

# Geographical variation in diaspore traits of an ant-dispersed plant (*Helleborus foetidus*): are ant community composition and diaspore traits correlated?

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## Summary

**1** We explored geographical variation in the interaction between the elaiosome-bearing seeds of *Helleborus foetidus* and ant dispersers. We looked for correlation across nine Iberian localities, between diaspore traits and structural and functional characteristics of ant communities.

**2** Mean diaspore traits did not show a distance-dependent pattern. Seed size-related traits (length, width, diaspore mass and seed mass) varied mostly among localities and ant reward-related traits (elaiosome mass and elaiosome to seed mass ratio) mainly within plants.

**3** Ant communities showed distance-dependent patterns in composition and abundance. Almost all ant species responded positively to diaspore offerings and preferred seeds with elaiosomes. The extent of the preference differed among species and was affected by ant size. Ant size was however, similar in almost all localities and the quality of the disperser guild, estimated as the ant response to seed offerings, did not vary.

**4** We found a large-scale lack of adjustment: seed traits could not be predicted from ant community composition or geographical distance. Nor could structural and functional ant community parameters explain variation in seed traits.

**5** Comparison of ant sizes, position on a Principal Components Analysis of seed traits, and indirect estimates of dispersal success, suggests that there is a mosaic of well-matched and mismatched situations which probably obscures the overall relationships among seed traits and ant assemblages. This is consistent with the role proposed for the geographical structure of interactions in recent coevolutionary theories.

*Key-words:* ant communities, ant–seed dispersal mutualism, elaiosome, geographical variation, *Helleborus foetidus*, seed size

*Journal of Ecology* (2002) **90**, 446–455

## Introduction

Ecologists have studied the mutualisms underlying the dispersal of seeds by ants since Sernander (1906) first described myrmecochory. An attached elaiosome, which attracts ants, is removed in the nest, leaving the seed dispersed and undamaged (Beattie 1985). Research has concentrated on the selective advantage of being dispersed by ants (Culver & Beattie 1978; Beattie 1985; Bond & Stock 1989) and, more recently, on the immediate consequences of this interaction for

plant recruitment (Hughes & Westoby 1992a; Levey & Byrne 1993; Horvitz & Schemske 1994).

Variation in diaspore (seed plus elaiosome) traits has been studied for some ant–seed interactions at both the intraspecific (Mark & Olesen 1996) and interspecific level (Hughes & Westoby 1992b; Byrne & Levey 1993; Gorb & Gorb 1995), and several assemblages of ant dispersers have been characterized (Beattie & Culver 1981; Wolff & Debussche 1999). However, multipopulation studies of the strength and direction of the selective pressures exerted, which are necessary to evaluate intraspecific and geographical variation of the interaction throughout a plant's range, have not been carried out. The generalist nature of this type of plant–animal

**Table 1** Location and description of study sites

Locality	Mountain range	Elevation	Geographical co-ordinates	Habitat type
Caurel Scrubland (CS)	Sierra del Caurel (NW Spain)	1150	42°39' N, 7°7' W	<i>Brachypodium sylvaticum</i> open scrubland pasture
Caurel Forest (CF)	Sierra del Caurel (NW Spain)	1200	42°39' N, 7°7' W	<i>Castanea sativa</i> forest
Roblehondo (RH)	Sierra de Cazorla (SE Spain)	1270	37°56' N, 2°52' W	<i>Pinus</i> forest
Correhuelas (CH)	Sierra de Cazorla (SE Spain)	1600	37°55' N, 2°50' W	<i>Pinus</i> forest
Collado de Góntar (CG)	Sierra de Segura (SE Spain)	1550	38°16' N, 2°32' W	Mediterranean open scrubland
Mágina Scrubland (MS)	Sierra Mágina (SE Spain)	1650	37°44' N, 3°28' W	Mediterranean open scrubland
Mágina Forest (MF)	Sierra Mágina (SE Spain)	1440	37°43' N, 3°30' W	<i>Quercus</i> forest
Sierra Nevada (SN)	Sierra Nevada (SE Spain)	1300	37°10' N, 3°28' W	Riverside open scrubland pasture
Sierra de Baza (SB)	Sierra de Baza (SE Spain)	1200	37°24' N, 2°51' W	<i>Pinus</i> forest

interaction, is shown by the variety of ants carrying elaiosome-bearing seeds whatever the vegetation type considered (reviews in Buckley 1982 and Hölldobler & Wilson 1990; see also Wolff & Debussche 1999) and, since the disperser guild will probably vary considerably, geographical variation is therefore likely to be important.

The evolution of such interactions cannot be fully understood without knowledge of spatial and temporal variation of the resultant selection pressures (Thompson & Pellmyr 1992; Thompson 1994; Travis 1996; Brody 1997; Gómez & Zamora 2000), since this could either limit or enhance the degree to which plant species may become adapted to their mutualists. Morphological matching between elaiosome-bearing seed traits and ant traits would be expected if ants effectively exert selection on propagule traits and, if different ants select for different traits or act on the same traits in different ways, then changes in ant composition would result in changing selective pressures. Population divergence might therefore be detected if matching is evaluated at large spatial scales.

We explore such variation in the interaction between the elaiosome-bearing seeds of *Helleborus foetidus* and their ant dispersers. More specifically, we investigate a number of *H. foetidus* populations from across its geographical range to determine the relationship between morphological characteristics of their diaspores and the structural and functional characteristics of their associated ant communities. Three specific questions are addressed. (i) Do *H. foetidus* diaspores show geographical variation in size, shape and elaiosome to seed mass ratio of *H. foetidus* diaspores? (ii) Do the abundance and species composition of local ant communities vary among *H. foetidus* populations and, if so, does this have consequences for dispersal? (iii) Is diaspore variation correlated with dispersal-related characteristics of the ants?

## Materials and methods

### STUDY SYSTEM AND SITES

*Helleborus foetidus* L. (Ranunculaceae) is a rhizomatous perennial herb distributed across Western Europe



**Fig. 1** Location of study sites. Abbreviations for locations are given Table 1.

(Werner & Ebel 1994). Details of the floral biology of the species in the Iberian Peninsula, where it appears in the understorey of deciduous and mixed forests, in patchy scrub and ruderal habitats, can be found in Herrera *et al.* (2001). Flowers have 1–5 carpels (most commonly 2–3), each of which develops 10–12 elaiosome-bearing seeds. Dehiscing from the end of June to early July releases these diaspores and many potential ant dispersers are attracted. Although rodents consume *H. foetidus* seeds, ant removal probably prevents this loss being substantial.

The study was conducted in 1998 and 1999 at nine sites (see Table 1 and Fig. 1), selected to represent the whole altitudinal range and almost the whole latitudinal distribution of this species in the Iberian Peninsula. A range of habitats and of ant communities are represented with distances between sites ranging from 3 to 690 km.

### SEEDS

At each study site, we collected 25 diaspores from dehiscing carpels of each of 17–20 plants. After measuring the length and width of each seed (i.e. disregarding the elaiosome), diaspores were dried during 10 days at 60 °C and dry mass determined for the whole diaspore and for the seed alone. We calculated elaiosome mass (an absolute measure of ant reward) and the ratio of elaiosome to seed mass (reward relative to the effort that ants must invest in carrying a seed).

## ANTS

Pitfall traps were regularly distributed in each locality (six along each of four transects) using cylindrical plastic vials (7 cm wide, 9 cm deep) half-filled with water and detergent and buried level with the soil surface. Ants were collected over a 24-h period as the carpels started to dehisce, and were taken to represent potential dispersers. Ant communities were characterized by species composition, diversity ( $H'$  Shannon index), richness (total number of species in each locality,  $S'$ ) and evenness ( $J$ ).

Head width, distance between mandible insertions, and the maximum width of the open mandibles of the ants were measured using a dissection microscope with micrometer. Only species accounting together for at least 80% of total captures at a locality were measured (10 individuals per species). Since the three variables were strongly correlated across species (Pearson's  $r = 0.81$ ,  $P < 0.01$ ,  $N = 36$ , for all the trait pairs and species), we used mean head width as an indicator of species-specific ant size (AS). Species-specific AS values were weighted by relative abundance in a locality to give a community-level AS for that site.

To evaluate whether a particular ant species was likely to carry the diaspores, seeds, with and without elaiosomes, were offered in the field to each of the abundant species at that site. A positive response was recorded when an ant collected and carried the diaspore (i.e. a dichotomous variable viewed from the perspective of seed dispersal rather than of ant behaviour). Species-specific ant response (AR) is defined as the proportion of offerings of seeds with elaiosomes to that species which elicited a positive response. Species-specific AR was weighted by relative abundance to give the probability of a positive response when a seed is offered to a randomly selected ant at a particular locality (community-level AR). In the absence of information on the fate of the seeds carried by each species, this is our most reliable estimate of the quality of the local disperser guild. We assume that success at the population level also depends on absolute disperser abundance at each locality and therefore we used the product of abundance and community-level AR as an indirect estimate of local dispersal success.

## DATA ANALYSES

*General aspects*

Between-localities pairwise matrices were obtained for geographical distance (MGeog), Mahalanobis distance on seed traits (MSeed), Euclidean distance on ant communities (MAnt-comm), dissimilarity in community-level AS (MAnt-size), and dissimilarity in community-level AR (MAnt-resp). Dissimilarity distances were transformed to Euclidean distances by applying Orloci's Method (Sneath & Sokal 1973).

We first analyse variation among localities in a target variable before testing for a significant distance-dependent pattern with Mantel's permutation test (Manly 1997; 5000 iterations) that correlates a between-localities pairwise matrix of a target variable with MGeog. Finally, when applicable, we look for evidence of geographical correlation between seed and ant traits.

Except for analyses of metric seed traits, which met the normality criterion, most of the analyses of variation among localities were conducted with Generalized Linear Models. We used the VGLZ Module of STATISTICA (StatSoft 2000). Rather than applying the canonical link function for each distribution, we tried all link functions applicable to the data under consideration choosing the one that minimized the deviance of the model (see Herrera 2000).

*Seeds*

Both univariate and multivariate tests were performed to explore variation in seed traits among *H. foetidus* populations. Plant was nested within locality, being both considered random effects and residuals determining the within-plant effect. Data were analysed using the SAS MIXED Procedure (SAS Institute 1999).

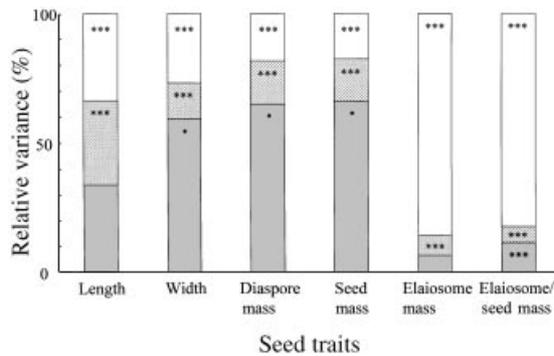
We explored patterns of covariation between seed length and width (both log transformed) among populations, among plants, and within plants. The SAS MIXED procedure was used to conduct an ANCOVA with logarithm of length as the dependent variable, and locality, width  $\times$  locality, and width  $\times$  plant as random factors.

Ants probably perceive traits in combination rather than individually and a multivariate analysis, using means of seed traits per plant, was therefore used to provide a between-locality pairwise Mahalanobis distance matrix on seed traits (MSeed). To avoid redundancy among traits, only length, width, seed mass, and elaiosome mass were considered in this analysis. We further conducted a Principal Components Analysis (PCA) to explore whether localities were segregated, without any a priori criteria, based on the seed traits.

*Ants*

To explore variation among localities in mean ant size, i.e. variation in community-level AS, we performed an ANOVA with the species-specific ant size as the dependent variable and the relative abundance of each species in each locality as a weighting variable.

We analysed ant response to seed offerings with a Generalized Linear Model considering a binomial response. We explored: the species-specific response, the overall response according to the ant species and to the presence or absence of elaiosome, differences among localities in ant response by using community-level AR as dependent variable, and the influence of ant size on ant response.



**Fig. 2** Variance of seed and diaspore traits accounted for Residual (within plant □), Plant (▨) and Locality (■) effects (for each component, \* $P < 0.05$ ; \*\*\* $P < 0.001$ ).

#### Relationship between ant community composition and seed traits

The correlation between MAnt-comm, MSeed and MGeog was analysed using the extension of the Mantel's test to three matrices (Manly 1997). This analysis is conceptually similar to a multiple regression analysis. We used MSeed as the dependent variable and MAnt-comm and MGeog as predictors.

The relationship between seed traits and ant communities (disregarding geographical distance) was further examined by fitting multiple and/or simple regression models to population means and coefficients of variation of seed size, elaiosome mass and ratio of elaiosome to seed mass (representing seed bulk, absolute reward and relative reward for the ants, respectively). Coefficients of variation were considered because large variation within plants and within localities was found (see Results). Separate analyses for each dependent variable were conducted with three groups of predictor variables: ant community structure parameters, community-level AS and community-level AR. Seed size in these analyses was represented by seed mass. To improve the accuracy of these models, which only include nine cases (or localities), we conducted bootstrap estimates (bias-corrected percentile limits, Manly 1997) of the regression coefficients and their 95% confidence limits. These regressions were conducted with SAS REG procedure (SAS Institute 1999) and the bootstraps with SAS JACKBOOT Macro (SAS Institute 1999).

## Results

### SIZE, SHAPE AND REWARD OF THE SEEDS

Diaspores differed considerably both among and within plants and, except for seed length and elaiosome mass, between localities (Fig. 2). Absolute variation for mean seed traits per plant ranged between 3.48 and 5.13 mm for length, 1.42–2.44 mm for width, 5.13–18.55 mg for diaspore mass, 4.57–17.46 mg for seed mass, 0.40–1.52 mg for elaiosome mass, and 0.03–0.16 mg for elaiosome to seed mass ratio. Locality

**Table 2** ANCOVA results of the seed shape analysis obtained by the MIXED procedure (SAS Institute 1999) using LogLength as dependent variable

Random effects	Z	P
Locality	1.68	0.0923
LogWidth × Locality	1.54	0.1231
LogWidth × Plant (Loc)	8.64	0.0001
Error	45.37	0.0001

Fixed Effect (Cov.)	NDF	DDF	F	P
LogWidth	1	8	80.98	0.0001

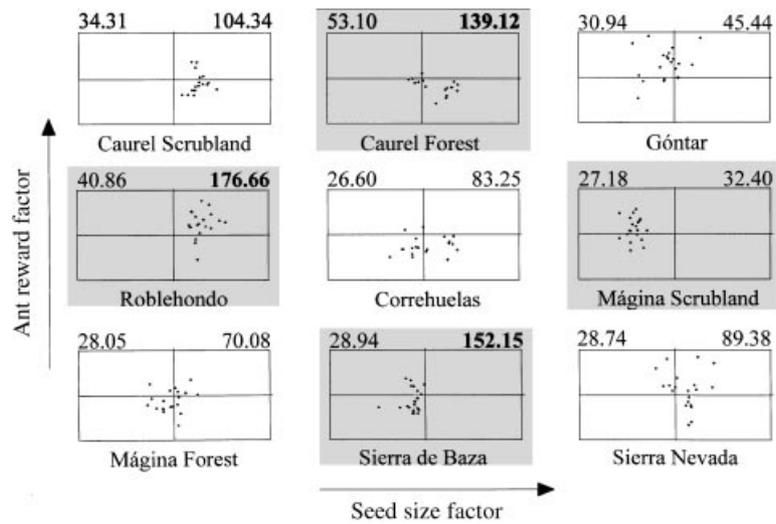
usually explained most variation in seed size traits (width, mass), but within-plant variation was critical for ant reward (elaiosome mass and elaiosome to seed mass ratio) and among-plant effects were always small (Fig. 2). Shape varied among plants within locality but not between localities (interactions in Table 2). MSeed and MGeog matrices were not significantly correlated, indicating a lack of any distance-dependent pattern in mean seed traits (Mantel test,  $r = 0.008$ ,  $P = 0.5$ ).

Principal components analysis on plant means indicated that a seed size component (correlated with length, width, seed mass and diaspore mass) explained 67% of the variation in diaspore traits and a second, ant-reward component (correlated with elaiosome mass and elaiosome to seed mass ratio) accounted for a further 25%. Plots of PCA scores for individual plants (Fig. 3), showed within-site variation, but separated Caurel forest, Caurel scrubland, and Roblehondo which had heavy seeds (and at Caurel, small rewards), from Sierra de Baza, Góntar and Mágina forest and scrubland (small seeds and, at Góntar and Mágina scrubland, high rewards). Interestingly, at many sites one of the two axes accounted for most of the variation, e.g. size varied at Correhuelas but reward was always low, compared with variable reward in the large seeds at Sierra Nevada.

Mahalanobis distances between localities (reflecting differences in seed traits) indicate that seed traits can be similar in both distant (e.g. Correhuelas and Caurel forest: Mahalanobis distance = 0.82, geographical distance = 640 km) and nearby localities (e.g. Caurel forest and Caurel scrubland: Mahalanobis distance = 1.48, geographical distance = 4 km) but dissimilarity is also possible (e.g. Caurel Scrubland and Mágina Scrubland: Mahalanobis distance = 30.19, geographical distance = 627 km, and Mágina Scrubland and Roblehondo: Mahalanobis distance = 28.96, geographical distance = 63 km).

### ANT COMMUNITY COMPOSITION

Overall, 36 ant species were trapped. Species richness, diversity and composition differed between sites (see Appendix 1) and correlation between MAnt-comm and MGeog (Mantel test,  $r = 0.69$ ,  $P = 0.006$ ) indicates that variation in community composition depended on



**Fig. 3** Factor scores for the two Principal Components generated from the analysis of seed traits for plants at different localities (all at the same scale). Local dispersal success (high values in bold type) and community-level ant size are shown for each locality. Sites where ant and seed traits are well matched are shaded.

**Table 3** Ant species-specific response to seed offerings. Proportion of positive responses to seeds with and without elaiosome are shown, together with the results of the Generalized Linear Model to test for differences in the response of each species to seeds with and without elaiosomes. Numbers in parentheses refer to species used in Fig. 4

Species name	Seeds with elaiosome	Seeds without elaiosome	Wald's Chi-squared	P
<i>Aphaenogaster iberica</i> (12)	0.85	0.44	8.30	0.0039
<i>Aphaenogaster senilis</i> (17)	0.85	0.10	25.44	0.0001
<i>Cataglyphis velox</i> (19)	0.92	0.18	38.68	0.0001
<i>Crematogaster scutellaris</i> (13)	1.00	0.00	55.45	0.0001
<i>Crematogaster sordidula</i> (3)	0.00	0.00	–	–
<i>Formica cunicularia</i> (14)	0.78	0.05	27.00	0.0001
<i>Formica decipiens</i> (15)	0.56	0.10	10.92	0.0009
<i>Formica lugubris</i> (18)	0.80	0.25	14.17	0.0001
<i>Formica rufibarbis</i> (16)	0.20	0.025	9.53	0.002
<i>Lasius niger</i> (7)	0.75	0.00	30.43	0.0001
<i>Leptothorax unifasciatus</i> (2)	0.00	0.00	–	–
<i>Messor capitatus</i> (20)	0.85	0.76	0.55	0.4562
<i>Myrmica aloba</i> (9)	0.95	0.67	6.55	0.0104
<i>Myrmica scabrinodis</i> (10)	1.00	0.00	31.77	0.0001
<i>Myrmica sabuleti</i> (11)	1.00	0.00	55.45	0.0001
<i>Pheidole pallidula</i> (5)	0.64	0.04	23.03	0.0001
<i>Plagiolepis pygmaea</i> (1)	0.00	0.00	–	–
<i>Tapinoma erraticum</i> (6)	0.67	0.00	29.11	0.0001
<i>Tapinoma nigerrimum</i> (4)	0.50	0.00	20.92	0.0001
<i>Tetramorium caespitum</i> (8)	0.90	0.00	40.83	0.0001

distance. Communities differed in the mean size of the ants ( $F_{8,45} = 2.16$ ,  $P < 0.05$ ), although SNK post hoc comparisons showed that this was due to bigger values in Caurel Forest than in any of the other localities ( $P < 0.001$ ), which did not differ. Weighted means (i.e. community-level AS) ranged between 53.10 mm in Caurel Forest and 26.62 mm in Correhuellas. A marginally significant distance-dependent pattern in ant size was detected (Mantel test,  $r = 0.368$ ,  $P = 0.08$ ).

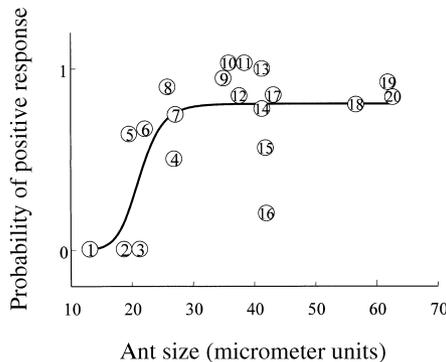
SEED OFFERINGS

All ant species that responded positively to the offerings were significantly more likely to respond to seeds with elaiosomes, except for *Messor capitatus* (Table 3),

and species, elaiosome, and their interaction all affected this proportion (Table 4). Although there was a significant, positive effect of ant size (Wald's  $\chi^2 = 11.249$ ,  $P = 0.0007$ ), species capable of carrying seeds (all except the three smallest; *Plagiolepis pygmaea*, *Crematogaster sordidula*, and *Leptothorax unifasciatus*), collected the majority of seeds offered (Fig. 4). At the community level, localities did not differ significantly in the proportion of positive responses (Wald's  $\chi^2 = 6.43$ ,  $P = 0.602$ ), although closer locations had more similar probabilities of a seed being carried when found (Mantel test:  $r = 0.385$ ,  $P = 0.0129$ ). The index of local dispersal success was extremely variable, ranging between 32.4 in Mágina scrubland and 176.7 in Roblehondo.

**Table 4** Factors affecting the ant response analysis

Source	d.f.	Log-likelihood	Chi-squared	<i>P</i>
Species	15	-465.41	114.41	< 0.0001
Elaiosome	1	-317.04	296.72	< 0.0001
Species × Elaiosome	8	-269.88	94.31	< 0.0001



**Fig. 4** Species-specific response to seed offerings as a function of the species-specific ant size (1 micrometer unit = 0.03125 mm). A logistic regression is fitted to the data ( $F_{2,17} = 9.53$ ,  $P = 0.0017$ ;  $r = 0.73$ ). (See Fig. 4 for species corresponding to each number).

#### RELATIONSHIPS BETWEEN ANT COMMUNITY COMPOSITION AND SEED TRAITS

The model predicting seed traits as a function of similarity in ant community composition (MAnt-comm) and geographical distance (MGeog) was not significant, nor did any of the independent variables explain the pattern of seed traits ( $P = 0.38$  for MGeog, and  $P = 0.53$  for MAnt-comm). Relationships between three seed traits and four ant community characteristics, irrespective of geographical distance between localities (Fig. 5) showed only three significant regressions (two for elaiosome mass and one for the elaiosome to seed mass ratio). The probability of obtaining by chance three significant relationships out of 24 possible is 0.15 (according to binomial probability distribution) and we cannot therefore rule out this option.

#### Discussion

##### PATTERNS OF VARIATION IN SEED TRAITS

Ant-dispersed plants largely rely on elaiosomes for seed dispersal (Van der Pijl 1982; Beattie 1985). Interspecific differences in a variety of diaspore traits have been related to attractiveness (Hughes & Westoby 1992b; Gorb & Gorb 1995) but data on intraspecific variation are scarce (but see Mark & Olesen 1996). Absolute reward for ants (elaiosome mass), relative reward (elaiosome to seed mass ratio), or total amount of bulk to be transported (seed mass), which vary within or among populations, as found in this study, must account for intraspecific patterns.

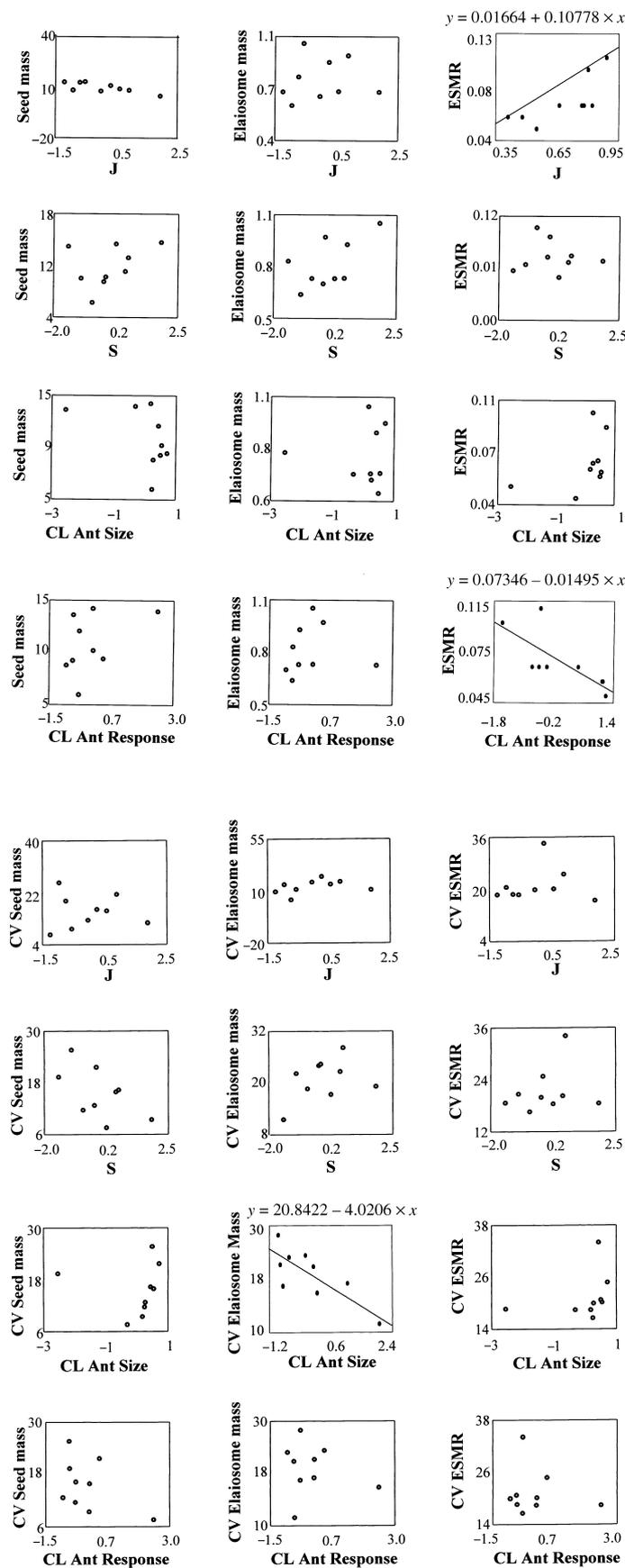
Seed mass is also frequently recognized as a fundamental trait determining the future survival of seedlings (Jurado & Westoby 1992; Saverimuttu & Westoby 1996; Eriksson & Eriksson 1998; Walters & Reich 2000). Diaspore traits may therefore be classified as related to ant reward (dispersability) and related to size (survival). The partitioning of variance of *H. foetidus* diaspore traits clearly differed between ant reward-related traits (variability in elaiosome mass and elaiosome to seed mass ratio occurred mostly within plants) and size-related traits, where among-locality differences may reflect possible divergence in seed size. Elaiosome mass did not differ among localities, and seed mass is therefore the main determinant of both relative reward and total ant load. The elaiosome-bearing seeds of *H. foetidus* thus differ somewhat from other types of seeds, where variation in seed size is often less pronounced among plants within the same population and within individual plants (e.g. Thompson 1984; Thompson & Pellmyr 1989; Obeso 1993; Méndez 1997; Vaughton & Ramsey 1997, 1998).

Principal component analysis (Fig. 3) clearly segregates localities according to seed size and ant reward factors. Interestingly, the upper left quadrant in the PCA (corresponding to the most suitable diaspores for the ants) is often empty for several localities, suggesting a trade-off between seed mass and elaiosome mass i.e. survival (providing resources for future growth) vs. dispersability (Ganeshiah & Uma Saanker 1991; Greene & Johnson 1993; Morse & Schmitt 1995). In some localities *H. foetidus* diaspores may be responding mainly to ant dispersal selective pressure by reducing seed mass, whereas in others different factors control the allocation of resources into the diaspore.

Pairwise comparisons of localities (Fig. 3 and analyses of Mseed) suggest the existence of a large scale mosaic for diaspore traits, with similarity unrelated to distance.

##### PATTERNS OF VARIATION IN ANT COMMUNITY COMPOSITION AND FUNCTION

Ant community composition varied considerably across the broad range of ecological conditions studied. There was a broad-scale distance-dependent pattern so that, for instance, typical Central European ants like *Myrmica scabrinodis* and *Formica lugubris* appeared only in some of the northern populations, but differences in habitat and/or vegetation type also contribute to create variation at smaller spatial scales (Wolff & Debussche 1999; Retana & Cerdá 2000), as between adjacent sites such as Caurel Forest and



**Fig. 5** Scatter-plots of seed traits (mean values and coefficients of variation) vs. ant community parameters (Evenness, *J* and Richness, *S*), and Community-level (CL) ant size (CL Ant Size) or response. ESMR indicates elaiosome to seed mass ratio. Bootstrap estimates of linear regression models were fitted to each scatter-plot but only significant regressions (i.e. those where the 95% confidence interval generated by bootstrapping did not include 0) are shown.

Caurel Scrubland. Combination of these two patterns creates a complex large-scale mosaic.

Almost all ant species responded positively to seed offerings and preferred seeds with elaiosomes (see also Wolff & Debussche 1999), and could therefore affect the ant-seed interaction. This preference was more marked in larger species (Gorb & Gorb 1995), although many of the smaller species carried more than 50% of the diaspores offered, and could therefore be effective dispersers. Given the positive influence of ant size on the response to diaspore, ant size at the community level could influence *H. foetidus* dispersal. Although average species size in the ant assemblage tends to increase with increasing latitude (Cushman *et al.* 1993) over much of Europe, only one of our localities had a significantly different average size and, furthermore, this parameter was not distance-dependent.

Do any differences in ant community composition translate into differential dispersal probabilities for *H. foetidus*? Local dispersal success, as estimated here (Fig. 3), suggests that dispersal probabilities will vary greatly, but this was due to differences in the absolute abundance of ants rather than in species composition. Thus community-level AR did not vary, showing that, once found, the probability of a seed being dispersed was independent of the substantial variation in ant community composition. Differences in community composition do not therefore necessarily result in functional differences in the quality of the disperser guild of *H. foetidus* diaspores.

#### RELATIONSHIPS BETWEEN ANT COMMUNITIES AND DIASPORE TRAITS: EVOLUTIONARY REMARKS

Local matching between animal and plant traits has generally been considered to be evidence of evolutionary adjustment between the interactors. However, recent formulations of the coevolutionary theory (Thompson 1994, 1997, 1999) have emphasized the role of the geographical structure of the interactions. Following this recent view, we have tested for correlation between the geographical variation in diaspore traits and dispersal-related characteristics of the local ant communities.

The absence of such a relationship found in this study was partially expected from the lack of distance-dependent variation in diaspore traits, although distance-independent matching may still occur. Seed size was the most variable, and therefore most selectable, trait in a broad geographical context but, as expected from a functional equivalence in disperser assemblages (Zamora 2000), mean local seed mass was not significantly related either to ant community structure, ant size at the community level, or ant response to diaspore at the community level (Fig. 5).

The general absence of relationships in this study shows that the spatial mosaic in seed traits of *H. foetidus* does not match with that of ant communities, but

recent theory (Thompson 1994, 1997, 1999) does not require, or even predict, that any specific interaction should generally show accurate matching. Instead a geographical mosaic of mismatched and well-matched situations will result from local selective forces and also, to some extent, from gene flow and genetic drift. Then, could the large-scale lack of adjustment reflected in this study be a consequence of such a mosaic? Our results suggest that this could be the case here: only at some sites is community-level AS correlated with their relative position in the PCA (Fig. 3). Thus Mágina Scrubland and Sierra de Baza, with relatively small ant sizes and small seeds, and Roblehondo and Caurel Forest, with the largest community-level AS and dominated by large-seeded plants, are well matched, unlike any of the other sites. In particular, Caurel Scrubland, one of the northern populations, and Sierra Nevada tend to have large seeds and medium to small ants. The mosaic pattern thus probably obscures any large-scale adjustment.

Well-matched situations may be interpreted as resulting from the selective pressures by the ant assemblage or, in contrast, from random variation in space of diaspore traits and ant assemblages. Most of the good matches (Caurel Forest, Sierra de Baza, and Roblehondo) also have high dispersal success, compared to lower values in mismatches (e.g. Sierra Nevada, Correhuelas) (Fig. 3) and may indicate the operation of selective pressure rather than independent random variation in seed traits and ant communities.

This study represents a first step in establishing the coevolutionary potential of the interaction between *H. foetidus* and its ant dispersers by studying its geographical structure. The study system potentially reflect a selection mosaic, where distance-dependent patterns are rare and where matching patterns are not established on a species by species basis (as suggested by Thompson 1994). Instead, habitat type, which strongly influences ant community composition and abundance, and the functional equivalence of the disperser assemblages (Zamora 2000) play more important roles.

Results of this study also suggest that close adjustments between plant and animal communities may not be apparent across multiple sites, because interactions may take different directions in different localities or even because at many localities such an adjustment may not occur. Thus, findings based on one or few localities can lead to erroneous conclusions about the evolution of the interactions (Travis 1996; Thompson 1999).

#### Acknowledgements

The authors thank A. Tinaut for generously determining ant species and J. M. Gómez for facilitating information about Sierra de Baza and Sierra Nevada. J. Guitián and M. Medrano provided housing facilities and helped us with the field work in Caurel. We also benefited from the technical support and/or field assistance

of A. M. Sanchez-Lafuente, R. Requerey, A. Manzaneda, J. Garrido and M. C. Anguita. We thank the Junta Rectora of Sierra de Cazorla, Segura y Las Villas and Sierra Mágina Natural Parks for providing working facilities. This study was supported by grant PB96-0856 from the Dirección General de Enseñanza Superior e Investigación, Ministerio de Educación y Cultura.

### Supplementary material

The following material is available from <http://www.blackwell-science.com/products/journals/suppmat/JEC/JEC680/JEC680sm.htm>

**Appendix 1** Ant community composition (number of ants of each species trapped in pitfall), ant community structure (diversity, evenness and richness indices), and ant-seed relationship parameters (community-level ant size and community-level ant response). Numbers in brackets referred to species used in Fig. 4.

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Received 22 May 2001

revision accepted 20 November 2001