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Dispersal mechanisms of the narrow endemic *Polygala vayredae*: dispersal syndromes and spatio-temporal variations in ant dispersal assemblages

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Abstract This study assesses the dispersal mechanisms of the narrow endemic *Polygala vayredae*, analysing the functioning of its dispersal syndromes (anemochory and myrmecochory), the spatio-temporal variability of the disperser assemblage, foraging behaviour and dispersal ability, and the role of the elaiosome in ant attraction and seed germination. The dispersion of diaspores begins when either (1) capsules or seeds fall beneath the mother plant (barochory) or (2) the seeds are directly collected in the suspended capsules by ants (myrmecochory). As capsules frequently open and expose/disseminate seeds before leaving the mother plant, the adaptation for anemochory appears to be reduced and rarely functional, possibly with only occasional events of long-distance dispersal (e.g. under extreme weather conditions). *P. vayredae* is essentially myrmecochorous and a diverse array of ant species are involved in seed manipulation, with the elaiosome playing a major role in ant attraction. From the plant's perspective for dispersal, the majority of ant species had a positive interaction with the seeds, but negative and potential neutral interactions were also observed. Overall, dispersal distances were limited and were mainly determined by ant body size. The frequency of interactions and the ant assemblage varied significantly both spatially and temporally, and these factors may have an effect on directing or disrupting the selection of plant traits. Low seed predation and similar germination rates of intact seeds compared with seeds without elaiosome indicate that seed predator avoidance and seed germination improvement after ant manipulation are not among the selective advantages of myrmecochory operating at present. Dispersal mechanisms that enhance seed dispersal within the population and only occasionally lead to long-distance dispersal events, along with the rarity and patchiness of suitable habitats, may be the main factors explaining the actual density and narrow distribution of this species.

Keywords Anemochory · Barochory · Elaiosome · Myrmecochory · Seed predation · Seed germination

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Introduction

During the process of evolution, as a result of different selective pressures exerted by various factors in diverse habitats, plants have developed an array of structures adapted to particular biotic and/or abiotic dispersal vectors. Among the diversity of diaspores found in flowering plants, species from the genus *Polygala* L. (Polygalaceae) have evolved several distinct dispersal syndromes (e.g. winged structures, elaiosomes) theoretically linked with specific dispersal mechanisms (anemochory, myrmecochory, ornitochory, diplochory and epizoochory; reviewed in Forest et al. 2007). The studies performed so far in *Polygala* species from temperate regions have revealed two major mechanisms of dispersal (diplochory): (1) dispersal by ants (myrmecochory; Lack and Kay 1987; Oostermeijer 1989; Sernander 1906) and (2) wind dispersal of capsules prior to seed dispersal (anemochory; Lack and Kay 1987; Sernander 1906). However, until now, most of the knowledge of the dispersal mechanisms of *Polygala* has derived from inferences based on morphological traits of diaspores and their actual functioning has in most cases not been demonstrated.

The seeds of myrmecochorous species characteristically present an elaiosome that attracts ants due to its richness in lipids and chemical similarity to the insect's hemolymph (Hughes et al. 1994; Lanza et al. 1992). This interaction has been described as mutualistic, with the ants benefiting from the nutritive resources of the elaiosome (e.g. Gammans et al. 2005; Morales and Heithaus 1998) and the plant profiting from seed dispersal by ants (e.g. Beattie 1985; van der Pijl 1982). Besides the direct dispersal-related benefits, myrmecochory may also bear other selective advantages for the plants, such as seed predator avoidance (e.g. Boulay et al. 2007; Manzaneda et al. 2005; and reviewed in Giladi 2006), reduction in parent-offspring conflict, sibling competition (e.g. Boyd 2001; Higashi et al. 1989) and competition with congeneric species (e.g. Handel 1978), relocation of the seeds to more favourable sites for germination and establishment (e.g. nutrient enriched, moist environments; Culver and Beattie 1978; Oostermeijer 1989; but see Horvitz and Schemske 1986), seed germination improvement (e.g. Culver and Beattie 1980; Gómez et al. 2003) and/or fire avoidance (e.g. Hughes and Westoby 1992a). For anemochory, diaspores have structural adaptations (such as membranaceous wings or pappus) that increase their dispersal distances, promoting gene flow and allowing them to reach new locations (van der Pijl 1982). Wind dispersal creates the opportunity for long-distance dispersal, but the fate of diaspores is also subjected to high levels of uncertainty, and this mechanism is considered less reliable when compared with dispersal mediated by biotic vectors (Nathan et al. 2005; van der Pijl 1982).

Spatial and temporal variations in the composition, visitation rates and dispersal behaviour of the plant visitor assemblage may result in different selection patterns operating on different plant traits (geographic mosaic hypothesis; Thompson 1994, 2005), such as morphological or biochemical adaptations of diaspores and/or adaptations in flowering and fruiting phenologies (e.g. Boulay et al. 2006; Guitián and Garrido 2006). For example, several studies have shown geographic selection mosaics for characters such as seed mass (Garrido et al. 2002), seed and elaiosome size (Alcántara et al. 2007; Edwards et al. 2006) and elaiosome chemistry (Boulay et al. 2006), as a result of the interactions with different ant assemblages and behaviours. In other studies, temporal variations in visitor activity and visitation rates suggest that myrmecochorous plants may adapt their phenologies to the seasonal availability of dispersers, improving dispersal services (Guitián and Garrido 2006; Oberrath and Bohning-Gaese 2002) and escaping seed predation and competition for dispersal (Boulay et al. 2007; Guitián and Garrido 2006). In this sense, analysis of the consequences of both temporal and spatial sources of variation in ant–plant interactions will potentially enable a better understanding of the evolutionary patterns of specialisation within plant communities, particularly in the evolution of mutualisms (Manzaneda and Rey 2009). However, despite several studies on spatial variation at local and broad multi-population scales (e.g. Guitián et al. 2003; Rey and Manzaneda 2007), the analysis of temporal variations in ant visitor assemblages remains largely neglected (e.g. Manzaneda et al. 2007).

The aim of this study was to assess the dispersal mechanisms of the narrow endemic *Polygala vayredae* Costa. This species, described as a relict that survived the Quaternary glaciations (Bolós 1946), has a restricted distribution of approximately 12-km^2 in the oriental pre-Pyrenees. In the few existing populations, the plant forms dense carpets of several barely distinguishable individuals. Similar to other species of the genus, *P. vayredae* presents two types of structurally distinct diaspores associated with particular dispersal syndromes, bicarpelar-winged capsules (anemochory) and seeds with ant-attractive elaiosomes (myrmecochory). However, so far there have been no studies focused on the functional aspects of these structures. In this study, we evaluated (1) the functioning of the dispersal syndromes of *P. vayredae* by assessing the outcomes of anemochory and myrmecochory and (2) the ant–plant interactions, both at spatial and temporal scales. Furthermore, we investigated seed predation, the role of the elaiosome in ant attraction and the effect of elaiosome removal by ants on seed germination. For this purpose, primary and secondary dispersal experiments, observations of ant assemblages and behaviours and in situ seed germinations were performed for three populations during three consecutive years.

Materials and methods

Plant and study area

Polygala vayredae Costa (Polygalaceae) is a small perennial shrub, up to 25-cm tall, distributed in a restricted area in Alta Garrotxa, Girona (Catalunya, Spain). This narrow endemic species occurs in a few dense populations in mesophytic and xeric meadows (*Mesobromion*) with *Pinus sylvestris* and *Buxus sempervirens* and in rocky places (*Saxifragion mediae*) mainly in the *Quercetum pubescentis* domain. New shoots are produced each year from a rootstock, resulting in dense clusters of barely distinguishable individuals. Reproductive ramets produce small axilar inflorescences of 1–3 flowers in early spring (April–May), with each flower having a bilocular ovary with one ovule per locule (Castro et al. 2008, 2009a). Flowers of *P. vayredae* are self-incompatible and strictly rely on pollination vectors to set fruits, with the long-tongued bees *Bombus pascuorum* queens and *Anthophora* sp. being the main pollinators of this species (Castro 2007). Fruiting occurs in late spring (May–June) with the production of a dehiscent capsule containing two seeds. The capsules are large (mean ± SD: 10.0 ± 1.04-mm long and 8.8 ± 0.79-mm wide, $n = 100$), winged (mean ± SD: 1.8 ± 0.27-mm wide, $n = 100$) and presented on a 6.3 ± 0.86-mm pedicel (mean ± SD, $n = 100$) at a variable angle relative to the ramet (mean ± SD: 104.8 ± 49.13°, $n = 100$). The hairy seeds (mean ± SD: 4.7 ± 0.24-mm long and 2.3 ± 0.09-mm wide, $n = 68$) present a large external elaiosome (mean ± SD: 3.0 ± 0.44-mm long, $n = 68$) and weigh 9.1 ± 1.62-mg (dry weight; mean ± SD, $n = 68$) (Castro 2007). The seeds germinate at the beginning of spring in the following year and are nearly absent from the soil seed bank of subsequent years (S. Castro, personal observations).

This study was conducted in the natural protected area of Alta Garrotxa (UTM DG57 and DG58) at three populations: Montmajor, Serrat dels Boixos and Colldecarrera (for site description see Castro et al. 2009b). Field observations revealed that seed dispersal is synchronous in the study sites. The experiments were conducted during the peak of the fructification period in three consecutive years (2004–2006) and displayed simultaneously at all populations. The study sites differ in the type of habitat and were selected to include the two distinct habitats occupied by this narrowly distributed species.

Primary dispersal

Primary seed dispersal was evaluated in all populations in three consecutive years. Forty ramets of *P. vayredae* with a mature fruit primed for dehiscence were randomly selected in every population each year (fruits from neighbouring plants within a 2-m radius were removed to control the origin of the diaspores). A circular aluminium tray with a 60-cm radius and a small hole at the centre was fitted to the base of each ramet. The aluminium plates were then densely coated with glue to ensure that the fallen diaspores remained adhered to the tray. The type of diaspore (either capsule or seed) and respective distance from the mother plant (primary seed dispersal) were recorded in each tray. All capsules and seeds used in the experiment were tracked, confirming that the dimensions of the aluminium trays were appropriate to determine primary seed dispersal in this species. Primary seed dispersal mediated by ants was assessed within section “*Disperser assemblage, frequency of interaction and foraging behaviour*” (see below).

Secondary dispersal and seed predation

Secondary seed dispersal and seed predation (preliminary observations suggested that rodents were the main seed predators) were investigated using selective exclusion experiments with four treatments: (1) free exposure to dispersers/predators, ten seeds were placed over a Petri dish; (2) rodent exclusion, ten seeds were placed over a Petri dish protected by a metallic cage, allowing access to ants but not to rodents; (3) ant exclusion, ten seeds were placed over a Petri dish with the borders imbued with glue to prevent the entry of ants but allowing access to rodents; and (4) ant and rodent exclusion (control group), ten seeds were placed over a Petri dish with glued borders and protected by a metallic cage (i.e. combination of treatments 2 and 3). Furthermore, to evaluate the role of the elaiosome in disperser attraction, the treatments were duplicated to contain one set with seeds bearing fresh elaiosomes and another set with seeds where the elaiosome was removed after it was dry. Ten seeds were used as they simulate the mean number of seeds available in a small cluster of plants. The exclusion experiments were installed in the early morning and maintained for a total of 3 days, with each Petri dish of the two sets of treatments randomly spaced over a circle of approximately 3.14-m^2. During this period, the number of seeds that had been removed from each treatment was recorded every 24-h. Also, the removed seeds were replaced by fresh ones so that a total of ten seeds were offered each 24-h. Three replicates were displayed within each population. The experiment was performed at all three sites simultaneously for three consecutive years.

Disperser assemblage, frequency of interaction and foraging behaviour

The disperser assemblage and foraging behaviour were assessed by direct observations of dehiscent mature fruits during two consecutive years (2005 and 2006) in the three populations. The observations were made in several randomly selected areas of approximately 1-m^2, in which all the fruits could be easily monitored. Visits were recorded during 15-min surveillance sessions at different hours of the day. A total number of 228 censuses, evenly distributed per population and year, were performed, corresponding to 57 h of net observation. During each session, the following variables were recorded: total number of fruits under observation, number of visited fruits, ant species interacting with the seeds and ant foraging behaviour. When individuals were detected removing and transporting seeds, they were tracked and dispersal distances were measured (primary seed dispersal by ants). Each ant–plant interaction was qualitatively classified as: (1) negative (−), when ants completely predate the elaiosome without transporting the seed or transported the seed to unsuitable places for germination, namely, to the nests built in the tree trunks; (2) potentially neutral (0), when ants predate minute portions of the elaiosome apparently without affecting posterior visits (S. Castro, field observations); or (3) positive (+), when ants effectively transported the seeds to suitable places for germination, namely, to the nests in the soil or when seeds were accidentally lost in the litter during transportation. Based on the most frequent type of interaction and dispersal ability, each ant species was organised into the following functional groups (from the plant perspective for dispersal): short-distance dispersers, long-distance dispersers, “light” predators and “heavy” predators. Ant specimens were collected for identification and vouchers were deposited at the Department of Biology, University of Aveiro.

Effect of elaiosome removal on seed germination

To analyse the effect of elaiosome removal on seed germination rates, after the fructification period of 2005, ten germination plots containing both seeds with elaiosomes and without this structure (artificially removed) were randomly distributed among the population of Colldecarrera. Furthermore, seeds with the elaiosome removed by two ant species, *Crematogaster scutellaris* and *Formica gagates*, were sown in two additional plots. These seeds were obtained during disperser censuses after seed manipulation by these species.

Data analysis

Differences in primary dispersal distances among populations and years were analysed with two-way

ANOVA using Generalised Linear Models (GLZs), with the dispersal distance adjusted to a Gamma distribution (as dispersal curves were strongly skewed to the left) and with a logarithmic link function for model responses. The Type 3 Likelihood Ratio test of effects was computed. Differences in the proportions of each dispersal unit (i.e. capsule or seed) leaving the mother plant were analysed using a z-test. Differences in dispersal distances achieved by each dispersal unit were analysed using the Mann–Whitney U-test.

The significance of the selective exclusion experiments (i.e. disperser guild and presence/absence of elaiosome), population and year on secondary seed removal was analysed with a factorial ANOVA using GLZs, with the number of removed seeds (transformed with square root of $x + 0.5$) being adjusted to a Gamma distribution and with a logarithmic link function for model responses. The Type 3 Likelihood Ratio test was computed for all effects and interactions. For each factor, when statistically significant differences were observed, the Kruskal–Wallis one-way ANOVA on ranks was performed to evaluate which groups were different. Dunn's method was used for post-hoc pair-wise multiple comparisons.

The frequency of ant–plant interactions (given as the number of visited fruits) among populations, years and ant functional groups was analysed with a factorial ANOVA using GLZs, with the dependent variable (number of visited fruits, transformed with square root of $x + 0.5$) adjusted to a Poisson distribution and with a logarithmic link function for model responses. The Type 3 Likelihood Ratio test was computed for all effects and interactions. Differences in dispersal distances observed among ant functional groups and between ants and barochory/anemochory were analysed using a Kruskal–Wallis one-way ANOVA on ranks, followed by Dunn's method for pair-wise multiple comparisons.

Differences in germination rates among treatments (i.e. seeds with intact elaiosome, elaiosome removed by ants and elaiosome removed artificially) were analysed with one-way ANOVA. Prior to the analyses, germination rates were normalised with an arcsine transformation.

All the statistical analyses were performed using the STATISTICA 7 software package (StatSoft Inc., Tulsa, OK, USA).

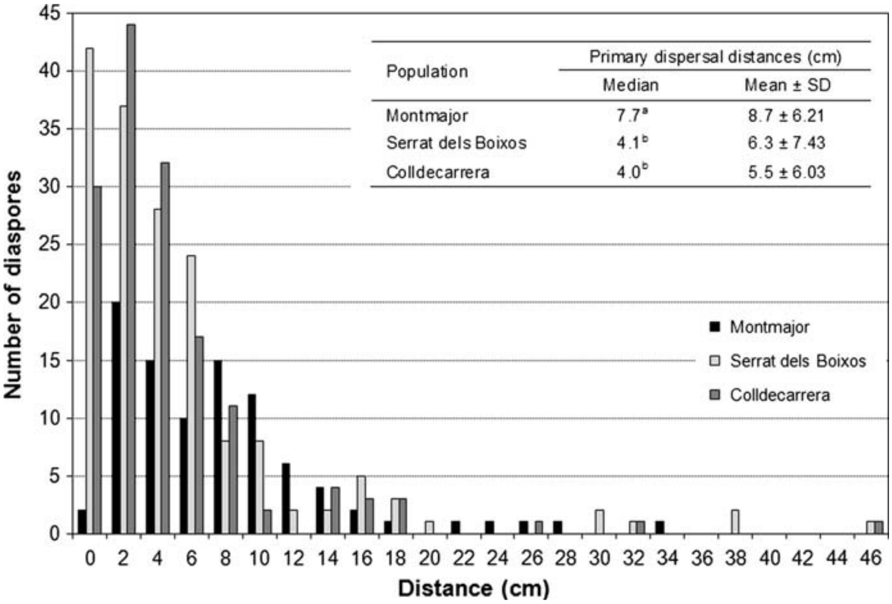
Results

Primary dispersal

During the process of maturation, the wings of capsules start to open and expose the seeds. A total of 407 diaspores were tracked in the primary dispersal trays. Overall, 56.5% of the diaspores leaving the mother plant were seeds, which fell mainly by gravity (barochory). The remaining 43.5% of the diaspores were capsules containing at least one seed. These proportions were significantly different ($z = 2.52$, $P = 0.012$). Also, despite the fact that the capsules presented wings, no statistically significant differences were observed in the dispersal distances between the two types of diaspores (seeds: mean ± SD of 5.9 ± 3.26-cm, median of 5.4-cm, $n = 230$; capsules: mean ± SD of 6.7 ± 3.00-cm, median of 5.9-cm, $n = 177$; $U = 18407.0$, $P = 0.098$). Analysis of the variation of primary dispersal distances with space and time revealed statistically significant differences among populations ($\chi^2 = 8.086$, $df = 2$, $P = 0.018$) but not among years ($\chi^2 = 4.959$, $df = 2$, $P = 0.084$) nor for the interaction year × population ($\chi^2 = 5.810$, $df = 4$, $P = 0.214$). The primary dispersal curves obtained for each population (with the data from all years pooled) were strongly skewed to the left (Fig. 1). Despite the significant differences observed among populations, primary dispersal distances were limited in any population and resulted mainly from gravity; 95% of the diaspores fell within 18-cm of the mother plant and none of them were able to disperse to a distance greater than 46-cm (Fig. 1). The results on primary seed dispersal mediated by ants are presented within section "*Disperser assemblage, frequency of interaction and foraging behaviour*" (see below).

Secondary dispersal and seed predation

The number of seeds removed from the selective exclusion treatments varied significantly among the studied factors and in some of the second-order interactions (Table 1). In the studied populations, ants were found to be the main dispersers of *P. vayredae* seeds, with rodents only occasionally involved in seed removal/predation ($P < 0.05$; Fig. 2). As a result, the number of seeds removed in the freely exposed treatments was not significantly



Population	Primary dispersal distances (cm)	
	Median	Mean ± SD
Montmajor	7.7^{a}	8.7 ± 6.21
Serrat dels Boixos	4.1^{b}	6.3 ± 7.43
Colldecarrera	4.0^{b}	5.5 ± 6.03

Fig. 1 Histogram of primary dispersal distances of *Polygala vayredae* diaspores in the three studied populations (with the data from all years pooled). An inset table with the median, mean and standard deviation of the mean (SD) obtained for each population is also provided (medians followed by different letters are significantly different at $P < 0.05$)

Table 1 Effect of the selective exclusion treatments, presence/absence of elaiosome, populations and years on secondary seed removal (only main effects and interactions of second-order between effects are provided)

Effect	df	χ^2	*P*
Treatment	2	409.62	<0.0001
Elaiosome	1	75.27	<0.0001
Population	2	26.02	<0.0001
Year	2	26.42	<0.0001
Treatment × Elaiosome	2	9.87	0.007
Treatment × Population	4	4.75	0.314
Treatment × Year	4	42.19	<0.0001
Elaiosome × Population	2	1.00	0.605
Elaiosome × Year	2	18.32	<0.0001
Population × Year	4	36.43	<0.0001

different from the number of seeds removed in the treatments where only ants were allowed ($P < 0.05$; Fig. 2). It was also clear that the elaiosome played a major role in ant attraction and subsequent seed transportation (76.2% of seed removal), as in its absence the number of removed seeds was significantly lower (42.6% of seed removal; $P < 0.05$; Fig. 2). The effects of presence/absence of elaiosome and exclusion treatment on seed removals were consistent across populations (Elaiosome × Population and Treatment × Population), but revealed to be variable across years potentially due to variable disperser abundances and/or assemblages among years (Elaiosome × Year and Treatment × Year; Table 1). Significant interactions between exclusion treatment and presence/absence of elaiosome were also observed, indicating that the main agents of seed removal may differ depending on the presence or absence of the elaiosome (Treatment × Elaiosome; Table 1). Spatial and temporal variations in the number of seeds removed were also observed (Table 1). For instance, in 2005, the proportions of seed removal were usually lower ($P < 0.05$), especially in Serrat dels Boixos and Colldecarrera (Fig. 2c–f). Also, while ants were common dispersers and presented similar seed removal rates among populations, rodents were scarce but more commonly involved in seed removal in Montmajor and Colldecarrera (Fig. 2a, b and 2e, f).

Disperser assemblage, frequency of interaction and foraging behaviour

A total of 297 interactions between the seeds of *P. vayredae* and ants were observed. A diverse array of ant species visited the capsules, each one responding positively to the presence of the elaiosome but presenting specific foraging behaviours (Table 2). According to the most frequent foraging behaviour and dispersal ability, ant species were arranged in four functional groups (from the plant perspective for

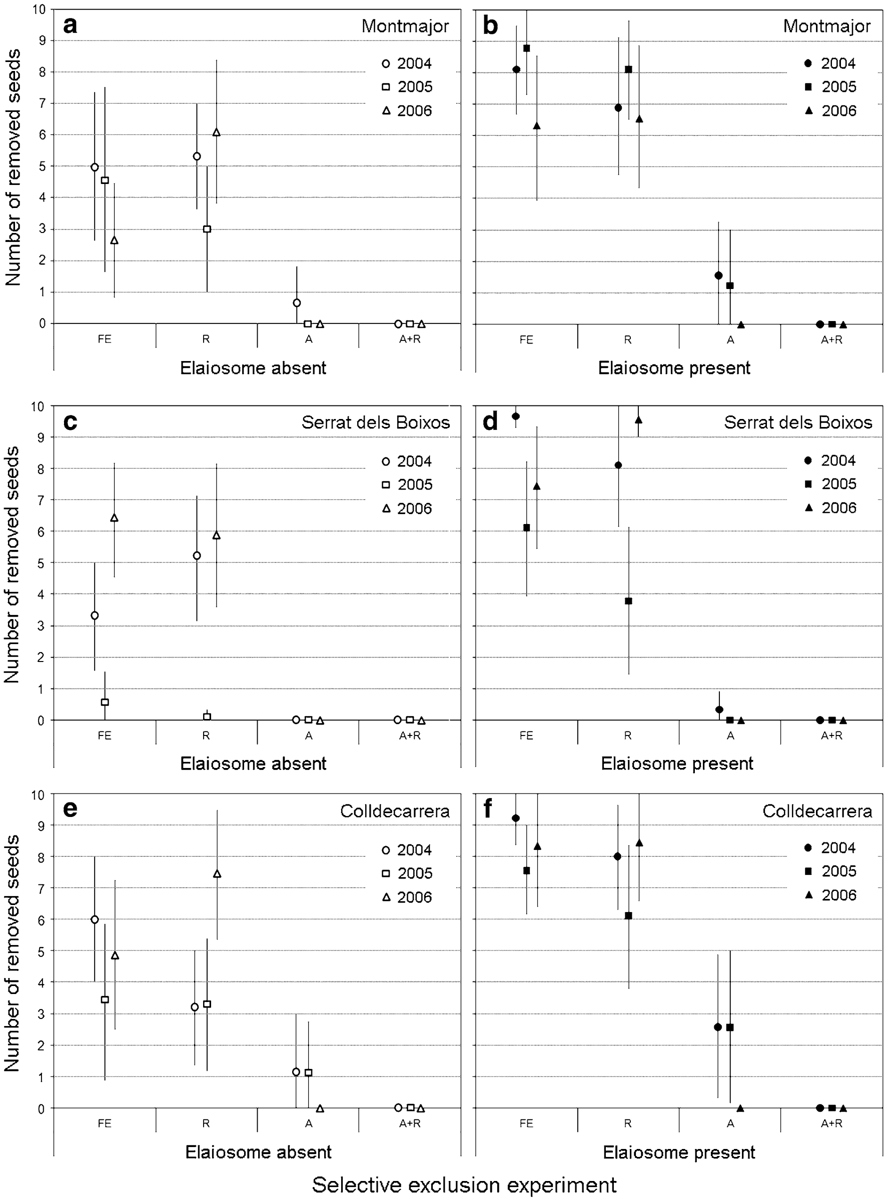


Fig. 2 Secondary seed removals in the selective exclusion experiment (*FE* free exposure to dispersers/predators, *R* rodent exclusion, *A* ant exclusion, *A*+*R* ant and rodent exclusion) investigated using seeds with removed (**a**, **c**, **e**; open symbols) and intact (**b**, **d**, **f**; closed symbols) elaiosomes, in the three studied populations (**a**, **b**: Montmajor; **c**, **d**: Serrat dels Boixos; **e**, **f**: Colldecarrera) during three consecutive years (2004–2006). The number of removed seeds is given as mean and standard error of the mean over a value of ten seeds offered by treatment

dispersal). The first group, short-distance dispersers, included species from the genera *Lasius* and *Myrmica* (Table 2). These species clearly recognised the seeds in the open capsules actively transporting them but due to their small body size (2.1–5.0-mm), seeds were easily lost in the forest litter, resulting in relatively small dispersal distances (Table 2). The second group, long-distance dispersers, included several species from the genus *Formica*, which were the largest ant species (4.0–7.5-mm) observed interacting with *P. vayredae* seeds (Table 2). These ants behave in a similar way as *Lasius* spp. and *Myrmica* spp., but due to their larger body size (4.0–7.5-mm) they were able to transport seeds to significantly larger distances into their nests (Fig. 3, Table 2). In the particular case of *Formica gagates* Latr., a curious behaviour was occasionally observed: these ants accumulated the seeds in small pockets in the moss close to their nests. The third group, “light” predators, included the smallest ant species seen

Table 2 Ant species, range of ant's body size (maximum and minimum), frequency of interaction (followed by proportion of the total number of visits) and dispersal distances (mean ± standard deviation of the mean, followed by the median) for each functional group observed in three populations during 2005 and 2006

Functional group	Species	Min–Max body size (mm)	Type of ant–plant interaction	Number of interactions						Dispersal distance (cm)	Photographs exemplifying each functional group
				Montmajor		Serrat dels Boixos		Colldecarrera			
				2005	2006	2005	2006	2005	2006		
Short-distance dispersers	*Lasius alienus* (Förster) *Lasius emarginatus* (Olivier) *Lasius platythorax* Seifert *Myrmica spinosior* Santschi	2.1–5.0	+	20 (77.0%)	32 (82.0%)	12 (26.1%)	5 (10.2%)	8 (10.1%)	9 (15.5%)	57.6 ± 72.61 (24.5)^{b}	
Long-distance dispersers	*Formica cunicularia* Latr. *Formica gagates* Latr. *Formica rufibarbis* Fabr.	4.0–7.5	+	1 (3.8%)	0 (0.0%)	15 (32.61%)	18 (36.7%)	17 (21.6%)	35 (60.3%)	415.9 ± 321.70 (459.0)^{a}	
"Light" predators	*Pheidole pallidula* (Nylander) *Plagiolepis pygmaea* (Latr.) *Tapinoma erraticum* (Latr.) *Temnothorax* spp.	1.1–4.9	–/0	4 (15.4%)	7 (18.0%)	10 (21.7%)	19 (38.78%)	8 (10.1%)	3 (5.2%)	–	
"Heavy" predators	*Crematogaster scutellaris* (Olivier)	2.9–5.2	–/0/+	1 (3.8%)	0 (0.0%)	9 (19.6%)	7 (14.3%)	46 (58.2%)	11 (19.0%)	62.5 ± 53.03 (62.5)^{a,b}	
	Total no. of observed fruits			122	169	268	140	231	313		
	Total no. of interactions			26 (21.3%)	39 (23.1%)	46 (17.2%)	49 (35.0%)	79 (34.2%)	58 (18.5%)		

Ant species were organised in the functional groups according with the most frequent type of interaction and dispersal ability; in each group the ant–plant interactions were qualitatively classified as negative (–), potentially neutral (0) or positive (+), from the plant's perspective for dispersal (see details in Material and Methods and Results). The total number of observed fruits and interactions are also provided. Medians followed by different letters are significantly different at $P < 0.05$. (a) *Crematogaster scutellaris*, bar = 1 mm; (b) *Formica gagates*, bar = 1 mm; (c) *Myrmica* sp., bar = 1 mm; (d) *Temnothorax* sp., bar = 0.5 mm interacting with *P. vayredae* seeds (1.1–4.9-mm), which mainly belonged to the genus *Temnothorax* [*T. nylanderi* (Förster), *T. parvulus* (Schenck), *T. rabaudi* (Bondroit), *T. racovitzai* (Bondroit), *T. unifasciatus* (Latr.) cf.]. In this case, ants were unable to transport the seeds but predated very small portions of the elaiosome, which likely progressively reduced its attractiveness (potentially neutral to negative interaction; Table 2). The last group, "heavy" predators, includes the acrobat ant *Crematogaster scutellaris* (Olivier), which presented several distinct interactions (Table 2). In most cases, individuals of this species were observed predating parts or the complete elaiosome, leaving the seed inside the capsule, sometimes even before the capsule was completely mature (potentially neutral to negative interaction); in fewer instances, they were seen actively transporting the seeds into their nest (in this particular case, the interaction is considered negative, because the ant nests are constructed in tree trunks, and thus, the seeds are deposited in unfavourable sites for germination), eventually losing some of them along the way (positive interaction). Another interesting feature of ant–seed interactions was the method of seed holding during transportation, which is determined by the relationship between the morphological features and sizes of diaspores and the sizes of the ant workers (Gorb and Gorb 2003; Ness et al. 2004). While the larger ants (*Formica* group) grabbed seeds by the elaiosome and transported them facing forward (see illustrations in Gorb and Gorb 2003), the smaller ants had more difficulty coping with the large size of the seeds, transporting them by reverse walking and dragging along the substrate (frequently losing them in the litter). The differences in dispersal distances among functional groups were statistically significant ($H = 31.69$, $df = 2$, $P \leq 0.001$), with the *Formica* group being able to transport the seeds to significantly larger distances than the *Lasius* group (Table 2). The analysis of primary seed dispersal distances revealed that ants dispersed the seeds to significantly larger distances than seed dispersal by means of barochory/anemochory ($H = 133.59$, $df = 1$, $P \leq 0.001$; Fig. 1 and Table 2). Several other ant species were present in the study sites [*Aphaenogaster subterranea* (Latr.), *Camponotus aethiops* (Latr.), *Camponotus cruentatus* (Latr.) and *Lasius flavus* (Fabr.)] but were never observed interacting with *P. vayredae* seeds, even after seed offering experiments.

The number of interactions varied significantly among years, populations and functional groups, as well as for the interactions among all factors (Table 3). With respect to spatial variation, there were usually higher ant–plant interactions in Colldecarrera and Serrat dels Boixos than in Montmajor, regardless of the year. Regarding temporal variation, while in Montmajor and Serrat dels Boixos the number of interactions was higher in 2006 (at least for the two major functional groups), in Colldecarrera the opposite was observed (Table 2). Ant guilds interacting with *P. vayredae* seeds revealed to be variable both across populations and years (Functional group × Population, Functional group × Year; Tables 2 and 3). Within populations, changes in ant

Fig. 3 Dispersal of *Polygala vayredae* seeds by *Formica gagates*; **a** mature capsule with exposed seeds; **b** ant exploration; **c** seed detection; **d** seed removal; **e** seed transportation; **f** empty capsule fixed to the mother plant

Table 3 Variation in the frequency of ant–plant interactions among populations, years, and functional groups

Effect	df	χ^2	*P*
Population	2	12.25	0.002
Year	1	10.04	0.002
Functional group	3	8.55	0.036
Population × Year	2	12.59	0.002
Population × Functional group	6	135.28	<0.0001
Year × Functional group	3	20.20	0.0002
Population × Functional group × Year	6	33.37	<0.0001

Table 4 Germination rates of *Polygala vayredae* seeds with intact, artificially and ant-removed elaiosomes

Elaiosome manipulation	*n*	Seed germination (%)
Intact	262	43.2 ± 21.15
Artificially removed	271	47.0 ± 28.47
Removed by ants	40	45.0 ± 30.00
One-way ANOVA		$F = 0.217$, $df = 2, 19$ $P = 0.807$

The proportion of seed germination is given as the mean and standard deviation of the mean; the total number of seeds sown (*n*) is also provided

guilds along time were especially clear in Colldecarrera population where a shift of the main functional group was observed (from *C. scutellaris* in 2005 to the *Formica* group in 2006), but were also evident in Serrat dels Boixos (Table 2).

Effect of elaiosome removal on seed germination

The germination rates in *P. vayredae* were highly variable and no statistically significant differences were observed among treatments (i.e. intact, artificially and ant-removed elaiosome) (Table 4).

Discussion

The study of the dispersal mechanisms operating in *Polygala vayredae* revealed new insights into the actual function of the morphological adaptations of its diaspores. In the absence of ants, primary dispersal occurs mainly by barochory (i.e. by the action of the diaspore weight), with the seed being the main diaspore leaving the mother plant. This appears to result from the maturation process of the capsules, which open their wings and expose the mature seeds before leaving the mother plant. Furthermore, when winged capsules were involved in primary dispersal instead of the seeds, the dispersal distances did not increase in any of the studied populations. Wind dispersal of capsules prior to seed release has been described as a dispersal mechanism in several other species of *Polygala* and in other genera within Polygalaceae (Sernander 1906; van Roosmalen 1985), having important effects, for example, on the genetic structure of the populations (Lack and Kay 1987). Nonetheless, experimental works confirming the actual role of this dispersal syndrome are scarce. In *P. vayredae*, the early opening of capsules and the consequent exposure of the seeds to other dispersal vectors had significant consequences for wind dispersal, reducing its importance in favour of barochory and myrmechocory (as ants responded positively to the elaiosome, seeds were often removed directly from the suspended capsules). Therefore, currently, it seems that the winged capsule may be losing its functionality (in the absence of ants, 56.5% of the diaspores leaving the mother plant were seeds); wind dispersal appeared to occur at low frequencies and long-distance dispersal may occur very rarely, e.g. under extreme weather conditions or through other vectors (Higgins et al. 2003) not observed during the course of these experiments. In this sense, particular characteristics of the plants, such as size or plant clustering, may affect primary seed dispersal by barochory. The seeds, either on the mother plant (primary dispersal) or in the soil (secondary dispersal), were actively searched for and rapidly transported by several ant species that constituted the main dispersal vector of this plant, significantly increasing seed dispersal distances. Furthermore, it is worth noting that the enclosure of the seed within the open capsule could potentially maintain the attractiveness of the elaiosome for longer periods. This could be especially important in exposed habitats, being a major advantage for myrmecochory.

Myrmecochory is a widely distributed and diffuse mutualism present in over 3,000 plant species (Beattie 1985; Berg 1975). In this mutualistic relationship, the elaiosome plays an important function in ant attraction (e.g. Beattie 1985; Hughes and Westoby 1992b; Hughes et al. 1994). For *P. vayredae*, the artificial removal of the elaiosome greatly reduced the rates of seed removal by ants (from 76 to 43%), revealing it to be a fundamental trait for seed dispersal. Nonetheless, a significant proportion of seeds without elaiosome was also transported. Similar seed removal patterns were observed in *P. vulgaris* by Oostermeijer (1989) and Lack and Kay (1987) who considered the possibility that ants formed a "search image" for the seeds of this species. Further detailed studies focused on how the presence or absence of the elaiosome and on how the quantitative variation of other seed traits affect seed removal and ant behaviour are needed to better understand the seed removal patterns of this species. Additionally, future studies should also address the effect of elaiosome predation by other ant species. As this behaviour may lead to a reduction of seed attractiveness, it can influence further interactions with other ant species, ultimately affecting seed dispersal (S. Castro, field observations and results herein; Rey and Manzaneda 2007).

The behaviour of the ant species interacting with the seeds of *P. vayredae* was found to be highly diverse. According to their ability to remove and transport seeds, it was possible to identify four different functional groups of ants: two effective dispersers differing in dispersal distances and two elaiosome predators differing in predation intensity. As for other myrmecochorous species, the mean dispersal distances for *P. vayredae* seeds were rather limited (reviewed in Gómez and Espadaler 1998a). Nonetheless, some ant species were able to transport seeds over considerably large distances (up to 7.4-m). These observations are in accordance with the characteristic dispersal curves generated by ants, i.e. a curve positively skewed to short distances with a long tail (e.g. Gómez and Espadaler 1998b; Horvitz and Beattie 1980). The dispersal distances attained by each ant species or group were primarily influenced by the ant's body size (see also Ness et al. 2004) and by the method of seed holding during transportation (see also Gorb and Gorb 2003), but factors such as foraging behaviour, nest density and/or spatial patterns of local ant communities may have also been involved with the achieved dispersal distances (Gómez and Espadaler 1998a, b). Overall, the limited dispersion ability observed in this plant species might be an important factor contributing to the formation/maintenance of its dense populations.

The assemblage of seed dispersers and the frequency of interactions between *P. vayredae* and each ant's functional group varied significantly for the spatial and temporal scales. Previous studies have also shown interpopulation variation in the composition of the ant-disperser assemblage (e.g. Manzaneda et al. 2007). Spatial variation in ant guilds may result from an array of different factors, namely landscape history (Ness and Morin 2008), habitat complexity (Lassau and Hochuli 2004), vegetation canopy (Feener and Schupp 1998; Retana and Cerdá 2000), interspecific competition (Andersen 1992; Cerdá et al. 1998), temperature (Cerdá et al. 1998) and/or degree of anthropogenic disturbance (Andersen and Majer 2004). In this study, it was evident that the Montmajor population presents specific characteristics that make it dissimilar to the remaining populations. This population is found on a rocky slope with small-sized rupicolous vegetation and is highly exposed to the sun, thus experiencing high temperatures during some hours of the day. The remaining populations are found in shadowy meadows with *Pinus sylvestris*. Interestingly, a similar spatial pattern has been observed for the pollinator's assemblage of this species, with major consequences for floral trait selection (Castro 2007; Castro et al. 2009b). Temporal variation was mainly observed in the Serrat dels Boixos and Colldecarrera populations, but while in the former population it reflects general differences in the abundance of ants, in the latter it represents a shift in the main ant group interacting with *P. vayredae* seeds. Such differences have already been found in other myrmecochorous systems and are usually associated with environmental parameters such as temperature, rainfall and/or moisture (Rico-Gray et al. 1998). The observed spatial variation may lead to the selection of different dispersal traits as a result of different foraging behaviours among different effective dispersers within each population. Traits such as seed and elaiosome sizes (Alcántara et al. 2007; Garrido et al. 2002; Hughes et al. 1994), elaiosome chemistry (Boulay et al. 2006), fruiting and dissemination phenologies, and rates and modes of seed presentation (Boulay et al. 2007; Hughes and Westoby 1992b; Oberrath and Bohning-Gaese 2002) constitute the major targets for selection by ants, determining the dispersal success of a myrmecochorous plant under a specific ant's community (Edwards et al. 2006; Giladi 2006). Preliminary surveys on several traits of *P. vayredae* seeds have already revealed significant differences between two of the studied populations for mean seed and elaiosome weight [mean ± SE (*n*): 8.9 ± 0.12 mg (101) vs. 8.3 ± 0.22 mg (50) and 1.2 ± 0.03 vs. 1.0 ± 0.04 mg, respectively] and elaiosome/seed mass ratio (S. Castro, unpublished results), indicating that different selective pressures could be operating on these diaspore traits (Mark and Olesen 1996). On the other hand, the temporal variation in ant communities may potentially lead to shifts in the strength and/or direction of selection operating within each population over time. Thus, in order to better understand the evolution of myrmecochory in this species, future studies should experimentally address how various plant traits affect the proportion and outcome of ant–plant interactions (including germination and establishment success after dispersal) and how they evolve across space and time.

Seed predation by rodents was only an occasional occurrence during the study period, and it did not lead to significant seed losses. Furthermore, granivorous ants are absent or extremely rare in the region inhabited by *P. vayredae* (X. Espadaler, personal observations). Thus, contrary to what has been observed in other species (e.g. Boyd 2001; Heithaus 1981), at present, predation of *P. vayredae* seeds is not among the selective pressures involved in ant-mediated dispersal. Regarding the influence of seed manipulation by ants on seed germination rates, no visible effects were observed in *P. vayredae*. In contrast, in several myrmecochorous plants, an enhancement in seed germination after elaiosome removal by ants has been described (e.g. Culver and Beattie 1980; Gómez et al. 2003; Horvitz and Beattie 1980), whereas in others, negative (e.g. *Centaurea corymbosa*, Imbert 2006) or neutral effects have been reported (e.g. *Fremontodendron decumbens*, Boyd 2001). Overall, it seems that the relative contribution of these features as selective advantages for myrmecochory varies with the plant and ant species, and with the ecosystem (Giladi 2006).

The distribution of plant species within populations and throughout their range of occurrence mainly depends on the distribution of suitable habitats for their establishment and growth, on their ability to disperse the diaspores, and on their recent history processes (e.g. Lesica et al. 2006; Münzbergova 2004; Navarro and Guitián 2003; Rey et al. 2006; van der Pijl 1982). This study provides valuable data on the dispersal mechanisms of the narrow endemic *P. vayredae*, revealing a low ability to disperse its diaspores. Future studies should now assess the availability of suitable sites (e.g. through introduction experiments in apparently suitable but unoccupied sites, Van der Veken et al. 2007) in an attempt to fully understand the factors responsible for its restricted distribution and ultimately to direct the implementation of appropriate management strategies for this species.

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