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# Growth forms, dispersal strategies and taxonomic spectrum in a semi-arid shrubland in SE Spain

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ABSTRACT

We have identified the dispersal strategies of major growth forms in a semi-arid Mediterranean shrubland of Cabo de Gata Natural Park (SE Spain), testing (1) whether dispersal strategies and antitelechoric mechanisms vary among growth forms and families, and (2) whether dispersal traits that identify dispersal strategies can be used to predict different ways of plant survival in response to seasonal changes in their habitat. In the survey, the data of 17 dispersal traits were collected of 140 species and analysed using cluster analysis and nonlinear principal components analysis. For shrubs and forbs, low diaspore release height, spheroidal diaspores with a low mass and small size and a low to high diaspore number were associated with restricted spatial dispersal. In contrast, medium to high release height, relatively large and heavy diaspores varying in shape and a high diaspore number were associated with developed spatial dispersal (telechory). Telechory is higher in shrubs than in forbs and grasses, where atelechory/antitelechory predominate. Dispersal was synchronized mainly with the drought period (July and August) and the beginning of the rainy season (October–December). 68% of shrubs and 61.6% of forbs were anemochores, whereas zoochory (6% of shrubs) and ballistic species (8% of shrubs and 6.9% of forbs) were less common. Ombrohydrochory was well represented among forbs (27.3%) but rare among shrubs (4%). The main antitelechoric mechanisms were: bradyspory (30.7%), myxospermy (15.7%) and trypanocarpy (29.4%, only for grasses). Species with restricted spatial dispersal and antitelechoric mechanisms are well adapted to survival in semi-arid climatic conditions, and should be taken into consideration in conservation planning.



## 1. Introduction

Seed dispersal determines many key aspects in plant biology (Grime, 2001; Ozinga et al., 2005) and in plant communities (Cain et al., 2000; Knevel et al., 2005). It is also a key factor in conservation biology (Haddad et al., 2003; Trakhtenbrot et al., 2005) and in restoration ecology (Palmer et al., 1997).

Seed dispersal is a critical event regulating the spatial and temporal distribution of plants. Aridity results in restricted dispersal capabilities because the space already occupied is usually the most suitable for growth. For this reason, species that do not possess any adaptations to promote spatial dispersal (atelechory) or that actively restrict dispersal (antitelechory) by mechanisms which protect diaspores from predation and other dangers, and that regulate the intra- and inter-year timing of dispersal and germination are frequent in arid and desert regions (Ellner and Shmida, 1981; van Rooyen et al., 1990; Fenner, 1992; Gutterman, 1993, 1994, 2001; Ehrman and Cocks, 1996; van Rheede van Oudtshoorn and van Rooyen, 1999). Recently, it has been demonstrated that restricted spatial dispersal could be selected under certain conditions (Lavorel et al., 1994) to ensure plant survival in situ and establishment, to facilitate plant coexistence (Green, 1989) and to reinforce spatial aggregation in arid plants (Puigdefabregas and Pugnaire, 1999). In contrast, spatial dispersal facilitates colonization of the landscape, even though the new sites may not be entirely appropriate for establishment, especially those exposed to unpredictable environmental conditions. Gutterman (1990, 2001) and Grime et al. (1981) have also demonstrated that dispersal in time, species in which part or all of its seeds are retained and protected on the mother plant long after seed maturity, is a frequent mechanism in arid plants for restricting germination to the most favourable season of the year, which corresponds with the beginning of the rainy season.

Under the framework of plant dispersal, we set out to validate the hypothesis that restricted spatial dispersal strategies and antitelechoric mechanisms are predominantly selected by shrub, forb and grass species. In addition to this, the coexistence of dispersal strategies is clearly advantageous in a semi-arid

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Mediterranean ecosystem to ensure survival in situ and to maintain ecosystem biodiversity.

Although the dispersal spectrum is considered a key factor in species coexistence and conservation (Strykstra et al., 2002), little attempt has been made to investigate the relationships between dispersal diversity, dominant dispersal strategy and taxonomic biodiversity in Mediterranean semi-arid shrublands.

In this paper we attempt to answer the following questions: (1) Do dispersal strategies vary among the major life forms (shrubs, forbs, and grasses) in a Mediterranean shrubland in Cabo de Gata Natural Park? (2) Do they show any response to seasonal changes in their habitat? (3) What are the dispersal traits associated with spatial dispersal? (4) Is the dispersal spectrum from this site similar to that of other arid communities of the Old and New World? and (5) Do the spatial dispersal strategies follow the same trends among taxonomic groups?

We also wish to summarize existing knowledge of dispersal and its interrelations with other attributes of plants and their habitats.

## 2. Materials and methods

### 2.1. Study site

Cabo de Gata Natural Park lies on the southeast coast of Spain in a volcanic mountain range (0–493 m asl). The climate is semi-arid Mediterranean characterized by mild summer temperatures with an average annual rainfall of 260 mm. The mean annual temperature is 17.7 °C (figures for 1953–1991) (Rivas Martinez and Rivas y Sáenz, 2007). The dominant vegetation is a shrubland of dwarf-palm (*Chamaerops humilis*) with *Ulex baeticus* and *Rhamnus lycioides* (Peinado et al., 1992). Open halophytic shrublands (*Salsola* spp.) with saline soils are scattered across the site.

### 2.2. The species sets

Data were gathered for 140 major representative species with the highest cover values (Navarro et al., 2006). We classified each species based on their growth form, which yielded three sets of species: 50 shrubs, 73 forbs and 17 grasses. These groups provided the possibility of describing natural correlations between dispersal traits and investigating different sets of traits among growth forms (Lavorel et al., 1997; McIntyre et al., 1999a, 1999b).

### 2.3. Dispersal traits

Field sampling and observations were carried out monthly between June 2005 and December 2006. Voucher specimens of the studied species were kept in the MGC Herbarium. Botanical nomenclature follows Castroviejo et al. (1986–2007). The family and class affiliation of each species were added using APG II (Angiosperm Phylogenetic Group) (2003). Seventeen easily measured dispersal traits, including resprouting ability (see Appendix A), were analysed. Four of these, dispersal mode, diaspore shape, size and mass (weight), constitute the main regenerative traits, according to Cornelissen et al. (2003). Additional information comes from regional floras.

The term diaspore is used to name the dispersal unit (Weiher et al., 1999). Whenever a diaspore lent itself to more than one type of dispersal mode, the mechanism judged to be predominant was assigned. The achenes of Asteraceae were measured with the pappus, Poaceae were measured with the persistent lemmas, which normally disperse and are considered as open balloons, while awns are considered long or short elongated appendages. Diaspores were collected when ripe, just before they started to fall off the plant. We determined the number of diaspores per plant and diaspore release height in 20 adult plants of a given species growing in a typical habitat and exposed to full sunlight. For each plant, 20 (100 for small seeded species) diaspores were air-dried, weighed, measured and averaged into ranges (Cornelissen et al., 2003).

The antitelechoric mechanisms (van Rheede van Oudtshoorn and van Rooyen, 1999) included bradyspory, basicarpy (Zohary, 1962; van Rooyen et al., 1990), synaptospermy (Zohary, 1937, 1962; Ellner and Shmida, 1981; van Rooyen et al., 1990), myxospermy (Zohary, 1937: van Rooyen et al., 1990), and trypanocarpy. Bradyspory was indicated for those species which delayed diaspore release, all or part of which are retained and protected by lignified floral structures or dry fruits. In the study area, bradysporic species retain the diaspores for between 2(3) and 6 months (Navarro et al., 1993).

We considered that species with developed spatial dispersal ability (telechory) are those whose diaspores are equipped with structures that facilitate spatial dispersal, such as flyer structures (pappi, barbs, wings) or fleshy fruits, in accordance with Ellner and Shmida (1981), Venable and Levin (1985), Willson (1993), Cain et al. (2000) and Higgins et al. (2003). We considered species with restricted spatial dispersal (atelechory/antitelechory) those whose diaspores lack of the dispersal-enhancing characters, according to Willson (1993). Species, family, dispersal traits and seasonal diaspore release time are available as a Supplementary electronic file.

### 2.4. Statistical analysis

Separate statistical analyses were carried out for the shrub, forb and grass datasets (McIntyre and Lavorel, 2001). We classified the species into different dispersal strategies using cluster analysis using Ward's method as clustering algorithms (Ward, 1963). A nonlinear principal components analysis (NLPCA, De Leeuw, 1982) was undertaken for comparison and visualization of the results and the identification of the decisive attributes that distinguish dispersal strategies similar to principal components analysis, NLPCA can be used for transforming attributes of a dataset into a new set of uncorrelated attributes (principal components), while still retaining as much of the variability of the dataset as possible. NLPCA can handle variables of different types simultaneously and deal with nonlinear relationships between variables. It is performed by the program CATPCA implemented in the software SPSSv 14.0 (SPSS Inc.). In addition, Cronbach's Alpha (Cronbach, 1951) was calculated for each extracted component. If the Alpha value of a specific component is high, it could be interpreted as indicating that the component has a strong opened dimensional structure, or that the dimension is reliable to account for the total variance. Generally, an Alpha value of 0.7 or greater is considered to be reliable (Bland and Altman, 1997). The association between ordinal traits was determined with a Tau–Kendall test, while the association between nominal traits was determined with the Pearson Chi-square test. All statistical analyses were carried out with SPSS 14. All the original matrices are available on request.

## 3. Results

### 3.1. Dispersal strategies and trait assessment

We distinguished six major shrub dispersal strategies on the basis of cluster analysis (Fig. 1; Appendix 1, electronic version only). The first principal component had high loadings from diaspore morphology, diaspore release mechanism, bradyspory, age of first reproduction, synaptospermy, aerial seed bank and resprouting capacity (Table 1). It separated escape species without bradyspory, such as ballistic shrubs (e.g. *U. baeticus*, DS6) and vertebrate dispersal shrubs (e.g. *Whitania frutescens*, *Lycium intricatum*, DS5), from wind-flyer shrubs with dispersal in time (e.g. *Teucrium* spp.,