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Floristic patterns and plant traits of Mediterranean communities in fragmented habitats

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ABSTRACT

Aim To contrast floristic spatial patterns and the importance of habitat fragmentation in two plant communities (grassland and scrubland) in the context of ecological succession. We ask whether plant assemblages are affected by habitat fragmentation and, if so, at what spatial scale? Does the relative importance of the niche differentiation and dispersal-limitation mechanisms change throughout secondary succession? Is the dispersal-limitation mechanism related to plant functional traits?

Location A Mediterranean region, the massif of Albera (Spain).

Methods Using a SPOT satellite image to describe the landscape, we tested the effect of habitat fragmentation on species composition, determining the spatial scale of the assemblage response. We then assessed the relative importance of dispersal-related factors (habitat fragmentation and geographical distance) and environmental constraints (climate-related variables) influencing species similarity. We tested the association between dispersal-related factors and plant traits (dispersal mode and life form).

Results In both community types, plant composition was partially affected by the surrounding vegetation. In scrublands, animal-dispersed and woody plants were abundant in landscapes dominated by closed forests, whereas wind-dispersed annual herbs were poorly represented in those landscapes. Scrubby assemblages were more dependent on geographical distance, habitat fragmentation and climate conditions (temperature, rainfall and solar radiation); grasslands were described only by habitat fragmentation and rainfall. Plant traits did not explain variation in spatial structuring of assemblages.

Main conclusions Plant establishment in early Mediterranean communities may be driven primarily by migration from neighbouring established communities, whereas the importance of habitat specialization and community drift increases over time. Plant life forms and dispersal modes did not explain the spatial variation of species distribution, but species richness within the community with differing plant traits was affected by habitat patchiness.

Keywords
Dispersal, floristic pattern, grassland, habitat fragmentation, life form, scrubland, Spain, spatial scale.

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INTRODUCTION

Unveiling the processes that determine the spatial distribution of species is a central goal for community ecology and biogeography. Hubbell (1997, 2001) suggested that the dispersal history of biological assemblages, rather than habitat specialization, provides the main explanation for spatial variation. Neutral theory predicts that among-site floristic similarity (beta-diversity or commonality) should decrease logarithmically with increasing geographical distance because

of seed-dispersal limitation (Chave & Leigh, 2002; Condit *et al.*, 2002). In contrast, niche theory predicts that most floristic differentiation among plant communities is caused by the adaptation of species to the environment. According to niche theory, plant species should be distributed within their fundamental niche defined by a range of environmental factors such as climate and edaphic conditions; this distribution may be described unimodally along an environmental gradient (Whittaker, 1956; Oksanen & Minchin, 2002). Testing neutral theory against niche theory has proven challenging, as environmental variables and species distributions tend to be spatially autocorrelated. On the one hand, species distributions are most often aggregated because of contagious biotic processes such as local dispersal; on the other, the environment is structured primarily by climate and geomorphological processes on land that cause gradients and patchy structures. Therefore values of these variables are not stochastically independent from one another. This may lead to misinterpretation of patterns using classical statistics when ecologists conclude that species–habitat associations are statistically significant, not realizing that type I error rates of their analyses have been inflated by the presence of spatial autocorrelation (Legendre, 1993; Harms *et al.*, 2001). To evaluate the relative importance of environmental segregation and limited dispersal in explaining species distributions, spatial structure (Legendre, 1993) must be considered.

An additional complication arises in disturbed and fragmented plant communities. In fragmented habitats, spatial diffusion processes and habitat patchiness may jointly influence diversity patterns (Hanski & Gilpin, 1997; Fahrig, 2003). For instance, some habitats may act as barriers for dispersal (Gómez, 2003). In contrast, wind-dispersed species may be favoured in open areas (McEuen & Curran, 2004). Wind dispersal patterns also depend on patch structure, as it alters the structure of the air-boundary layer and thus propagule uplift (Schupp, 1995; Nathan & Muller-Landau, 2000). At the community level, area, isolation, edges and the matrix surrounding habitat patches affect plant diversity and composition (Laurance *et al.*, 1998, 2002; Honnay *et al.*, 1999; Bascompte & Rodríguez, 2001; Eriksson *et al.*, 2002; Ross *et al.*, 2002; Deutschewitz *et al.*, 2003; Murphy & Lovett-Doust, 2004). Yet tests of spatial species-turnover models implicitly assume that sites are stable and separated by a homogeneous environment. Therefore it is critical to include information about landscape structure in such tests.

To address these issues, we contrasted the spatial floristic patterns between Mediterranean grasslands and scrublands along a gradient of habitat fragmentation. Grasslands correspond to early stages of secondary succession, and are usually replaced by scrubland vegetation. The Mediterranean region ranks among the richest areas on Earth for plant diversity (Médail & Quézel, 1997), and is also a good region within which to study permanently fragmented yet diverse habitats. Here we ask three central questions: (1) are plant assemblages affected by habitat fragmentation, and if so, at what spatial scale? (2) does the relative importance of the niche

differentiation and dispersal-limitation mechanisms change throughout secondary succession? (3) is the dispersal-limitation mechanism related to plant functional traits?

The following hypotheses were formulated to address the first question. A major effect of habitat fragmentation is the reduction of area available for the community, hence the reduction in the size of the local species pool (Zobel, 1997). However, this 'species-pool effect' is expected to have a maximal effect if species are clumped spatially and if population sizes are small. We would therefore need to know whether the effect of habitat patchiness on plants is local, or extends over large distances. To test this, we analysed the influence of landscape structure on species composition at different spatial scales. We expect that landscape structure influences species composition maximally at a particular spatial scale, which reflects the spatial extent at which surrounding populations contribute to the species composition of the local community. The greater the dispersal rate between two islands of an archipelago, the larger the spatial covariance in abundance of a species (Hubbell, 2001). Hence a group of species with poor dispersal efficiency will respond strongly to habitat fragmentation, and at small spatial scales; whereas species of an efficient dispersal group will be widespread over the landscape, therefore their response to habitat fragmentation will be weaker and at larger scales.

To address the relative importance of niche differentiation and dispersal limitation throughout secondary succession, we formulated a null expectation based on succession theory. Niche breadth and overlap are expected to decrease over time as species sort out along environmental gradients (Odum, 1969; Christensen & Peet, 1984). Because of the unpredictable nature of disturbances, initial stages of secondary succession should not show any spatial structuring (Shugart, 1984). Since grasslands are more prone to disturbances, we expect both limited dispersal and niche differentiation to control species composition more weakly in grasslands than in scrublands.

The third question asks if dispersal limitation is related to plant functional traits. In neutral communities, distance decay in community similarity is faster at low dispersal rates (Hubbell, 2001; Chave & Leigh, 2002). The main plant traits used to quantify plant dispersion are dispersal syndrome (by wind, animals or other means); seed size; and reproduction rate. In heterogeneous landscapes, the effective movement of propagules could be reduced (Nekola & White, 1999; Nathan & Muller-Landau, 2000). We tested the association of the spatial structure of Mediterranean assemblages and habitat fragmentation to plant life forms and dispersal modes. We expected: (1) since species with a strong aggregation are likely to be more dispersal-limited (Jacquemyn *et al.*, 2001), plants with assisted seed dispersal (by wind or animals) will be less clumped than plants with unassisted dispersal (Svenning & Skov, 2002); (2) short-lived and small species colonize open areas better (Lavorel *et al.*, 1997), and will be more homogeneously distributed than perennial plants over the landscape; (3) the number of species with different traits will differ with respect to both fragmentation and the type of surrounding vegetation.

METHODS

Study area

The study area, in the southern foothills of Albera massif (eastern Pyrenees, Spain), is 15 × 25 km (Fig. 1). The area ranges from sea level (lowland plains) to *c.* 550 m a.s.l., and consists mainly of granites and schists. The soils are siliceous and relatively acid. The vegetation is mostly evergreen due to the Mediterranean climate, with dry summers, mild winters and maximum rainfall in early autumn. Three main vegetation types occur within this area: forests, scrublands and grasslands. Forests are dominated by sclerophyllous trees (cork oak, *Quercus suber* and holm oak, *Quercus ilex*), and scrubs. At the northern boundaries of the study area, pubescent oaks (*Quercus pubescens*) form deciduous forests. The scrubland community is dominated by *Cistion mediomediterraneum* Alliance: heliophilous and xerophytic scrubs between 0.5 and 2 m in height (Bolòs, 1983; Franquesa, 1995). This community may develop from abandoned grasslands or from degraded cork oak or holm oak forests. It spans large areas in the eastern part of the massif due to the high frequency of fire (Díaz-Delgado *et al.*, 2002). Grasslands are dominated by *Helianthemion guttati* Alliance (Bolòs & de Vigo, 1984). Some of these grasslands are encountered in old grazed or recently burned areas, others as fallows or in abandoned vineyards and olive orchards. Agriculture and pastures are mainly located in the lowland plains, whereas forest remnants occur at high altitudes to the north west.

Floristic sampling

All vascular plant species were censused at 78 scrubland sites and at 48 annual-rich grasslands (or grass-prairie) sites in June 2002 and May 2004 (Fig. 1). Sites were distributed within a moderate elevation range (*c.* 425 m), and in different landscape types. We selected sites surrounded by closed forests, scrubs, agricultural land, and a mosaic of these land covers.

We defined a sampling unit of 100 m^2 for censusing scrublands and 4.5 m^2 for grasslands, based on a preliminary study of species-accumulation curves. We identified a total of 335 plant species: 245 species in scrublands and 237 in grasslands. One hundred and forty-seven species were shared between the two types of community. Average species richness per site was 31.8 (SD = 8.4) in scrublands and 36.1 (SD = 8.2) in grasslands.

Plant traits

Species were classified according to life form and dispersal mode (Fig. 2). Life forms included perennial woody plants, biennial or perennial herbs, and annual herbs. Dispersal modes included wind, water, animal, and unassisted. Among all species, 255 species (78%) could be classified according to dispersal type: 193 were classified into dispersal syndromes using values from the literature (Molinier & Müller, 1938; Rameau *et al.*, 1993; Tweddle *et al.*, 2003, see also http://www.rbgkew.org.uk/data/sid); and 62 species were classified further based on their diaspore morphology (e.g. wings, fleshy fruit). Water-dispersed species were omitted from the analysis because of their low frequency (nine species). The two types of community are dominated by species with distinct biological traits (Fig. 2). While annuals largely dominate grasslands (58%), the percentage of woody plants in scrublands is twice that of grasslands. Differences in dispersal syndrome are smaller: grasslands present relatively more wind-dispersed and fewer animal-dispersed species than scrublands.

Environmental data and landscape descriptors

We acquired five environmental variables: elevation, mean annual precipitation (mm year^{-1}), mean annual temperature, annual seasonality, and potential solar radiation. Annual seasonality is the difference between the mean temperature of the hottest month (July) and that of the coldest month (January), as defined by Ninyerola *et al.* (2000) for the Mediterranean climate. Potential solar radiation is measured in kJ m^{-2} day^{-1}) and is computed taking into account the sun's path, the sun–earth distance, atmospheric attenuation, incident angles on each point, and cast-shadow effects on each

Figure 1 Study area of Albera (south-east Pyrenees, Spain). Land cover classified from a SPOT image: closed forest (dark grey); scrublands (light grey); agricultural areas and grasslands (white); other land (black). A filter based on the median has been applied to the land-cover classification, eliminating isolated pixels for illustration purposes. Floristic sampling of grasslands (circles) and scrubland (triangles) indicated by symbols.
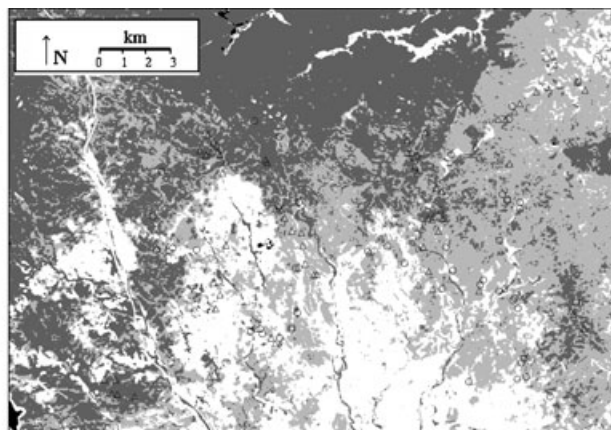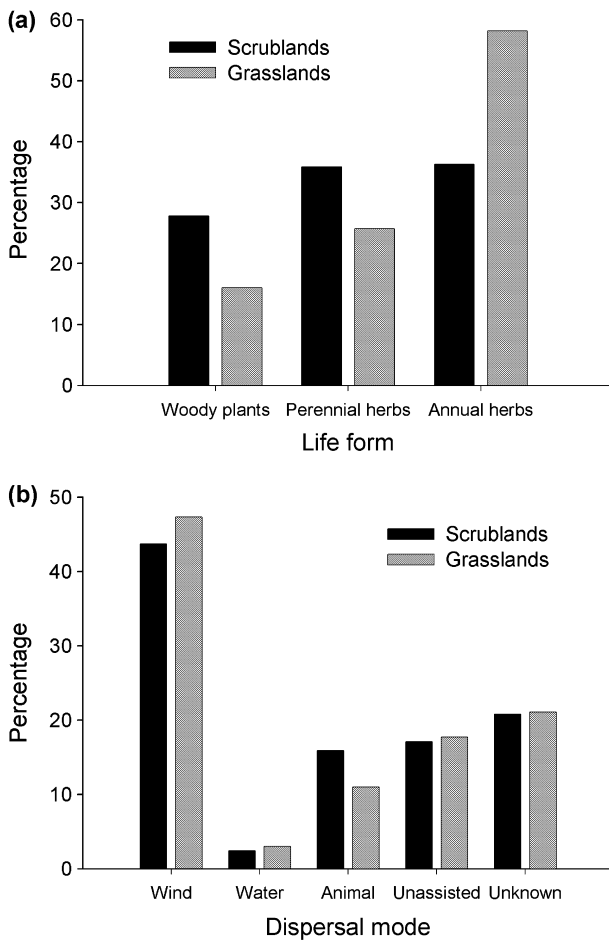
Figure 2 Number of species (percentage) in scrublands and grasslands as functions of (a) life forms; (b) dispersal types.

point (Pons, 1996). The four climatic variables were acquired from the digital climatic atlas of Catalonia at 180-m grid spacing (Pons, 1996; Ninyerola *et al.*, 2000), available online at http://magno.uab.es/atles-climatic/catala/cartografia.htm.

We used optical satellite imagery to generate a land-cover map of the area and to extract landscape descriptors. We selected an image from the SPOT HRVIR satellite sensor that covered the Albera massif on 30 June 1998. SPOT HRVIR has a spatial resolution of 20×20 m and records the image with four spectral bands (green, red, near-infrared and mid-infrared wavelengths).

Land-cover data were generated through a supervised classification of the SPOT image into four classes: closed forest (sclerophyllous and deciduous forests); scrubland; grasslands and agricultural land (arable fields); and other land covers (water surfaces, irrigated land, coniferous plantations). Land covers were classified with a maximum-likelihood procedure using all four spectral bands. The errors of omission and commission (Stehman, 1997) were, respectively, closed forest, 3.2 and 17.2%; scrubland, 23.6 and 14.1%; agricultural and herbaceous land, 16.3 and 11.4%; other land covers, 0.1 and 0%.

A multi-scale approach (Pearman, 2002; Chust *et al.*, 2003) was used to characterize the fragmentation of habitats at different scales. The method uses spatially nested landscapes surrounding each sampling site to calculate the proportion of each land cover (closed forest; scrubland; agricultural and herbaceous land) at different spatial scales (from 60×60 m to 5×5 km grain size).

Statistical analysis of fragmentation effects and floristic patterns

We compared floristic spatial patterns in grass prairies and scrublands. The role of niches in each community type was evaluated indirectly by the analysis of environmental decay in species similarity. The role of dispersal limitation was measured by the distance decay in species similarity and the effects of habitat fragmentation. The explanation for the distance decay in similarity under the neutral model is that large steady-state differences exist in the meta-community abundances of species, coupled with dispersal limitation, which is increasingly severe in ever-rarer species (Hubbell, 2001). First, we computed a similarity matrix of species for each plant community using the Jaccard index, defined as the number of species shared between two sites divided by the total number of species observed in the two sites. As the Jaccard index is influenced by species richness (Kuhn *et al.*, 2003), we also calculated the Simpson similarity (Simpson, 1943) based on $S_S = a/[a + \min(b,c)]$, where a is the number of shared species, and b and c are those unique to one site or the other. Similarity matrices of landscape descriptors, elevation and climatic variables were obtained from the Gower coefficient (Gower, 1971). Gower's similarity index (S_G) between sites A and B with p descriptors is defined as:

$$S_G(\text{site A, site B}) = \frac{1}{p}\sum_{j=1}^{p} s_j,$$

where $s_j = 1 - (|X_{Aj} - X_{Bj}|/R_j)$, which is a normalized distance transformed into a similarity, with X_j the value of the environmental or landscape variable j, and R_j the range of the variable. We calculated one similarity matrix for each environmental variable separately, and one matrix for each spatial scale using the proportion of three land covers. The geographical distance among the sampling sites was measured by Euclidean distance. We used Mantel tests to determine the correlation between similarity in species occurrence and explanatory variables (landscape similarity across spatial scales, geographical distance, elevation, annual precipitation, mean temperature and annual seasonality) for each site (Legendre & Legendre, 1998). The Mantel statistic r_M is a measure of the correlation between the two matrices, and is tested by a permutation test. When comparing a distance matrix with a similarity matrix, we converted the similarity measure to a distance measure ($= 1 - \text{similarity}$).

The Mantel statistic was calculated in a comparison between species similarity and landscape descriptors at different spatial

scales. The effects of landscape structure are evaluated with partial Mantel tests, that is, by correlating species and landscape similarities while controlling for geographical distance. We then detected the scale (or scales) at which landscape pattern maximally influences species composition (henceforth 'optimal scale').

We tested the correlation between species similarity and geographical distance or logarithmically-transformed geographical distance using a Mantel test. The slopes of the distance decay in similarity index were also estimated for each plant community.

We evaluated the relative importance of environmental factors and dispersal-related variables (geographical distance; habitat fragmentation at the optimal scale) by conducting a multiple regression analysis of species similarity (Legendre *et al.*, 1994). Backward elimination was applied to select statistically significant terms at $\alpha = 0.05$. We performed this for each plant community. Since the two community types are very different, we also performed the analysis on the set of 147 shared species to test if the differences in patterns between scrublands and grasslands might be caused by the traits of community-specific species, or by historical processes. Multiple regression analyses were run with PERMUTE! 3.4 (alpha version), available online at :http://www.bio.umontreal.ca/Casgrain/en/labo/permute/index.html.

Statistical analysis of plant life form and dispersal mode

Since dispersal-related factors causing variation in species distribution may differ among reproductive strategies and dispersal abilities, we tested the association between these factors and plant traits (life form and dispersal type) in two ways. First, we quantified the pattern of species clumping by analysing the spatial autocorrelation for each species occurring in at least five sites (Moran's I index at 1-km resolution; Legendre & Legendre, 1998). We then contrasted the patterns of species clumping among plant traits using a χ^2 test. We emphasize that, in principle, care must be taken when interpreting analyses among plant traits because of phylogenetic correlation. If, however, no correlation is observed in a test that ignores phylogenetic structure, it is very unlikely that a phylogenetic contrast test will be statistically significant.

Second, we analysed the effect of habitat fragmentation on species richness for each plant trait, because the local species richness within a given plant trait might be affected by the degree of fragmentation of the community type and the type of surrounding vegetation. To test the effects of habitat fragmentation on species richness of plant traits, we used the fourth-corner method (Legendre *et al.*, 1997). The fourth-corner method tests for the association between biological traits to habitat at locations where the corresponding species are found, a common issue in community ecology, although it has seldom been used in vegetation studies (but see Charest *et al.*, 2000). To apply the fourth corner, three matrices were used: A ($k \times m$) contained data on the presence or absence of k species

at m locations; B ($k \times n$) described n plant traits (life forms or dispersal modes) of the k species; and C ($p \times m$) contained p explanatory variables (habitats: closed forest, scrubland, and agricultural zone and grassland) at m locations. The fourth-corner matrix D ($p \times n$) is computed as the matrix product $D = C \times A' \times B$, where A' is the transpose of matrix A, and provides a table containing the number of occurrences of each of the associations between the traits of species and those of location. The method provides an F statistic by which a global measure of association between species traits and sites can be evaluated; and a correlation coefficient, r, indicating the strength of association of occurrences of each species trait to small or large values of the explanatory variables. The significance of these associations is tested by permutation.

RESULTS

Effects of habitat fragmentation at the community level

First, we compared the Jaccard index of similarity with the Simpson index. The correlation between these two indices of species similarities was very high, $r = 0.92$ for grasslands and 0.85 for scrublands. For this reason, and since the Jaccard index is a classical coefficient of similarity, we considered only the Jaccard index in the analysis.

We analysed the correlation between the Jaccard index of species similarity, geographical distance and landscape similarity across spatial scales (Fig. 3). The correlation between landscape similarity and geographical distance increased with scale in both plant community types, indicating that landscape descriptors were more strongly spatially autocorrelated at larger spatial scales. In scrublands, the correlation between Jaccard and landscape similarity, partialling out geographical distance, reached a maximum at a scale of 220×220 m (partial Mantel correlation $r_{pM} = 0.27$, $P = 0.001$). From 1 to 5 km, the partial Mantel correlation plotted against scale was relatively flat and close to the maximum value (0.22–0.26, $P = 0.001$). In grasslands, species similarity correlated with landscape similarity at larger scales: 3.2×3.2 km ($r_{pM} = 0.25$, $P = 0.001$). In both types of community, the response to landscape structure varied little between intermediate and large spatial scales.

Floristic patterns across spatial and environmental gradients

The Jaccard similarity of both types of community correlated more strongly with the logarithm-transformed geographical distance, ln(GD), than with untransformed distance (Table 1), as predicted by neutral theory. Similarity in scrublands correlated more strongly with ln(GD) and the slope of the corresponding linear regression was slightly steeper (regression coefficient −0.034) than for grasslands (−0.029). Hence among-site community similarity decreased more with distance in scrublands than in grasslands.
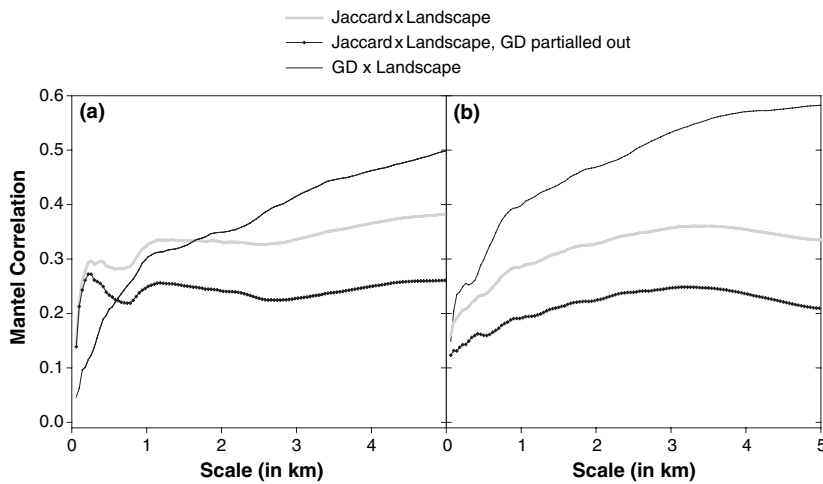
Figure 3 Mantel and partial Mantel correlation statistics among Jaccard similarity values on species occurrence of (a) scrublands; (b) grasslands; geographical distance (GD) and landscape similarity at different spatial scales.

Table 1 Mantel correlation statistic (r_M) between Jaccard species similarity (in scrublands and grasslands) and explanatory variables (geographical distance, elevation and climatic factors)

	Scrubland	Grassland
Geographical distance	0.340 (0.001)	0.296 (0.001)
ln(geographical distance)	0.399 (0.001)	0.315 (0.001)
Elevation	0.264 (0.001)	0.263 (0.002)
Precipitation	0.386 (0.001)	0.339 (0.001)
Temperature	0.299 (0.001)	0.314 (0.001)
Seasonality	0.225 (0.001)	0.204 (0.001)
Solar radiation	0.184 (0.002)	0.151 (0.042)

Probability values are in parentheses.

Table 2 Standardized regression coefficients and multiple correlation coefficient (R^2) of multiple linear regression models on distance matrices

	Scrubland	Grassland
ln(geographical distance)	−0.262 (0.001)	−
Landscape structure	0.189 (0.001)	0.286 (0.001)
Precipitation	−0.194 (0.001)	−0.225 (0.002)
Temperature	−0.094 (0.007)	−
Solar radiation	0.088 (0.010)	−
R^2	0.279 (0.001)	0.184 (0.001)

Probability values are in parentheses.

We analysed the correlation between Jaccard similarity and environmental factors separately, and found that all environmental variables were significant (Table 1). We then performed a multiple regression on distance matrices taking the logarithm of geographical distance, all environmental variables and landscape descriptors (at the optimal scale) as entries. In scrublands, a backward procedure retained five variables (Table 2). The standardized coefficients revealed that geographical distance was the most important factor, although precipitation and landscape structure presented slightly lower

weights. By contrast, the multiple regression model in grasslands retained only landscape structure and mean precipitation with a lower multiple correlation (Table 2).

Finally, the effects of habitat fragmentation and floristic patterns restricted to the 147 species shared by scrublands and grasslands were similar to those including all species of the plant community. Optimal scales of response to landscape were 260×260 m for scrublands and 3.7×3.7 km for grasslands. Scrublands were more strongly correlated with log geographical distance ($r = 0.37$) with a steeper slope (−0.036), than grasslands ($r = 0.26$, slope −0.028). The variables retained in the multiple regression model for scrublands were: logarithm of geographical distance, landscape structure, precipitation, and solar radiation; for grasslands: landscape structure and precipitation. The R^2 was also higher for scrublands (0.250) than for grasslands (0.197). Thus environmental, spatial and landscape factors affected the same set of species differently as a function of their establishment in either scrublands or grasslands.

Dispersal-related factors and plant traits

The association between local spatial aggregation and plant traits was tested for 129 species in scrublands and 117 species in grasslands (occurring in at least five sites). Fifty-seven per cent of scrubland species and 32% of grassland species were significantly autocorrelated at 1 km distance. This difference agrees with the steeper slope of distance decay in species similarity in scrublands. The χ^2 tests were not significant in any plant trait (Table 3), hence spatial clumping was not associated with dispersal modes or life forms.

The fourth-corner analysis was applied at the optimal scale of landscape structure: 220×220 m for scrublands and 3.2×3.2 km for grasslands (Table 4). In scrublands, life form and dispersal type were significantly associated with the proportion of closed forest and scrubland covers surrounding that plant community (F test, Table 4). In grasslands, however, life form and dispersal mode were not associated with landscape structure. Correlation statistics are reported in

Table 3 Percentage of species spatially autocorrelated at 1 km distance for each life form and dispersal type

	Scrubland	Grassland
Life form		
Woody plants	62.5	33.3
Biennial and perennial herbs	52.8	46.7
Annual herbs	53.3	25.0
Dispersal type		
Wind	52.6	33.9
Animal	57.1	25.0
Unassisted	70.8	15.8
Total	56.6	31.6

χ^2 tests were not significant (at $\alpha = 0.05$) in any plant trait.

Table 4 Probability values of the F test of the fourth-corner analysis relating plant traits (life form and dispersal mode) and fragmentation gradient

	Scrubland		Grassland	
Habitat cover	Life form	Dispersal type	Life form	Dispersal type
Closed forest	0.0004	0.0016	0.5508	0.7894
Scrubland	0.0014	0.0062	0.2820	0.5986
Agricultural zone and grassland	0.1406	0.3148	0.6644	0.8786

Table 5 Correlation coefficients (r) and probability values (P) of the fourth-corner method applied to scrublands relating plant traits (life form and dispersal mode) to significant habitats (according to F test; Table 4)

	Closed forest cover		Scrubland cover	
	r	P	r	P
Life form				
Woody plants	0.117	0.0002	−0.093	0.001
Biennial and perennial herbs	−0.034	0.0436	0.001	0.4902
Annual herbs	−0.095	0.0008	0.101	0.0006
Dispersal type				
Wind	−0.063	0.0016	0.05	0.0072
Animal	0.074	0.0002	−0.064	0.002
Unassisted	−0.001	0.482	0.006	0.357

Percentage cover of the two habitats (closed forest and scrubland) calculated at the 220 × 220-m scale.

Table 5 for those cases in which the F test was significant. Scrublands in landscapes dominated by closed forest had more woody plants and animal-dispersed plants, and fewer annual herbs and wind-dispersed species (Fig. 4). Conversely, woody plants and animal-dispersed plants were poorly represented in scrubland-dominated landscapes, and annual herbs and wind-dispersed species were more abundant when embedded in that environment. Biennial and perennial herbs and unassisted dispersers were not preferentially associated with a specific landscape type.

DISCUSSION

Our results address the questions raised about floristic patterns and the importance of habitat fragmentation in the two Mediterranean community types. (1) Species composition in scrublands depends on the surrounding vegetation at a smaller spatial scale than in grasslands. (2) Both niche differentiation and dispersal limitation were more important in scrubby assemblages than in grasslands. (3) Dispersal mode and life form were unrelated to species clumping, but the number of species with alternative traits was affected by habitat patchiness in scrublands.

Species respond individually to the landscape structure at different spatial scales, and this may generate an overall community-level 'response'. But when we tested the scale at which the community shows the strongest response to the surrounding vegetation, we found that grasslands correlated with habitat patchiness at larger scales than did scrublands. Overall, this indicates that the establishment of a significant fraction of plants of a local scrubby community depends on the proximity of sources, and that they do not establish at random from the same species pool.

Floristic similarity was more strongly correlated with the logarithm of geographical distance and had a higher slope in scrublands than in grasslands. This agrees with the higher percentage of scrubland species that were spatially autocorrelated as compared with grassland species. Hence scrublands had a larger spatial species turnover. The lower floristic similarity in grasslands might be caused by long-distance dispersal. Grasslands hold many disturbance-prone, small species with short life spans that can colonize rapidly in open areas (Lavorel et al., 1997). Wind-dispersed species, abundant in grasslands, produce flatter seed-dispersal probability distributions (seed shadows) than animal-dispersed plants (Jordano & Godoy, 2002). This could explain why species composition in grasslands responded to landscape at larger spatial scales. However, we found no correlation between species clumping and dispersal mode, probably because other processes operating between seed dispersal and seedling establishment, smooth out the initial aggregation of seeds (Schupp, 1995).

That species composition in scrublands depends on geographical distance, habitat fragmentation, and climate-related conditions appears to be consistent with patterns of dispersal limitation, as emphasized in the neutral theory of biodiversity (Hubbell, 2001) and niche-based arguments of environmental segregation. Other studies also support the importance of both processes in determining plant distribution (Svenning & Skov, 2002; Jacquemyn et al., 2003; Chust et al., 2006). We are unable to favour either theory based solely on this data set and on our approach. However, our tests are perhaps weak because, although the joint weight of dispersal-limited
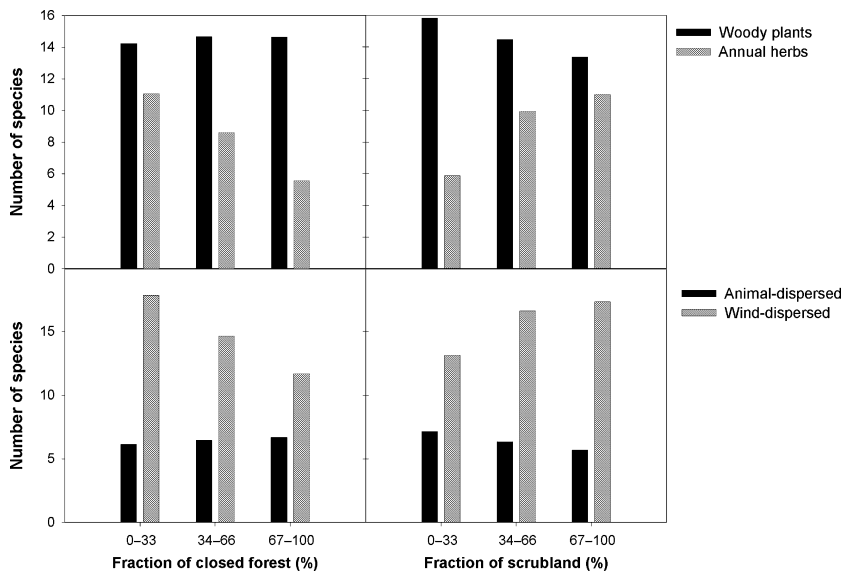
Figure 4 Average species number of woody plants, annual herbs, animal- and wind-dispersed species in scrublands against the percentage cover of closed forest and scrubland at 220 × 220 m. The test of the correlation statistic of the fourth-corner method was significant in all four cases (Table 5).

factors is higher than environmental requirements, these differences are not striking. Also, environmental gradients are weak in the study area, and we did not measure edaphic heterogeneity (texture, pH, depth, nutrient and mineral content). Future work will address this issue. Finally, our limitation may be inherent in the definition of the niche, a topic that has fuelled a considerable amount of debate (Chase & Leibold, 2003). The niche concept provides a useful way of thinking about ecological relationships of populations, but not necessarily a practical one (Brown, 1995).

Landscape structure appeared to be the main factor affecting the floristic composition of grasslands. This suggests that, in early communities, plant establishment is driven primarily by migration from vegetation surroundings when competition is low, while the role of habitat association increases over time, as expected from known successional trends (Margalef, 1968; Odum, 1969; Christensen & Peet, 1984). In other words, the greater structuring in scrubland community is a result of a longer historical process. This idea is reinforced by the analysis of the 147 species shared by scrublands and grasslands: these species showed greater spatial structuring and environmental dependence in scrublands than in grasslands. Therefore the importance of both dispersal limitation and niche-differentiation processes increases over time for each species, rather than because of differences in species traits.

Although dispersal influences the structure of these plant communities, plant traits were not related to species aggregation, contrary to our expectations. Several studies have found that dispersal mode affects tree species aggregation in forests, whether temperate (Svenning & Skov, 2002), boreal (Nekola & White, 1999) or tropical (for review see Levine & Murrell, 2003), although there are also counter-examples in non-forests. For instance, Eriksson & Jakobsson (1998) found that dispersal mode was unrelated to abundance and geographical range for over 80 grassland plants in Sweden. In special cases, such as wind dispersal in the Asteraceae, dispersal mode can be

used as a proxy for the shape of the seed dispersal probability distribution (Levine & Murrell, 2003). Seed dispersal before recruitment of individuals is a complex process, including secondary dispersal (Wang & Smith, 2002); scale-dependent mutualistic relationships between fruits and frugivores (Gómez, 2003; Burns, 2004); density-dependent seed predation (Janzen-Connell effects, Janzen, 1970); and complex interactions between fruit, seed dispersers and seed predators (Herrera, 1984; Fragoso *et al.*, 2003; Moore, 2003).

The lack of association between life form and species clumping in our study indicates that the type of plant growth is not directly linked to the resulting species distribution at landscape scales. Our expectation that annual plants are distributed more randomly than perennials was not supported, although the percentage of annuals spatially autocorrelated was higher (albeit not significantly so) than woody species. Our initial hypothesis was based on the assumption that annuals are able to colonize rapidly in open areas (Lavorel *et al.*, 1997). However, Nekola & White (1999) found that the rate of distance decay was twice as high for herbs than for woody plants in North American spruce–fir forests. Thus the structure of habitat interacts with reproductive strategies. This is in accordance with our finding that annual herbs were poorly represented when scrublands were embedded in closed forests, and more abundant in scrubland-dominant landscapes. Woody species were more abundant near closed forests and scarcer around scrublands. This suggests that the proximity to forests favours a scrubland-to-forest transition by facilitating the dispersal of woody plants. On the other hand, animal-dispersed plants were abundant in landscapes dominated by closed forests, suggesting that the seed dispersers are mainly forest-dwelling. Thus forest plants in isolated fragments might need more time to disperse successfully over new areas because of the absence of their disperser. We conclude that the proximity of vegetation types is a key factor in explaining the distribution of plants; in particular, the richness of woody and

animal-dispersed plants is high when that of annual herbs and wind-dispersed species is low, and vice versa.

In conclusion, plant establishment in early and disturbed communities appears to be driven primarily by migration from vegetation surroundings, whereas habitat association and community drift become increasingly important over time. The structuring of Mediterranean scrubland communities results from a longer historical process than that of grass prairies, comprising environmental segregation and limited dispersal. Plant life forms and dispersal modes were unrelated to species clumping, suggesting that these plant functional traits do not contribute to the variation of plant dispersal parameters. However, the number of species within the community with differing plant traits was affected by habitat fragmentation, which has consequences for biodiversity conservation at the landscape scale and for forest regeneration.

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