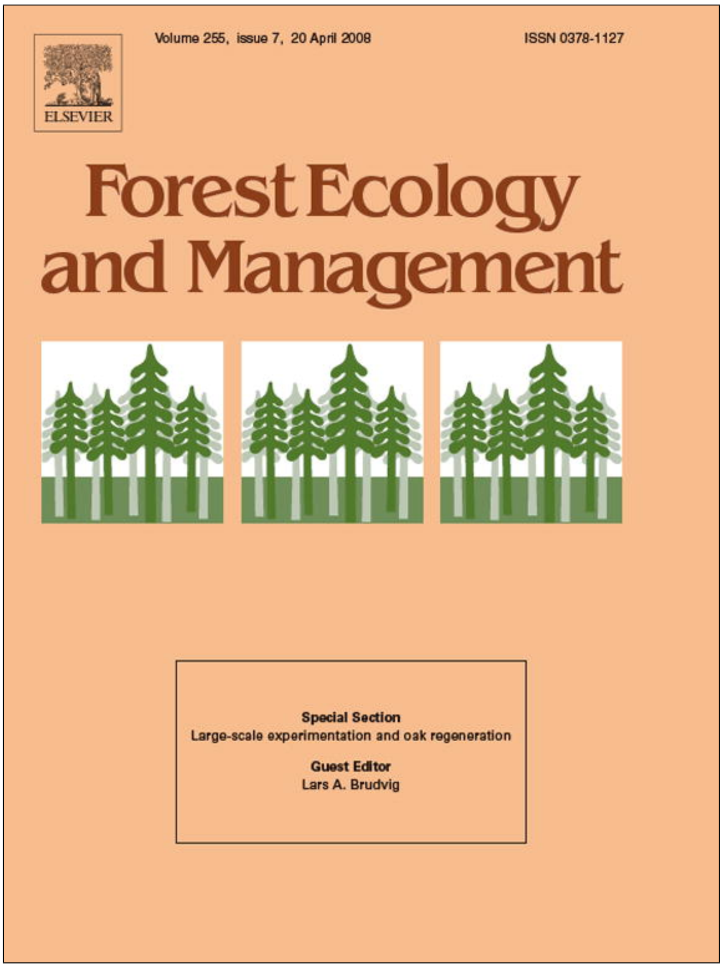

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Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes

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Abstract

While maximizing plant species richness continues to be central in the design, conservation and reforestation action plans, plant life histories are receiving increasing attention in assessments for the conservation of biodiversity in fragmented landscapes. We investigated the determinants of woody plant species (trees, shrubs and climbers) richness in the forest patches of the Guadalquivir river valley, a Mediterranean agricultural landscape with ~1% forest cover. We analyzed three species richness variables, total, and those corresponding to species with short-distance (ballistic, barochorous, myrmecochorous and short-distance anemochorous) and long-distance (anemochorous, endozochorous, exozoochorous, hydrochorous and dyszoochorous) dispersal systems, which significantly characterize earlier and late successional stages, respectively. We selected eleven predictor variables related to habitat structure (patch area, shape, distances to the nearest patch and reserve, and general isolation), physical environment (temperature, precipitation, elevation, and lithological heterogeneity), and anthropogenic influences (disturbance and proportion of old-growth forest). We used ordinary-least-squares multiple regression (OLS) and the Akaike's information criterion (corrected for spatial autocorrelation) and derived indices to generate parsimonious models including multiple predictors. These analyses indicated that plant species richness increase primarily along with increasing patch area and decreasing disturbance, but also detected secondary effects of other factors when dispersal was considered. While the number of species with potential long-distance dispersal tended to increase in more isolated patches of areas with greater precipitation and lithological heterogeneity (e.g. highlands at the valley edges), the number of species with short-distance dispersal increased towards drier and less lithologically complex zones with shorter between-patch distances (e.g. central lowlands). Beyond emphasizing the need to consider dispersal in fragmentation studies, our results show that woody plant species richness would be favoured by actions that increase patch area and reduce anthropogenic disturbances particularly in lowland forests.

Keywords: Biodiversity conservation; Habitat fragmentation; Mediterranean forest restoration; Seed dispersal; Woody plant species richness

1. Introduction

Deforestation begun in Europe ~6.0 ka BP when Neolithic agriculturalist settlements began to clear forests for cultivation, grazing, and obtaining fodder (Williams, 2000). This process of forest destruction and fragmentation has been particularly intense and severe in the Mediterranean region (Valladares et al., 2004), where forest fragments are frequently sparsely distributed across an agricultural matrix of extensive cultivations. Still, this region is considered a hot spot for biological diversity (Médail and Quézel, 1997), and although its relictual forested landscape (*sensu* McIntyre and Hobbs, 1999) is far from a pristine example of Mediterranean vegetation, it often contains unique populations of endemic plant species (Garrido et al., 2002; Aparicio, 2005).

It is important to understand the function of these landscapes as plant diversity reservoirs and how their diversity relates to characteristics of the remaining habitat fragments. Among these, forest cover is considered the pre-eminent determinant of forest species richness (Boutin and Hebert, 2002; Fahrig, 2003). However, for the case of relict landscapes, where the amount of forest cover drops to 10% or below (McIntyre and Hobbs, 1999), habitat structure-related attributes such as patch size, shape and spatial configuration may also have strong impacts

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on plant species richness (Saunders et al., 1991; Boutin and Hebert, 2002). The main goal of this study is to document relationships of woody species richness with habitat configuration in the forest patches of the Guadalquivir river depression, a relict landscape of southwestern Spain where natural or semi-natural forest retention is about 1% (Aparicio, 2008).

Because maximizing species richness has been central to set targets for conservation and to design conservation and reforestation action plans in general (Honnay et al., 1999; Godefroid and Koedam, 2003; Peintinger et al., 2003; Desmet and Cowling, 2004; Wilsey et al., 2005), species richness has often been explored within the species–area relationship as theoretical framework (Lomolino, 2000). However, the generally highly stochastic processes of extinction and recolonization determining within patch species richness do not only depend on patch area, but also on characteristics of the physical environment, disturbance regimes, and, notably, plant life histories (Honnay et al., 1999; Butaye et al., 2001). Consequently, the study of life history traits of plant species is receiving increasing attention in assessments for the conservation of biological diversity in fragmented landscapes (Graae and Sunde, 2000; Benítez-Malvido and Martínez-Ramos, 2003; Kolb and Diekmann, 2005; Purves and Dushoff, 2005; Wiegand et al., 2005; Chust et al., 2006; but see Yates and Ladd, 2005). In particular, seed dispersal is considered a functional core trait with relevance for both understanding and predicting ecological patterns and processes associated with population dynamics and evolution (Herrera, 1992; Weiher et al., 1999; Duminil et al., 2007), not only at the species level but also for species assemblages (Jacquemyn et al., 2001). In this regard, the spatial scale at which dispersal operates is fundamental in biological conservation since short-distance dispersal is primarily related to local population recruitment, whereas long-distance dispersal is much more influential on the potential of colonization of new habitats, the migration capacity of the species and the spatial genetic structuring of populations (Calviño-Cancela et al., 2006).

According to Ozinga et al. (2005), the critical question for conservation is not whether dispersal is an important process, but whether differences in dispersal translate into differences in local plant diversity. The response of each plant species to habitat fragmentation may depend largely on its potential for long-distance dispersal, relying on the type of diaspore (Butaye et al., 2001; Ozinga et al., 2005; Chust et al., 2006). In principle, from a functional perspective, morphological adaptations of diaspores for animal- and wind-mediated dispersal (fleshy pulps, wings, hooks, hair tufts) provide longer dispersal distances compared to diaspores lacking such morphological adaptations, or bearing food bodies for ant dispersal (Willson, 1993; Hughes et al., 1994). Thus, in theory, those species in which long-distance dispersal can be facilitated by the intervention of animals or wind should be less sensitive to habitat fragmentation than species lacking this possibility, or that are disseminated by animals with reduced home ranges such as ants.

Along with dispersal, responses of plant species richness to both environmental variation and anthropogenic modifications of habitat characteristics may be conditioned by a number of interrelated life history characteristics including flowering time, longevity, vegetative spread or life form (e.g. Tilman et al., 1994; Kolb and Diekmann, 2005), but reliable information to assign accurately these other traits to large plant species sets rarely exists (Herrera, 1984, 1992). Yet Herrera (1992) compiled up to ten of such morphological and functional characters for up to 66 of the woody plant genera that inhabit in the Mediterranean southwestern Spain. This allowed him to classify the woody vegetation of this region into two well-defined groups, each characterized by genera exhibiting a particular association of traits or character syndrome (Herrera, 1992; see also Verdú et al., 2003). Among other traits, the first syndrome corresponds to non-sclerophyllous, insect-pollinated, small-seeded dry-fruited lineages evolved during the Quaternary (e.g. *Cistus*, *Halimium*, *Thymus*, *Lavandula*, *Erica* or *Calluna*) and the second syndrome involves sclerophyllous, wind-pollinated, large-seeded fleshy-fruited lineages already evolved during the Tertiary (e.g. *Pistacia*, *Osyris*, *Juniperus*, *Rhamnus*, *Quercus* or *Myrtus*). On the other hand, Verdú (2000), Pausas and Verdú (2005) and Paula and Pausas (2006) have shown that post-disturbance resprouting capacity (as opposed to diaspore germination) is another common functional trait among the genera representative of the Tertiary set of species and that the Quaternary species are more drought-tolerant and fire-adapted. In all, while Tertiary species are characteristic of pre-forestal, more successionally mature communities, Quaternary species characterize earlier successional stages or woody pioneer plants (Herrera, 1992).

We asked three questions in this study. First, to what extent characteristics of habitat configuration, physical environment and anthropogenic influence determine total woody species richness variation across the studied forest patches? Second, do major plant dispersal potentials condition the response of species richness to these factors? Third, what are the implications of the observed relationships for the conservation of woody species richness in Mediterranean relict landscapes?

To address these questions we have used data from the 'Island-Forests of Western Andalusia' database BIANDOCC (property of the Andalusian Regional Government) generated from a complete sampling that involved all the woody species and all the forest patches currently occurring in the Guadalquivir river valley (Aparicio, 2008).

2. Methods

2.1. Study area

The study area in the project BIANDOCC extends from the Atlantic coast through the mean and lower stretches of the Guadalquivir river valley, a landscape of about 21,100 km^2 dominated by a fairly uniform agricultural matrix (Fig. 1). The climate is mild Mediterranean, with cool humid winters and warm, dry summers. Annual precipitation ranges from 460 to 1027 mm and mean annual temperature from 15.1 to 18.5 °C.

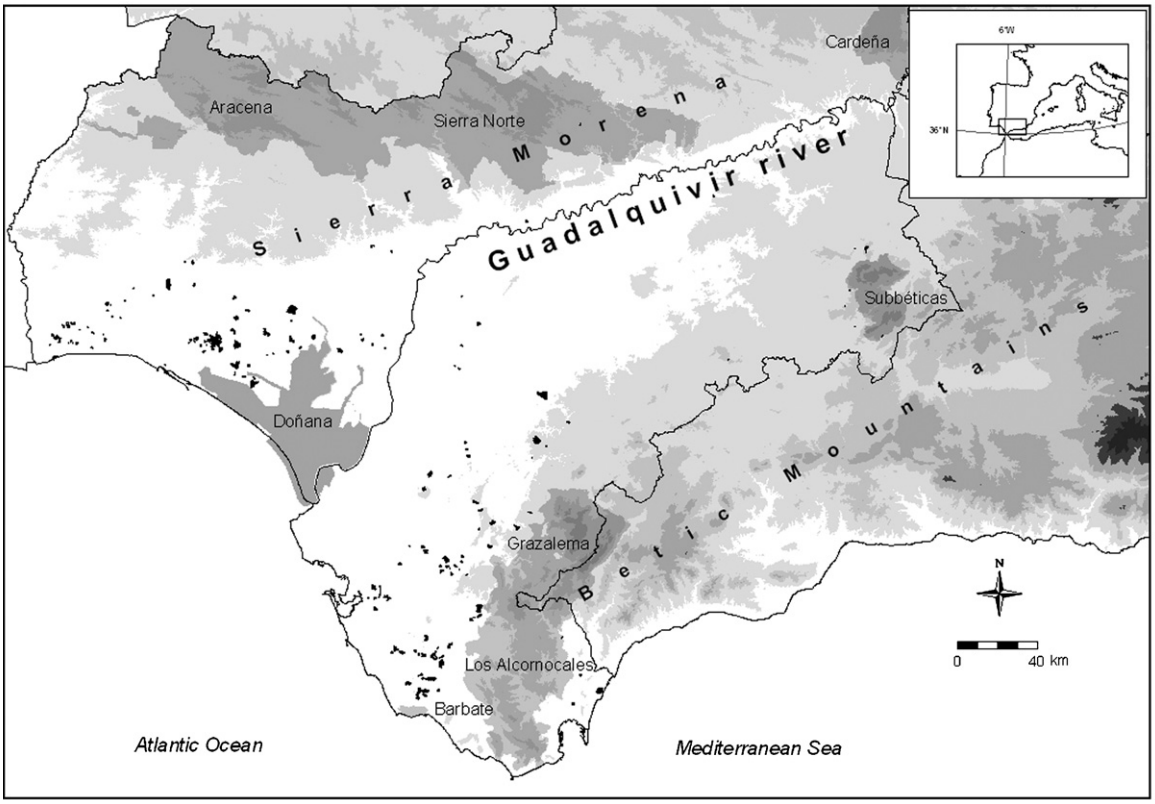

Fig. 1. Studied area in Western Andalusia (outlined). Light colour is the Guadalquivir river valley (<200 m in altitude) where the studied forest patches are embedded. For this study, forest stands having high three (>50%) and shrub (>25%) cover and at least four native woody species were selected ($N = 237$). National Parks and Natural Parks in Western Andalusia are shaded and labelled.

The dominant orography consists in low plains intermixed with small hills and the elevation ranges from sea level to 200 m. Lithologically, the area is made up of sediments from the Miocene to the Quaternary, and its soils are derived from marls, clays, limestones, chalkstone calcareous and siliceous sandstones, and silty alluvials from the Guadalquivir river and its tributaries (Jordán, 1999). The dominant tree species within the area are *Quercus ilex* subps. *ballota*, *Q. suber*, *Pinus pinea*, *P. pinaster* and *P. halepensis*, while the dominant cultivations consist of olives, cereals, sunflower, beetroot, cotton, legumes, opium poppies, vineyards, orchards, and greenhouses, along with oranges, figs, pine trees, and *Eucalyptus* plantations (a detailed description of BIANDOCC project can be found in Aparicio, 2008).

2.2. Forest patches and botanic sampling

We focused our analyses on 237 forest patches embedded in the agricultural matrix of the Guadalquivir river depression covering in all 0.64% of the area (i.e. 135.2 km^2). These units represent all woody vegetation patches showing clear natural or semi-natural forest characteristics with tree cover $\geq$50%, a shrub cover $\geq$25%, and, at least, four native woody species. We excluded all exotic tree plantations, as well as all other highly managed woody vegetated areas that were too open and impoverished in tree/shrub species as to be considered as forests (e.g. patches of 'dehesa' which are savannah-like formations typical of Spanish extensive farmlands). Following sampling procedures described in Gotelli and Colwell (2001), the botanic sampling of the forest patches was done between 1998 and 2001 and involved two to three researchers randomly walking the patches until identifying all woody species. For each patch, the time devoted to sampling was proportional to its area and visual heterogeneity (cf. Kirby et al., 1986).

2.3. Dispersal abilities and richness variables

We generated three measures of woody plant species richness for each patch: (1) total species richness; (2) short-distance dispersal species richness, and (3) long-distance dispersal species richness. We categorized each species as having either short-distance dispersal (S) (including ballistic, barochorous, myrmecochorous and short-distance anemochorous) or potential for long-distance dispersal (L) (including anemochorous, endozochorous, exozoochorous, hydrochorous and dyszoochorous) by surveying the primary botanical literature (including the Seed Information Database, Flynn et al., 2006) for specific information on dispersal modes, either referred to particular species or to congenerics (see Appendix A). We obtained information for 86% of the species, while for the rest the dispersal mode was assigned assuming a standard dispersal system (Higgins et al., 2003) and taking into account diaspore morphologies as described in the regional flora (Valdés et al., 1987). Given the low number of candidate species (see Appendix A) and our broad interest in detecting patterns of species richness at the regional scale, we have ruled out the influence of non-standard long-distance and secondary dispersal events (Higgins et al., 2003).

In addition, we have also investigated to what extent our assignment of woody species to these two dispersal categories could be used as indicative of the broader complexes of life history traits analyzed by Herrera (1992). For this, we focused on the 50 genera common to both studies and performed a genera-level analysis. Firstly, we ranked these genera from 1 to 3 according to their dispersal potentials, with 1 indicating long-distance dispersal (26 genera), 3 short-distance dispersal (21 genera), and 2 the genera with either type of dispersal (3 genera). Then we related this ordinal (rank order) variable with Herrera's (1992) 'Dimension 1', a composite, continuous variable that corresponds to the first dimension of an ordination plane generated by this author using Nonmetric Multidimensional Scaling (NMDS). According to Herrera (1992), this variable provides a coherent synthesis of the across-genera similarities of 10 functional and morphological traits – referred to habit (deciduousness, spinescence, and sclerophylly), flower biology (flower size and sexuality, perianth colour and degree of reduction, and pollinating agent) and seed dispersal (seed size and dispersal agent) – (for details see Herrera, 1992).

2.4. Predictor variables

We generated eleven potential predictor variables indicative of major characteristics of (i) habitat structure, (ii) the physical environment, and (iii) current and past anthropogenic influences (see Jacquemyn et al., 2003; Maestre, 2004).

2.4.1. Habitat structure

Fragmentation is a process causing the division of the original habitat into a constellation of habitat remnants differing in size, shape, and connectivity (Franklin et al., 2002; Fahrig, 2003). Accordingly, we used (1) patch area (in hectares), (2) the Patton's I shape index (Patton, 1975) computed as:

$$I = \frac{P}{200\sqrt{\pi A}}$$

where P is patch perimeter in meters, and A its area in hectares), (3) the Euclidean distance (edge-to-edge) to the nearest neighbouring patch and to the nearest reserve, and (4) the general proximity index (Gustafson and Parker, 1992), taking into account the combined effects of the amount and spatial configuration of the forested area existing in the vicinity of each patch. This index is computed as:

$$\text{proximity} = \sum_{k=1}^{n} \frac{A_{ik}}{d_{ik}^2}$$

where A_{ik} is the area (in hectares) of the patch i within a user-specified neighbourhood radius, and d_{ik} is the distance (in meters) between the focal patch and the patch i. The greater the occupancy of the neighbourhood by forest patches and, especially, the shorter the distances of these patches to the focal patch, the higher the value of the index. To optimize this variable, we assayed six neighbourhood radiuses from 250 to 10,000 m seeking the highest correlation between *proximity* and the response variables. Finally, we used the proximity index at 5000 m.

We obtained all these variables either directly from digital coverages superimposed on digitized aerial orthophotos taken in 2002 (available at http://desdeelcielo.andaluciajunta.es) or from a 30 m cell grid generated with ArcGis 9.0. Euclidean distance and the proximity index were computed in FRAGSTATS 3.3 (McGarigal et al., 2002).

2.4.2. Physical environment

Environmental heterogeneity is responsible for species richness at landscape scales (Pausas et al., 2003). So, we used mean annual temperature and annual precipitation to capture major gradients of warmth and humidity across the landscape. These data were taken at the patch centroids from 1-km resolution rasters generated by the Instituto Nacional de Meoteorología (www.inm.es) using interpolated meteorological station records for the period 1971–2000. We also obtained the patch-centroid elevation to use it as a surrogate for patch microclimate characteristics not taken into account by the other variables (data taken from: www.juntadeandalucia.es/medioambiente). Finally, we assessed lithological heterogeneity at patch level by counting the number of lithological units existing within each patch (lithological data from Jordán, 1999).

2.4.3. Anthropogenic influence

Current human disturbance level was visually assessed in the field with respect to a range of activities (including forest management practices, public use, cattle grazing and/or trampling, fires, hunting, tracks, and buildings). This allowed us to generate a semi-quantitative variable in which each patch is assigned with a value between 1 and 4, where 1 represents minimum human pressure. In addition, from a short-term historical perspective, we found, comparing two sets of digitized aerial orthophotos dating from 1956 and 2002 (a 46 years time span), that forest patches have either decreased or increased their total area. Accordingly, we generated a variable that takes into account the proportion of old-growth forest area relative to the total area for each patch by clipping the two digital coverages (i.e. forest patches from 1956 to 2002) in ArcGis 9.0, and classifying as old-growth forest the corresponding overlapping surfaces.

2.5. Data analysis

Gamma correlation is the rank order index to be used when the data contain an elevated number of tied observations (StatSoft, 2001) – as it is the case of the variable 'dispersal potential' –, so we used this index to check the degree of association between our assigned dispersal categories and Herrera's (1992) ''Dimension 1'' (see above).We generated models including multiple predictors for each species richness variable by using ordinary-least-squares (OLS) multiple regression, which is known to perform poorly when using highly collinear variables. To overcome this, we first calculated the Pearson's correlation for all possible pairs of predictors and excluded those showing high correlation with at least another predictor ($r > |0.5|$; Booth et al., 1994). Additionally, we used a model selection procedure based on Information Theory which deals efficiently with collinearity among predictor variables (see Burnham and Anderson, 2002; Johnson and Omland, 2004). This procedure is based on generating information indexes of relative support for all possible models (i.e. for all possible combinations of predictors). We utilized the Akaike's information criterion (AIC) complemented with the ΔAIC index (i.e. the difference between the AIC of each model and the minimum AIC found) to identify which models have substantial support (i.e. $\Delta\text{AIC} \leq 2$) and fit almost equally well as the best model (Burnham and Anderson, 2002). Also, we used the 25 models with lowest AICs to calculate their Akaike's weighting (w_i), an index that can be interpreted as the probability that the model i is actually the best explanatory model.

Additionally, we took into account that our species richness and environmental data may display spatial autocorrelation due to the varying proximities of the analysis units (i.e. forest patches) in the studied landscape. This spatial dependence of the analysis units may generate bias in common statistical procedures due to overestimation of the sample size. Accordingly, we used the modified t-test of Dutilleul (1993) to obtain spatially unbiased significance estimates of Pearson's correlations (e.g. Legendre et al., 2002). We acknowledge that this is a highly conservative correction that we used as a way to identify particularly strong relationships and thus give more focus to our interpretations (JAF Diniz-Filho pers. comm.). Also we computed all AICs and derived indexes using corrected variances for the presence of spatial autocorrelation in the residuals of the regression models (for a detailed description of this method see Olalla-Tárraga et al., 2006; Olalla-Tárraga and Rodríguez, 2007). Finally, we investigated the effectiveness of our models to account for spatially structured patterns in the data by generating Moran's I spatial correlograms for both the three response richness variables, and the residuals resulting after fitting the models (Diniz-Filho et al., 2003).

We applied log or angular transformation to all variables as appropriate before analysis (Tabachnick and Fidell, 1996), and performed all statistical analyses in STATISTICA 6.0 (StatSoft, 2001) and SAM 1.1 (Spatial Analysis in Macroecology; Rangel et al., 2006).

3. Results

Mean (±SD) area of the forest patches was 55 (±100) hectares (range 0.3–752), and the median was 2.27 ha ($N = 237$). Mean Euclidean distance (edge-to-edge) among patches was 827 (±1570) m (range 60–20 701). The number of woody plant species was 143 with a mean (±S.D.) of 18.96 (±7.7) species per patch. The sets of short- and long-distance dispersal species were comprised by 83 (58%) and 60 (42%) species (see Appendix A), with mean (±SD) patch values of 9.05 (±4.72) and 9.87 (±4.83) species, respectively. The association between our 'dispersal potential' variable and Herrera's (1992) 'Dimension 1' (see Methods), was very high (Gamma $r = 0.806$, $P \ll 0.001$), thus supporting that our assignation of broad dispersal characteristics is to a large extent capturing the characteristic trait syndromes described by this author for the genera in the flora of south-western Spain.

On the other hand, after correcting probability levels for spatial autocorrelation, all species richness variables were significantly positively correlated with patch area and negatively with current disturbance, and total and long-distance species richness were also significantly positively correlated with patch shape and lithological heterogeneity (Table 1). Due to collinearity among predictor variables and weak relationships with richness (Table 2), patch shape, proximity and elevation were excluded from the analysis, and thus we used a final set of eight variables for multiple regression modelling.

3.1. Total species richness

Out of the 255 possible multiple-regression models for total species richness, 13 models had a $\Delta\text{AIC} \leq 2$ and accounted for

Table 1
Pearson's product moment correlations between response (total species richness, short- and long-distance dispersal species richness) and predictor (habitat structure, physical environment, anthropogenic influence) variables used for model construction

	Total species	Short-distance dispersal species	Long-distance dispersal species
Habitat structure			
Area[a]	0.454***	0.199**	0.486***
Shape	0.312***	0.107	0.350***
Distance to nearest reserve	−0.088	0.177	−0.282
Distance to nearest neighbour	−0.036	−0.159	0.107
Proximity	0.098	0.042	0.077
Physical environment			
Temperature	−0.081	0.096	−0.225
Precipitation	0.026	−0.337	0.340
Elevation	0.026	−0.137	0.154
Lithological heterogeneity	0.193***	−0.130	0.413*
Anthropogenic influence			
Current disturbance	−0.367***	−0.371***	−0.205*
Proportion of old-growth forest	0.047	−0.049	0.108

[a] Significance levels have been corrected for spatial autocorrelation by the t-test of Dutilleul (1993). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2
Pearson's correlation matrix among predictor variables

	Area	Shape	Distance to nearest reserve	Distance to nearest neighbour	Proximity	Temperature	Precipitation	Elevation	Lithological heterogeneity	Current disturbance
Habitat structure										
Area[a]										
Shape	0.686***									
Distance to nearest reserve	−0.262	−0.245								
Distance to nearest neighbour	−0.064	−0.136	0.036							
Proximity	0.223**	0.295**	−0.417*	−0.524***						
Physical environment										
Temperature	0.094	0.003	0.311	−0.107	−0.139					
Precipitation	0.22	0.254	−0.652	0.035	0.402***	−0.287				
Elevation	0.061	0.14	−0.426	−0.007	0.262*	−0.718***	0.367*			
Lithological heterogeneity	0.426***	0.437***	−0.242	0.138	0.072	−0.188	0.435	0.169		
Anthropogenic influence										
Current disturbance	−0.122	−0.001	0.082	−0.043	−0.049	0.166	0.115	−0.109	0.019	
Proportion old-growth forest	0.238**	0.166*	−0.242	−0.164	0.109	0.256	0.139	−0.179	0.145	0.002

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

[a] Significance levels have been corrected for spatial autocorrelation by the *t*-test of Dutilleul (1993).

similar proportions of variance (ca. 31%) (Table 3). Only two variables entered in all the models: patch area with positive sign and current disturbance with negative sign. Other variables entered in some models, but were of secondary importance according to their low standardized regression coefficients (see Table 3). The Moran's *I* correlogram for total species richness showed no evidence of spatial autocorrelation across all distance classes (Fig. 2a).

3.2. Short-distance dispersal species richness

On the basis of a $\Delta\text{AIC} \leq 2$, six models were equivalent in describing short-distance species richness (Table 3), and accounted for similar proportions of variance (ca. 31%). However, based on Akaike's weightings, none of the models received an overwhelming support, with the best four models having w_i values from 0.20 to 0.06. Five variables entered in all six models, which were related to habitat features (patch area and distance to the nearest neighbour), physical environment (precipitation), and anthropogenic influence (current disturbance and proportion of old-growth forest). Based on the standardized regression coefficients, precipitation and current disturbance were the strongest predictors of short-distance dispersal especies richness, both with negative sign. Distance to the nearest neighbour and, notably, patch area showed discrete negative and positive associations with this richness variable,

Table 3
Standardized regression coefficients of the variables and coefficients of determination (r^2) of the multiple regression models obtained for total, short- and long-distance dispersal species richness

Model	Habitat structure			Physical environment			Anthropogenic influence		r^2	AIC[a]	w_i[b]
	Area	Distance to nearest reserve	Distance to nearest neighbour	Temperature	Precipitation	Lithological heterogeneity	Current disturbance	Proportion of old-growth forest			
Total richness											
Best	0.429						−0.317	−0.053	0.308	−123.250	0.122
Average (13 models)	0.429	0.014	−0.001	−0.030	−0.008	0.003	−0.310	−0.025	0.309	−121.823	
Short-distance dispersal richness											
Best	0.247		−0.160		−0.338		−0.301	−0.095	0.305	−82.105	0.203
Average (6 models)	0.255	0.005	−0.153	0.012	−0.319	−0.030	−0.305	−0.098	0.307	−81.086	
Long-distance dispersal richness											
Best	0.394		0.101	−0.141	0.169	0.138	−0.212		0.381	−171.121	0.327
Average (4 models)	0.395	0.059	0.104	−0.155	0.186	0.132	−0.174	0.049	0.383	−169.877	

For brevity, we report only two models for each species group: the best model (the one with the lowest AIC) and an average model obtained from averaging all models with (AIC $\leq$ 2 (see Section 2). The number of models averaged in each case is indicated in parentheses.

[a] Values of Akaike Information Criterion (AIC) computed with corrected variances for the presence of spatial autocorrelation in the residuals.

[b] Akaike's weightings (w_i) calculated over the 25 models with the lowest AICs.

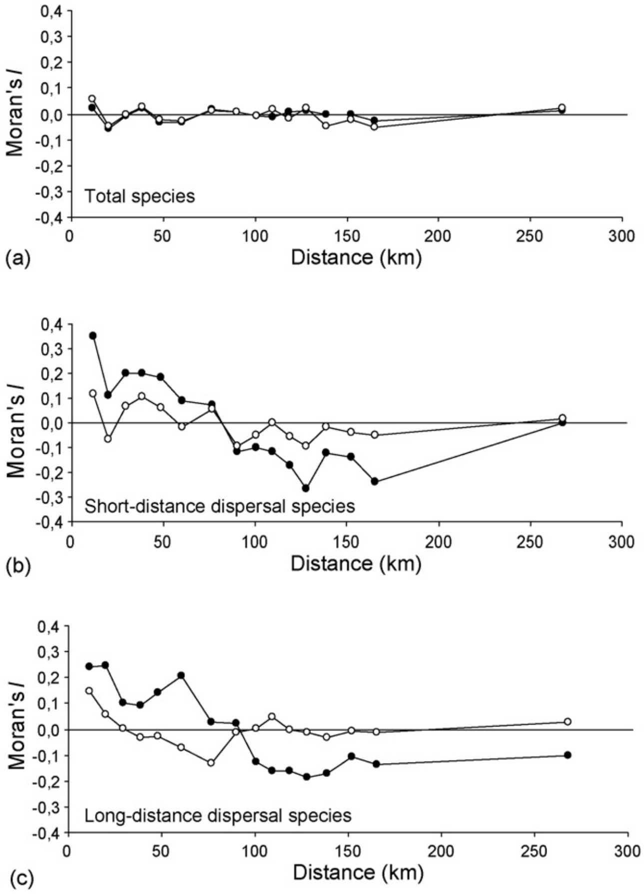

Fig. 2. Spatial correlograms using Moran's *I* for woody species richness (solid circles) and residuals of the best-fitted multiple models (open circles). All spatial correlograms were computed for 16 distance (in km) classes.

respectively. The amount of old-growth forest also entered in all the selected models displaying a slight negative effect. The pattern of spatial autocorrelation for short-distance dispersal species richness was characteristic of a cline with positive autocorrelation at shorter distances and gradually becoming negative at larger distances, except for the largest one, which showed negligible autocorrelation (Fig. 2b). The best multiple regression model removed most of this pattern, indicating that our environmental models are sufficient to account for the spatially structured variation of short-distance dispersal species richness in the studied landscape.

3.3. Long-distance dispersal species richness

Finally, four models were equivalent in explaining long-distance species richness variation (Table 3), all of them accounting for similar proportions of variance (ca. 38%). Six predictor variables (namely, patch area, distance to the nearest neighbour, temperature, precipitation, lithological heterogeneity, and current disturbance) were present in all the models, of which patch area exhibited the highest standardized regression coefficient. Notably, although patch area and current disturbance show the same signs (positive and negative, respectively) as those obtained for short-distance dispersal species richness, this was not the case for the other predictors, which exhibited opposite signs in each case (Table 3). This indeed suggests that each species richness variable is responding differently to environmental variation. On the other hand, the pattern of spatial autocorrelation for long-distance dispersal species richness was again representative of a cline (Fig. 2c), and the model with the highest w_i accounted for virtually all of this pattern.

4. Discussion

4.1. Determinants of richness

We have investigated the influence of habitat structure, physical environment and anthropogenic disturbance on woody plant species richness across the forest patches that exist sparsely in the agricultural matrix of the Guadalquivir river valley, a relictual Mediterranean landscape intensively managed since pre-Roman times. Because dispersal capabilities might determine species responses to habitat fragmentation, we explored three richness variables, one including all species, and the other two involving species with either short- or long-distance seed dispersal system. In all three cases, species richness decreased with intra-patch disturbance levels, and increased along with increasing forest patch area, the latter being a result commonly reported in the literature on habitat fragmentation (reviewed by Fahrig, 2003).

We also found weak associations between total woody species richness and the rest of the predictors, which could be interpreted as that neither fragmentation nor major aspects of the physical environment are relevant for plant richness variation. However, the patterns exhibited by short-distance versus long-distance dispersal species richness could lead to a different interpretation. First, with regard to fragmentation, the regression models suggested that distance to the nearest neighbouring patch had detectable effects in determining the spatial variation of both species richness variables, albeit these effects were not as strong as those of habitat area and disturbance (Table 3). In addition, the regression models also indicated that each group of species was differently associated with this distance, so that an increasing separation between forest patches led to the increase of species with good dispersal abilities and to the diminution of species with limited dispersal. Bearing in mind that both plant groups show fairly high species numbers in the study area (83 and 60 species, respectively), these contrasting trends are likely to have counterbalanced each other when all species were pooled together to attain total richness values. In other words, considering that dispersal limits species responses to habitat fragmentation (Jacquemyn et al., 2001; Purves and Dushoff, 2005), the lack of relationships we observed between total richness and fragmentation variables might be accounted for by the occurrence of woody species with different dispersal potentials.

Second, with regard to the effects of other aspects of the environment on species richness, these were also highlighted once dispersal abilities were taken into account. Thus, the regression models detected clearer effects of temperature, lithological heterogeneity, proportion of old-growth forest and, specially, precipitation when species richness was separately analyzed for short-distance versus long-distance dispersal species, and, interestingly, that the effects of each of these variables on each plant group were opposite in sign (Table 3). On the one hand, such contrasted responses are, again, likely to have counterbalanced each other when both plant groups were summed up to obtain total species richness values, thus explaining why total species richness showed so low association with these environmental variables. On the other hand, some of the relationships of short- and long-distance dispersal species richness with these variables are easily interpreted as direct responses of vegetation to its surrounding environment (Pausas et al., 2003), but some others do not. For example, the preference of plants for more mesic areas under semiarid climates (Pugnaire and Lázaro, 2000) agrees with the increase of long-distance dispersal species towards higher precipitation areas, but contrasts with the negative association between short-distance dispersal species richness and precipitation. Such difference is difficult to understand unless it reflects indirect effects via competition between these two trait syndrome cohorts at patch level; that is, an increase in the number of long-distance dispersal species with precipitation causes a reduction in the number of short-distance dispersal species, which are known to be more drought-tolerant (Paula and Pausas, 2006). Similar arguments could be used to interpret the rest of the contrasted trends exhibited by both plant cohorts, but this would be highly speculative given the non-experimental nature of our investigation. Consequently, we prefer to emphasize that our data clearly put forward that the potential for long-distance dispersal appears to determine, either directly or indirectly, the responses of plant richness to many factors, including characteristics of both habitat structure and physical environment.

4.2. Maximizing species richness and successional rates

Our multiple regression models were built to be explanatory (i.e. to identify key factors for the spatial variation of richness in the studied landscape), not as predictive models to be used for evaluating alternative scenarios in real conservation/restoration projects. For this, a predictive approach should be adopted (e.g. including higher order and interaction terms in the regressions), thus making it possible to generate models that are less limited than ours in accounting for richness variance (see Table 3) and, hence, that could generate more accurate richness predictions. Even so, we have statistically shown that the two dispersal categories in our study actually synthesize broader complexes of life history traits (Herrera, 1992; Verdú et al., 2003), which allows discussing our model results in the context of ecological succession. Thus, while short-distance dispersal is common among non-sclerophyllous, insect-pollinated, dry-fruited, seeder species, typical of pioneer woody Mediterranean communities (e.g. *Cistus*, *Halimium*, *Thymus*, *Lavandula*, *Erica*, *Calluna*), long-distance dispersal often occurs in species that exhibit complementary character states, and that are typical of mature communities (e.g. *Pistacia*, *Osyris*, *Juniperus*, *Rhamnus*, *Myrtus*) (Herrera, 1984, 1992). Therefore our regression models can be used as indicative of the sort of actions that might push ecological succession forward across the forest patches of the study area.

Specifically, our models suggest that a clear starting point to enhance within-patch woody species richness is to increase patch area while minimizing anthropogenic disturbance, particularly because we have identified these two factors as the ones most strongly associated with total, short- and long-distance dispersal species richness (Table 3). Beyond this, our models also inform about where, in environmental terms, controlling these factors is likely to have stronger effects on richness and succession. For example, model regression coefficients indicate that increasing patch area and reducing disturbance would be more effective in promoting long-distance dispersal species richness – and, hence, pre-forestal communities – in wet, cool areas with greater lithological heterogeneity (e.g. at higher elevations in the edges of the Guadalquivir river valley). Conversely, in lowlands, similar effects on long-distance dispersal species richness and succession would require larger increments of patch area and reductions of disturbances, as these areas typically have more homogeneous substrates, and warmer and drier climate.

To conclude, the most salient finding of our study is that woody plant species richness not only responds to variation in habitat area and human disturbance, as it is commonly reported in the fragmentation literature, but also, and secondarily, to habitat structure (nearest neighbour distance), climate and characteristics of the substrate. However, these secondary effects were only evident after discriminating between major plant dispersal potentials, which emphasizes the need to consider dispersal if we are to understand the determinants of plant species richness in highly fragmented landscapes.

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Appendix A

We show in this section the complete list of the 143 autochthonous (including *Pinus* spp.) woody and climber plant species used in this study, the number of patches where they were collected (N), and the assigned dispersal category accounting for their long-distance dispersal ability. For 86% of the taxa, dispersal mode was obtained from the literature, including the Seed Information Database (Flynn et al., 2006). For the remaining taxa (14%) for which apparently no bibliographic data were available (empty cells in the last two columns), the dispersal category was assigned assuming a standard-dispersal system (Higgins et al., 2003) based in the diaspore morphology described in the regional flora (Valdés et al., 1987). Thus, the long-distance dispersal species category (L, $N = 60$) includes anemochorous (partly), endozochorous, exozoochorous, hydrochorous and dyszoochorous species, and the short-distance dispersal species category (S, $N = 83$) includes ballistic, barochorous, myrmecochorous and short-distance anemochorous species.

	N	Assigned dispersal category	Type of dispersal	Reference
Adenocarpus gibbsianus Castroviejo & Talavera	1	S		
Adenocarpus telonensis (Loisel.) DC.	30	S		
Anagyris foetida L.	11	S		
Anthyllis cytisoides L.	3	S	Wind, local dispersal	Pugnaire et al. (2006)
Arbutus unedo L.	15	L	Animal	Flynn et al. (2006)
Aristolochia baetica L.	84	S	Ants	Berjano (2006)
Asparagus acutifolius L.	155	L	Animal[a]	Flynn et al. (2006)
Asparagus albus L.	55	L	Animal[a]	Flynn et al. (2006)
Asparagus aphyllus L.	70	L	Animal[a]	Flynn et al. (2006)
Bryonia dioica Jacq.	27	L	Animal	Flynn et al. (2006)
Bupleurum gibraltaricum Lam.	1	S		
Calicotome villosa (Poiret) Link	20	S		
Calluna vulgaris (L.) Hull	37	S	Wind[a], local dispersal[a]	Bullock and Moy (2004)
Ceratonia siliqua L.	11	L	Animal	Flynn et al. (2006)
Chamaerops humilis L.	61	L		
Cistus albidus L.	43	S	Unassisted[a]	Flynn et al. (2006)
Cistus crispus L.	137	S	Unassisted[a]	Flynn et al. (2006)
Cistus ladanifer L.	71	S	Unassisted	Flynn et al. (2006)
Cistus libanotis L.	36	S	Unassitsed	Flynn et al. (2006)
Cistus monspeliensis L.	42	S	Unassisted[a,b]	Flynn et al. (2006)
Cistus populifolius L.	3	S	Unassisted[a]	Flynn et al. (2006)
Cistus psilosepalus Sweet	8	S	Unassisted[a]	Flynn et al. (2006)
Cistus salvifolius L.	175	S	Unassisted, Ants	Troumbis and Trabaud (1986)
Clematis cirrhosa L.	37	L	Wind[a]	Flynn et al. (2006)
Clematis flammula L.	16	L	Wind	Flynn et al. (2006)
Colutea hispanica Talavera & Arista	1	L	Wind	Flynn et al. (2006)
Coronilla juncea L.	8	S		
Crataegus monogyna Jacq.	62	L	Animal	Flynn et al. (2006)
Cytisus arboreus (Desf.) DC.	21	S	Auto, ants[a]	Flynn et al. (2006)
Cytisus grandiflorus DC.	59	S	Auto, ants[a]	Flynn et al. (2006)
Cytisus scoparius (L.) Link	1	S	Auto, ants[c]	Malo (2004)
Cytisus striatus (Hill) Rothm.	1	S	Auto, ants[a]	Flynn et al. (2006)
Daphne gnidium L.	158	L	Animal	Flynn et al. (2006)
Dorycnium hirsutum (L.) Ser.	1	S	Short-distance[a]	Bouza et al. (2002)
Dorycnium pentaphyllum Scop.	8	S	Short-distance[a]	Bouza et al. (2002)
Dorycnium rectum (L.) Ser.	4	S	Short-distance[a]	Bouza et al. (2002)
Erica andevalensis Cabezudo & Rivera	1	S	Wind[a], local dispersal[a]	Bullock and Moy (2004)
Erica arborea L.	8	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Erica australis L.	6	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Erica ciliaris L.	1	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Erica lusitanica Rudolphi	1	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Erica scoparia L.	46	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Erica umbellata L.	30	S	Wind[a] local dispersal[a]	Bullock and Moy (2004)
Ficus carica L.	8	L	Animal	Flynn et al. (2006)
Flueggea tinctoria (L.) G. L. Webster	2	L	Animal[a]	Flynn et al. (2006)
Fraxinus angustifolia Vahl	2	L	Wind[a]	Flynn et al. (2006)
Fumana ericifolia Wallr.	2	S	Short-distance[a]	Thanos et al. (1992)
Fumana juniperina (Lag ex Dunal) Pau	2	S	Short-distance[a]	Thanos et al. (1992)
Fumana thymifolia (L.) Spach ex Webb	22	S	Short-distance[a,b]	Thanos et al. (1992)
Genista ancistrocarpa Spach	2	S	Ants[a]	Gómez and Oliveras (2003)
Genista cinerea (Vill.) DC.	2	S	Ants[a]	Gómez and Oliveras (2003)
Genista hirsuta Vahl	49	S	Ants[a]	Gómez and Oliveras (2003)
Genista polyanthos R. de Roemer ex Willk.	1	S	Ants[a]	Gómez and Oliveras (2003)
Genista triacanthos Brot.	62	S	Ants[a]	Gómez and Oliveras (2003)
Genista tridens (Cav.) DC.	4	S	Ants[a]	Gómez and Oliveras (2003)

Appendix A (*Continued*)

	N	Assigned dispersal category	Type of dispersal	Reference
Genista umbellata (L'Hér.) Poiret	1	S	Ants[a]	Gómez and Oliveras (2003)
Globularia alypum L.	4	S		
Halimium calycinum (L.) K. Koch	77	S	Short-distance[a]	Thanos et al. (1992)
Halimium halimifolium (L.) Willk.	109	S	Short-distance[a]	Thanos et al. (1992)
Helianthemum hirtum (L.) Mill.	12	S	Unassited[a]	Flynn et al. (2006)
Helianthemum marifolium (L.) Mill.	1	S	Unassited[a]	Flynn et al. (2006)
Helianthemum syriacum (Jacq.) Dum.-Courset	1	S	Unassited[a]	Flynn et al. (2006)
Helichrysum italicum (Roth) G. Don fil.	1	L	Wind[a]	Flynn et al. (2006)
Helichrysum picardii Boiss. & Reuter	63	L	Wind[a]	Flynn et al. (2006)
Helichrysum stoechas (L.) Moench	47	L	Wind[a]	Flynn et al. (2006)
Jasminum fruticans L.	18	L	Animal[a]	Flynn et al. (2006)
Juniperus oxycedrus L.	6	L	Animal	Flynn et al. (2006)
Juniperus phoenicea L.	10	L	Animal[a]	Flynn et al. (2006)
Lavandula stoechas L.	140	S	Unassisted, Animal	Sánchez and Peco (2002)
Linum suffruticosum L.	3	S		
Lonicera implexa Aiton	23	L	Animal	Flynn et al. (2006)
Lonicera periclymenum L.	3	L	Animal[a]	Flynn et al. (2006)
Micromeria graeca (L.) Bentham ex Reichenb.	14	S		
Myrtus communis L.	100	L	Animal	Traveset et al. (2001)
Nerium oleander L.	4	L	Water	Herrera (1991)
Olea europaea L.	144	L	Animal	Alcántara et al. (2000) and Rey and Alcántara (2000)
Osyris alba L.	32	L	Animal[a]	Flynn et al. (2006)
Osyris lanceolata Hochst. & Steudel	15	L	Animal	Flynn et al. (2006)
Phagnalon rupestre (L.) DC.	8	L	Water, wind	Flynn et al. (2006)
Phagnalon saxatile (L.) Cass.	32	L	Water, wind[a]	Flynn et al. (2006)
Phillyrea angustifolia L.	70	L	Animal	Flynn et al. (2006)
Phillyrea latifolia L.	3	L	Animal	Flynn et al. (2006)
Phlomis lychnitis L.	3	L	Wind	Aparicio (1997)
Phlomis purpurea L.	73	S	Unassisted	Aparicio (1997)
Pinus halepensis Miller	18	L	Wind or animal[a]	Nathan and Ne'eman (2004) and Flynn et al. (2006)
Pinus pinaster Aiton	24	L	Wind or animal[a]	Flynn et al. (2006)
Pinus pinea L.	144	S		
Pistacia lentiscus L.	165	L	Animal	Verdú and García-Fayos (2001)
Pistacia terebinthus L.	3	L	Animal	Flynn et al. (2006)
Populus alba L.	6	L	Wind[a]	Flynn et al. (2006)
Populus nigra L.	1	L	Wind	Flynn et al. (2006)
Pterospartum tridentatum (L.) Willk.	3	S		
Pyrus bourgaeana Decne	20	L	Animal[a]	Flynn et al. (2006)
Quercus coccifera L.	117	L	Animal[a]	Gómez Reyes (2003) and Pons and Pausas (2007)
Quercus faginea Lam.	12	L	Animal[a]	Gómez Reyes (2003) and Pons and Pausas (2007)
Quercus ilex L.	64	L	Animal	Gómez Reyes (2003) and Pons and Pausas (2007)
Quercus suber L.	111	L	Animal	Pons and Pausas (2007)
Retama monosperma (L.) Boiss.	4	L	Animal	Dellafiore et al. (2006)
Retama sphaerocarpa (L.) Boiss.	53	S	Wind, local dispersal	Pugnaire et al. (2006)
Rhamnus alaternus L.	49	L	Animal	Flynn et al. (2006)
Rhamnus lycioides L.	66	L	Animal[a]	Flynn et al. (2006)
Rosa canina L.	6	L	Animal	Flynn et al. (2006)
Rosa sempervirens L.	4	L	Animal[a]	Flynn et al. (2006)
Rosmarinus officinalis L.	80	S	Ants	Bouman and Meeuse (1992)
Rubia agostinhoi Dansereau & P. Silva	1	L	Animal[a]	Flynn et al. (2006)
Rubia peregrina L.	45	L	Animal	Flynn et al. (2006)
Rubus ulmifolius Schott	44	L	Animal	Flynn et al. (2006)
Ruscus aculeatus L.	30	S	Unassisted	Martínez-Palle and Aronne (1999)
Salix alba L.	1	L	Wind, water	Flynn et al. (2006)
Salix atrocinerea Brot.	6	L	Wind, water[a]	Flynn et al. (2006)
Santolina pectinata Lag.	1	S		
Satureja obovata Lag.	2	S	Wind[d] or animal[a]	Bouman and Meeuse (1992)
Scrophularia canina L.	12	S		
Sideritis arborescens Salzm. ex Bentham	7	S		
Smilax aspera L.	75	L	Animal	Flynn et al. (2006)
Spartium junceum L.	2	S		
Staehelina dubia L.	6	L		

Appendix A (*Continued*)

	N	Assigned dispersal category	Type of dispersal	Reference
Stauracanthus boivinii (Webb.) Samp.	10	S		
Stauracanthus genistoides (Brot.) Samp.	44	S		
Tamarix africana Poiret	2	L	Wind[a]	Flynn et al. (2006)
Tamus communis L.	26	L	Animal	Flynn et al. (2006)
Teline linifolia (L.) Webb	5	S		
Teucrium capitatum L.	29	S	Wind[d]	Bouman and Meeuse (1992)
Teucrium fruticans L.	45	S	Wind[d]	Bouman and Meeuse (1992)
Teucrium haenseleri Boiss.	3	S	Wind[d]	Bouman and Meeuse (1992)
Teucrium pseudochamaepitys L.	10	S	Wind[d]	Bouman and Meeuse (1992)
Thymbra capitata (L.) Cav.	27	S	Wind[d]	Bouman and Meeuse (1992)
Thymelaea argentata (Lam.) Pau	1	S	Ants[a]	de la Bandera and Traveset (2005)
Thymelaea hirsuta (L.) Endl.	6	S	Ants[a]	de la Bandera and Traveset (2005)
Thymelaea pubescens (L.) Meissner	1	S	Ants[a]	de la Bandera and Traveset (2005)
Thymelaea villosa (L.) Endl.	2	S	Ants[a]	de la Bandera and Traveset (2005)
Thymus albicans Hoffmanns. & Link	9	S	Wind[d]	Bouman and Meeuse (1992)
Thymus mastichina (L.) L.	74	S	Wind[d]	Bouman and Meeuse (1992)
Thymus zygis Loefl. ex L.	3	S	Wind[d]	Bouman and Meeuse (1992)
Ulex argenteus Welw. ex Webb	8	S	Ants	López-Vila and García-Fayos (2005)
Ulex australis Clemente	73	S	Ants	López-Vila and García-Fayos (2005)
Ulex baeticus Boiss.	6	S	Ants	López-Vila and García-Fayos (2005)
Ulex eriocladus C. Vicioso	18	S	Ants	López-Vila and García-Fayos (2005)
Ulex minor Roth	13	S	Ants	López-Vila and García-Fayos (2005)
Ulex parviflorus Pourret	25	S	Ants	López-Vila and García-Fayos (2005)
Ulmus minor Miller	3	L	Wind[a]	Flynn et al. (2006)
Viola arborescens L.	1	S	Ants[a]	Flynn et al. (2006)
Vitis vinifera L.	5	L	Animal	Flynn et al. (2006)

[a] Reported in related congeneric species.

[b] Candidate for non-standard long-distance dispersal (Ramos et al., 2006).

[c] Candidate for non-standard long-distance dispersal (Manzano et al., 2005).

[d] Probably local (Casper, 1987).

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