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Functional traits and phylogeny: What is the main ecological process determining species assemblage in roadside plant communities?

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Abstract

Question: What is the main ecological process determining species assemblage in roadside herbaceous plant communities?
Location: Roadside slopes (roadcuts and embankments) in the south (Málaga, mesic Mediterranean) and east (Valencia, dry and continental) of the Iberian Peninsula.
Methods: We identified 417 plant species, from which we selected the 331 most abundant (within the 70th abundance percentile) at each site. We compiled information on 28 functional traits and on the biogeographic range of each of these 331 species. We quantified the phylogenetic signal of each trait for the species of each community and determined the number of functional convergences or divergences over the phylogenetic tree for each of the four situations (roadcuts and embankments in the two sites).
Results: There was a significant phylogenetic signal in many traits, being positive in Valencia embankments and negative in Valencia roadcuts with almost no signal in any type of slope in Málaga. Each trait was significantly correlated with 20% - 35% of all other traits but correlation coefficients were low. No significant phylogenetic signal was found for the species' distribution range in any of the four communities studied, which might be the consequence of the complex mixture of biogeographic origins of the species found in these communities.
Conclusion: The lack of a phylogenetic signal in most traits in Málaga, a climatically favourable locality, suggests that competitive exclusion was the main process involved in the assemblage of these communities. The significant and either positive or negative phylogenetic signal (in embankments and roadcuts respectively), the latter coupled with a significant number of functionally convergent nodes in the phylogenetic tree, suggests that environmental filtering is the most likely process involved in the harsh locality of Valencia.

Keywords: Environmental gradient; Mediterranean; Phylogenetic signal; Plant community; Road slope.

Abbreviation: AOT = Analysis of traits.

Introduction

We have little knowledge of the mechanisms determining the assemblage of the species that make up a community and, although it has been known for some time now that neither plants nor their functional traits are distributed randomly (Raunkiær 1934; Diamond 1975), numerous studies are still attempting to determine the processes that give rise to community structure (e.g. Keddy & Weiher 2001; Temperton & Hobbs 2004). From an ecological point of view, two main hypotheses might account for the non-random distribution of a group of species and their functional traits (Tofts & Silvertown 2000). On one hand, the classical theory of competitive exclusion states that competition is directly proportional to the similarity among species, which brings co-existing species to maximise the difference for a given functional trait (Johansson & Keddy 1991). This trait is, in turn, distributed among the species of the community in an overdispersed manner (i.e. exhibiting phenotypic repulsion) regarding a null hypothesis of random distribution of species and functional traits (Armbruster et al. 1994; Wilson & Watkins 1994; Wilson & Gitay 1995). On the other hand, community structure might result from the influence of environmental filters and only those species possessing specific attributes would persist in the community (Montalvo et al. 1991; Fernández-Alés et al. 1993; Díaz & Cabido 1997; Díaz et al. 2001). In this case, the species would be more similar than what would be expected by chance and a given trait would be clustered (i.e. exhibiting phenotypic attraction) regarding a null hypothesis of randomness. Neither hypothesis is exclusive, so that competitive exclusion and environmental filters concur, although their relative importance can differ depending on environmental conditions (Weiher &

Keddy 1995). Thus, the combination of both ecological and phylogenetic forces acting on the evolution of traits can give rise to two dominant processes of community assembly: habitat filtering and competitive exclusion (Cavender-Bares et al. 2006; Webb et al. 2002).

Community theories based exclusively on species interactions, however, do not fully explain the processes giving rise to a determined community structure (Weiher & Keddy 1995). Any comparison between the structures of different communities should take into account their respective biogeographic and phylogenetic histories (Ackerly & Donogue 1995; Harvey 1996; Losos 1996; Silvertown & Dodd 1997; Webb et al. 2002; Arroyo et al. 2004). Omitting previous historical information can lead to erroneous interpretations (Harvey & Pagel 1991; Herrera 1992; Westoby et al. 1995). Therefore the distribution of a given trait in the species making up a community can be considered as the result both of ecological processes and of the phylogenetic relationships between the species (Olson & Miller 1958; Berg 1960; Antonovics 1976; Chevereud 1988; Silvertown et al. 2001). Ecological and phylogenetic determinants have both been inextricably linked throughout the history of lineages and communities (Pigliucci 2003). Thus, if we could breakdown the role played by the phylogenetic structure of the community, the study of key functional traits would become a crucial tool for determining the predominant ecological process in community structuring (Webb et al. 2002). This breakdown should involve the quantification of the phylogenetic signal in the functional traits considered, as it estimates the relative influence of phylogeny in the phenotypic repulsion or attraction of the species making up a community (Blomberg & Garland 2002; Silvertown et al. 2006; Table 1).

Habitat filtering can be said to be an important process if the species living in a community either (a) share close phylogenetic ancestors (i.e. phylogenetic clustering) and the trait conferring tolerance is evolutionarily conserved (i.e. trait conservatism) or (b) do not share close ancestors (i.e. phylogenetic overdispersion) and the trait conferring tolerance has evolved repeatedly in distant lineages (i.e. trait convergence). Competition exclusion can be considered the dominant process when the combination of either trait conservatism and phylogenetic overdispersion or phylogenetic clustering and trait convergence (or random dispersion of traits) are found (see Table 1).

The current study was conducted in roadside plant communities, which are species-rich and common worldwide, being the basis of novel or emerging ecosystems *sensu* Hobbs et al. (2006). However, and despite this ubiquity, they are still poorly understood from an ecological perspective (Martinez-Alonso & Valladares 2002; Schaffers & Sýkora 2002; Matesanz et al. 2006). We compared communities at two sites within the Iberian Peninsula that are markedly different in terms of drought and temperature (Málaga, oceanic climate and Valencia, drier and more continental) growing on two types of slopes at each site, roadcuts (excavation slopes) and embankments (accumulation slopes), which also vary with regard to water availability, slope angle and soil conditions (Andrés & Jorba 2000; Martinez-Alonso & Valladares 2002; Bochet & García-Fayos 2004). This study firstly attempts to establish the mechanisms giving rise to the structure of the communities studied, considering both ecological and phylogenetic information. We assume that community composition is primarily influenced by one dominant ecological process that can be inferred from its phylogenetic structure and the distribution of functional traits (Webb et al. 2002; Ackerly 2003); competitive exclusion and environmental filters are assumed to be the two main processes, with other processes (stochastic processes, density-dependent mortality, etc.) only marginally explaining species assembly. Secondly, this study seeks to determine whether this mechanism changes with environmental conditions. Our specific hypotheses were that adverse environmental conditions, in our case Valencia (vs Málaga) and roadcuts (vs embankments), (1) maximise the importance of environmental filters as the ecological process structuring the communities (Weiher & Keddy 1995) and (2) increase the number of correlations among traits as the result of selection of functional strategies involving highly integrated phenotypes.

Material and Methods

Study area, species and sampling protocol

The study area comprised roadside slopes (roadcuts and embankments) located in two different regions, in the south (Málaga, oceanic site) and east (Valencia, continental site) of Spain. On each slope, we sampled an area of ca. 1 ha, always choosing the central zone, as the upper and lower slope zones were considered as buffer zones and excluded. The first study area was located at the Costa del Sol (Málaga, Spain, 36º25' N; 05º09' W), between kilometers 110 and 147 of the Costa del Sol motorway. The mean elevation above sea level was 100-200 m and mean annual rainfall and temperature were 1017 mm and 18.5 °C respectively (16 year time series obtained from the National Meteorology Institute, Spain). The proximity of the study area to the Mediterranean Sea was seen in an increase in mean temperature and a decrease in temperature variations throughout the year which, together with the influence of the sea breeze, attenuated the adverse conditions typical of the Mediterranean climate in more xeric areas: The vegetation surrounding the study

Table 1. Theoretical diagram modified from Webb et al. (2002) showing the four possibilities for distribution of a given set of functional traits in all the species making up a given community, considering both the ecological processes and the phylogenetic history of the species involved. It also shows the expected phylogenetic signal in these traits, which is positive when closely-related species are functionally similar and negative when they are not. The two cases in which traits present negative phylogenetic signals can be differentiated by whether there is a significant number of functional convergences or divergences (i.e. nodes at which functional traits exhibit a different level of similarity among descendants and ancestors from what could be expected by chance).

	Phylogenetically conserved traits	Phylogenetically convergent traits
Environmental filtering	CLUSTERED TRAITS Positive phylogenetic signal	OVERDISPERSED TRAITS Negative phylogenetic signal with a significant number of functional convergences over the phylogenetic tree. Distant species have similar trait values
Competitive exclusion	OVERDISPERSED TRAITS Negative phylogenetic signal with a non-significant number of functional convergences or divergences over the phylogenetic tree. Close species have different trait values	RANDOM TRAITS No phylogenetic signal

area consisted of shrublands of *Chamaerops humilis* and *Pistacia lentiscus* alternating with cornfields, castor plant crops (*Ricinus communis),* very open *Quercus suber* (cork oak) *dehesas* and small stands of *Quercus coccifera*. The second study area was located in the La Plana de Utiel-Requena region (Valencia, Spain 39º 29' N; 1º 06' W). The roadside slopes selected were situated between the Siete Aguas and Venta del Moro sites in the section between Km 267 and 307 of the A-3 motorway linking Valencia and Madrid. Mean annual rainfall was half that recorded in Málaga (418 mm) and mean annual temperature was 4 °C less (14.2 ºC), with greater temperature differences, both daily and seasonal (Pérez 1994). Rainfall distribution within and over the years was very variable showing two peaks, one in May and the other in October. The climate was more continental, with frequent frosts in winter. The growth period of the plants was significantly shorter than for Málaga, due to the greater duration of adverse conditions, throughout both winter and summer. Most of the surrounding area comprised crop fields (mostly vines, olive and almond trees), although there were also small patches of shrubland and open forest of *Pinus halepensis* as the most abundant tree, with *Rosmarinus officinalis*, *Thymus vulgaris*, *Genista scorpius* and *Quercus coccifera* as accompanying shrubs, and *Brachypodium retusum*, *Koeleria vallesiana*, *Stipa offneri* and *Helictotrichon filifolium* (*Poaceae*) as the dominant herbaceous species.

In Málaga, nine roadcuts and 12 embankments were visited on several occasions throughout the growth period of the plants (from February to July 2002) and two transects were established on each slope parallel to the motorway in order to obtain the list of spontaneous flora (see App. 1 for a complete species list). In Valencia, we chose ten roadcuts and ten embankments and visited the study area to complete the list of spontaneous flora following the same procedure as explained for the slopes in Málaga. In order to capture the species with different phenologies, floristic composition was sampled on roadslopes from early spring to early summer of 2000. In both localities, data collection was carried out 3-4 years after construction. All the slopes were initially hydroseeded with a commercial mixture of *Leguminoseae* and *Poaceae* (see App. 1 for the species), which is common practice for accelerating the formation of an initial plant cover. The hydroseeded species, however, represented only 5% of all the species recorded on the slopes and these species generally constituted marginal components of the community from the start. This is a result of both a relatively high natural colonisation of the slopes and the rapid disappearance of hydroseeded species as reported in a previous study (Matesanz et al. 2006).

Nomenclature of species, functional traits and biogeographic range

The Iberian Flora (Castroviejo 1986) and the Flora of Western Andalucia (Valdés et al. 1987) were used for species nomenclature s well as the identification keys of the Flora of Valencia (Mateo Sanz & Crespo Villalba 1986), the flora of Italy (Pignatti 1982) and the Flora of Catalonia (Bolós de & Vigo 1984) were used to identify the species that were not included in the main Floras. Furthermore, we gathered information on 28 traits related to three of the most important aspects of the biology and ecology of the species, based both upon personal observations in the field and on checklists of the local flora, assigning qualitative values to each trait. The 28 traits considered (Table 2) are based on previous studies (Gomez Sal et al. 1986; Fitter & Peat 1994) although we simplified these traits in order to avoid ambiguities and overlapping of concepts and definitions. We also obtained the biogeographic information from the reference checklists of the local flora and classified the species according to one of the following four categories: Cosmopolitan, Palaeotemperate, truly Mediterranean or Stenomediterranean.

Table 2. Definition of traits and groups of traits used in the study, together with their abbreviations as used in Tables and Appendices. The possible values are also shown for each particular trait and for the biogeographic range.

SPA	**Characteristics related to spatial occupation**	
DEN	Density of spatial occupation	1. High (concentrated biomass) 2. Intermediate 3. Low (Biomass not concentrated)
GRO	Plant growth trends	1. Preferably vertical (Erect or climbing) 2. Without preferable direction of growth 3. Preferably horizontal
ADU	Most common size of adult plant	1. Less than 50 cm 2. Between 50 cm and 1 m 3. Between 1 and 2 m 4. More than 2 m
PER	Plant persistence	1. Annual 2. Variable 3. Perennial/Biennial
FIL	Plant phyllotaxis	1. Alternate 2. Both/Indefinite 3. Opposite
STE	Number of stems per plant	1. Acauline 2. Unicauline 3. Multicauline
RAM	Stem branching	1. No branched 2. Branched
TEX	Stem texture	1. Woody 2. Fibrous 3. Herbaceous
SEP	Stem epidermal characteristics	1. Glabrous 2. Hispid 3. Lanate or very tomentose
FOM	**Characteristics related to foliar morphology**	
ABU	Relative abundance of leaves	1. More than 75% 2. Between 25% and 75% 3. Less than 25%
SIT	Predominant leaf situation	1. Basal rosette or leaves only at the base of the stem 2. All over the plant, both basal and along stems 3. Along single stem
DIF	Differences in leaf shape and size	1. No differences 2. Different size or shape 3. Different size and shape
SPI	Spinescence	1. Not spiny 2. Spiny
FOE	Leaf epidermal Characteristics	1. Glabrous 2. Hispid 3. Lanate or very tomentose
FOS	Relative leaf size	1. Big (> 30 cm) 2. Intermediate (10cm - 30 cm) 3. Small (< 10 cm)
FOL	Relative leaf length	1. Long and narrow (length/width > 1) 2. Isodiametric (length/width = 1) 3. Short and wide (length/width < 1)
LOB	Leaf lobulation	1. Low 2. Intermediate 3. High/Compose
REP	**Characteristics related to reproduction and seed dispersal**	
CLO	Vegetative reproduction	1. Absence 2. Presence
FLD	Flower distribution	1. Close to stem-root joint 2. All over the plant 3. At the top of the flowering stem
INF	Type of inflorescence	1. Cimose 2. Both 3. Racemose
SUB	Subterranean structures	1. Absence 2. Presence
SES	Seed size	1.Big (> 4 mm) 2. Intermediate (1 mm - 4 mm) 3. Small (< 1 mm).
FLS	Flower size	1.Big (corolla > 20 mm) 2. Intermediate (5 mm - 20 mm) 3. Small (corolla < 5 mm)
SEX	Flower sexuality	1. Monoic 2. Dioic 3. Hermaphrodite
FLC	Colour of the flower	1. Brown-greenish 2. White or coloured
DIM	Dispersal mode (Fruit type)	1. Indehiscent fruit 2. Fleshy fruit 3. Dehiscent fruit
DIT	Dispersal type	1. Anemochorous 2. Barochorous 3. Zoochorous
BIO	Biogeographic range (area of distribution of the species)	1. Cosmopolitan/Naturalized 2. Paleotemperate, Circumboreal, Mediterranean - Turanian or north African 3. Eumediterranean 4. Stenomediterranean

Phylogenetic reconstruction and validations of the matrix of phylogenetic distances

We now have complete information on the phylogenetic relationships occurring among most vascular plants thanks to an extensive study of molecular genetics (Clark et al. 1995; Soltis et al. 2000; Davies et al. 2004). However, phylogeny based on phenotypic characters and on taxonomic information is sometimes the only way to approach phylogeny at the infrageneric level, particularly when the number of species of the phylogenetic tree is very high. In order to determine the reliability of using this type of phylogeny with the communities studied in this paper, we chose a subgroup of 31 species with which we constructed phylogenetic distances, using Soltis et al. (2000) to classify the species into the different taxa, and Jordano (1995) for coding the distance values: (1) if the two species belong to the same genus, (2) if they are from different genera within the same family, etc.. Thus, we obtained a matrix of discrete distances among species. Moreover, we constructed a matrix of molecular distances using data from the sequence of the chloroplastic rubisco rbcl marker obtained for each of the 31 species in the 'Genebank' database (http://www.ncbi.nlm.nih.gov). The 31 species considered were:

Chamaerops humilis, Schoenus nigricans, Carex monostachya, Hyparrhenia hirta, Bromus inermis, Hordeum jubatum, Iris germanica, Anagalis arvensis, Coris monspeliensis, Herniaria glabra, Silene gallica, Galium aparine, Lavandula stoechas, Prunella vulgaris, Olea europaea, Plantago coronopus, Plantago lanceolata, Verbena officinalis, Convolvulus arvensis, Daucus carota, Cichorium intybus, Urtica dioica, Adenocarpus complicatus, Calicotome villosa, Cytisus scoparius, Lotus corniculatus, Lupinus luteus, Medicago sativa, Retama sphaerocarpa, Spartium junceum, and *Ulex parviflorus*.

Once the sequences were obtained, and for correct construction of the distance matrix, the sequences were aligned using the programme Clustal X 1.83 (Thompson et al. 1997). With the programme MEGA2 (Kumar et al. 2001), we constructed nine distance matrices, each one of these based upon a different model of molecular phylogenetic distances. In order to compare the matrix of distances and the nine matrices of molecular distances, we used a Mantel correlation test (Mantel Nonparametric Test Calculator 2.0, 1999, Adam Liedloff, Queensland University of Technology, Australia). All data for Mantel tests were previously standardised. The values of Z (Mantel coefficient), g (standard normal variate) and r (correlation coefficient) were calculated from the two matrices specified. The obtained values of g were then compared with critical values for the most common levels of significance ($P = 0.01$, $P = 0.025$ and $P = 0.05$). The program also generated a user-specified number of random permutations of the first matrix to determine the possible variation within the data. In our case, 1000 random iterations were calculated for each distance (or dissimilarity) matrix and the values of g and Z were obtained in each case from the randomised distribution. Euclidean distances were used for the matrices and the zeros of the diagonal were excluded from the analyses as recommended by Legendre & Legendre (1983). Comparison with the subgroup of species revealed that the distances calculated with a discrete phylogeny based on phenotypic and taxonomic characters were significantly correlated with the distances calculated with molecular data. Mantel correlation coefficient was always greater than 0.83 and the associated probability after correction (Rice 1989) less than 0.001 for the all models: number of differences ($r = 0.864$), p-distance value ($r = 0.869$), Jukes Cantor's distance ($r = 0.866$), Tajima Nei's distance ($r = 0.852$), Kimura model with 2 parameters ($r = 0.862$), Tamura model with 3 parameters ($r = 0.831$), Tamura-Nei model ($r = 0.859$), F84 model ($r = 0.833$) and logDet model ($r = 0.830$). More details on the properties of each model can be obtained in Kumar et al. (2001) and Felsenstein (2004). This result supports the use of discrete phylogeny in studies of large numbers of species, particularly when there is insufficient molecular information for many of the species, as is the case of much of the spontaneous flora on roadside slopes.

Phylogenetic and statistical analyses

For each of the four communities studied (roadcuts and embankments in Málaga and Valencia) we constructed a matrix of phylogenetic distances and 33 matrices of Euclidian distances: one for each of the 28 traits and five more, grouping the traits into those relating to spatial occupation, leaf morphology, form of reproduction and for all the traits together. We constructed another matrix of Euclidian distances with the species' distribution range. We tested for the presence of phylogenetic signal in the dataset; the term phylogenetic signal refers to the tendency of phylogenetically related species to occur together in the communities (Webb et al. 2002; Blomberg & Garland 2002). We quantified the phylogenetic signal by comparing functional and phylogenetic matrices, using Mantel's test as in the aforementioned comparison of the two types of matrices of phylogenetic distances among species.

We obtained the number of significant correlations of a given trait with the rest of traits and considered this number as an estimator of the association of characters in syndromes. To avoid the problem of giving all species the same weight in their contribution to trait features, we selected the 331 most abundant species, which represented the species within the 70th abundance percentile, for the phylogenetic and functional analyses. The 70th percentile was chosen after visual inspection of the abundance histogram for all species, which revealed a sharp decline of abundance after this value due to very rare and non-representative species (see App. 1).

The analysis of traits (AOT version 3.0, Ackerly 2004) module of Phylocom (www.phylodiversity.net/phylocom) was used to further explore the phylogenetic signal and to carry out node-level analyses of trait means and diversification. Phylomatic, a tool associated with Phylocom was used to generate the initial tree in the Newick format; the obtained tree was checked and corrected manually for species not yet included in the web database. Branch length was adjusted introducing available information from fossil records together with the information in Davies et al. (2004) regarding node age of angiosperms. At the end still some branch lengths were unknown so we used the relatively well known branch lengths and reconstructed the rest following the protocol of BLADJ (branch length adjusting) of Phylocom. The phylogenetic signal is estimated in AOT by the mean divergence deviation relative to the null hypothesis (randomizations of trait values across the tips of the tree). If closely related species are highly divergent, there will be many large contrasts near the tips of the tree, while if the trait evolution is conserved, the divergence will be small. To handle polytomies, we have generated a suite of randomly resolved polytomies and used mean phylogenetic distances obtained for the distribution of distances over all possible trees regarding doubtful nodes and polytomies.

Significance testing for the patterns of traits conservatism was conducted by randomization of trait values across the tips of the phylogeny; 10 000 randomizations were carried out for the results presented here. The number of nodes exhibiting significant conservatism or divergence was calculated. Conservatism was taken as significant when standard deviation was significant in the low tail of the null distribution, and divergence when standard deviation was significant in the high tail of the null distribution. Functional convergence was estimated for the nodes with descendent trait values being more similar than could be expected by chance.

Trait values assigned to each species were, in most cases, in an ordinal scale, so functional distances among species could be directly calculated. However, distance values between species had to be reduced to either zero (same value for a given pair of species) or one (different values for each species of a given pair) for some traits (e.g. DIT, SEX, FLC, DIM etc. see Table 2). In order to analyse the relationships among variables we used Pearson's correlation test and for the comparisons of means we employed ANOVA, LSD test for subsequent analysis. To reduce the probability of type I and type II errors when obtaining multiple estimates of p we used a Rice sequential correction (Rice 1989). We used the program STATISTICA (2001, StatSoft Inc, version 6 Tulsa, OK, US) for all statistical analyses except for the aforementioned specific matrix and phylogenetic analyses.

Results

We recorded 417 plant species in the four communities studied (see App. 1 for a full list with their relative abundance). The percentage of palaeotemperate species was significantly the highest (54 ± 23%) followed by the other three groups, cosmopolitan (14.03 ± 5.93%), truly Mediterranean (13.88 ± 8.24%) and stenomediterranean (9.46 ± 6.63%) ($F = 88.61$, $p < 0.00001$), and this was true in both localities (Málaga vs Valencia, $p = 0.088$) and in both types of slope (roadcuts vs embankments; $p = 0.41$), as shown by the non-significant interactions between factors (Fig. 1). The percentage of truly Mediterranean species, however, was lower in Málaga ($p < 0.0001$), although this did not vary between slope types ($p = 0.535$). Lastly, the stenomediterranean species showed no differences with regard to proportion, both between sites ($p = 0.167$) and between slope types ($p = 0.111$).

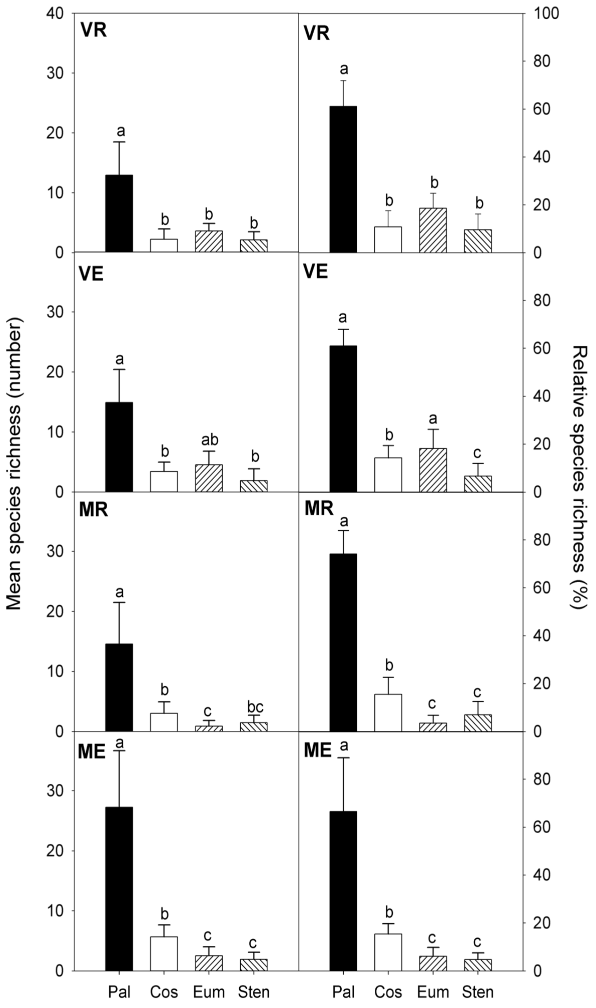

Fig. 1. Mean species richness (left) and relative species richness (%, right) per slope at both sites (Málaga and Valencia) and for each of the two types of slopes (roadcuts and embankments) according to the biogeographic range (cosmopolitan = Cos, Palaeotemperate = Pal, Mediterranean = Eum and Stenomediterranean = Sten). The letter code indicates significant differences (ANOVA, $p < 0.05$, corrected by Rice). VR = Valencia roadcuts, VE = Valencia embankments, MR = Málaga roadcuts, ME = Málaga embankments.

With regard to the number of traits with which a given trait showed correlations, we found no significant differences between sites, although the species from the embankment communities presented a higher number of traits clustered in syndromes than those from the roadcut communities as revealed by a larger number of correlations among traits ($F = 31.75$, $p < 0.001$) (Table 3; see App. 2 for trait values of the 331 most abundant species).

Several traits presented a significant phylogenetic signal (Table 4), and we found a lower percentage of traits or groups of traits with a phylogenetic signal in Málaga (14.2% on embankments and 21.5% on roadcuts) than in Valencia (46.4% on embankments and 43% on roadcuts; the critical probability value corrected by Rice for each trait). No differences were found among the values observed and expected for no phylogenetic signal, positive and negative signal in the embankments in Málaga (23, 4 and 1 compared with the expected 28, 0, 0; $\chi^2 = 0.893$, $p = 0.640$), and the

Table 3. Number of traits with which a given trait presented significant correlations at both sites and on both types of slopes. The number of traits with significant correlations was calculated separately for each trait (see Table 2 for abbreviations).

	Málaga		Valencia	
	Embankments	Roadcuts	Embankments	Roadcuts
DEN	11	9	4	4
GRO	9	4	12	8
ADU	10	9	16	8
PER	10	4	8	7
FIL	10	6	9	5
STE	13	5	12	9
RAM	11	7	7	8
TEX	13	9	7	6
SEP	8	3	7	7
ABU	3	3	3	3
SIT	13	8	11	7
DIF	12	8	9	8
SPI	11	3	4	4
FOE	7	2	4	3
FOS	17	9	14	8
FOL	13	8	4	6
LOB	14	9	14	6
CLO	9	6	8	3
FLD	15	6	6	7
INF	12	7	10	8
SUB	8	3	10	7
SEN	12	9	3	5
SES	8	5	9	5
FLS	10	6	4	2
SEX	3	0	0	1
FLC	9	6	14	1
DIM	8	7	11	10
DIT	9	6	9	6

same occurred in the roadcuts at the same site (22, 6, 0 compared with 28, 0, 0; $\chi^2 = 1.285$, $p = 0.526$). By contrast, in the embankments of Valencia, the number of traits with a positive phylogenetic signal was higher than expected (14, 13, 1 compared with 28, 0, 0; $\chi^2 = 7.\ 00$, $p = 0.0302$) and the same occurred on the roadcuts, but with traits showing a negative phylogenetic signal (16, 0, 12 compared with 28, 0, 0; $\chi^2 = 6.03$, $p = 0.048$). There was no significant phylogenetic signal in the biogeographic range of the species of any of the four communities studied (Table 4; $p > 0.05$). The number of nodes of the phylogenetic tree that showed divergences or convergences was significant only in the case of the roadcuts of Valencia. In total 54 nodes of the phylogenetic tree of the communties from the roadcuts of Valencia exhibited significant convergence, revealing that distant taxa were more similar than could be expected by chance (Table 5). This latter finding agrees with the negative phylogenetic signal detected in the roadcut communities of Valencia (Table 4).

Table 4. Correlations between phylogenetic distance and the functional distances between the species (phylogenetic signal) at both sites and on both types of slopes (see Table 2 for abbreviations). The functional distances among species were calculated separately for each trait. Correlation was also calculated for the biogeographic distribution range (BIO). Mantel's statistic (*g*) is shown for each case. * indicates statistical significance, the critical *p*-values have been corrected taking into account Rice's sequential correction.

	Málaga		Valencia	
	Embankments	Roadcuts	Embankments	Roadcuts
	g	*g*	*g*	*g*
DEN	-0.84	1.41	-0.56	-0.39
GRO	0.68	1.91	-0.64	-1.29
ADU	-1.20	0.15	-1.72 *	-2.85 *
PER	1.35	0.99	1.65 *	-3.14 *
FIL	1.25	1.46	2.01 *	-1.21
STE	0.87	0.84	3.9 *	-0.79
RAM	1.26	1.63	1.21	-1.18
TEX	0.19	1.01	1.28	-0.73
SEP	2.63 *	0.97	3.46 *	-1.19
ABU	-0.24	-0.33	0.55	-1.93 *
SIT	-2.04 *	-0.59	3.4 *	-0.31
DIF	2.51 *	0.73	5.13 *	-0.41
SPI	-0.81	0.72	2.69 *	-0.78
FOE	3.84 *	0.58	-0.11	-3.21 *
FOS	-1.16	1.02	2.31 *	-1.87 *
FOL	1.34	-0.59	0.93	-0.03
LOB	1.08	-0.33	1.71 *	-1.58
CLO	0.48	1.53	-0.53	-2.56 *
FLD	1.71 *	2.22 *	0.04	-1.90 *
INF	0.26	5.86 *	0.98	-1.24
SUB	2.42 *	3.22 *	0.98	-2.18 *
SEN	0.83	3.93 *	4.54 *	0.49
SES	1.71	0.86	1.24	-2.34 *
FLS	0.69	2.63 *	3.52 *	-1.92 *
SEX	-0.18	0.00	-1.49	1.22
FLC	1.21	0.99	3.49 *	-2.97 *
DIM	0.28	1.9 *	0.09	-3.67 *
DIT	0.67	1.45	4.52 *	1.17
BIO	0.67	0.34	1.53	-1.54

Discussion

Ecological processes, phylogeny and the distribution of traits in the communities

Extending from the theoretical framework suggested by Webb and collaborators (2002) we can infer the mechanisms that lead to the observed community structure using the phylogenetic signal present in the functional traits of the species (Table 1). The theory predicts four different distribution patterns of a determined trait in the species of the community as a result of considering, on the one hand, the ecological processes taking place – competitive exclusion or environmental filter – and, on the other hand, the phylogenetic relationships among the members of a community for a given trait – a phylogenetically conserved trait or a converging trait that is not phylogenetically conserved. A positive phylogenetic signal – the more closely related the species in the community, the greater the functional similarity - provides evidence in

Table 5. Number of traits exhibiting positive, negative or no phylogenetic signal in both types of slopes and at the two study sites, and the number of nodes of the phylogenetic tree exhibiting either significant or no significant divergences and convergences. The most likely ecological process determining the species assemblage is suggested for each combination of slope and locality according to the conceptual framework of Table 1. Asterisks indicate significantly higher values than those expected from a null hypothesis of no phylogenetic signal or functional convergence or divergence (χ^2, degrees of freedom = 1; $p < 0.01$). Results supporting the conclusion on the dominant process are shown in boldface

	Málaga		Valencia	
	Embankments	Roadcuts	Embankments	Roadcuts
Number of traits with a positive phylogenetic signal	4	6	**13** *	0
Number of traits with a negative phylogenetic signal	1	0	1	**12** *
Number of traits with no significant phylogenetic signal	23	22	14	16
Number of nodes exhibiting significant divergences	12	11	13	9
Number of nodes exhibiting significant convergences	11	5	15	**54** *
Number of nodes exhibiting no significant divergences or convergences	**251**	**258**	**246**	211
SUGGESTED DOMINANT ECOLOGICAL PROCESS	COMPETITIVE EXCLUSION (phylogenetically converging traits)	COMPETITIVE EXCLUSION (phylogenetically converging traits)	ENVIRONMENTAL FILTERING (phylogenetically converging traits)	ENVIRONMENTAL FILTERING (phylogenetically converging traits)

favour of a phylogenetically conserved trait, whereas a negative phylogenetic signal – the more closely related the species in the community, the bigger the differences for the functional trait considered – can indicate two situations: a phylogenetically conserved trait in a scenario of competitive exclusion or a shared trait by means of adaptational convergence when environmental filters prevail in community structuring. The fourth possible situation, the absence of a phylogenetic signal, could indicate the prevalence of competitive exclusion. The number of significant correlations between each trait and the other ones enables us to distinguish between the two situations that bring a trait to present a negative phylogenetic signal. This number of correlations is an estimate of the degree of association in syndromes with which a determined species presents its functional traits, as has been highlighted in studies of dispersal and pollination systems (Ridley 1930; Janson 1983; Neal et al. 1998), tolerance to shade (Kitajima 1994), functional traits of Mediterranean woody flora (Herrera 1992) and of bushes beneath the tropical tree canopy (Mulkey et al. 1993). This association in syndromes of the characters results from historic effects, sorting processes, phylogenetic relationships and environmental filters (Herrera 1992). With the exception of environmental filters, all the factors act at regional (100 -1000 km) but not at local scales (Webb et al. 2002). It can be argued that the harder the environmental conditions, the higher the number of traits a given trait will correlate with due to the existence of an environmental filter which is selecting in favour of specific life strategies (Weiher & Keddy 1995). Under these adverse conditions that give rise to syndromes, the most likely situation is that the traits will be similar due to convergence, rather than being phylogenetically conserved. Even though the number of correlations among traits did not increase with the adversity of the habitat we have found, as a support for this hypothesis, that the only situation where the number of functional convergences within the phylogenetic tree was significant was in the most adverse, i.e. roadcuts in Valencia (Table 5). Collectively these results suggest that environmental filters were the dominant ecological process in the dry and continental site (Valencia), both in embankments (positive phylogenetic signal) and in roadcuts (negative signal and significant convergence among nodes).

By contrast, the lack of phylogenetic signal in the functional traits of the communities in the humid and mild site (Málaga) suggested that the most likely ecological process involved in structuring communities in this site was competitive exclusion (Tables 4 and 5). This process is considered to be fundamental to community structure in a wide range of environmental conditions (Armbruster et al. 1994; Wilson & Watkins 1994; Wilson & Gitay 1995; Wright 2002). No phylogenetic signal was found in the functional traits of plants from meadow communities, which was interpreted as an evidence for rapid evolution of coexisting and closely related species (Silvertown et al. 2006) in contrast to the notion of niche conservatism and slow evolution of plant traits supported by other studies (Webb et al. 2002). This lack of phylogenetic signal supported, in turn, the idea of interspecific competition as an important process involved in the assembly of these communities. Grime (2006) argued that filters both with divergent and convergent effects may operate simultaneously during the assembly of a community on recruitment from the local species pool and impose contrasted effects on the similarity of the trait values exhibited by coexisting species in grassland communities. In these communities, local disturbances were argued to have diversifying effects on plant traits (divergence) while productivity related traits were considered less variable (convergence).

Competitive exclusion leads to a broad distribution of the trait values among the species, which is also seen in a low degree of association of these traits in syndromes (Johansson & Keddy 1991). This situation was manifest in the communities studied, where the number of traits correlating to a given trait was relatively low. However, and contrary to our hypothesis, this number did not increase with environmental adversity.

It must be noted that plant communities can be very dynamic, exhibiting remarkable changes in species composition over time. This is particularly the case for many human-influenced communities such as the herbaceous roadside communities studied here. These communities have been shown to exhibit a highly dynamic species composition with a Sørensen similarity index of only 0.3-0.5 between years (Matesanz et al. 2006). In a study of the relationships between change in α-diversity and habitat homogenizations in terms of species composition and plant functional traits for the 1978-1998 period in British human-modified ecosystems, Smart et al. (2006) observed that as α-diversity declined, plant communities became functionally more similar, but less similar in terms of species composition. This finding suggested that different communities converged on a narrow range of trait syndromes with species identities remaining historically contingent over time. Since roadside plant communities are only recently receiving attention in ecological studies, there is a scarcity of long-term data sets but we have observed that species composition becomes more stable over time after the first 3-4 years since colonization of the road slopes (unpubl. data). The species considered for the current study were the most abundant ones (within the 70th abundance percentile) so we not only minimised the influence of unrepresentative species in our inferences of the ecological processes underlying species assembly but also maximised the chances of including the species that are continuously present in the communities over time since temporal compositional changes affect primarily the least abundant species (Matesanz et al. 2006).

Relationships between phylogeny and biogeographic range

There was no significant phylogenetic signal in the biogeographic range of the species in any of the four communities studied. Few studies associate phylogeny with the biogeographic distribution range of species and all of these found a positive phylogenetic signal – the phylogenetically closer the species, the more similar their distribution range (Jablonski 1987; Ricklefs & Latham 1992; Brown 1995). This has been explained by the fact that phylogenetically related species tend to be closer in evolutionary age than less related ones, and as evolutionary age is related to current distribution area, distribution area is found to be a phylogenetically conserved attribute (Willis 1992; Fjeldsa & Lovett 1997). For Mediterranean vascular flora, however, Herrera (1992) showed that the same distribution area can be shared by lineages of different evolutionary age, which attenuates the phylogenetic signal. This is more likely to occur in communities with a mixture of biogeographic origins, as occurs in the roadside communities studied, which develop in the south of the Iberian Peninsula, a diversity hotspot (Médail & Quézel 1997). Moreover, the four communities share a high percentage of species with a wide distribution range, coinciding with what was found for this type of roadside herbaceous plant communities in other parts of the world (Heindl & Ullmann 1991; Ullmann et al. 1998; Godefroid & Tanghe 2000). The differences are seen, however, in the percentage of species with a limited distribution range (Mediterranean), which is lower on the slopes in Málaga. The fact that environmental filtering was likely to be a dominant ecological process in the continental and dry Valencia site is associated with a larger fraction of Mediterranean species in the communities and coincides with the well established relationship between distribution range and enviromental adversity (Wilson et al. 1992; Ullmann et al. 1995).

Limitations of the study and research perspectives

The main limitations of our study stems from (1) the coarse-grained estimation of functional attributes and phylogenetic distances among species and (2) the observational, correlative approach. With these limitations we can only suggest what the main ecological processes influencing the assemblage of the species could be. For instance, the lack of an increase in correlations among traits with environmental adversity obtained here might be due to limitations associated with the discrete nature of our data set, although the hypothesis deserves further attention. We cannot disregard other processes such as stochastic processes or factors influencing density-dependent mortality that also affect the assembly of species (Kembel & Hubbell 2006; Webb et al. 2006). Observational studies involving no manipulation or experimental approach are the first approach to most plant communities and, for some, they provide the only source of information currently available. However, we must admit important limitations in our understanding of the real ecological processes involved in the assemblage of plant communities derived from correlative, observational studies such as the present one; although we argue that the influence of the main processes can still be detected by a thorough examination of the distribution of functional traits over the species of the community and their phylogenetic relationships.

An additional problem when testing for the relative importance of competitive exclusion vs habitat filtering is the confounding effect of the different scale of action of each process. This has been discussed by Webb et al. (2002, 2006) and Cavender-Bares et al. (2006), and the available evidence suggests that competitive exclusion should have greater importance at smaller spatial scales while environmental filtering should predominate at larger spatial scales. Cavender-Bares et al. (2006) also reported that the increasing conservatism of traits at broader phylogenetic scales shifts the functional trait pattern from overdispersion to clustering, rising caution on the definition of plant communities: when they are broadly defined, they include greater phylogenetic diversity, which in turns increases trait conservatism and affects our understanding of the ecological processes underlying species assembly. This issue of scale is underlying the notions of α and β niches (corresponding to the scales at which α and β diversity are measured) as discussed by Silvertown et al. (2006). In meadow plant communities α niche has been found to be more evolutionarily labile than β niche, which can reconcile contrasting evidences but it requires more research with plant communities that contain a more complete sampling of the clades from which the community is assembled than those studied so far (Silvertown et al. 2006). Ideally, phylogenetic approaches to plant communities should handle both large numbers of species and thorough determination of functional traits, but the work load involved in each of these tasks leads to studies involving either a large number of species such as the present one with some 300 species, for which a simplified estimation of the functional traits of each species is obtained, or a reduced number of species, for which functional traits and phylogenetic distances among species are accurately determined, as in the study by Cavender-Bares et al. (2004) that focused on 17 *Quercus* species, or the study by Silvertown et al. (2006) that focused on 55 meadow species. However, more and more phylogenetic and functional information is becoming available for an increasing number of plant communities, facilitating detailed and extensive analyses of plant communities. We conclude that such analyses explicitly including the relative abundance of the species and a quantitative and thorough characterization of the functional traits of each species, particularly of those traits that are relevant for the habitat in question, together with the phylogenetic distances among them will render sound insights into the processes involved in the assemblage of plant communities.

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References

Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: S165-S184.

Ackerly, D.D. 2004. *Analysis of traits (AOT), v3.0: A module of PHYLOCOM, v3.21 by C. Webb, S. Kempel, D. Ackerly*. Stanford University, Stanford, CA, US.

Ackerly, D.D. & Donoghue, M.J. 1995. Phylogeny and ecology reconsidered. *Journal of Ecology* 83: 730-733.

Andrés, P. & Jorba, M. 2000. Mitigation strategies in some motorway embankments (Catalonia, Spain). *Restoration Ecology* 8: 268-275.

Antonovics, J. 1976. The nature of limits to natural selection. *Annals of the Missouri Botanical Garden* 63: 224-247.

Armbruster, W.S., Edwards, M.E. & Debevec, E.M. 1994. Floral character displacement generates assemblage structure of Western Australian triggerplants (*Stylidium*). *Ecology* 75: 315-329.

Arroyo, J., Carrión, J.S., Hampe, A. & Jordano, P. 2004. La distribución de las especies a diferentes escalas espacio-temporales. In: Valladares, F. (ed.) *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, EGRAF, S.A., Madrid, ES.

Berg, R.L. 1960. The ecological significance of correlation pleiades. *Evolution* 14: 171-180.

Blomberg, S.P. & Garland, T.J. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* 15: 899-910.

Bochet, E. & García-Fayos, P. 2004. Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology* 12: 166-174.

Bolós, O. de & Vigo, J. 1984. *Flora del Països Catalans*. Editorial Barcino, Barcelona, ES.

Brown, J.H. 1995. *Macroecology*. University Chicago Press, Chicago, IL, US.

Castroviejo, S. 1986. *Flora Ibérica: plantas vasculares de la Península Ibérica e Islas Baleares*. CSIC, Madrid, ES.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist:* 163: 823-843.

Cavender-Bares, J., Keen, A. & Miles, B. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87: S109-S122.

Chevereud, J.M. 1988. The evolution of genetic correlation and developmental constraints. In: de Jong, G.D. (ed.) *Population genetics and evolution*, pp. 94-101. Springer-Verlag, Berlin, DE.

Clark, L.G., Zhang Weiping & Wendel, J.F. 1995. A phylogeny of the grass family (Poaceae) based on ndhF sequence data. *Systematic Botany* 20: 436-430.

Davies, T. J., Barraclough, T. G., Chase, M.W., Soltis, P. S., Soltis, D.E. & Savolainen, V. 2004. Darwin´s abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* 101: 1904-1909.

Diamond, J.M. 1975. Assembly of species communities. In: Cody, M.L. & Diamond J.M. (eds.) *Ecology and evolution of communities*, pp. 342-444. Belknap Press, Cambridge, UK.

Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change: a multiscale approach. *Journal of Vegetation Science* 8: 463-474.

Díaz, S., Cabido, M. & Casanoves, F. 2001. Functional implications of trait-environment linkages in plant communities. In: Díaz, S., Cabido, M. & Casanoves, F. (eds.) *Functional implications of trait-environment linkages in plant communities*, Cambridge University Press, Cambridge, UK.

Felsenstein, J. 2004. *Inferring phylogenies*. Sinuauer, Sunderland, MA, US.

Fernández-Alés, R., Laffarga, J.M. & Ortega, F. 1993. Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science* 3: 313-322.

Fitter, A.H. & Peat, H.J. 1994. The ecological flora database. *Journal of Ecology* 82: 415-425.

Fjeldsa, J. & Lovett, J.C. 1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation* 6: 325-346.

Gittleman, J.L. & Kot, M. 1990. Adaptation: Statistic and a null model for estimating phylogenetic effects. *Systematic Zoology* 39: 227-241.

Godefroid, B. & Tanghe, M. 2000. Influence of small climatic variations on the species composition of roadside grasslands. *Phytocoenologia* 30: 655-664.

Gomez Sal, A., De Miguel, J.M., Casado, M.A. & Díaz Pineda, F. 1986. Successional change in the morphology and ecological responses of a grazed pasture ecosystem in Central Spain. *Vegetatio* 67: 33-44.

Grime, P.J. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 255-260.

Harvey, P.H. 1996. Phylogenies for ecologist. *Journal of Animal Ecology* 65: 255-263.

Harvey, P.H. & Pagel, M.D. 1991. *The comparative method in evolutionary biology*. Oxford Universwity Press, Oxford, UK.

Heindl, B. & Ullmann, I. 1991. Roadside vegetation in Mediterranean France. *Phytocoenologia* 20: 111-141.

Herrera, C.M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. *The American Naturalist* 140: 3 421-446.

Hobbs, R.J., Arico, A.J., Baron, J.S., Bridgewater, P., Cramer, W.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D.,. Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1-7.

Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of cretaceous mollusks. *Science* 238: 360-363.

Janson, S.H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187-189.

Johansson, M.E. & Keddy, P.A. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity – an experimental study on 2 guilds of wetland plants. *Oikos* 60: 27-34.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interaction. *The American Naturalist* 145: 163-191.

Keddy, P.A. & Weiher, E. 2001. *Ecological Assembly Rules: Perspectives, advances, retreats*. Cambridge University Press, Cambridge, UK.

Kembel, S.W. & Hubbell, S.P. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87 (Suppl): S86-S99.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98: 419-428.

Kumar, S., Tamura, K., Jakobsen, I. B. & Nei, M. 2001. *MEGA2: Molecular evolutionary genetics analysis software*. Arizona State University. Tempe, AZ, US.

Legendre, P. & Legendre, L. 1983. *Numerical ecology*. Elsevier, Amsterdam, NL.

Losos, J.B. 1996. Phylogenetic perspectives on community ecology. *Ecology* 77: 5 1344-1354.

Mateo-Sanz, G. & Crespo-Villalba, M. B. 1986. *Manual para la determinación de la flora valenciana*. 2. ed. Corregida y Ampliada. Editorial Moliner, Valencia, ES.

Martínez-Alonso, C.& Valladares, F. 2002. La pendiente y el tipo de talud alteran la relación entre la riqueza de especies y la cobertura de las comunidades herbáceas. *Ecología* 16: 59–71.

Matesanz, S., Valladares, F., Tena, D., Costa-Tenorio, M. & Bote, D. 2006. Early dynamics of plant communities in revegetated motorway slopes from southern Spain: is hydroseeding always needed? *Restoration Ecology* 14: 297-307.

Médail, F. & Quézel, P. 1997. Hot-spot analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden* 84: 112-127

Montalvo, J., Casado, M.A., Levassor, C. & Pineda, F.D. 1991. Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. *Journal of Vegetation Science* 2: 655-666.

Mulkey, S.S., Wright, S.J. & Smith, A.P. 1993. Comparative physiology and demography of three neotropical forest shrubs: alternative shade adaptive character syndromes. *Oecologia* 96: 526-536.

Neal, P. R., Dafni, A. & Giurfa, M. 1998. Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypothesis. *Annual Review of Ecology and Systematics* 29: 345-373.

Niinemets, U. & Valladares, F. 2006. Tolerance to shade, drought and waterlogging of temperate, Northern hemisphere trees and shrubs. *Ecological Monographs* 76: 521-547.

Olson, E.C. & Miller, R.L. 1958. *Morphological integration*. University of Chicago Press, Chicago, IL, US.

Pérez, A.J. 1994. *Atlas Climàtic de la Comunitat Valenciana (1961-1990)*. Consellería dÓbres Publiques, Urbanisme i Transports, Valencia, ES.

Pigliucci, M. 2003. Studying mutational effects on G matrices. In: Pigliucci M. (ed.) *The evolutionary biology of complex phenotypes*. Oxford University Press, Oxford, UK.

Pignatti, S. 1982. *Flora d'Italia*. Edagricoltore, Bologna, IT.

Raunkiær, O. 1934. *The life forms of plants and statistical plant geography*. Clarendon Press, Oxford, UK.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Ricklefs, R. E. & Latham, R.E. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *The American Naturalist* 139: 1305-1321

Ridley, H.N. 1930. *The dispersal of plants throughout the world*. Reeve, Ashford, Kent, UK.

Schaffers, A.P. & Sýkora, K.V. 2002. Sinecology of species-rich plant communities on roadside verges in the Netherlands. *Phytocoenologia* 32: 29-83.

Silvertown, J. & Dodd, M. 1997. Comparing plants and connecting traits. In: Silvertown, J., Franco, M. & Harper, J.L. *Plant life histories: ecology, phylogeny and evolution*. Cambridge University Press, London, UK

Silvertown, J., Dodd, M. & Gowing, D. 2001. Phylogeny and the niche structure of meadow plant communities. *Journal of Ecology* 89:428-435.

Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A. & Dolphin, K. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B Biological Sciences* 273: 39-44.

Smart, S.M., Thompson, K., Marrs, R.H., Duc, M.G.L. Maskell, L.C. & Firbank, L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B Biological Sciences* 273: 2659-2665.

Soltis, D.E., Soltis, P.S. & Chase, M.W. 2000. Angiosperm phylogeny inferred from 18S rDNA rbcL, and atpB sequences. *Botanical Journal of the Linnean Society* 133: 381-461.

Temperton, V. M. & Hobbs, R. J. 2004. The search for ecological assembly rules and its relevance to restoration ecology. In: Temperton V.M., Hobbs R.J., Nuttle T. & Halle S. (eds.) *Assembly rules and restoration ccology – Bridging the gap between theory and practice*. Island Press, Washington, DC, US.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25: 4876-4882.

Tofts, R. & Silvertown, J. 2000. A phylogenetic approach to community assembly from a local species pool. *Proceedings of the Royal Society of London B : Biological Sciences* 267: 363-369.

Ullmann, I., Bannister, P. & Wilson, B. 1995. The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. *Journal of Vegetation Science* 6: 131-142.

Ullmann, I., Bannister, P. & Wilson, B. 1998. Lateral differenciation and the role of exotic species in roadside vegetation in southern New Zealand. *Flora* 193: 149-164.

Valdés, B., Talavera, S. & Fernández-Galiano, E. 1987. *Flora Vascular de Andalucía Occidental*. Ketres Editora S.A., Barcelona, ES.

Webb, C., Ackerly, D.D., Mc Peek, M. & Donogue, M.A. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475-595.

Webb, C.O., Gilbert, G.S. & Donoghue, M.J. 2006. Phylodiversity-dependent seedling mortality, size structure and disease in a Bornean rain forest. *Ecology* 87 (Suppl.): S123-S131.

Weiher, E. & Keddy, P.A. 1995. Assembly rules, null models and trait dispersion: new question from old patterns. *Oikos* 74: 159-164

Westoby, M., Leishman, L.R. & Lord, J. 1995. On misinterpreting the phylogenetic correction. *Journal of Ecology* 83: 531-534.

Willis, J.C. 1992. *Area and age: A study of geographical distribution and origin in species*. Cambridge University Press, Cambridge, UK.

Wilson, J.B., Rapson, G., Sykes, M., Watkins, A. & Williams, P. 1992. Distributions and climatic correlations of some exotic species along roadsides in South Island, New Zealand. *Journal of Biogeography* 19: 183-194.

Wilson, J.B. & Gitay, H. 1995. Community structure and assembly rules in a dune slack – variance in richness, guild proportionality, biomass constancy and dominance/diversity relations. *Vegetatio* 116: 93-106.

Wilson, J.B. & Watkins, A.J. 1994. Guilds and assembly rules in lawn communities. *Journal of Vegetation Science* 5: 591-600.

Wright, S.J. 2002. Plant diversity in tropical forest: a review of mechanisms of species coexistence. *Oecologia* 130: 1-14.

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App. 1. List of the 417 recorded plant species and their mean abundance in each locality; abundance values are frequency of appearance multiplied by mean cover, both variables in a 0-1 scale; † hydroseeded species; most abundant species (within the 70 abundance percentile) in Malaga or Valencia are indicated with M or V respectively.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**
Achillea ageratum L.	0.00	0.09	*V*
Adenocarpus complicatus (L.) Gay	0.18	0.00	*M*
Aegilops geniculata Roth	0.00	1.66	*V*
Aegilops neglecta Req. ex Bertol.	0.22	0.00	*M*
Aegilops triuncialis L.	0.10	0.53	*M* *V*
Agropyron pectinatum (Bieb.) Beauv. †	0.00	0.62	*V*
Agropyron repens (L.) P. Beauv.	0.06	0.00	
Ajuga chamaepytis (L.) Schreb.	0.00	0.09	*V*
Ajuga iva (L.) Schreb.	0.00	0.03	
Allium ampeloprasum L.	0.18	0.33	*M* *V*
Allium roseum L.	0.14	0.00	*M*
Althaea hirsuta L.	0.00	0.15	*V*
Alyssum granatense Boiss. & Reut.	0.00	0.00	
Alyssum simplex Rudolphi.	0.00	1.13	*V*
Amaranthus graecizans L.	0.00	0.06	*V*
Ammi bisnaga (L.) Lam.	0.38	0.00	*M*
Ammi majus L.	0.00	0.03	
Anacyclus clavatus (Desf.) Pers.	0.46	2.05	*M* *V*
Anacyclus radiatus Loisel.	0.60	0.00	*M*
Anagallis arvensis L.	1.65	0.00	*M*
Anchusa azurea Rchb. an Miller	0.87	0.00	*M*
Andryala integrifolia L.	1.37	0.00	*M*
Anthemis arvensis L.	0.66	0.06	*M* *V*
Anthyllis cytisoides L.	0.72	0.00	*M*
Anthyllis montana ssp. *hispanica* L.	0.00	0.06	*V*
Anthyllis tetraphylla L.	0.59	0.00	*M*
Arenaria aggregata L.	0.00	0.03	
Arenaria hispanica Sprenger	0.24	0.00	*M*
Argyrolobium zanonii (Turra) P.W. Ball.	0.00	0.09	*V*
Arisarum simorrhinum Durieu	0.40	0.00	*M*
Arrhenatherum album (Vahl) W.D. Clayton	0.03	0.00	
Artemisia absinthium L.	0.00	0.03	
Arundo donax L.	0.10	0.00	*M*
Asparagus albus L.	0.03	0.00	
Asperula aristata L.	0.00	0.15	*V*
Asphodelus fistulosus L.	0.00	0.18	*V*
Asphodelus ramosus L.	0.06	0.00	
Asteriscus aquaticus (L.) Less.	0.20	0.00	*M*
Asterolinon linum-stellatum (L.) Duby	0.03	0.00	
Astragalus echinatus Murray	0.20	0.00	*M*
Astragalus hamosus L.	0.00	0.15	*V*
Astragalus sesameus L.	0.00	0.09	*V*
Astragalus stella L.	0.00	0.06	*V*
Atractylis humilis L.	0.00	0.44	*V*
Atriplex halimus L.	0.06	0.09	*V*
Avena barbata Pott ex Link	0.30	2.25	*M* *V*
Avena sterilis L.	1.92	0.68	*M* *V*
Avenula bromoides (Gouan) H.Scholz	0.00	0.18	*V*
Beta vulgaris L.	0.00	0.12	*V*
Biscutella baetica Boiss. & Reuter	0.55	0.00	*M*
Biscutella valentina (Loefl. ex L.)	0.00	0.03	
Biserrula pelecinus L.	0.03	0.00	

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App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Brachypodium dystachion (L.) Beauv.	1.10	0.18	*M*	*V*
Brachypodium retusum (Pers.) Beauv.	0.10	0.24	*M*	*V*
Brassica nigra (L.) Koch	0.90	0.00	*M*	
Brassica oleracea L.	0.20	0.09	*M*	*V*
Brassica repanda (Willd.)	0.00	0.03		
Briza maxima L.	0.26	0.00	*M*	
Bromus diandrus Roth.	0.12	0.52	*M*	*V*
Bromus inermis Leyss. †	0.00	2.25		*V*
Bromus madritensis L.	0.25	0.00	*M*	
Bromus rubens L.	0.09	1.51	*M*	*V*
Bromus scoparius L.	0.10	0.03	*M*	*V*
Bromus sterilis L.	0.37	0.00	*M*	
Bromus tectorum L.	0.00	1.72		*V*
Bupleurum fruticosum L.	0.00	0.09		*V*
Bupleurum lancifolium Hornem.	0.09	0.00	*M*	
Calendula arvensis L.	0.74	0.62	*M*	*V*
Calicotome villosa (Poiret) Link	1.35	0.00	*M*	
Cardaria draba (L.) (Desv.)	0.00	0.00		
Carduncellus caerulens (L.) C. Presl.	0.10	0.00	*M*	
Carduus borgeanus L.	0.10	0.00	*M*	
Carduus picnocephalus L.	0.73	1.28	*M*	*V*
Carex humilis Leyss	0.00	0.03		
Carlina corymbosa L.	0.12	0.00	*M*	
Carthamus lanatus L.	0.30	0.74	*M*	*V*
Catananche caerulea L.	0.00	0.30		*V*
Centaurea calcitrapa L.	0.12	0.06	*M*	*V*
Centaurea melitensis L.	0.20	0.27	*M*	*V*
Centaurea pullata L.	0.92	0.00	*M*	
Centaurea solstitialis L.	0.20	0.00	*M*	
Centaurea sphaerocefala L.	0.10	0.00	*M*	
Centaurium erythraea Rafn.	0.12	0.00	*M*	
Centranthus macrosiphon Boiss.	0.06	0.00		
Cerastium gracile Dufour	0.00	0.03		
Cerastium pumilum Curtis	0.00	0.24		*V*
Cerastium purpureum L.	0.06	0.03		*V*
Cerastium semidecandrum L.	0.00	0.00		
Chaenorhinum serpyllifolium (Lange) Lange	0.00	0.03		
Chenopodium album (Mulh. ex Willd.) Coss. & Germ.	0.02	0.15		*V*
Chenopodium murale L.	0.03	0.00		
Chenopodium opulifolium Schrader	0.03	0.00		
Chrysanthemum coronarium L.	0.93	0.00	*M*	
Cichorium endivia L.	0.00	2.14		*V*
Cichorium intybus L.	0.00	0.09		*V*
Cirsium arvense (L.) Scop.	0.24	0.06	*M*	*V*
Cistus monspeliensis L.	0.03	0.00		
Cistus salvifolius L.	1.06	0.00	*M*	
Coleostephus myconis L.	0.03	0.00		
Convolvulus altheoides L.	0.21	2.16	*M*	*V*
Convolvulus arvensis L.	0.00	0.06		*V*
Convolvulus lineatus L.	0.10	0.00	*M*	
Convolvulus meonanthus Hoffmanns	0.10	0.00	*M*	
Convolvulus tricolor L.	0.00	0.21		*V*
Conyza bonariensis (L.) Cronq.	0.00	0.09		*V*
Conyza canadensis (L.) Cronq.	0.00	0.03		

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Conyza sumatrensis (Retz) E. Walker.	0.06	0.00		
Coridothymus capitatus (L.) Reichb.	0.06	0.21		*V*
Coris monspeliensis L.	0.00	0.03		
Coronilla minima L.	0.00	0.53		*V*
Coronilla scorpioides ssp. *lotoides* (L.) Koch.	0.06	0.00		
Corrigiola littoralis L.	0.00	0.00		
Crambe filiformis Jacq.	0.00	0.09		*V*
Crataegus monogyna Jacq.	0.06	0.00		
Crepis capillaris (L.) Wallr.	0.00	0.71		*V*
Crepis foetida L.	0.00	0.03		
Crepis pulchra L.	0.74	1.57	*M*	*V*
Crepis vesicaria L.	0.06	0.00		
Crucianella angustifolia L.	0.00	0.06		*V*
Crupina crupinastrum (Moris) Vis.	0.03	0.00		
Cynara scolymus L.	0.30	0.44	*M*	*V*
Cynodon dactylon (L.) Pers. †	0.06	0.00		
Cynosurus echinatus L.	0.06	0.00		
Cytisus scoparius (L.) Link.	0.57	2.61	*M*	*V*
Dactylis glomerata L. †	1.32	0.56	*M*	*V*
Daucus carota L.	0.34	0.09	*M*	*V*
Desmazeria rigida (L.) Tutin	0.40	2.02	*M*	*V*
Diplotaxis erucoides (L.) DC.	0.48	0.00	*M*	
Diplotaxis virgata (Cav.) DC.	0.00	0.03		
Dipsacus fullonum L.	1.11	0.18	*M*	*V*
Ditrichia viscosa (L.) Greuter	0.00	0.03		
Dorycnium pentaphyllum Scop.	0.00	0.06		*V*
Echinaria capitata (L.) Desf.	0.03	0.00		
Echinops strigosus L.	0.00	0.00		
Echium creticum L.	0.68	0.00	*M*	
Echium plantagineum L.	0.10	0.53	*M*	*V*
Elymus repens (L.) Gould †	0.00	0.00		
Erodium ciconium (L.) L´herit.	0.46	1.48	*M*	*V*
Erodium cicutarium (L.) L´herit.	0.10	0.56	*M*	*V*
Erodium malacoides (L.) L´herit.	0.30	0.00	*M*	
Erodium moschatum (L.) L´herit.	0.30	0.00	*M*	
Erodium primulaceum Wel. ex Lange	0.00	0.15		*V*
Eruca vesicaria (L.) Cav.	0.00	1.54		*V*
Eryngium campestre L.	0.00	0.00		
Euphorbia exigua L.	0.44	0.18	*M*	*V*
Euphorbia falcata L.	0.10	0.06	*M*	*V*
Euphorbia helioscopia L.	0.28	0.36	*M*	*V*
Euphorbia minuta Loscos & Pardo	0.03	0.06		*V*
Euphorbia peplus L.	0.81	0.00	*M*	
Euphorbia segetalis L.	0.40	0.00	*M*	
Euphorbia serrata L.	0.00	1.90		*V*
Euphorbia sulcata De Lens ex Loisel	0.10	0.00	*M*	
Euphorbia terracina L.	0.00	0.03		
Fedia cornucopiae (L.) Gaertner	0.40	0.00	*M*	
Fedia scorpioides Dufresne	0.10	0.00	*M*	
Festuca arundinacea Schreber †	0.56	0.06	*M*	*V*
Filago pyramidata L.	0.13	0.89	*M*	*V*
Fumana ericifolia Wallr	0.00	0.03		
Fumana ericoides (Cav.) Gandg.	0.00	0.06		*V*
Fumana hispidula Loscos & Pardo	0.00	0.09		*V*
Fumana laevipes (L.) Spach	0.00	0.03		

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Fumana laevis (Cav.) (Gross.)	0.00	0.09		*V*
Fumana thymifolia (L.) Spach.	0.06	0.03		*V*
Fumaria officinalis L.	0.20	0.00	*M*	
Fumaria parviflora Lam.	0.30	0.00	*M*	
Galactites tomentosa Moench.	2.10	0.92	*M*	*V*
Galium divaricatum Pourret ex Lam.	0.06	0.03		*V*
Galium murale (L.) All.	0.03	0.03		*V*
Galium parisienne	0.40	0.00	*M*	
Galium spurium L.	0.03	0.00		
Gastridium ventricosum (Gouan) Schinz et Thell.	0.10	0.00	*M*	
Gaudinia fragilis (L.) Beauv.	0.00	0.95		*V*
Genista hirsuta Vahl.	0.00	0.95		*V*
Genista scorpius L.	0.00	0.95		*V*
Geranium columbinum L.	0.40	0.00	*M*	
Geranium dissectum L.	0.30	0.00	*M*	
Geranium molle L.	0.18	0.03	*M*	*V*
Geranium purpureum Vill. In L.	0.30	0.00	*M*	
Geranium rotundifolium L.	0.27	0.03	*M*	*V*
Gladiolus communis L.	0.03	0.00		
Glaucium corniculatum (L.) J.H. Rudolph.	0.00	0.18		*V*
Glyceria notata Chevall.	0.20	0.00	*M*	
Gynandriris sisyrinchium (L.) Parl.	0.20	0.00	*M*	
Halimium spec.	0.00	0.27		*V*
Hedipnois cretica (L.) Dum.-Courset	0.26	0.27	*M*	*V*
Hedysarum coronarium L.	1.90	0.00	*M*	
Helianthemum asperum Lag Ex Dunal	0.00	0.36		*V*
Helianthemum hirtum (L.) Miller	0.00	0.12		*V*
Helianthemum ledifolium (L.) Miller	0.00	0.03		
Helianthemum marifolium (L.) Miller	0.00	0.15		*V*
Helianthemum siriacum (Jacq.) Dum.- Courset	0.00	0.09		*V*
Helichrysum serotinum (Boiss.) P. Fourn	0.00	0.68		*V*
Helichrysum stoechas (L.) Moench.	0.00	0.44		*V*
Herniaria glabra L.	0.00	0.00		
Herniaria hirsuta L. Heywood	0.00	0.09		*V*
Hippocrepis ciliata Willd.	0.00	0.06		*V*
Hippocrepis bourgaei (Nyman) Hervier	0.00	0.42		*V*
Hirsfeldia incana (L.) Lagrèze-Fossat	0.78	1.07	*M*	*V*
Hordeum leporinum Link.	0.22	1.19	*M*	*V*
Hormatophylla lapeyrousiana Guterm	0.00	0.03		
Hypericum perforatum L.	0.20	0.00	*M*	
Hypochaeris achyroporus L.	0.00	0.00		
Iberis crenata Lam.	0.09	0.00	*M*	
Iris germanica L.	0.03	0.06		*V*
Jasione montana L.	0.06	0.00		
Juncus bufonius L.	0.03	0.00		
Kickxia spurea (L.) Dumort.	0.16	0.03	*M*	*V*
Koeleria vallesiana L.	0.00	0.30		*V*
Lactuca sativa L.	0.00	0.03		
Lactuca serriola L.	0.58	0.68	*M*	*V*
Lamarckia aurea (L.) Moench.	0.06	0.00		
Lamium amplexicaule L.	0.20	0.06	*M*	*V*
Lathyrus angulatus L.	0.10	0.00	*M*	
Lathyrus annuus L.	0.00	0.03		
Lathyrus aphaca L.	0.37	0.00	*M*	
Lathyrus cicera L.	0.60	0.12	*M*	*V*

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Lathyrus clymenum L.	0.33	0.00	*M*	
Lathyrus ochrus (L.) DC.	0.64	0.00	*M*	
Launaea fragilis (Asso) Pau.	0.00	0.03		
Launaea pumila (Cav.) O. Kuntze	0.00	0.00		
Lavandula stoechas L.	0.06	0.00		
Leontodon longirostris Finch & P.D. Sell	0.00	0.24		*V*
Leontodon taraxacoides (Finch & P.D. Sell) Talavera	1.33	0.00	*M*	
Lepidium graminifolium L.	0.00	0.06		*V*
Leuzea conifera (L.) DC.	0.00	0.12		*V*
Linaria latifolia Desf.	0.00	0.12		*V*
Linaria simplex (Willdenow) A.P. de Candolle	0.00	0.50		*V*
Linum bienne Miller	0.45	0.00	*M*	
Linum narbonense L.	0.00	0.09		*V*
Linum strictum L.	0.18	0.06	*M*	*V*
Lobularia maritima (L.) Desv.	0.23	0.03	*M*	*V*
Logfia gallica (L.) Cosson & Germ.	0.18	0.00	*M*	
Lolium multiflorum Lam. †	0.54	0.00	*M*	
Lolium rigidum Gaudín †	0.18	1.54	*M*	*V*
Lophochloa cristata	0.00	0.12		*V*
Lotus corniculatus L. †	0.74	0.18	*M*	*V*
Lotus edulis L.	0.06	0.00		
Lotus ornithopodiodes L.	0.32	0.00	*M*	
Lupinus angustifolius L.	0.00	0.00		
Lupinus luteus L.	0.20	0.00	*M*	
Malope trifida Cav.	0.06	0.00		
Malva hispanica L.	0.84	0.00	*M*	
Malva neglecta Wallr.	0.00	0.53		*V*
Malva parviflora L.	0.75	0.00	*M*	
Mantisalca salmantica (L.) Briq .& Cav.	0.10	0.03	*M*	*V*
Marrubium supinum L.	0.00	0.33		*V*
Matthiola fruticulosa (L.) R. Br.	0.00	0.24		*V*
Medicago littoralis Rohde ex Loisel	0.18	0.36	*M*	*V*
Medicago lupulina L.	0.00	0.09		*V*
Medicago minima (L.) Bartal	0.10	1.19	*M*	*V*
Medicago orbicularis (L.) Bartal	0.23	0.15	*M*	*V*
Medicago polymorpha L.	0.60	0.15	*M*	*V*
Medicago rigidula L. All.	0.81	0.18	*M*	*V*
Medicago sativa L. †	1.06	4.12	*M*	*V*
Medicago scutellata (L.) Mill.	0.00	0.03		
Medicago trunculata Gaertner	0.00	0.00		
Melica ciliata L.	0.00	0.09		*V*
Melica magnolii Gren. & Godron	0.00	0.27		*V*
Melilotus officinalis Lam. †	0.15	0.44	*M*	*V*
Melilotus sulcata Desf.	0.23	0.27	*M*	*V*
Mercurialis annua L.	0.67	0.00	*M*	
Mercurialis tomentosa L.	0.00	0.30		*V*
Micromedia graeca (L.) Benth.	0.06	0.00		
Micropyrum tenellum (L.) Link.	0.00	0.00		
Misopates orontium (L.) Rafin	0.45	0.00	*M*	
Muscari neglectum Guss ex Ten.	0.00	0.27		*V*
Neslia paniculata (L.) Desv.	0.00	0.03		
Nigella damascena L.	0.06	0.00		
Onobrychis viciifolia Scop. †	1.91	3.44	*M*	*V*
Ononis mitissima L.	0.40	0.00	*M*	

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Ononis natrix L.	0.94	0.00	*M*	
Ononis pusilla L.	0.00	0.47		*V*
Onopordum acanthium L.	0.00	0.12		*V*
Ornithopus compressus L.	0.03	0.00		
Orobanche amethystea Thuill.	0.66	0.00	*M*	
Orobanche ramosa L.	0.10	0.00	*M*	
Otospermum glabrum (Lag.) Willk.	0.52	0.00	*M*	
Oxalis pes-caprae L.	0.86	0.00	*M*	
Pallenis spinosa (L.) Cass.	0.00	0.98		*V*
Papaver rhoeas L.	0.69	0.74	*M*	*V*
Papaver somniferum L.	0.20	0.00	*M*	
Parentucellia viscosa L.	0.06	0.00		
Parietaria judaica (L.) Béguinot	0.00	0.03		
Paronychia argentea Lam.	0.22	0.06	*M*	*V*
Paronychia capitata (L.) Lam.	0.00	0.39		*V*
Paronychia echinulata Chater	0.12	0.03	*M*	*V*
Petrorhagia prolifera (L.) P.W. Ball &	0.00	0.33		*V*
Phagnalon saxatile (L.) Cass.	0.48	0.12	*M*	*V*
Phalaris coerulescens Desf.	0.50	0.00	*M*	
Phalaris minor Retz	1.15	0.00	*M*	
Phlomis lychnitis L.	0.20	0.00	*M*	
Phlomis purpureus L.	0.20	0.00	*M*	
Phoeniculum vulgare Mill.	0.53	0.89	*M*	*V*
Picris echioides L.	0.87	0.12	*M*	*V*
Piptatherum miliaceum L. Cosson	0.62	0.47	*M*	*V*
Piptatherum paradoxum	0.06	0.03		*V*
Pistacia lentiscus L.	0.10	0.00	*M*	
Plantago afra L.	0.38	0.00	*M*	
Plantago coronopus L.	0.19	0.18	*M*	*V*
Plantago lagopus L.	0.24	0.09	*M*	*V*
Plantago lanceolata L.	0.92	0.65	*M*	*V*
Plantago major L.	0.40	0.00	*M*	
Plantago sempervirens	0.00	0.59		*V*
Polycnemum majus A. Braun	0.00	0.09		*V*
Polypogon maritimus Willd	0.10	0.00	*M*	
Polypogon monspeliensis (L.) Desf.	0.15	0.00	*M*	
Polypogon viridis (Gouan) Breistr.	0.00	0.03		
Potentilla reptans L.	0.00	0.09		*V*
Prunus dulcis (Mill.) DA Webb.	0.00	0.15		*V*
Psoralea bituminosa L.	1.20	0.00	*M*	
Pulicaria dysenterica (L.) Bernh.	0.09	0.00	*M*	
Quercus coccifera L.	0.03	0.03		*V*
Ranunculus arvensis L.	0.03	0.00		
Ranunculus muricatus L.	0.09	0.00	*M*	
Raphanus raphanistrum L.	0.68	0.00	*M*	
Raphistrum rugosum (L.) All.	0.68	0.47	*M*	*V*
Reichardia intermedia (Schultz) Samp	0.62	0.00	*M*	
Reseda lutea L.	0.24	0.00	*M*	
Reseda phyteuma L.	0.23	0.98	*M*	*V*
Retama sphaerocarpa (L.) Boiss.	0.30	0.00	*M*	
Rhamnus alaternus L.	0.00	0.62		*V*
Rhamnus oleoides L.	0.54	0.00	*M*	
Ricinus communis L.	0.06	0.00		
Ridolfia segetum (L.) Moris	0.20	0.09	*M*	*V*
Roemeria hybrida L.	0.00	0.03		

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Rosmarinus officinalis L.	0.00	0.21		*V*
Rostraria cristata (L.) Tzvelev	0.06	0.15		*V*
Rubia peregrina L.	0.00	0.21		*V*
Rubus ulmifolius L.	0.10	0.06	*M*	*V*
Rumex conglomeratus Murray	0.47	0.00	*M*	
Rumex pulcher L.	0.26	0.15	*M*	*V*
Salvia verbenaca L.	0.10	0.77	*M*	*V*
Sanguisorba minor Scop. †	0.65	1.93	*M*	*V*
Santolina chamaecyparissus L.	0.00	0.95		*V*
Satureja innota (Pau) G. López	0.00	0.03		
Scabiosa atropurpurea L.	0.26	0.56	*M*	*V*
Scabiosa simplex Desf.	0.00	1.57		*V*
Scabiosa stellata L.	0.00	0.15		*V*
Scandix pecten-veneris L.	0.03	0.00		
Schoenus nigricans L.	0.03	0.00		
Scolymus baetica L.	1.03	0.21	*M*	*V*
Scolymus hispanica L.	1.03	0.21	*M*	*V*
Scorpiurus muricatus L.	0.00	0.33		*V*
Scorpiurus sulcatus L.	0.55	0.00	*M*	
Scorpiurus vermiculatus L.	0.40	0.00	*M*	
Scorzonera angustifolia L.	0.00	0.56		*V*
Scorzonera laciniata L.	0.00	1.84		*V*
Scrophularia canina L.	0.00	0.03		
Scrophularia sambucifolia L.	0.10	0.00	*M*	
Sedum album L.	0.00	0.03		
Sedum sediforme (Jacq.) Pau.	0.00	0.09		*V*
Senecio gallicus Chaix	0.00	0.62		*V*
Senecio vulgaris L.	0.10	0.68	*M*	*V*
Sesamoides canescens (L.) O.Kuntze	0.06	0.00		
Sherardia arvensis L.	1.00	0.00	*M*	
Sideritis angustifolia L.	0.00	0.03		*V*
Sideritis arborescens Salzm. ex Bent.	0.00	0.03		*V*
Sideritis incana L.	0.00	0.12		*V*
Silene colorata Poiret	0.13	0.15	*M*	*V*
Silene conica L.	0.00	0.09		*V*
Silene gallica L.	0.43	0.00	*M*	
Silene nocturna L.	0.06	1.39		*V*
Silene vulgaris (Moench) Garcke	0.15	0.18	*M*	*V*
Silybum marianum (L.) Gaertner	0.75	0.33	*M*	*V*
Sinapis arvensis L.	0.30	0.00	*M*	
Sisymbrium irio L.	0.00	0.15		*V*
Sisymbrium orientale L.	0.00	0.21		*V*
Solanum nigrum L.	0.35	0.00	*M*	
Sonchus asper (L.) Hill.	1.21	0.00	*M*	
Sonchus oleraceus L.	0.60	2.88	*M*	*V*
Spartium junceum L.	0.12	0.00	*M*	
Stachys arvensis (L.) L.	1.29	0.00	*M*	
Stachys germanica (L.)	0.20	0.00	*M*	
Stegia trimestris (L.) Luque & Devesa	0.60	0.00	*M*	
Stipa capensis Thumb.	0.33	0.03	*M*	*V*
Stipa offneri Breistr.	0.00	0.24		*V*
Stipa parviflora Desf.	0.00	0.09		*V*
Taeniatherum caput-medusae (L.) Nevski	0.00	0.03		*V*
Taraxacum vulgare L.	0.00	0.12		*V*
Tetragonolobus purpureus Moench.	0.65	0.00	*M*	

App. 1, cont.

Species	**Abundance in Malaga**	**Abundance in Valencia**	**Species above 70th abundance percentile**	
Teucrium capitatum L.	0.10	0.15	*M*	*V*
Teucrium gnaphalodes L´hérit.	0.00	0.09		*V*
Teucrium pseudochamaepitys L.	0.00	0.12		*V*
Thesium humile Vahl.	0.01	0.00		
Thymus vulgaris L.	0.00	0.47		*V*
Tolpis barbata (L.) Gaertner	0.32	0.00	*M*	
Torilis nodosa L. Gaertner	1.63	0.00	*M*	
Tragopogon dubius Scop.	0.00	0.74		*V*
Tragopogon porrifolius L.	0.00	0.00		
Trifolium angustifolium L.	0.54	0.00	*M*	
Trifolium campestre Schreber	0.34	0.00	*M*	
Trifolium glomeratum L.	0.23	0.00	*M*	
Trifolium lappaceum L.	0.16	0.00	*M*	
Trifolium pratense L.	0.19	0.00	*M*	
Trifolium repens L. †	0.37	0.15	*M*	*V*
Trifolium scabrum L.	0.13	0.00	*M*	
Trifolium squamosum L.	0.32	0.00	*M*	
Trifolium stellatum L.	0.35	0.00	*M*	
Trifolium sylvaticum Gérad ex Lois	0.10	0.00	*M*	
Trigonella monspeliaca L.	0.00	0.03		*V*
Trigonella polyceratia (L.) Trautv.	0.00	0.30		*V*
Trisetaria panicea (Lam.)	0.00	0.00		
Triticum durum Desf.	0.30	0.00	*M*	
Ulex parviflorus Pourret	0.87	0.44	*M*	*V*
Urospermum picrioides (L.) Scop.	1.32	0.12	*M*	*V*
Urtica dioica L.	0.00	0.00		
Valerianella discoidea (L.) Loisel.	0.06	0.00		
Verbascum sinuatum L.	0.05	0.07		*V*
Verbena officinalis L.	0.05	0.00		
Veronica polita Fries	0.00	0.06		*V*
Vicia cracca L. †	0.56	0.00	*M*	
Vicia laxiflora Brot.	0.30	0.00	*M*	
Vicia lutea L.	0.83	0.00	*M*	
Vicia peregrina L.	0.00	0.44		*V*
Vicia sativa L.	1.37	0.15	*M*	*V*
Vulpia ciliata Dumort.	0.00	0.15		*V*
Vulpia myuros (L.) C.C. Gmel.	0.06	0.00		