

## Seed dispersal spectra of plant communities in the Iberian Peninsula

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### Abstract

We studied the seed dispersal spectra of 46 Iberian plant communities of five types: potential woodland, forest fringe, substitutional scrubland, nitrophile communities and montane communities. There were no significant differences between the spectra of communities of the same type from Mediterranean and Eurosiberian regions. Biotic dispersal is most common at mature stages of succession, and abiotic dispersal at immature stages.

### Introduction

Seed dispersal is one of the central topics of modern plant biology, with numerous implications for the ecology and biogeography of plant communities. As such, there have been studies on the presence of the various types of dispersal in different plant communities (Danserau & Lems 1957; Luftensteiner 1979, 1984) or taxonomic groups (Beattie & Lyons 1975; Van der Pijl 1982), on certain dispersal syndromes (Sorensen 1986; Beattie 1983; Murray 1986; Howe 1986) and on the geographical distribution of such syndromes (Howe & Smallwood 1982; Willson *et al.* 1989, 1990). There is nevertheless little published information on seed dispersal by higher plants in the Iberian Peninsula, and what there is concerns mainly endozoochores (plants with fleshy fruits consumed by vertebrates), especially plants dispersed by birds (Pérez-Chiscano 1983; Herrera 1984; Jordano 1984; Guitián 1984; García & Obeso 1988; Fuentes 1991). In the work reported here, we studied the types of dispersal present in

46 Iberian plant communities with a view to determining the geographical distribution of dispersal syndromes and the relationship between dispersal and successional maturity.

### Methods

We worked with vegetation inventories for 10 regions of the Iberian Peninsula that were judged to be jointly sufficiently representative of the great variety of Iberian vegetation. For each region, we considered five types of community: potential woodland, forest fringe, substitutional scrubland, nitrophile herb communities and montane communities (Fig. 1). In accordance with the terminology of Van der Pijl (1982) and Luftensteiner (1984), we distinguished the following types of dispersal unit: winged anemochorous; villous anemochorous (including all anemochorous units without wings); semachorous, with no special morphology for dispersal; barochorous, with no special morphology for dispersal; autochorous;

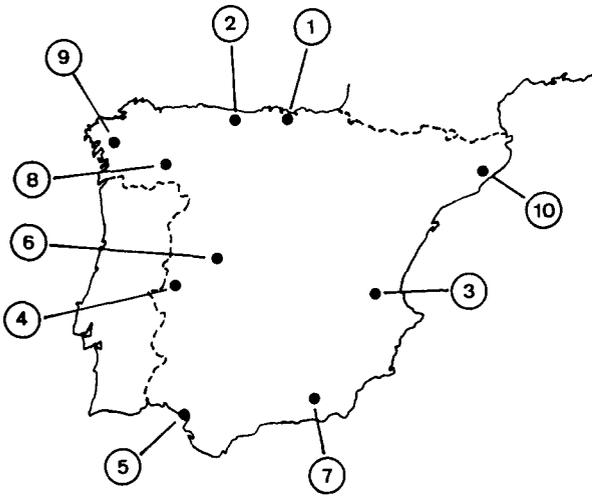


Fig. 1. Sources of data, with references. 1, Basque Country (Onaindía 1986); 2, Asturias, Picos de Europa (Rivas-Martínez & al. 1984); 3, Valencia, Sierra Martes (Figuerola 1983); 4, Cáceres, Monfragüe (Belmonte 1986); 5, Huelva, Doñana (Rivas-Martínez & al. 1980); 6, Avila, Sierra de Gredos (Sánchez-Mata 1986); 7, Granada, Sierra de Baza (Gómez-Mercado & Valle 1988); 8, Mediterranean Galicia (Gutián ined.); 9, Atlantic Galicia (Gutián ined.); 10, Barcelona, Montseny (O. de Bolós 1983).

endozoochorous (mainly ornithochorous); exozoochorous; and myrmecochorous. In this classification based on morphological and functional aspects of the vector, small seed diaspores with no special morphology are grouped, following Van der Pijl (1982), as semachorous rather than anemochorous diaspores; Willson (1990) includes them in her 'no special device' group.

Each species in the inventories was treated as having a single dispersal mechanism, which was assigned on the basis of the work of Luftensteiner (1982), our own field observations and the morphology of the diaspores. Whenever a diaspore might lend itself to more than one type of dispersal mechanism, it was assigned the mechanism we judged to be the predominant one. In the single inventory in which the Braun-Blanquet cover/abundance class '+' appeared, we ignored the accidental species.

The inventories used (some 400 in all, comprising some 5000 records) covered 46 communities. We calculated the dispersal spectrum of each community by expressing the number of species

with each type of dispersal as a percentage of the total number of species present in the community. It should be pointed out that lack of information on the natural history of many plants present may have distorted our analysis somewhat, since our own observations and those of Jordano (unpublished data) suggest that in certain regions of the Iberian Peninsula mechanisms such as myrmecochory have greater importance than is reflected in the present data. In spite of this *caveat*, we believe that the general conclusions drawn from the present study are perfectly valid.

The data were analysed statistically using Wilcoxon's non-parametric test (Siegel 1988). Differences were considered to be significant if  $p < 0.05$  using Bonferroni's modification (Rice 1989).

## Results and discussion

The climatic differences that justify the current division of the Iberian Peninsula in two chorological regions, the Mediterranean and the Eurosiberian, do not greatly affect the dispersal spectra of their plant communities.

For communities of the same kind, the dispersion spectra of those located in the Eurosiberian region are very similar of those of Mediterranean communities (Table 1). The only significant differences concern wing-borne anemochores in forest fringe communities, which make up 5.1% of the species in the Mediterranean region but are absent from Eurosiberian fringes, and myrmecochores in potential woodland, which account for 9.7% of the species in the Eurosiberian communities but only 1.5% in the Mediterranean region. It seems possible that these differences may be due to lack of information on the natural history of many species.

### *Anemochores*

In all the various types of community considered, most anemochores are villous rather than winged (2.9–20.3% as against 1.1–3.2%, with differences of 0.4–17.6%). Villous and winged anemochores

Table 1. Mean prevalence rates of each dispersal mechanism in each type of community, for the Eurosiberian and Mediterranean regions and the whole Iberian Peninsula.

| Eurosiberian  |      |       |       |      |       |       |       |      |
|---------------|------|-------|-------|------|-------|-------|-------|------|
|               | Z    | Y     | X     | V    | U     | T     | S     | R    |
| Woodland      | 4.77 | 3.96  | 42.11 | 8.76 | 4.70  | 22.78 | 3.23  | 9.67 |
| F. fringe     | 0.00 | 4.50  | 28.72 | 9.00 | 2.38  | 52.00 | 1.39  | 0.00 |
| Scrubland     | 0.00 | 5.13  | 59.07 | 1.04 | 13.39 | 11.28 | 1.92  | 8.17 |
| Nitrophiles   | 3.75 | 17.36 | 48.62 | 1.67 | 10.30 | 3.53  | 12.77 | 0.00 |
| Montane       | 0.00 | 1.28  | 68.31 | 0.00 | 9.58  | 18.25 | 0.00  | 2.25 |
| Mediterranean |      |       |       |      |       |       |       |      |
|               | Z    | Y     | X     | V    | U     | T     | S     | R    |
| Woodland      | 1.57 | 4.27  | 41.32 | 6.78 | 8.95  | 34.22 | 1.43  | 1.45 |
| F. fringe     | 5.10 | 1.33  | 25.70 | 2.87 | 6.13  | 54.25 | 2.22  | 1.67 |
| Scrubland     | 2.12 | 8.71  | 61.23 | 5.25 | 9.15  | 10.32 | 1.25  | 0.38 |
| Nitrophiles   | 1.50 | 23.16 | 51.52 | 6.54 | 3.24  | 5.29  | 8.74  | 0.00 |
| Montane       | 4.31 | 18.27 | 52.30 | 0.00 | 7.20  | 11.51 | 5.13  | 0.00 |
| Total         |      |       |       |      |       |       |       |      |
|               | Z    | Y     | X     | V    | U     | T     | S     | R    |
| Woodland      | 3.17 | 4.11  | 41.72 | 7.77 | 6.83  | 28.50 | 2.33  | 5.56 |
| F. fringe     | 2.55 | 2.91  | 27.21 | 5.93 | 4.25  | 54.12 | 1.80  | 0.83 |
| Scrubland     | 1.06 | 6.92  | 60.15 | 3.14 | 11.27 | 10.80 | 1.59  | 4.27 |
| Nitrophiles   | 2.63 | 20.26 | 50.07 | 4.10 | 6.77  | 5.41  | 10.75 | 0.00 |
| Montane       | 2.16 | 9.78  | 60.31 | 0.00 | 8.39  | 14.88 | 2.56  | 1.28 |

Z, winged anemochory; Y, villous anemochory; X, semachory; V, barochory; U, autochory; T, endozoochory; S, exozoochory; R, myrmecochory.

together are most prevalent in nitrophile communities, and least in forest fringe (Fig. 2), the difference being statistically significant.

The various types of community differ with respect to the relative numbers of villous anemochores, but not as regards winged anemochores. Only the prevalence rates observed in nitrophile and montane communities are within the range reported by Willson *et al.* (1990) for temperate zone communities (10–30% of species anemochorous); the prevalence of anemochores is slightly lower in scrubland (8%), and lower still in potential woodland and forest fringe. Our data are nevertheless in keeping with Willson's (1983) conclusion that villous anemochory is more important in open (nitrophile, montane and scrubland)

communities than in closed communities (woodland and forest fringe); Howe & Smallwood (1982) suggested that the prevalence of villous anemochores in closed communities is low because in this situation only arboreal or climbing species can reach the canopy and be efficiently dispersed by wind. In keeping with the findings of Fenner (1985), we found anemochores to be more prevalent in immature communities than in those closer to climax.

#### *Semachores and barochores*

Like anemochores, semachores are less prevalent in potential woodland and forest fringe than in

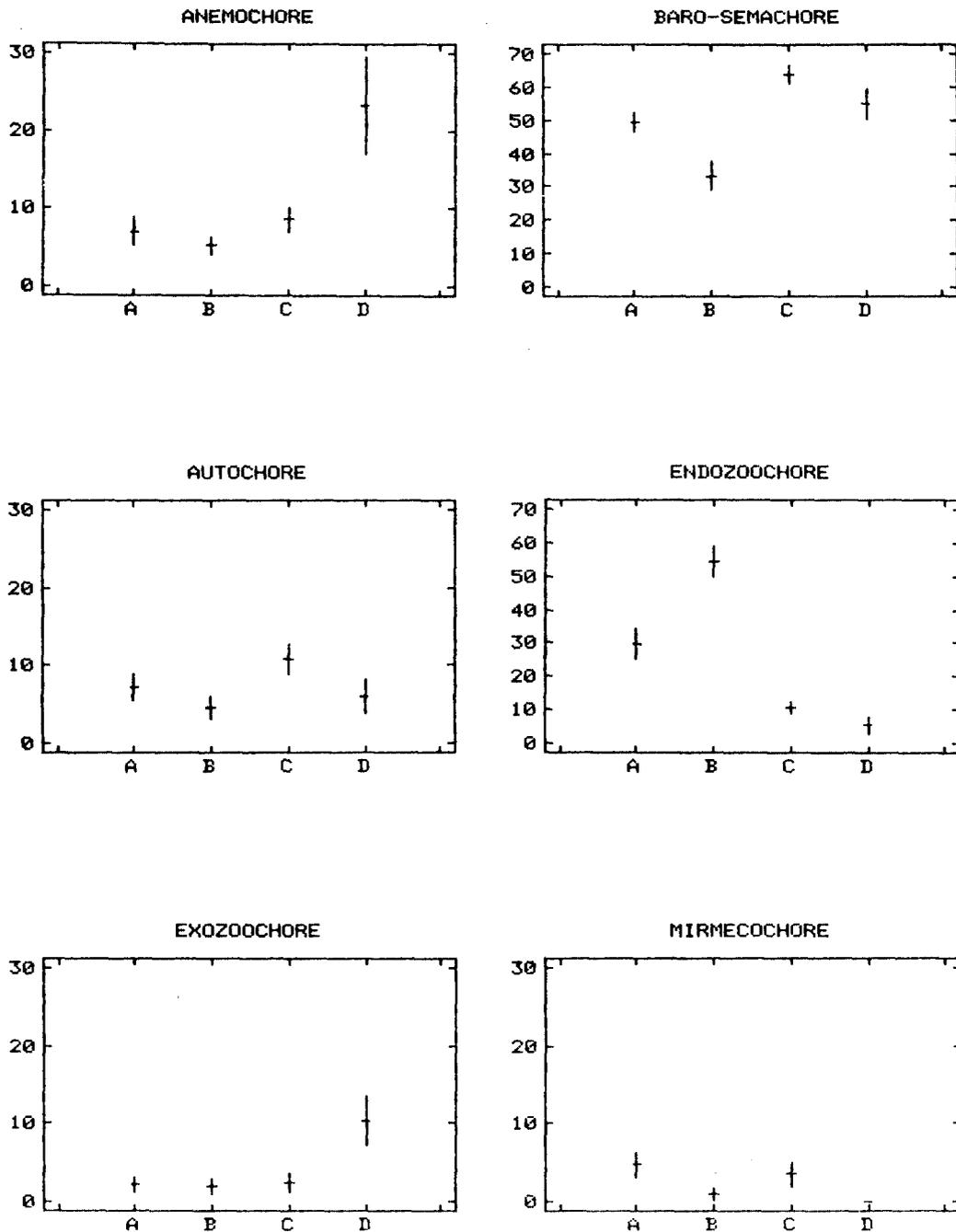


Fig. 2. Mean prevalence of the various dispersal mechanisms considered in each type of community. A, potential woodland; B, forest fringe; C, scrubland; D, nitrophile communities. Vertical bars indicate standard deviations.

the other three types of community considered. Their greatest prevalence, 60.3% is reached in montane communities, followed by scrubland and nitrophile communities. Their prevalence in for-

est fringe was significantly lower than in all the other types of community. Woodland differed significantly from both forest fringe and scrubland in this respect.

Barochores account for fairly similar proportions of the total number of species in all except the montane communities, from which they are absent. Only the difference between their prevalence rates in montane and potential woodland communities is statistically significant. Barochores are included with semachores in Figure 2.

We included in these classes all those plants whose seeds or fruits have no morphological features obviously related to dispersal (unknown dispersal mechanism). It is therefore possible that their prevalence has been overestimated due to the inclusion of anemochores whose only adaptation is the small size of their seeds, zoochores that are transported and stored by animals in spite of having no special adaptation (see Price & Jenkins 1986) and autochores with no evident dispersal mechanism (see Willson *et al.* 1990). It seems unlikely, however, that correction of any error due to such inclusions would alter our findings that semachory is the predominant dispersal mechanism in all types of community except forest fringe, and that these two illdefined dispersal mechanisms are least prevalent in the two most mature communities. The latter result is in keeping with the observations of Gentry (1982) and Luftensteiner (1979), though in the Iberian Peninsula the prevalence of geochores (semachores plus barochores) is anomalously less in forest fringe than in woodland, the prevalence of endozoochores increasing at their expense.

#### *Autochores*

In all five types of community, the prevalence of autochores is medium-to-low (Fig. 2); there are no statistically significant differences among these figures. The maximum of 11.3% attained in scrubland is due to the abundance of autochorous leguminosae.

In agreement with the findings of Willson *et al.* (1990), the prevalence of autochores was fairly uniformly low in all communities (4.3–11.3%), with no significant differences among the various types of community in this respect. Such low fre-

quencies can be attributed to both taxonomic and ecological causes, including the fact that signs of autochory are not always obvious. Our data are more or less in keeping with Ridley's (1930) assertion that autochory is more common among small plants than woody species, the communities in which autochory is most prevalent being predominantly composed of small plants (Fig. 2).

#### *Endozoochores*

Endozoochory is most prevalent in forest fringes, where it clearly predominates, being the mechanism used by 54.1% of species. In woodland it has a significantly lower prevalence rate, 28.5% (Fig. 2). Both these figures differ significantly from those observed in the other communities (5.4–14.9%), except for the difference between the prevalence rates in potential woodland and nitrophile communities, which is not statistically significant.

Like Snow (1971), Howe & Smallwood (1982), Gottsberger (1983), Garcia & Obeso (1988) and Willson *et al.* (1989), we found endozoochory to be significantly more prevalent in woody communities than in others. Our results are also in keeping with those of Willson *et al.* (1989) in that the prevalence rate of endozoochory varied widely, from 5.4% in nitrophile communities to 54.1% in forest fringe. The prevalence of endozoochores tended to increase with the complexity of the vegetation, but peaked in forest fringe communities (i.e. in the first stages of arborization) rather than in woodland itself, which may perhaps be interpreted as supporting the 'directed dispersal' hypothesis (Howe & Smallwood 1982; Howe 1986).

#### *Exozoochores*

The prevalence rate of exozoochores exceeds 3% only in the nitrophile communities, in which it reaches 10.8% (Fig. 2). It is smallest (1.6%) in scrubland. There are no significant differen-

ces among any of the communities in this respect.

Like Willson *et al.* (1990) and Sorensen (1986), we found the prevalence of exozoochory to be low in all the types of community considered, in keeping with the small percentage of exozoochorous taxa in the flora as a whole (10% of all families, and less than 5% of angiosperm species; see Sorensen 1986). Most exozoochores are herbaceous (Rockwood 1985), generally with heights of 1 m or less (Sorensen 1986), which tends to maximize the number of their contacts with dispersal vectors (Hawthorn & Hayne 1978; Lacey 1981; Sorensen 1986); these characteristics are typical of the communities that we, like Sorensen (1986), found exozoochores to be most prevalent in, the nitrophile communities.

### *Myrmecochores*

The proportion of species dispersed by ants ranges from a maximum of 5.6% in potential woodland to zero in nitrophile communities (Fig. 2); these two communities are the only pair differing significantly in this respect.

In keeping with the literature (Willson 1983; Willson *et al.* 1990), the prevalence of myrmecochores was low in all the communities studied. Though myrmecochory is both geographically and taxonomically widespread (Beattie 1983), both for primary dispersal and for secondary dispersal of seeds that have already been disseminated by other means, these low rates are probably in part due to lack of information on whether many taxa are myrmecochorous or not (Willson *et al.* 1990). Worldwide, myrmecochory appears to be most prevalent among communities established on poor soils (Willson *et al.* 1990).

### Conclusions

The salient features of the above results are as follows.

- 1) for communities of a given type, the dispersal spectra of communities from Mediterranean and Eurosiberian regions are similar.
- 2) In most types of community, the majority of seeds is classified to semachory/barochory (unknown dispersal mechanism). Its estimated degree of prevalence may in future fall as more is learnt of the less obvious dispersal mechanisms.
- 3) The prevalence of biotic dispersal increases as the climax vegetation is approached; abiotic dispersal is most prevalent at immature stages of succession.
- 4) In view of the foregoing, the differences among the dispersal spectra of the various types of community cannot be wholly explained in geographical or successional terms; it is also necessary to consider phylogenetic and ecological factors such as diaspore characteristics or the availability of dispersal vectors.

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## Appendix 1. Communities considered, numbered as in Figure 1.

### Woodlands

1. *Tamo-Quercetum roboris*
2. *Carici sylvaticae-Fagetum*
3. *Violo-Quercetum rotundifoliae*
4. *Pyro-Quercetum rotundifoliae*
5. *Oleo-Quercetum suberis*
6. *Luzulo-Quercetum pyrenaicae*
7. *Paeonio-Quercetum rotundifoliae*
8. *Genisto-Quercetum rotundifoliae*
9. *Rusco-Quercetum roboris*
10. *Brachypodio-Fraxinetum excelsioris*

### Forest fringes

1. *Berberidion*
2. *Pruno-Berberidetum cantabricae*
3. *Rosetum micrantho-agrestis*

4. *Lonicero-Rubetum ulmifolii*
5. *Lonicero-Rubetum ulmifolii*
6. *Rubo-Rosetum corymbiferae*
7. *Lonicero-Berberidetum hispanicae*
8. *Rubo-Rosetum corymbiferae*
9. *Pruno-Rubion ulmifolii*
10. *Rubo-Coriarietum myrtifolii*

#### Scrublands

1. *Daboecio-Ulicetum galli*
2. *Lithodoro-Genistetum occidentalis*
3. *Thymo-Cistetum landaniferi*
4. *Lavandulo-Cistetum albidii*
5. *Erico-Ulicetum australis*
6. *Halimio-Cistetum psilosepali*
7. *Halimio-Cistetum laurifolii*
8. *Cisto-Genistetum hystricis*
9. *Ulici-Ericetum cinereae*
10. *Violo-Callunetum vulgaris*

#### Nitrophyle communities

1. *Carduo-Cirsietum richteriani*
2. *Chenopodio-Senecietum durieui*
3. *Carduo-Sylibetum mariani*
4. *Verbasco-Onopordetum illyrici*
5. *Scolymo-Silybetum mariani*
6. *Urtico-Sambucetum ebuli*
7. *Medicago-Aegilopetum geniculatae*
8. *Carduo-Silybetum mariani*
9. *Coleostepho-Galactitetum tomentosae*
10. *Arctio-Urticetum dioicae*

#### Montane communities

1. *Agrostidi-Festucetum gautieri*
2. *Daphno-Arctostaphylletum uva-ursi*
6. *Junipero-Cytisetum oromediterranei*
7. *Genisto-Juniperetum nanae*
8. *Junipero-Vaccinietum uliginosi*
10. *Genisto-Arctostaphylletum uva-ursi*