

## Seed dispersal and germination patterns in a rare Mediterranean island endemic (*Anchusa crispa* Viv., Boraginaceae)

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**Abstract** — We analyse and discuss patterns of seed dispersal and germination of a rare endemic plant species, *Anchusa crispa* Viv. (Boraginaceae) from Corsica and Sardinia. This coastal plant inhabits dunes and back-dunes, and currently numbers only a few thousand individuals which generally occur in isolated populations. This study included experiments conducted in the field in Corsica and also under controlled conditions in the laboratory. Short-distance dispersal of *A. crispa* is performed by ants, both by myrmecochory and dyszoochory. The invasion of an exotic species of ant, *Linepithema humile*, could locally modify the dispersal system and possibly the population dynamics of *A. crispa*. Long-distance dispersal may occur by water transport since seeds can germinate after at least 1 week of immersion in seawater and readily float on the surface. Burial of seeds is favourable for germination, percentage germination being maximised at a depth of 1–2 cm below the soil surface. *A. crispa* has a seed bank of about ten viable seeds per m<sup>2</sup>, which may contribute to the survival of this species which exists in small populations with a short life span. Due to its seed dispersal and germination patterns, the conservation of this species will necessitate that human disturbance, which can destabilise the surface of the sand is prevented and that new populations are introduced to favourable sites. © 2000 Éditions scientifiques et médicales Elsevier SAS

**Dispersal / myrmecochory / hydrochory / seed bank / germination / endemic plant species / rarity / Mediterranean island / human impact**

### 1. INTRODUCTION

The Mediterranean basin is an important centre of biodiversity for vascular plants due to the presence of some 25 000–30 000 species [27, 55, 57]. Of particular importance are the numerous islands which are rich in endemic taxa, many of which are endangered [28, 56]. Island endemic species can be vulnerable because of: 1) the difficulties or impossibilities of finding refuge areas during large-

scale ecological changes; 2) the often reduced size of their populations; 3) the major habitat changes caused by human impacts; and 4) the large number of exotic species [47, 53, 68, 70, 71]. In addition, rapid changes in land use (e.g. the abandonment of traditional agriculture and extensive grazing) and the spectacular recent growth of tourism in coastal areas are identified as serious threats [45, 46, 48].

Understanding the ecological factors which regulate small populations is critical for the conservation of rare species. Small-sized populations are particularly susceptible to extinction

because of reduced fitness resulting from inbreeding depression and to random demographic and environmental effects [5, 22, 40, 62, 64]. Recently, Schemske et al. [60] have argued that knowledge of the demographic mechanisms and parameters of rare species is essential for the development of appropriate strategies of management for the survival of rare species. In this context, knowledge of dispersal mechanisms is crucial for our understanding of the life cycle of rare plant species [41], whether this be dispersal within the site close to the seed producer, or over long distances to other sites

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where new populations may establish [35]. A key moment in the life cycle of the plants, seed dispersal, may enable a population to reduce the threat of extinction [19, 63, 74]. Due to dormancy, the existence of a seed bank may buffer the small populations against disturbances, and may reduce the effect of genetic drift, through the germination of seeds produced by previous generations [33, 65, 72].

In this context, our aim here is to quantify the dispersal and germination patterns of a rare Mediterranean island endemic, *Anchusa crispa* Viv. (Boraginaceae). This species occurs in isolated populations in coastal habitats that are disturbed by human activities and is currently protected by law. We thus discuss the conservation implications of our data.

## 2. STUDY SPECIES AND STUDY AREA

*Anchusa crispa* Viv. is a Mediterranean endemic species occurring on the islands of Corsica (France) and Sardinia (Italy). In Corsica, five populations occur on the west coast and two on the east coast (figure 1). In the Mediterranean basin, many taxa also have separate isolated populations [10, 26, 67] which have arisen for a variety of reasons: 1) the basin's complex geological history characterised in particular by many movements of land masses and tectonic plates, and variations in sea level (e.g. [17, 44]); 2) the effects of glaciations (e.g. [37]); and 3) a long history of human activities (e.g. [42]). The total number of plants in each population in Corsica varies from a few individuals to several hundreds and the total number of observed plants in the last 10 years has varied from 800 to 2 300 flowering individuals [58]. *A. crispa*, a short-lived (up to 4 years with 2–3 flowering years [58]) hemicyc-

tophyte, grows on coastal dunes and back-dunes, on sandy soils in open herbaceous vegetation (with *Matthiola tricuspidata* (L.) R.Br., *Elymus farctus* (Viv.) Runemark, *Glaucium flavum* Crantz, *Medicago marina* L.), and on the margins of shrublands dominated by *Pistacia lentiscus* L. and *Tamarix africana* Poiret [50, 51]. The plant forms a rosette of hispid, undulate, lanceolate leaves up to 15–20 cm long. Flowering takes place from March to July. The small flowers (7–10 mm in diameter) with a pale blue to violet blue corolla are born on 10–35 cm long scorpioid cymes. The fruits comprise four fused carpels that develop into nutlets which bear an elaiosome. Dispersal takes place from June to September when the small achenes ( $2\text{--}4\cdot 10^{-3}$  g) are released from the infructescences and fall to the ground. *A. crispa* is a species listed under the Berne Convention since 1979, has been protected by law in France since 1982, and has figured on the list of protected species of the European Community since 1992.

Field studies took place in southern Corsica in the Capu Laurosù and Portigliolo populations situated on either side of the mouth of the river Rizzanese, near Propriano (figure 1). The climate is sub-humid Mediterranean with a mild winter (average rainfall:  $650\text{ mm}\cdot\text{year}^{-1}$ ; mean of the maximum temperature of the warmest month:  $29\text{ }^{\circ}\text{C}$ ; mean of the minimum temperature of the coldest month:  $5\text{ }^{\circ}\text{C}$ ; adapted from Lombardo [43], and Ascensio [3]). The sites are affected by extensive cattle grazing, cows frequently cross the sites and occasionally graze flowering stems and leaves of *A. crispa* (see also [50]). In summer, heavy tourist pressure occurs in this habitat, as a result the sandy soil can be greatly destabilized, and *A. crispa* plants can be trampled and crushed by off-road vehicles.

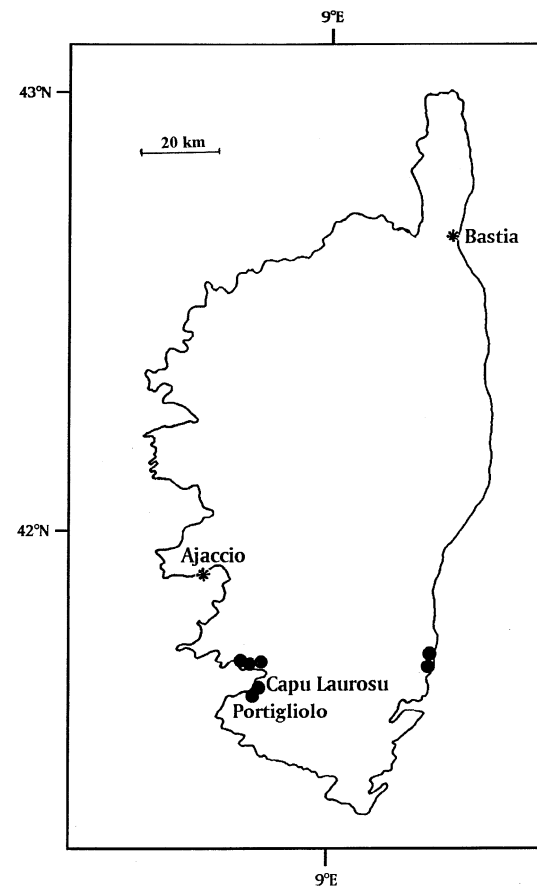


Figure 1. Location of the seven populations of *Anchusa crispa* Viv. in Corsica.

## 3. METHODS

### 3.1. Initial dispersal

The initial dispersal distance of seeds was measured in July 1997 at the Portigliolo site under and around ten plants of similar size (diameter:  $46.8 \pm 10.0$  cm), using wooden boards  $100 \times 30$  cm in size, covered with Soveurode® glue, and placed in contact with the plant stem. After 8 d, the distribution of the seeds on the collecting devices was mapped in relation to the distance from the plant stem.

### 3.2. Dispersal by ants

Preliminary observations showed that seeds falling to the ground could

be transported by ants. To assess the impact of this transport and the role played by the seed's elaiosome, two experiments were conducted.

Intact seeds and seeds on which the elaiosome had been removed were offered in August 1998 to the most abundant ant species in three sites (hereafter A, B and C) within the Portigliolo and Capu Laurosu populations. The ant species were *Linepithema humile* at Capu Laurosu (site A), *Aphaenogaster spinosa* (site B) and *Tapinoma nigerrimum* and *Tetramorium semilaeve* (site C) at Portigliolo. Twenty offer experiments, each including two seeds from each treatment (i.e. with and without elaiosome) were made; these two seeds were placed on the soil surface with a different ant individual. The first two species were tested separately, the latter two were tested together since they could not be distinguished in the experimental conditions. At each site (A, B, C), the experiment was conducted in an area with *A. crispa* and in an area without *A. crispa*, the two areas being situated 10–20 m apart. The type of seed (with and without elaiosome) that was first touched by an ant and the type of seed that was first removed by an ant were recorded. The seeds used in this experiment had been collected from the same study sites.

At the same date, three pairs of grids measuring  $3.5 \times 3.5$  m, and with 50 cm-mesh were set out, one pair at Capu Laurosu (site A) and the two other pairs at Portigliolo (sites B and C) (see also [8, 73]). One of the two grids in each pair covered an area containing *A. crispa* plants, whereas the other situated 10–20 m from the former, covered an area without *A. crispa* plants. The dominant ant species occurring at each of the three sites were the same as above. Thirty-two intact seeds and 32 seeds without an elaiosome were randomly placed at the 64 intersections of each of the grids. To prevent access by potential predators such as birds and rodents, each seed was placed below a Petri

dish raised 1 cm above soil level by paperclips. The experiment was conducted on the same day on all six grids. The number of seeds disappearing was recorded after 15, 30, 60, 120 and 180 min. The seeds offered were collected from the study sites.

### 3.3. Hydrochory

After having reached the soil, seeds of *A. crispa* can also be carried away by wind and swept into the sea. In some places, they can also be carried by river floods to the river mouth. The seeds can float on salt- or freshwater [58] during a period which varies from several hours to 1 d before sinking (Debussche, pers. obs.). Dispersal by water could thus contribute to seed movement and colonisation of new sites.

We designed experiments to quantify the capacity of seeds to withstand immersion in water without altering their germination capacity, and the role that the elaiosome may play in seed dispersal by water. Intact seeds and seeds whose elaiosome had been removed were kept submerged at 20–25 °C, in flasks filled with sea- or freshwater. Germination capacity was tested after 1, 2, 7, or 30 d immersion. Each flask contained 25 seeds.

The temperature and light conditions needed for seed germination are known for this species; scarification of the seeds reduces the latency period before germination (2–3 weeks) [4]. Germination was conducted at 18–20 °C under normal day-night conditions, by placing the 25 scarified seeds on filter paper and cotton soaked to saturation in Petri dishes (five seeds per Petri dish). Germination was considered to be successful when a radicle 1 mm long emerged from the seed; each seed that germinated was removed from the Petri dish. The number of seeds germinating was recorded daily for 1 month, no further germination took place after this date.

### 3.4. Seed bank

As the life span of the species is limited to a few years and the soil

surface is naturally disturbed, we attempted to determine whether a seed bank of the species existed in the soil. Since the seeds float, we placed the dry soil samples in water and collected and counted seeds which rose to the surface. To determine the accuracy of this method, we took three dry samples of sandy soil not containing any seeds and of the same particle size as the study samples and placed twenty seeds in each sample. The method allowed to recover 55 out of 60 seeds i.e. 92 %. We therefore considered our method to provide a reliable estimate of the seed bank.

Field observations on natural populations and on reinforced populations [2] showed that germination occurs mainly twice a year, in October–November and in April–May. In March 1998, after the autumnal germination peak and before ripe fruits release their seeds, soil samples were collected under ten plants in the Capu Laurosu population. Each sample contained the soil from 20 cm around the plant stem down to a depth of 10 cm. The seeds were separated by flotation. Seed viability was tested by germinating them under optimal conditions in Petri dishes (see above).

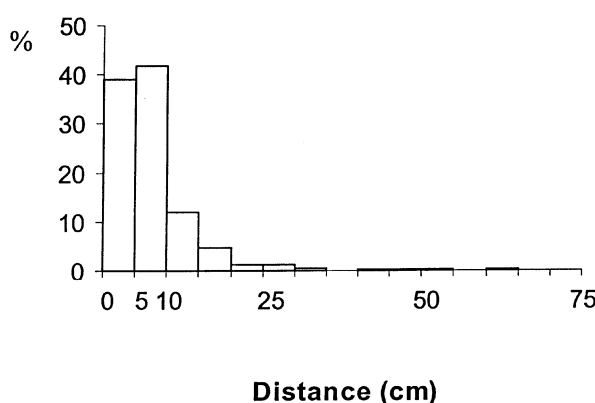
### 3.5. Germination of buried seeds

The frequency of disturbances to the soil surface caused by various factors (wind, waves, trampling by cattle and tourists and passage of vehicles) led us to determine whether there are germination requirements in terms of depth of burial in the soil. The experiment was conducted at 18–20 °C under day-night conditions using scarified seeds. The seeds were buried at different depths (0, 1, 2, 5 and 10 cm) in plastic pots containing sand from Capu Laurosu. Each pot contained ten seeds sampled from the same population. Two treatments were applied. First, at the beginning of the experiment the sand was water saturated with freshwater, then left to dry for the rest of the experiment,

with no further addition of water. This treatment simulates an isolated heavy rainfall event, which occurs frequently in the Mediterranean region. Second, after wetting to saturation the pots were placed in tanks containing 0.5 cm water throughout the experiment, this water maintaining moisture of the soil simulated a long period of rainy weather or the presence of a water table close to the surface during periods of high water table. There were three replicates per treatment. The number of seedlings emerging was counted daily.

### 3.6. Data analyses

Seed detection and seed removal by ants were analysed using a  $\chi^2$  test. The proportions of 1) germinated seeds after immersion and 2) after being buried, and the proportions of 3) ant-removed seeds were compared using an analysis of covariance, with time as the covariate, with a binomial error [24]. Explanatory factors were: for 1) water type, seed type and immersion length; for 2) burial depth and watering regime; for 3) ant species, seed type and presence of *A. crispera*. Data overdispersion in the different models was corrected using Pearson's  $\chi^2$  [16]. When interactions between factors were not significant they are not mentioned.



**Figure 2.** Initial seed dispersal of *Anchusa crispera* Viv. with percentage of seeds collected according to the distance to the stem ( $n = 584$  seeds dispersed).

## 4. RESULTS

### 4.1. Initial dispersal

Initial dispersal of collected seeds occurred over very short distances ( $m = 7.6 \pm 0.1$  cm; range 0–70 cm;  $n = 584$ ) from the plant stem (figure 2).

### 4.2. Dispersal by ants

The presence of *Anchusa crispera* individuals had no significant influ-

ence on seed choice ( $\chi^2 = 0$ ,  $P > 0.05$ ). On the other hand, there were significant differences in behaviour between ant species, both in the first seed touched ( $P < 0.01$ ) and the first removed ( $\chi^2 = 7.05$ ,  $P < 0.05$ ). *Linepithema humile* was the species more sensitive to the presence of an elaiosome since 80% of the seeds removed had an elaiosome. *Aphaenogaster spinosa* had a tenfold more seeds with an elaiosome (60% of cases), but it then showed no preference with regards to the seeds it removed. The other two species were indifferent to the presence of an elaiosome.

The patterns of seed removal differed between the sites and this difference varied over time (interaction Site  $\times$  Time significant;  $\chi^2 = 27.4$ ,  $P < 0.001$ ). Removal was particularly rapid at site B (figure 3). The effect on removal of the presence or absence of an elaiosome differed between sites, hence the significant Site  $\times$  Elaiosome effect ( $\chi^2 = 19.8$ ,  $P < 0.001$ ) (figure 3). There was no difference in the removal of seeds with or without an elaiosome at site B; at site C, more seeds with an elaiosome were removed by the end of the experiment, and at site A many more seeds with an elaiosome were

**Table I.** Choice of seeds by ants at the three sites (A, B, C), in relation to the presence or absence of *Anchusa crispera* and the presence or absence of an elaiosome. FT, first touched; FR, first removed (see Methods).

		<i>Anchusa crispera</i>			
		Present		Absent	
		With elaiosome	Without elaiosome	With elaiosome	Without elaiosome
Capu Laurosu (site A) with <i>Linepithema humile</i>	FT	14	6	14	6
	FR	17	3	15	5
Portigliolo (site B) with <i>Aphaenogaster spinosa</i>	FT	14	6	13	7
	FR	9	11	10	10
Portigliolo (site C) with <i>Tapinoma nigerrimum</i> and <i>Tetramorium semilaeve</i>	FT	9	11	8	12
	FR	10	10	11	9

removed than those without an elaiosome. These results confirm the results of the experiment in which seeds were offered to individual ant species, particularly concerning *L. humile* (table I). The presence of *A. crispa* in the experimental area had a positive effect on seed removal ( $\chi^2 = 10.24$ ,  $P < 0.01$ ), with 40 % more seeds removed compared to areas without *A. crispa*.

### 4.3. Hydrochory

Under optimal conditions, the germination capacity of non-submerged seeds was 92 % for intact seeds and 88 % for seeds with the elaiosome removed; the time taken to reach half the final germination capacity was 4 d in both cases (table II). Submersion quickly reduced the germination capacity after a few days immersion and was lethal for the seeds when seeds were submerged for 1 week in one treatment and in both treatments after 1 month. When the lethal submersion period was approached the speed of germination decreased greatly (table II). The type of water had no significant effect on germination capacity ( $\chi^2 = 1.33$ ,  $P > 0.05$ ), nor did the presence or absence of an elaiosome ( $\chi^2 = 2.52$ ,  $P > 0.05$ ).

### 4.4. Seed bank

In the sand samples analysed ( $n = 10$ )  $3.6 \pm 1.1$  seeds were found per sample, i.e.  $28.7 \pm 8.8$  seeds·m<sup>-2</sup>. The method used recovered 92 % of the seeds (see methods). At the end of winter there were thus about 30 seeds·m<sup>-2</sup> in the immediate proximity of *A. crispa* plants. Only 31 % of the seeds found germinated under optimal conditions.

### 4.5. Germination of buried seeds

The maximum germination was recorded in the two treatments when seeds were buried to a depth of 1 cm (table III). Percentage germination was low on the soil surface, and also low or even zero in one treatment when the seeds were buried at a depth

of 5 cm or more. Percentage germination depended both on the depth of burial and the watering treatment (interaction Depth × Treatment significant;  $\chi^2 = 10.6$ ,  $P < 0.05$ ). The deeper the seed was buried the longer the germination time.

## 5. DISCUSSION

### 5.1. Short-distance dispersal

We examined the seed dispersal types that were most likely to favour the survival of the species at the sites where it occurs, by avoiding competition with the parent plants by dispersing and by reaching microsites favourable for installation. The initial dispersal from the seed-bearer is very localised and occurs over a few centimetres to tens of centimetres, seeds falling essentially under the canopy of the parent plant. This spatial pattern is negative for seedling establishment as it will favour competition with the parent plants [15, 38]. Two dispersal types are responsible for most active dispersal within sites: 1) wind; and 2) ants attracted by the food represented by the seed and/or the elaiosome. We did not quantify the role of the wind, which would be difficult to do in the field, as its role would depend on very local factors such as the microtopography and the particle size of the substrate.

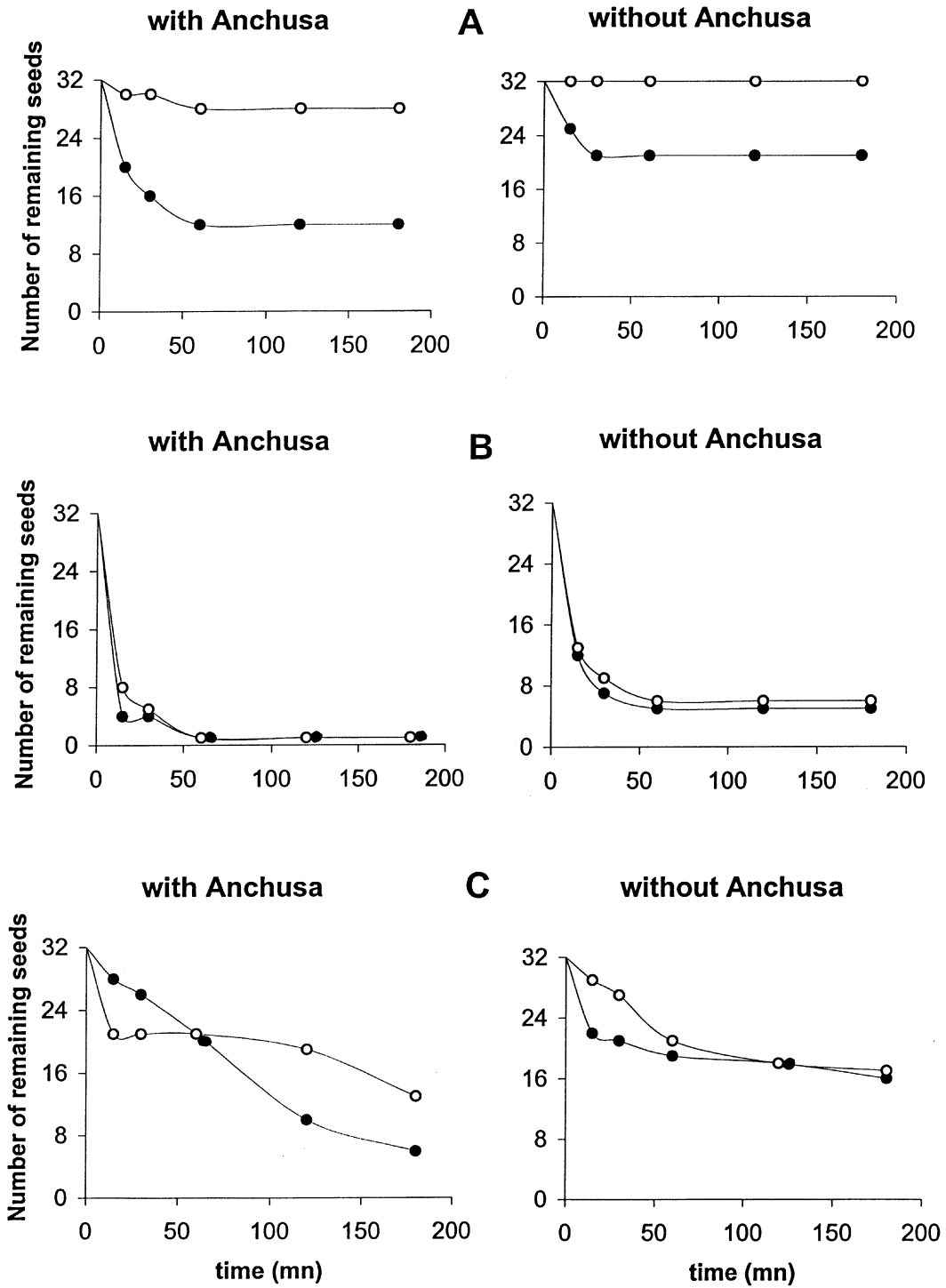
In the Mediterranean region, two types of dispersal are conducted by ants, myrmecochory and dyszoochory [73]. The dispersal distance realised by ants is usually only a few centimetres to metres [25]. Myrmecochory involves seeds with an ant-attractive appendage, the elaiosome. Ant workers take the whole diaspore to the nest, where only the nutritive elaiosome is eaten (e.g. [31]). The inedible seed (for these ant species) is then abandoned unharmed in the nest or rejected outside. Elaiosome-bearing seeds are dispersed by a wide variety of ant species (see review in [9]). The second type of ant dispersal called dyszoochory is performed by

seed-eating ants which collect the seeds of many plant species occurring in their habitat (e.g. [13, 23]), whether they have an elaiosome or not. Although most seeds taken to the nest by these ants are eaten, some happen to escape predation. Our results showed that *Anchusa crispa* is very probably concerned both by myrmecochory, because elaiosome-bearing seeds were removed by ants (see also [61]), and by dyszoochory, because seeds artificially deprived of this appendage were also removed by ants.

The four most abundant ant species recorded in the study sites are omnivorous. At other sites, at least three of these species are aphid and scale insect tenders, and one of these (*Tetramorium semilaeve*) is also a granivore [6, 7, 73]. The granivory of *T. semilaeve* is illustrated in this case by the fact that the seeds with or without an elaiosome were all equally attractive. The attractiveness of seeds with an elaiosome for the other ant species (pronounced attractiveness for *Linepithema humile*; slight for *Aphaenogaster spinosa*), does not however signify that these species do not consume part of the seeds, or the cotyledons at germination, since they are all omnivorous. It has however been established that *A. spinosa* plays a clear role in dispersal since many seedlings of *A. crispa* are observed after the autumnal germination in the immediate proximity of the nests of this species (Quilichini, pers. obs.). Detailed observations which cover the period from seed removal to predation or germination success in and around the ant nests for the different ant species, would be worthwhile to assess the respective importance of myrmecochory and dyszoochory.

### 5.2. The impact of exotic ant species

*L. humile* is an exotic species first recorded in Corsica in 1959. Since then it has become abundant in coastal plant communities and on



**Figure 3.** Removal (number of seeds remaining) of *Anchusa crisper* Viv. seeds with (filled circles) and without (open circles) an elaiosome, in the presence and in the absence of the plant species, for different ant species, *Linepithema humile* (A), *Aphaenogaster spinosa* (B), and *Tapinoma nigerrimum* and *Tetramorium semilaeve* (C).

**Table II.** Germination capacity of seeds, in percentage, in relation to the submersion period, in either fresh- or seawater, and either with the seed intact (a) or with its elaiosome removed (b). The time, in days, taken to reach half germination capacity is shown in parentheses.  $n = 25$  seeds per treatment.

		0 d	1 d	2 d	7 d	30 d
Freshwater	a	92 (4)	72 (7)	32 (8)	0	0
	b	88 (4)	72 (10)	68 (5)	20 (6)	0
Seawater	a	92 (4)	48 (4)	56 (5)	32 (10)	0
	b	88 (4)	72 (4)	72 (3)	20 (14)	0

some beaches [12] where it has a very varied diet and is an active aphid and scale insect tender [6]. The consequences of its invasion are documented in several case studies: it has an impact on the mutualism between plants and ants [8], between ants and aphids (e.g. [69]), on the composition of native ant communities [20, 36] and on other arthropods [14].

The impact of *L. humile* on the seed dispersal and the population dynamics of *A. crispa* is difficult to predict precisely. However, the presence of this exotic species may cause changes in the spatial distribution of the plant population by increasing the density of seeds under and near adult plants and therefore increasing the adverse effects of competition of adult plants on seedlings [15, 38]. In fact, *L. humile* frequently makes its nest right in the tap root of *A. crispa*, in the hollow gall produced by a beetle larva (*Pachycerus* sp., Curculionidae), which frequently parasitises plants more than 8 years old (Quilichini, pers. obs.). Indirectly it

could also influence the composition of the ant community which disperses *A. crispa*, by its competitiveness. Such changes in the interactions occurring in the life cycle of small-sized populations could have major effects on the dynamics of these populations and ultimately on their survival.

**5.3. Long-distance dispersal**

We also examined the possibilities for long-distance dispersal allowing new sites to be colonised, and therefore ensuring the survival of the species if conditions become unsuitable at sites already occupied. Long-distance dispersal can explain the distribution of populations of *A. crispa* and some of its genetic characteristics on Corsica and Sardinia [59]. Long-distance dispersal could occur by hydrochory since the seeds float for several hours and some are still capable of germinating after a week’s submersion in seawater. Long-distance colonisation across the sea surface must be a very rare event

but one whose reality is abundantly documented for islands (e.g. [11, 18]). Non-intentional introduction by man could also ensure long-distance colonisation [21, 30]; this has also been abundantly documented for other species on islands (e.g. on Corsica [49]). In the present case, fishermen who have crossed from Sardinia to Corsica with their boats and nets for centuries may have played a role. In more recent times, medium-distance dispersal by a terrestrial route could also have been produced by cattle that graze the plants, including the flowering stems ([50]; Quilichini and Debussche, pers. obs.), and could therefore in their movements disperse any mature seeds that survive digestion [39].

**5.4. Seed bank**

For many plant species, the existence of a seed bank provides an escape in time from temporarily unfavourable conditions. This can be decisive for a plant species with a small population size and short life

**Table III.** Percentage germination in relation to depth of seed burial and water regime. The time in days to reach half the germination capacity is shown in parentheses.  $n = 3 \times 10$  seeds per treatment.

	0 cm	1 cm	2 cm	5 cm	10 cm
One watering	6.7* (2)	66.7 ± 14.5 (15.0 ± 1.0)	13.3 ± 8.8 (16.5 ± 2.4)	10.0 ± 0.0 (25.3 ± 1.6)	0
Constant watering	16.7 ± 6.7 (9.0 ± 0)	70.0 ± 0 (11.0 ± 1.4)	66.7 ± 3.4 (13.0 ± 1.4)	13.3 ± 6.7 (15.0 ± 0)	26.7 ± 14.7 (21.3 ± 2.8)

\* Germination only occurred in one replicate.

span. A seed bank exists in *A. crispa*; we have estimated it to be about 10 viable seeds·m<sup>-2</sup> near adult plants after the autumnal germination, which is the most abundant, but we have not measured the seed bank after the spring germination. The numbers of seeds are however low (e.g. for seed densities in seed banks [32]). We do not know how long seeds survive in this seed bank, but the seed morphology (thick cuticle whose scarification promotes germination) suggests that seeds may survive several years. The survival of the species therefore seems to be assured even if all the existing plants have just been destroyed, but the low numbers of seeds that we recorded in the seed bank make this assurance a fragile one.

### 5.5. Germination of buried seeds

The seeds of *A. crispa* germinate over a temperature range of 10–20 °C [1]. This is consistent with the two germination peaks observed in autumn and in spring, these two seasons also being the most rainy in the Mediterranean region. Although the presence of an elaiosome plays a role in the dispersal by certain ant species, our results suggest that its presence has no effect on germination. Germination can take place both in the light and in the dark [1], i.e. for a seed on the soil surface or buried in the soil. We have however shown that the optimum burial depth for germination is 1–2 cm. Few seeds on the surface germinate because the sand dries out too quickly, and the seedlings they produce wither and die for the same reason. Seeds at a depth of 5 cm or more have a low germination success because the seeds probably do not have enough reserves to allow the cotyledons to reach the surface. A further experiment has shown that no germination took place, whatever the type of watering, at a burial depth of 20 cm (Quilichini and Debussche, unpub. data).

The position of the seeds in the sandy soil when the germination con-

ditions become favourable therefore appears to be important for the population dynamics of *A. crispa*. We suggest that the burying of seeds by ants has a positive influence on seedling establishment in *A. crispa*, provided the seeds are not buried too deep. Local modifications in the soil related to ants' nests (enrichment in organic matter and nutrients, improved water retention, etc.) are also probably positive (review in [9, 34]), particularly in a sandy poorly-developed and poorly-structured soil, such as those where this plant species grows. On the other hand, trampling and the passage of vehicles, that are frequent at *A. crispa* sites and whose effects are accentuated by the wind, destroy the fragile soil structure and lead to a spatial instability of the seed distribution and their burial depth. They probably also have an adverse effect on the survival of ants' nests. These human impacts are certainly a negative factor for germination and installation success. The positive role of structures that locally stabilise the sand, whether they are dead vegetation, flotsam deposited by the sea or planks associated with constructions, is demonstrated by the high frequency of germination that is observed at their contact (Quilichini and Debussche, pers. obs.).

### 5.6. Implications for conservation

*A. crispa* is a plant species that occurs in the ecotone between the unstable habitat of the beach, whose sand is constantly being reworked by the wind and waves, and habitats that are either shady or too competitive for it and where it cannot install or survive such as *Pistacia lentiscus* and *Tamarix africana* shrubland, and the dense grasslands of back-dunes.

Unfortunately we have no quantitative information on the state of the plant populations before the recent tourist boom. A qualitative assessment suggests that 40 years ago, *A. crispa* was much more abundant than at present at the mouth of the Rizzanese, where our experiments were

conducted [54]. A precise demographic study is thus needed (see [60]). It is however clear that *A. crispa* has always been a rare species, particularly because of the very reduced number of populations [66]. The recent and strong tourist pressure on its sites during summer is without doubt the most serious danger for the species' survival. The passage of vehicles and trampling by walkers and bathers destroy plants, destabilise the sandy soils, affect ant populations acting as dispersers, and change the disturbance regime which drives the depth of the seeds in the soil and the fate of the seed bank.

Although it would be very difficult to control the invasion of the exotic ant species *L. humile*, whose adverse effect on *A. crispa* remains to be demonstrated, there are however several measures that could be proposed aimed at maintaining: 1) the stability of the sand; and 2) the openness of the vegetation. Protecting the habitat by prohibiting automobile traffic and limiting human disturbance is an essential prerequisite of such measures. The extensive cattle grazing seems to play a positive role for *A. crispa* (despite some grazing of adult plants) by limiting the expansion of shrublands and highly competitive perennial herbs. The herbivory exerted by cattle and the soil trampling that it causes seems negligible compared to their positive role.

On Corsica, each *A. crispa* site constitutes a sort of terrestrial island of favourable sandy habitats surrounded by sea, bare sand, rocks, shrublands and dense grasslands where the species is unable to grow. Because its dispersal is mainly over short distances, it is unable to cross these surrounding unfavourable areas to colonise other sites suitable for its installation. Long-distance dispersal allowing it to cross these barriers is a significant phenomenon on an evolutionary time scale, but is evidently too rare with respect to the urgent need to conserve the species. It is therefore essential to create new

populations, from seeds or seedlings (e.g. [29]), in favourable habitats protected from human disturbance (e.g. [52]).

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