that is missing (i.e. the fourth table that would relate the environmental variables to species traits). Two methods have been described to tackle this problem. RLQ analysis (Dolédec et al. 1996) provides a simultaneous multivariate ordination of the three tables, whereas fourth-corner analysis (Legendre et al. 1997; Dray & Legendre 2008) tests the correlation between the environmental variables and the species traits. Here we used the former approximation because ordination allows the visualization of trait combinations and environmental gradients that combine more than one variable.

We constructed three data tables with the information on: (1) species frequencies (columns) in each patch (rows; table L, App. S4); (2) the values of environmental variables (columns) at each patch (rows; table R, App. S5); and (3) the traits (columns) for each species (rows; table Q, App. S6). We transformed the species frequency table (L) using the Hellinger transformation (Rao 1995) to reduce the effect of the most abundant species (Lacourse 2009) and solve the inherent problems of the Euclidean distance (Legendre & Gallagher 2001). Then, we investigated the relationship between species composition and the main environmental gradients using an ordination analysis of species frequencies (L) constrained by environmental variables (R). Since a detrended correspondence analysis (DCA) on the frequency table resulted in gradient lengths  $< 2$  SD, we used a linear constrained ordination (redundancy analysis, RDA) to relate community composition to

environmental variables. We applied a step-wise selection to obtain a model for the constrained ordination that avoided multicollinearity and to compare the variance explained by this model in to the variance explained by all ten environmental variables considered in the analysis. We performed ANOVA-like permutation tests (Legendre & Legendre 1998) with 9999 permutations to assess the statistical significance of the association between species composition and the variables selected, for the entire model and for each axis. We conducted the RDA analysis using the *vegan* package in R (R Core Development Team, Vienna, Austria).

We constructed a matrix of pair-wise phylogenetic distances among species. The distance metric used was the square root of the sum of branch lengths along the shortest path that connects species, which provides Euclidean distances (Pavoine et al. 2011). To test whether species traits had a phylogenetic signal, we constructed a matrix of pair-wise trait distances among species using the mixed-variables coefficient of distance (Pavoine et al. 2009) and applied the root-skewness test developed in Pavoine et al. (2010) with 999 Monte Carlo simulations. Species traits show a phylogenetic signal if trait diversity is biased to the root of the phylogenetic tree, otherwise (trait diversity biased to the tips or at random) no phylogenetic signal in traits can be identified.

Then, in order to relate species traits to environmental variables through species composition, we conducted a RLQ analysis (Dolédec et al. 1996), which consists of a simultaneous ordination of species traits (Q), environmental variables (R) and species frequencies (L). We also incorporated the phylogeny in the analysis, using the extended RLQ approach described in Pavoine et al. (2011). We first analysed the distance matrix of traits and the distance matrix of phylogeny by principal coordinates analysis (PCoA) with row weights equal to column weights of the correspondence analysis (CA) of table L, standardized the row coordinates by dividing them by the square root of the first eigenvalue of the respective analysis, and juxtaposed these two tables, obtaining the Q table of traits and phylogeny. Then we analysed the three tables (R, L and Q) separately to allow comparisons with the results of the joint analysis. We used a correspondence analysis (CA) of table L to obtain the simultaneous ordination of species and patches. We conducted a principal components analysis (PCA) of table R with row weights equal to row weights of the CA and another PCA of table Q with row weights equal to column weights of the CA. Then we used a version of RLQ based on the CA of the species frequencies in patches to study the joint structure of the three tables. This method is a trade-off among the three separate ordinations and, since the frequency table is processed by CA, it maximizes the covariance between patches and species scores

(Dolédéc et al. 1996), resulting in the best joint combination of the ordination of the three data tables: patches–environment (R), species frequencies–patches (L) and species–traits and phylogeny (Q; Ribera et al. 2001). We tested the global statistical significance of the analysis by comparing the total inertia value in the RLQ analysis obtained from the data to the distribution of the total inertias obtained from 999 Monte Carlo permutations of the rows of tables R and Q (Dolédéc et al. 1996). To investigate the strength of the association between tables of environmental variables and species traits, we compared the RLQ results with the results of the separate analyses of the three tables. The results of this RLQ analysis were also compared with the results of a standard RLQ analysis (without including phylogeny), as proposed by Tremlová & Münzbergová (2007) for analyses involving species traits and landscape attributes. In this analysis, table Q was the raw species traits table and it was analysed using a multi-variate analysis with mixed quantitative variables and factors (Hill & Smith 1976) with row weights equal to column weights of the CA. We obtained the distance matrices and performed RLQ analysis using the ade4 package (Chessel et al. 2004) in R.

## Results

### Constrained ordination of the species frequencies by the environmental variables

In the direct gradient analysis performed with RDA, the full model including ten environmental variables explained almost half (45.3%) of the total variance in the species frequencies. The reduced model obtained by the step-wise procedure still explained substantial variance (27.1%) and included only three environmental variables: UTM<sub>y</sub>, percentage of grassland area in the current landscape, and mean temperature (Table 1; Fig. 1). The permutation tests for this model revealed a highly significant overall association between species composition and constraining variables ( $P < 0.0001$ ) as well as a statistical significance for the first two axes ( $P < 0.0001$  and  $P = 0.005$ , respectively).

Axis 1 of this RDA explained 14.8% of the variance in species composition and had relatively high correlations with two geographic and climatic variables: latitude (positively correlated) and mean temperature (negatively correlated; Fig. 1). Species such as *Genista hispanica* and *Satureja montana* plotted on the negative side, being significantly associated, respectively, with southern study sites ( $r^2 = 0.20$ ) and warm sites ( $r^2 = 0.14$ ). *Narcissus assoanus*, *Staehe-lina dubia*, *Helianthemum oelandicum italicum*, *Arctostaphylos uva-ursi*, *Stipa offneri*, *Linum tenuifolium suffruticosum*, *Globularia vulgaris*, *Lithospermum fruticosum* and *Koeleria vallesiana* plotted on the positive side of the first axis, all significantly associated with northern and cooler sites ( $r^2$  between 0.14

**Table 1.** Redundancy analyses (RDAs) of the species frequency table: variance explained by each environmental variable alone and results of the step-wise selection procedure.

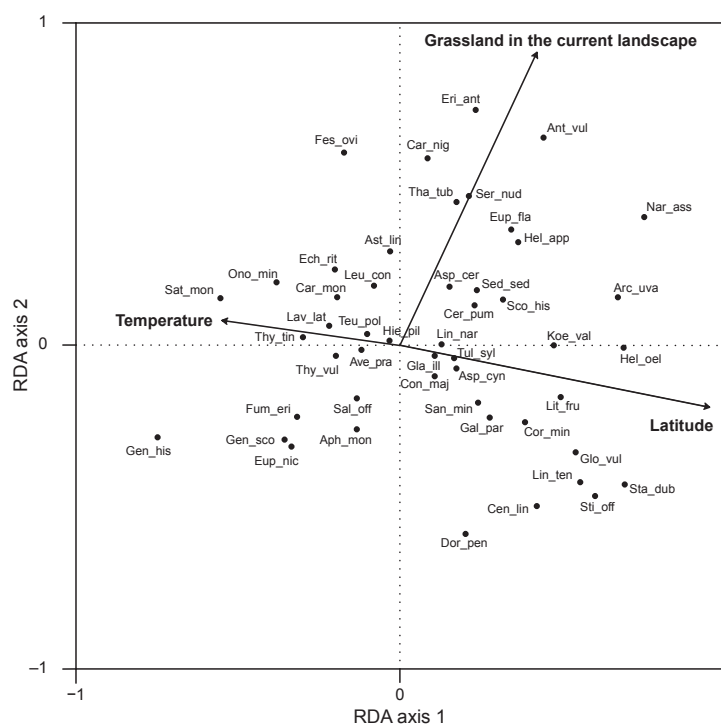
Environmental variable	RDA models	Step-wise model	
	Variance (%)	F	P-value
Latitude (UTM <sub>y</sub> )	14.1	3.74	<0.001
Percentage of grassland area in the current landscape	9.0	2.76	<0.001
Mean annual temperature	7.6	1.70	0.033
Mean annual precipitation	11.7	1.15	0.27
Longitude (UTM <sub>x</sub> )	13.2	1.14	0.28
Percentage of grassland area in the past landscape	6.5	0.99	0.45
Past patch area	4.8	0.83	0.66
Percentage of grassland area reduction in the landscape	4.8	0.84	0.69
Percentage of patch area reduction	4.7	0.82	0.73
Current patch area	7.5	0.73	0.81
Variance explained by the selected model <sup>1</sup> (%)			
Axis 1			14.8
Axis 2			7.8
All three axes			27.1

<sup>1</sup>The selected model includes the first three environmental variables.

and 0.41 for latitude and between 0.17 and 0.43 for temperature), except *Staehe-lina dubia* that was only associated with northern sites ( $r^2 = 0.36$ ). RDA axis 2 explained 7.8% of the variance and was most strongly correlated (positively) to percentage of grassland area in the current landscape. *Dorycnium pentaphyllum pentaphyllum*, *Centaurea linifolia linifolia* and *Stipa offneri* plotted on the negative side, but none of them was significantly associated with current landscapes with small grassland area. On the other hand, *Erinacea anthyllis*, *Anthyllis vulneraria fontqueri*, *Festuca ovina*, *Carduus nigrescens nigrescens* and *Serratula nudicaulis* plotted on the positive side of the second axis, and were significantly associated with current landscapes with abundant grassland ( $r^2$  between 0.23 and 0.37; *Festuca ovina* only marginally with  $r^2 = 0.13$  and  $P = 0.054$ ).

### RLQ analysis relating species traits to environmental variables

Traits had a significant phylogenetic signal, as trait diversity was biased towards the root in the root-skewness test ( $P < 0.001$ ). Thus, RLQ analysis was performed including phylogeny, but it yielded very similar results to the standard RLQ, although the phylogenetic approach explained less variance of the Q table (45–39% of the first and second axes, respectively, compared to 59–55% of the standard approach). Hence, only the results from the simpler, standard RLQ are reported in the text. Results from RLQ analysis including phylogeny are given in App. S7.



**Fig. 1.** Redundancy analysis (RDA) of species and environmental variables selected with the step-wise procedure. The first and second RDA axes, which explain 14.8% and 7.8% of the total variation, respectively, are plotted. The length of the projection of an arrow onto an axis indicates the correlation between the environmental variable and the RDA axis. Abbreviations are: Ant\_vul, *Anthyllis vulneraria fontqueri*; Aph\_mon, *Aphyllanthes monspeliensis*; Arc\_uva, *Arctostaphylos uva-ursi*; Asp\_cyn, *Asperula cynanchica*; Asp\_cer, *Asphodelus cerasiferus*; Ast\_lin, *Asterolinon linum-stellatum*; Ave\_pra, *Avenula pratensis iberica*; Car\_mon, *Carduncellus monspeliensis*; Car\_nig, *Carduus nigrescens nigrescens*; Cen\_lin, *Centaurea linifolia linifolia*; Cer\_pum, *Cerastium pumilum*; Con\_maj, *Conopodium majus ramosum*; Cor\_min, *Coronilla minima*; Dor\_pen, *Dorycnium pentaphyllum pentaphyllum*; Ech\_rit, *Echinops ritro*; Eri\_ant, *Erinacea anthyllis*; Eup\_fla, *Euphorbia flavicoma mariolensis*; Eup\_nic, *Euphorbia nicaeensis nicaeensis*; Fes\_ovi, *Festuca ovina*; Fum\_eri, *Fumana ericoides montana*; Gal\_par, *Galium parisiense*; Gen\_his, *Genista hispanica*; Gen\_sco, *Genista scorpius*; Gla\_ill, *Gladiolus illyricus*; Glo\_vul, *Globularia vulgaris*; Hel\_app, *Helianthemum appeninum*; Hel\_oel, *Helianthemum oelandicum italicum*; Hie\_pil, *Hieracium pilosella*; Koe\_val, *Koeleria vallesiana*; Lav\_lat, *Lavandula latifolia*; Leu\_con, *Leuzea conifera*; Lin\_nar, *Linum narbonense*; Lin\_ten, *Linum tenuifolium suffruticosum*; Lit\_fru, *Lithospermum fruticosum*; Nar\_ass, *Narcissus assoanus*; Ono\_min, *Ononis minutissima*; Sal\_off, *Salvia officinalis lavandulifolia*; San\_min, *Sanguisorba minor*; Sat\_mon, *Satureja montana*; Sco\_his, *Scorzonera hispanica crispatula*; Sed\_sed, *Sedum sediforme*; Ser\_nud, *Serratula nudicaulis*; Sta\_dub, *Stachelina dubia*; Sti\_off, *Stipa offneri*; Teu\_pol, *Teucrium polium*; Tha\_tub, *Thalictrum tuberosum*; Thy\_tin, *Thymelaea tinctoria*; Thy\_vul, *Thymus vulgaris*; Tul\_syl, *Tulipa sylvestris australis*.

The first and second axes of the RLQ analysis extracted 68.9% and 20.2%, respectively, of the total inertia of the cross-matrix of the environmental variables and species traits. Hence, we only considered these two axes, since together they accounted for 89.1% of the variance in the analysis. The results of the permutation test of the rows of the R and Q tables indicate a significant ( $P < 0.001$ ) statistical association between environmental variables and species traits. Since the RLQ analysis represents the partial ordination between the three separate tables (R, L and Q), the variance corresponding to each table was compared to the variance from the separate analyses of the three tables (Table 2). RLQ axis 1 accounted for 96%, 42.6% and 59.3%, and axis 2 accounted for 87.4%, 32.7% and 54.8% of the variability explained in the separate analyses of patches–environment (R), species frequencies–patches (L)

and species–traits (Q) tables, respectively. The variance of the Q table accounted for by the RLQ analysis is relatively low, but within the range of previous studies (Dolédéc et al. 1996; Ribera et al. 2001; Choler 2005; Cleary et al. 2007; Lacourse 2009). Since RLQ analysis maximizes the covariance between R and Q tables, it accounted for more variability of these two tables than it did for the species frequency table (L). The species and patches scores in the RLQ analysis had a correlation of 0.159 and 0.116 in the first and second axes, respectively, compared to the maximum possible correlation of 0.373, given by the square root of the first eigenvalue of the CA of the frequency table. The first RLQ axis maximizes the covariance between these two sets of scores, giving a value almost twice that in the second axis (0.446 and 0.241, respectively).

**Table 2.** Results of the RLQ analysis and the three separate analyses. Panel (a) shows the results of the separate analyses for the environmental variables table (R), the species composition table (L) and the species traits table (Q). Panel (b) gives the results of the RLQ analysis: variance explained by environmental variables and species traits, and covariance and correlation between sites and species for the first two axes. Panel (c) shows the comparison between the RLQ analysis and each separate analysis for the first and second axes.

(a) Separate analyses		
Analysis	Variance axis 1	Variance axis 2
PCA of R	3.635 (36.3%)	2.633 (26.3%)
CA of L	0.139 (16.0%)	0.126 (14.5%)
Mix model of Q	3.808 (17.3%)	3.424 (15.6%)
(b) RLQ analysis		
1. Variance		
Analysis	Variance axis 1	Variance axis 2
R/RLQ	3.490	2.302
Q/RLQ	2.257	1.878
2. Covariance		
Covariance axis 1	Covariance axis 2	
0.446	0.241	
3. Correlation		
Correlation axis 1	Correlation axis 2	
0.159	0.116	
(c) Comparison of RLQ and separate analyses		
	Explained variance (%)	
	RLQ axis 1	RLQ axis 2
R/RLQ	96.0	87.4
L/RLQ	42.6	32.7
Q/RLQ	59.3	54.8
Inertia	68.9	20.2

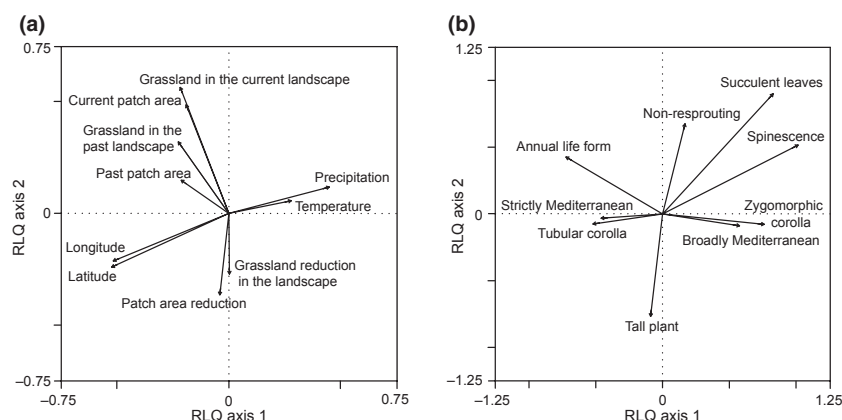
Climatic and geographic environmental variables, especially latitude and longitude (both negatively) and mean precipitation (positively), were correlated to the first RLQ axis (Fig. 2a). The species traits most correlated to this axis

were plant spinescence, leaf succulence, zygomorphic corolla (all positively correlated), annual life form (negatively correlated), broadly Mediterranean phytoecography (positively correlated), tubular corolla and strictly Mediterranean phytoecography (both negatively correlated; Fig. 2b). The RLQ second axis, on the other hand, was most strongly correlated to variables related to habitat amounts and dynamics: percentage of grassland area in the current landscape and current patch area (both positively correlated), resulting in a gradient from currently small patches with little grassland in the current surrounding landscape to patches of large size and having more grassland in the current landscape. This axis had the highest correlations with leaf succulence (positively correlated), large plant height (negatively correlated), non-resprouting ability after fire and spinescence (both positively correlated).

## Discussion

The present study shows that current but not historical landscape composition explains species distributions in the study patches. Moreover, we found a weak but statistically significant relationship between biological and ecological species traits and environmental variables.

Current habitat amount in the landscape plays a significant role in explaining the frequencies of broad specialist species in the studied communities, as it was the variable first selected in the step-wise RDA model after accounting for the effects of geographical location, which was the factor explaining most variance alone (Table 1). This result suggests that the grasslands studied work as metacommunities, where dispersal between habitat fragments plays an important role in maintaining species composition (Holoak et al. 2005). Specifically, since some grassland species increased their within-patch frequency when the patch was surrounded by more grassland habitat in the landscape, propagules for these species probably originated partly in



**Fig. 2.** RLQ analysis of environmental variables (a) and species traits (b). Only traits with a normed score > 0.45 on the first or second axis are shown.

grassland habitat outside the patch. Increased within-patch frequencies likely result in enhanced population persistence. Moreover, none of the measures of historical landscape structure was important in our study, contrary to some previous studies, suggesting that plant species in our habitats have already responded to habitat change. Lindborg et al. (2005) and Vellend (2005) found effects of land-use history on patch occupancy and population size and dynamics in several grassland and forest plants, respectively. Past area and isolation are also important for explaining the richness of plant specialists in some grasslands (e.g. Helm et al. 2006; Krauss et al. 2010; but see Adriaens et al. 2006). However, unlike the present study, none of these previous studies investigated the relationship between landscape structure and species composition of most plant specialists.

Even though we detected a phylogenetic signal in species traits, results did not change appreciably whether phylogeny was taken into account or not in the RLQ analysis, suggesting that the trait patterns observed are caused by ecological drivers. The lower variance of the separated analysis of table Q explained by the RLQ analysis including phylogeny may be due to the higher number of variables included in the traits and phylogeny Q table (68 variables) compared to the traits Q table (32 variables). Several plant traits were associated with habitat amount at the patch and landscape scales. However, we think the relationship between species traits and environmental variables, although statistically significant, was weak because: (1) the variance explained by the first two axes of the separate analysis of the species–traits table (Q) was relatively small; (2) the RLQ axes accounted for much less variance of the first two axes of species–trait table (Q; 59–55%) than of the first two axes of the patches–environment table (R; 96–87%); and (3) the contribution of the Q table to the joint ordination was small because environmental gradients in RDA and RLQ were almost identical. Besides, four out of the five traits most correlated to the RLQ second axis were represented by few species in our data set (i.e. succulent leaf anatomy, annual life form, spinescence and, to a lesser extent, tall plant). The fifth trait, the lack of resprouting ability, was most positively associated with current grassland area and negatively associated with grassland reduction. Non-resprouting species were regionally less frequent on average than resprouter species, and this could result in small populations vulnerable to local extinctions in small patches or in patches with little grassland in the landscape. In contrast, viable populations could persist in large patches and patches with more grassland in the landscape. Moreover, the most frequent non-resprouting species (*Fumana ericoides montana*, *Helianthemum appeninum*, *Helianthemum oelandicum italicum* and *Ononis minutissima*) germinate after fire (Arnán et al. 2007; Paula & Pausas 2008) and could also take advantage of other disturbances prone to

occur in open habitats, thus enhancing population regeneration in large patches. Tall plant specialists were most negatively associated with current grassland area and positively associated with grassland reduction, suggesting that they could take some advantage of habitat reduction and woody encroachment. Tall plants might have better competitive advantage and dispersal capacity than small plants when patches become smaller, more isolated and encroached by woody plants. However, since RLQ is a correlational method, the relationships between the traits we used and species responses to landscape variables are not necessarily cause–effect.

Many previous studies have stressed the importance of several plant traits in mediating plant response to land-use change in grasslands of central and northern Europe (Adriaens et al. 2006; Lindborg 2007) and in other fragmented habitats (Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Verheyen et al. 2003; Kolb & Diekmann 2005). In our study, life form was not related with either current patch area or current grassland amount in the landscape. This result indicates that plant responses to landscape patterns and dynamics were, on average, similar between woody species and herbaceous perennials; although our data set contained only three annual species. Plants with no specific dispersal mechanism were not more associated with large and connected grasslands than anemochorous or zoochorous species, suggesting that dispersal limitation is not strong enough or that realized dispersal does not differ in the study area among these plant groups. As in our case, Chust et al. (2006) could relate neither life form nor dispersal to landscape structure in Mediterranean grasslands. Neither corolla type nor flower size was related to current landscape composition in our study, even though generalist corollas and large flowers or inflorescences could provide an advantage if specialized pollinators are more affected by habitat loss and fragmentation than generalist pollinators. However, other factors like autogamy could affect this relationship, since autogamous species could persist more easily in small and fragmented habitats (Aguilar et al. 2006). Seed size has been related with dispersal strategy, establishment success and fecundity, although the advantage of larger seeds in seedling success is more important in shady habitats (Westoby et al. 1996) than in the open grasslands studied here. Lindborg (2007), like us, did not find a significant relationship between a similar trait (seed mass) and either habitat area or connectivity in grasslands. The same study, in contrast, found that vegetative spread and seed bank longevity were negatively associated with past connectivity, and vegetative spread was negatively associated with area. Our study did not find any correlation between vegetative spread and environmental gradients, possibly because of the low resolution of this attribute (yes/no). Moreover, the scarce information available for seed



bank longevity in Mediterranean plant species prevented us from including this trait in our analysis.

These contrasting results with other studies could be attributed either to different methodology or different study system. The RLQ analysis is not directly comparable with the methods used previously to assess the role of plant traits in land-use change, although it has proven useful to relate bird and insect traits to habitat and landscape fragmentation (Barbaro & van Halder 2009) and plant traits to various treatments of grazing, mowing, mulching and abandonment in semi-natural grasslands (Römermann et al. 2009; Pakeman & Marriott 2010). Effects of species traits on species' responses to landscape changes have been poorly studied in Mediterranean grasslands, unlike other European grasslands. Perhaps the role of traits is not as marked in Mediterranean conditions, where grasslands are often rich in woody species that might show life strategies similar to those dominating the surrounding open-canopy forests or scrub. This might lessen the environmental and biological contrast between grasslands and adjacent habitats, and suggests that future analyses of these communities could benefit from the 'continuum' model (Fischer & Lindenmayer 2006), which assumes individualistic species responses to either gradual or abrupt changes in environmental variables.

Additional variation in species composition may be explained by other climatic and geographic variables, edaphic factors or disturbance indicators for which information was not available in this study. More information on the landscape history of the study area, especially on grazing pressure and time since pasture abandonment, which are expected to affect landscape patterns and species composition, would provide a more complete view of vegetation dynamics. More information on poorly studied plant traits that possibly determine plant persistence in fragmented habitats is needed, especially on autogamy. Aguilar et al. (2006) showed that habitat fragmentation more negatively affected self-incompatible species than self-compatible ones. Seed bank longevity is also an important trait for plant persistence in fragmented boreal grasslands (Lindborg 2007), where the proportion of plants with persistent seed banks was negatively associated with past connectivity. Exploration of new plant traits or those known to be important in other communities is thus key to further our understanding of plant responses to habitat loss and fragmentation in Mediterranean grasslands.

Finally, if none of the considered traits succeeds in explaining species composition along environmental gradients, a different approach is needed. In relation to land-use change, we could measure demographic traits (e.g. vegetative regeneration, seed production, germination and survival rates) along a gradient of landscape composition and dynamics. This approximation would show the population

performance of different specialist species in response to the generalized reduction and fragmentation of Mediterranean grasslands and would help to identify species vulnerable to landscape change.

## Conclusions

We conclude that species composition is related to current landscape structure in Mediterranean grasslands of southern Catalonia, although climatic and geographic variables play a primary role. Species responses to these changes in habitat amount seem to be relatively fast, as present habitat amount was a better predictor of current species frequencies than was habitat amount 50 yr ago. A single, three-table ordination analysis used to relate biological and ecological plant traits to environmental variables yielded weak but significant relationships between environmental gradients and plant traits, indicating that species response to habitat reduction in these communities is not largely mediated by the traits we considered. These results suggest the need to investigate other factors like grazing pressure, other species traits like autogamy and seed bank persistence, and the role of demographic rates.

## Acknowledgements

We thank J.M. Ninot, C. Casas, A. Rodrigo, J. Bosch, X. Arnan, M. Riba, J. Bartolomé and P. Casals for supplying information on plant traits, R. Vilatersana for the *Cardueae* phylogeny, M. Greenacre for statistical support and F. Lloret and two anonymous referees for valuable comments on the manuscript. This study was funded by the EU in the 6th framework project COCONUT (SSPI-CT-2006-044346), by MICINN (Spain) in the project LANDPOLNET (CGL2009-12646) and by the Spanish Consolider-Ingenio 2010 programme in the project MONTES (CSD2008-00040). G. Bagaria was supported by a Pre-doctoral FPU fellowship (AP2009-4599) from the Ministerio de Educación y Ciencia (Spain).

## References

- Adriaens, D., Honnay, O. & Hermy, M. 2006. No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biological Conservation* 133: 212–224.
- Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9: 968–980.
- APG III Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105–121.

- Arnan, X., Rodrigo, A., Retana, J. & Collins, B. 2007. Post-fire regeneration of Mediterranean plant communities at a regional scale is dependent on vegetation type and dryness. *Journal of Vegetation Science* 18: 111–122.
- Barbaro, L. & van Halder, I. 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography* 32: 321–333.
- Bolòs, O., Vigo, J., Masalles, R.M. & Ninot, J.M. 2005. *Flora manual dels Països Catalans*. Pòrtic, Barcelona, ES.
- Bruun, H.H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography* 23: 641–650.
- Chessel, D., Dufour, A.B. & Thioulouse, J. 2004. The ade4 package – I: one-table methods. *R news* 4: 5–10.
- Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research* 37: 444–453.
- Chust, G., Pérez-Haase, A., Chave, J. & Pretus, J.L. 2006. Floristic patterns and plant traits of Mediterranean communities in fragmented habitats. *Journal of Biogeography* 33: 1235–1245.
- Cleary, D.F., Boyle, T.J., Setyawati, T., Anggraeni, C.D., Loon, E.E. & Menken, S.B. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. *Ecological Applications* 17: 1184–1197.
- Debussche, M., Lepart, J. & Dervieux, A. 1999. Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography* 8: 3–15.
- Dolédéc, S., Chessel, D., ter Braak, C. & Champely, S. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* 3: 143–166.
- Dorp, D.V., Hoek, W.V.D. & Daleboudt, C. 1996. Seed dispersal capacity of six perennial grassland species measured in a wind tunnel at varying wind speed and height. *Canadian Journal of Botany* 74: 1956–1963.
- Dray, S. & Legendre, P. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89: 3400–3412.
- Dupré, C. & Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* 90: 796–805.
- Eriksson, O., Cousins, S.A. & Bruun, H.H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science* 13: 743–748.
- Fischer, J. & Lindenmayer, D.B. 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112: 473–480.
- Grime, J. 2002. Declining plant diversity: empty niches or functional shifts? *Journal of Vegetation Science* 13: 457–460.
- Hedges, S.B. & Kumar, S., eds. 2009. *The timetree of life*. Oxford University Press, New York, NY, US.
- Helm, A., Hanski, I. & Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9: 72–77.
- Hill, M.O. & Smith, A.J.E. 1976. Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* 25: 249–255.
- Holyoak, M., Leibold, M.A. & Holt, R.D., eds. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, IL, US.
- Jacquemyn, H., Butaye, J. & Hermy, M. 2003. Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography* 26: 768–776.
- Kahmen, S. & Poschlod, P. 2004. Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* 15: 21–32.
- Kolb, A. & Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19: 929–938.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefane-scu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters* 13: 597–605.
- Lacourse, T. 2009. Environmental change controls postglacial forest dynamics through interspecific differences in life-history traits. *Ecology* 90: 2149–2160.
- Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.
- Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier, Amsterdam, NL.
- Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78: 547–562.
- Lindborg, R. 2007. Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *Journal of Ecology* 95: 555–564.
- Lindborg, R. & Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. *Ecology* 85: 1840–1845.
- Lindborg, R. & Eriksson, O. 2005. Functional response to land use change in grasslands: comparing species and trait data. *Ecoscience* 12: 183–191.
- Lindborg, R., Cousins, S.A.O. & Eriksson, O. 2005. Plant species response to land use change – *Campanula rotundifolia*, *Primula veris* and *Rhinanthus minor*. *Ecography* 28: 29–36.
- Maina, G.G. & Howe, H.F. 2000. Inherent Rarity in Community Restoration. *Conservation Biology* 14: 1335–1340.
- McIntyre, S. & Lavorel, S. 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology* 89: 209–226.
- Millennium Ecosystem Assessment. 2005. Biodiversity. In: Hassan, R., Scholes, R. & Ash, N. (eds.) *Ecosystems and human well-being. Volume 1. Current state and trends*, pp. 77–122. Island Press, Washington, DC, US.
- Moss, D., Wyatt, B., Cornaert, M.H. & Roekaerts, M. 1990. *CORINE Biotopes – The design, compilation and use of an inventory of sites of major importance for nature conservation in the European*

- Community*. Directorate-General Environment, Nuclear Safety and Civil Protection, Brussels, BE.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Pakeman, R.J. & Marriott, C.A. 2010. A functional assessment of the response of grassland vegetation to reduced grazing and abandonment. *Journal of Vegetation Science* 21: 683–694.
- Paula, S. & Pausas, J.G. 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. *Journal of Ecology* 96: 543–552.
- Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S. & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.
- Pavoine, S., Baguette, M. & Bonsall, M.B. 2010. Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* 80: 485–507.
- Pavoine, S., Vela, E., Gachet, S., de Bélair, G. & Bonsall, M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology* 99: 165–175.
- Pino, J., Vilà, M., Álvarez, N., Seguí, J.M. & Guerrero, C. 2009. Niche breadth rather than reproductive traits explains the response of wetland monocotyledons to land-cover change. *Applied Vegetation Science* 12: 119–130.
- Rao, C.R. 1995. A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Qüestió* 19: 23–63.
- Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82: 1112–1129.
- Rivas-Martínez, S., Fernández-González, F., Loidi, J., Lousa, M. & Penas, A. 2001. Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level. *Itinera Geobotanica* 14: 5–341.
- Römermann, C., Bernhardt-Römermann, M., Kleyer, M. & Poschlod, P. 2009. Substitutes for grazing in semi-natural grasslands – do mowing or mulching represent valuable alternatives to maintain vegetation structure? *Journal of Vegetation Science* 20: 1086–1098.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- Stöcklin, J. & Fischer, M. 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950–1985. *Oecologia* 120: 539–543.
- Tremlová, K. & Münzbergová, Z. 2007. Importance of species traits for species distribution in fragmented landscapes. *Ecology* 88: 965–977.
- Vellend, M. 2005. Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biological Conservation* 124: 217–224.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91: 563–577.
- WallisDeVries, M.F., Poschlod, P. & Willems, J.H. 2002. Challenges for the conservation of calcareous grasslands in north-western Europe: integrating the requirements of flora and fauna. *Biological Conservation* 104: 265–273.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098–2100.
- Weiher, E., Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.
- Westoby, M., Leishman, M. & Lord, J. 1996. Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society, London: Biological Sciences* 351: 1309–1318.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108: 261–280.

## Supporting Information

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

**Appendix S1.** Supplementary information on the phylogeny construction.

**Appendix S2.** Species traits and sources.

**Appendix S3.** Environmental variables and sources.

**Appendix S4.** Table L: Species frequencies by patches.

**Appendix S5.** Table R: Environmental variables by patches.

**Appendix S6.** Table Q: Biological and ecological traits by species.

**Appendix S7.** Results from the RLQ analysis including phylogeny.

**Appendix S8.** Environmental variables correlation matrix; Pearson correlation coefficients.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.