

Article

An Ant-Plant Mesocosm Experiment Reveals Dispersal Patterns of Myrmecochorous Plants

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Abstract: For Central European herbs, ants are one common dispersal vector acting at relatively small spatial scales. Though extensively studied concerning the different benefits to plants, specific dispersal patterns mediated by ants have been reportedly very sparsely and without any validation. Thus, we studied the seed dispersal pattern of a set of myrmecochorous plant species in a novel mesocosm experiment. We examined the seed dispersal distances of four forest herbs (Hollow Root–*Corydalis cava* (L.) Schweigg. & Körte, Alpine Squill–*Scilla bifolia* L., and Common Dog-violet–*Viola riviniana* Rchb. and the annual Ivy-leaved Speedwell–*Veronica hederifolia* L.) by the red ant *Myrmica ruginodis* Nylander in 8.25 m² large plots under natural conditions with and without ants. In the presence of *Myrmica* ants, the bulb geophytes *C. cava* and *S. bifolia* showed a significantly higher fraction of dispersed seedlings and a maximum dispersal distance of 322 cm. Estimated by nearest neighbor analyses, distances between single *C. cava* seedlings were significantly higher in ant plots than in enclosures without ants. The annual species *Veronica hederifolia* showed a few dispersed seedlings in ant plots only, while the diplochorous hemicryptophyte *Viola riviniana* germinated in a widely scattered manner with distances up to 241 cm due to ballochorous dispersal in both ant and enclosure plots, but with a maximum of 324 cm only by means of ants. Our results indicate the escape from the mother plant and dispersal for distance as an important benefit for myrmecochorous species, potentially accompanied by benefits through reduced competition.

Keywords: myrmecochory; seed dispersal; mesocosm; ant enclosures

1. Introduction

The mutualism of seed dispersal by ants, i.e., myrmecochory, has been investigated in a series of field studies which mainly tested three main hypotheses: distance dispersal, directed dispersal (e.g., to nutrient-enriched microsites), and predator avoidance. Out of these, dispersal for distance and avoidance of predators were noted as the most common benefits for plants, supported by 75% of related studies [1].

A serious problem of studies testing these hypotheses is the complexity and unpredictability of environmental variables, which affect myrmecochorous plants in the field, while the benefits for ants can be studied easily in laboratory experiments. Thus, it has been shown experimentally that ants may gain nutritional benefits from elaiosomes through which colony growth or sexual production is facilitated [2–6]. However, related studies concerning the investigation of the benefits for plants under controlled conditions are currently lacking. Such studies should provide the opportunity to capture the fate of adult plants, their seeds, and emerging seedlings in a given population [7].

Regarding distance dispersal of seeds by ants in the field, Gomez and Espadaler [8] calculated a mean dispersal distance of 1.16 m with a maximum of 70 m within the northern hemisphere. In this context, the mean seed dispersal distance seemed to decrease with increasing latitude while a more comprehensive study did not find a significant relationship for ant-dispersed species [9]. Heinken [10] reported the spread of the myrmecochorous Field Cow-wheat (*Melampyrum pratense* L.) in deciduous woodland with an annual mean migration rate of 0.91 meters within a simple sowing experiment—but with the uncertainty whether other dispersal vectors than ants could have affected that dispersal pattern, too. Myrmecochorous distance dispersal curves usually exhibit a narrow peak with a long tail. Escape from the mother plant or dispersal for distance is considered to be a major benefit to ant dispersed plants because it can lead to a decreased intraspecific competition as well as to the colonization of a new habitat [11,12].

The hypothesized benefit of directed dispersal has been supported by about half of all related studies [1]. Ant nests and garbage dumps can provide more solar light or nutrients than surrounding areas [13,14] and may favor seedling emergence [15]. However, this benefit is primarily found with large-sized ants, e.g., *Formica* sp. or the jet black ant, *Lasius fuliginosus* Latreille, as they have long-lasting nest sites. Kjellsson [16] found that seeds dispersed by red ants, *Myrmica ruginodis* Nylander, may be transported to the nest and remain there, but they may also be displaced to special garbage dumps or be lost along the foraging trail [16]. Overall, the dispersal and seedling patterns of myrmecochorous plants in space and time remain widely undiscovered [17].

While seed dispersal away from the mother plant might reduce sibling competition [12,18], the effect of subsequent seed aggregation around the nests could counteract this benefit: Oostermeijer [13] showed a closer aggregation of Common Milkwort (*Polygala vulgaris* L.) and Wild Pansy (*Viola curtisii* E. Forst) plants near ant nests than around, and Gorb et al. [19] mentioned aggregations of seedlings of Asarabacca (*Asarum europaeum* L.) and Sweet Violet (*Viola odorata* L.) on the territory borders of *Lasius fuliginosus*, which indicates a secondary relocation of seeds of these species to so-called garbage dumps. Nevertheless, it is questionable whether this aggregation may lead to an effectively higher competition between seedlings or if the mosaic structure of fluctuating ant nest sites is minimizing this effect likewise [20].

In the present study, we wanted to validate the formation of myrmecochorous dispersal patterns, e.g., as simulated by Gorb and Gorb [21,22] or indicated by Heinken [10]. Therefore, we aimed at totally excluding all other biotic dispersal vectors except ants in order to examine the importance of ant dispersal for a set of common myrmecochorous species which occurs in forests. We used a near-natural environment under controlled conditions: in a novel outdoor mesocosm experiment, we investigated the seed dispersal of four myrmecochorous plant species by *Myrmica ruginodis*, which is a common and frequent ant species in Central Europe and which is assumed to play a major role in myrmecochory with individual dispersal distances of up to 1.4 m (for the Pill Sedge, *Carex pilulifera* L. [16]).

Our main work hypothesis supposes benefits by a spatial spread of populations through myrmecochorous seed dispersal (distance dispersal), which generally leads to a reduced intraspecific competition favoring seedling establishment. Specific dispersal towards the ant nest or to a garbage dump (directed dispersal) might also occur. This pattern could result in benefits for seedlings through favorable environmental conditions at a nest or garbage dump.

2. Methods and Materials

2.1. Study Species

We used four indigenous myrmecochorous plant species covering different life forms, different seed sizes, and occurring in forests (Table 1). Thus, we chose two geophytes (Hollow Root, *Corydalis cava* (L.) Schweigg. & Körte and Alpine Squill, *Scilla bifolia* L.), a forest therophyte (Ivy-leaved Speedwell, *Veronica hederifolia* L.), and a forest hemicryptophyte (Common Dog-violet, *Viola riviniana* Rchb.).

Table 1. Some ecological traits of the studied plant species in *Myrmica* mesocosms.

Species	Life form	Life cycle	Time of seed set in experiment	Seed weight (mg) ¹	Elaiosome structure
Hollow root, <i>Corydalis cava</i> (L.) Schweigg. & Körte	geophyte	perennial	May	10.1	soft appendage
Alpine Squill, <i>Scilla bifolia</i> L.	geophyte	perennial	May	19.0	soft appendage
Ivy-leaved Speed-well, <i>Veronica hederifolia</i> L.	therophyte	annual	May–June	4.11	thickened cell wall
Common Dog-violet, <i>Viola riviniana</i> Rchb.	hemicryptophyte	perennial	July–August	1.43	dry appendage

¹ data from BIOPOP [23].

The red ant, *Myrmica ruginodis*, has a medium body size of 3.65 to 5 mm [24]. It was chosen because its workers are known to carry and disperse elaiosome-bearing seeds [15,25]. Nests harbor several hundreds of workers and are found in rotten logs, dead wood or grass tussocks in forests.

2.2. Mesocosms

We established 14 mesocosms which were protected by a wire cage of a 1 cm mesh width against disturbances by roaming animals or humans. Each mesocosm with the size of 3.3 m × 2.5 m was initially filled with sand and grit. To create a suitable habitat for plants, we added a 10 cm layer of heat-sterilized compost. Greenhouse experiments showed only grass and goosefoot seedlings emerging from this special compost soil. All mesocosms were surrounded with 30 cm high polyester plastic walls daubed with Tanglefoot® (Contech Enterprises, Grand Rapids, MI, USA) preventing ants from migrating between plots.

In April 2004, two to four individuals from each of the four species *Corydalis cava* (1), *Scilla bifolia* (2) *Veronica hederifolia* (4), and *Viola riviniana* (3) were planted in each plot. The spatial order of species groups was randomly chosen to exclude effects between the species. Biodegradable pots of 15 cm diameter were used. The maximum possible distance from the mother plants to the farthest edge in this experiment was approximately 325 cm. In seven out of the 14 mesocosms (“ant plots”), a nest of *Myrmica ruginodis* was settled opposite to the plants, with rotten wood and an empty *Helix pomatia* snail shell as an alternative nest site and with a 2.5 meter distance to each plant group in the arena (see Figure 1). The other seven remained without ants.

Ants were collected in a deciduous woodland area along the river Pfatter near Regensburg—(Germany; 48°56′ N, 12°22′ E) where our study plant species did not occur to exclude the occurrence of seeds in the nest material. Study plants were grown from seeds (annuals) or collected in various field localities around Regensburg (geophytes, hemicryptophyte). The experiment started in the beginning of May. Beginning with the foliation of trees and ending with its defoliation, a shading mat was used to obtain near-natural forest light conditions. To provide suitable conditions for the ants, they were fed with honey and cockroaches at random locations within the plot twice a week. We operated in the plots using small stepping stones in order to avoid soil damage or seed transfers by shoes.

All emerging seedlings of the study species were marked at the time of their emergence in late autumn and early spring of the following year. Afterwards, all seedling positions were measured and recorded. For the perennial geophytes *C. cava* and *S. bifolia*, the rediscovery of seedlings in spring of the following year was noted as establishment.

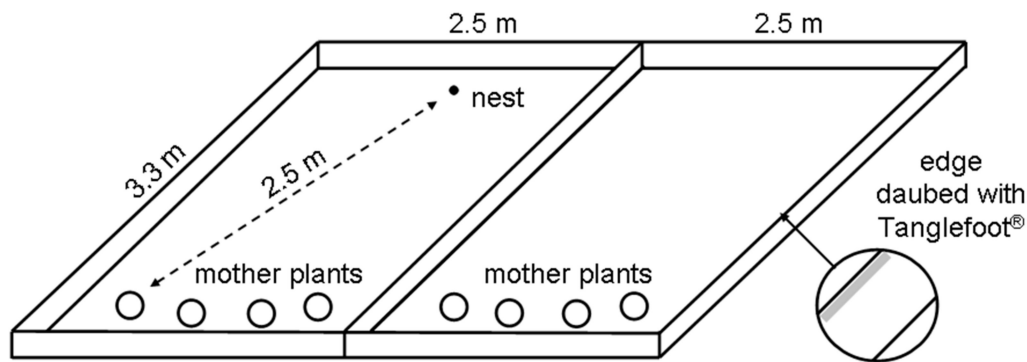


Figure 1. Schematic view of the mesocosm experiment with *Myrmica* showing one ant plot and one enclosure plot.

2.3. Statistical Analyses

After data input by means of Cartesian co-ordinates, we plotted and analyzed the seedling distribution patterns. To classify seedlings in the mesocosms into dispersed and non-dispersed seedlings, we discriminated the direct seed-fall shadow around the mother plants from the area of possible dispersal by ants. We generally used a radius of 50 cm around the respective mid-point of each plant group and added a second radius of 200 cm when analyzing *V. riviniana*. We compared the respective frequencies of dispersed seedlings, conducted nearest neighbor analyses [26], and calculated the neighborhood density function (NDF) to examine the spatial point pattern formed by the seedlings [27,28]. The density corrected NDF simplifies the display and interpretation of our point patterns as the reference value under spatial randomness is 1. NDF values above 1 indicate increasing spatial aggregation and NDF values below 1 indicate a pattern that is more regular than expected by random. The corrected NDF was calculated for pooled data sets at 5 cm intervals up to 125 cm. Confidence envelopes of NDF of 99% were estimated from 499 simulations of a random point process.

Statistical comparisons were conducted by means of Mann–Whitney U tests discriminating between ant plots and enclosures. Seedling numbers and nearest neighbor distances are given as mean values \pm SD. We used the program Microsoft Excel with the add-in SpPack Version 1.37 (Department of Geography, King’s College London, Strand, London [29]) and ‘SPSS for Windows 12.0’ (IBM, Armonk, NY, USA).

3. Results

The study plants set fruits between May and July. Seed set was similar between the treatments. *Myrmica* colonies successfully occupied the offered nesting sites and their workers were seen to be active during the whole season. Only one nest that moved within the plot had to be resettled in late April. First seedlings of *Veronica hederifolia* emerged in October, while *Corydalis cava*, *Viola riviniana*, and *Scilla bifolia* germinated the following year from March and April on. In all the species, seedlings in ant plots were dispersed the furthest, and in *C. cava* and *S. bifolia*, significantly more seedlings were spread beyond the 50 cm radius around mother plants by means of ants than in enclosures (see Figure 2 and Table 2).

3.1. *Corydalis cava*

The spatial distribution of *C. cava* in ant plots shows a highly scattered pattern of dispersed seedlings without particular aggregates or clumps (see Figures 2 and 3). The mean nearest neighbor for a *C. cava* seedling without ants was 10.55 ± 1.95 cm compared to 37.19 ± 5.37 cm in ant plots (Mann–Whitney U = 7.0; $p = 0.008$). The neighborhood density function (NDF) indicates higher levels of aggregation at small distances in enclosure plots with a maximum NDF value of 30.8 compared to an NDF value of 10.6 in ant plots (Figure 4). The maximum dispersal distance in this species was

279 cm. Regardless of distance, plots with ants contained more *Corydalis cava* seedlings than exclosures (12.57 ± 4.80 vs. 4.71 ± 1.19). One year later, 52% of prior seedlings in ant plots and 56% in exclosures had established as young vegetative plants and new seedlings emerged showing a similar distribution than in 2005.

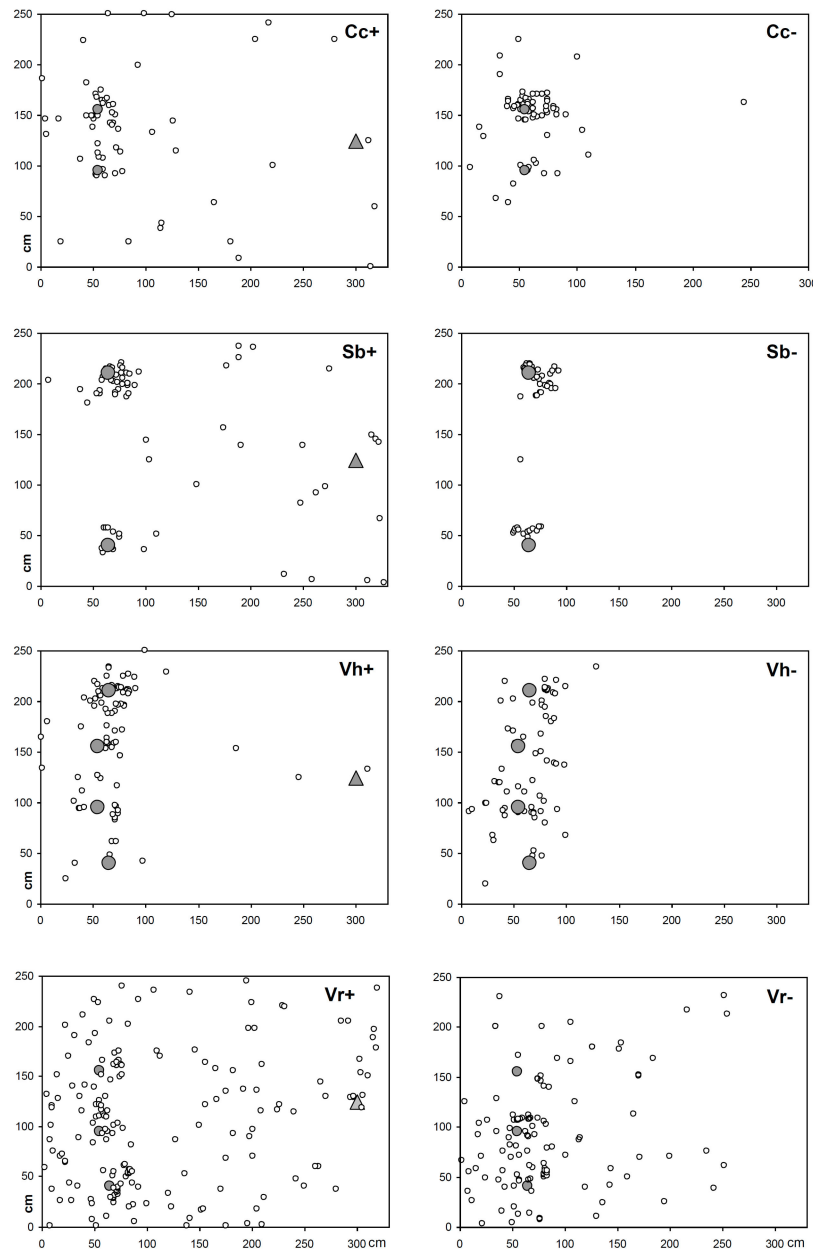


Figure 2. Spatial distribution of seedlings in *Myrmica* mesocosms. Seven replicates are plotted in one graph each. The open circles show the positions of seedlings. The grey circles represent each center of two to four initial mother plants (Cc—*Corydalis cava*, Sb—*Scilla bifolia*, Vh—*Veronica hederifolia*, Vr—*Viola riviniana*; + with ant nest, – without ant nest) and the triangles indicate the position of the *Myrmica* ant nest. The x- and y-axes represent the spatial mesocosm dimensions in cm.

Table 2. Mean of seedlings dispersed beyond a specified distance (a = 50 cm; b = 200 cm) in *Myrmica* ant plots and exclosures.

Species	%Seedlings		n seedlings		Mann-Whitney test		
	Exclosures	Ant plots	Exclosures	Ant plots	n	U	p
<i>Corydalis cava</i> ^a	7.5%	27.8%	0.50 ± 0.27	2.63 ± 1.10	7	11.0	0.021
<i>Scilla bifolia</i> ^a	2.3%	37.7%	0.43 ± 0.30	3.86 ± 1.62	7	9.0	0.027
<i>Veronica hederifolia</i> ^a	5.6%	10.0%	10.57 ± 2.36	11.29 ± 3.24	7	23.5	0.898
<i>Viola riviniana</i> ^a	36.9%	49.3%	6.71 ± 6.26	12.71 ± 7.83	7	14.0	0.180
<i>Viola riviniana</i> ^b	1.0%	12.5%	0.29 ± 0.76	3.43 ± 2.82	7	5.5	0.009

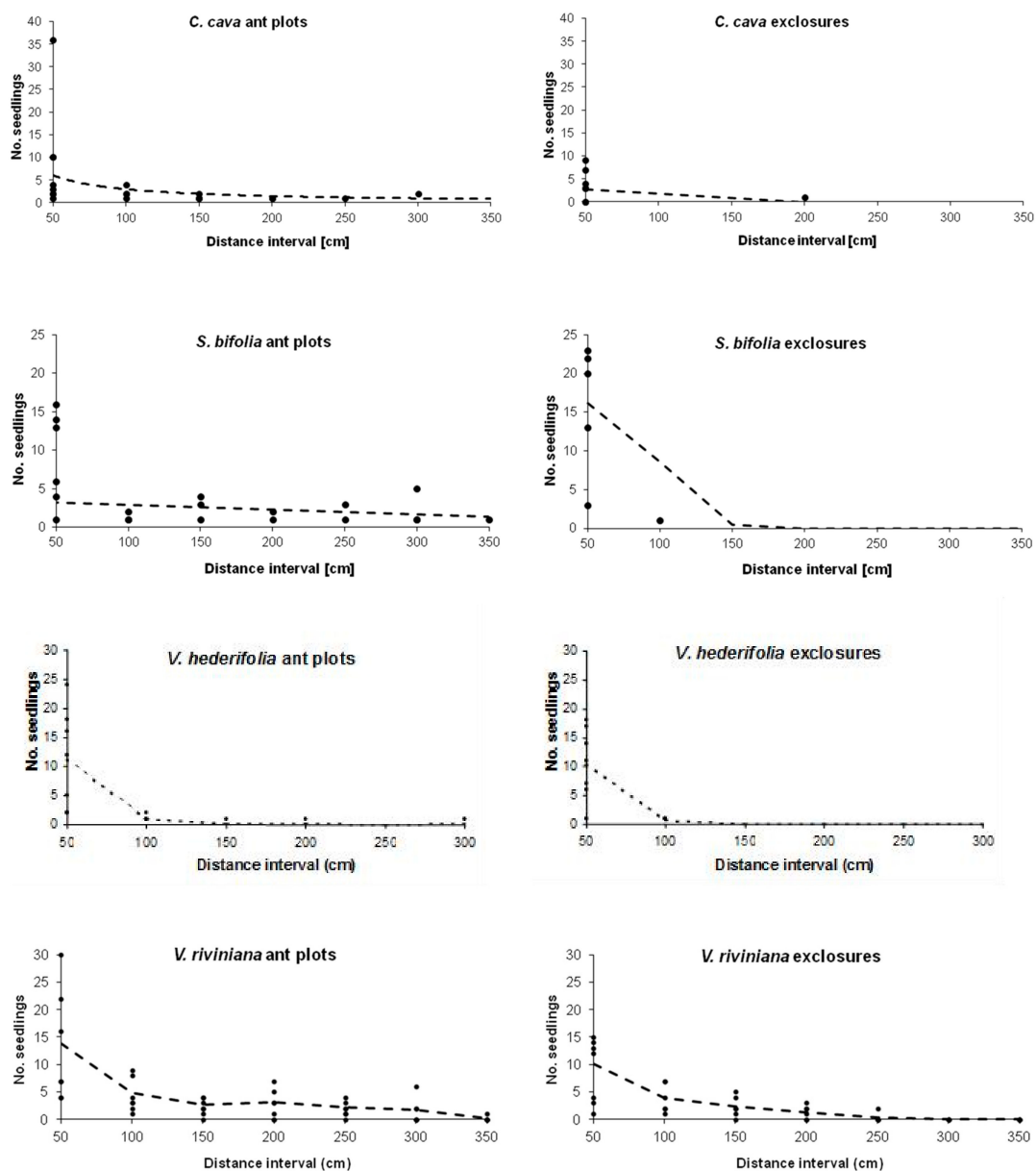


Figure 3. Dispersal curves of the seeds of the four study species (*Corydalis cava*, *Scilla bifolia*, *Veronica hederifolia*, and *Viola riviniana*) in ant plots and exclosures. Distances are given in 50 cm intervals beginning with 0–50 cm from the mother plants. The dashed line represents the mean dispersal curve of seedlings averaged over seven replicates and the dots represent the number of seedlings in single plots.

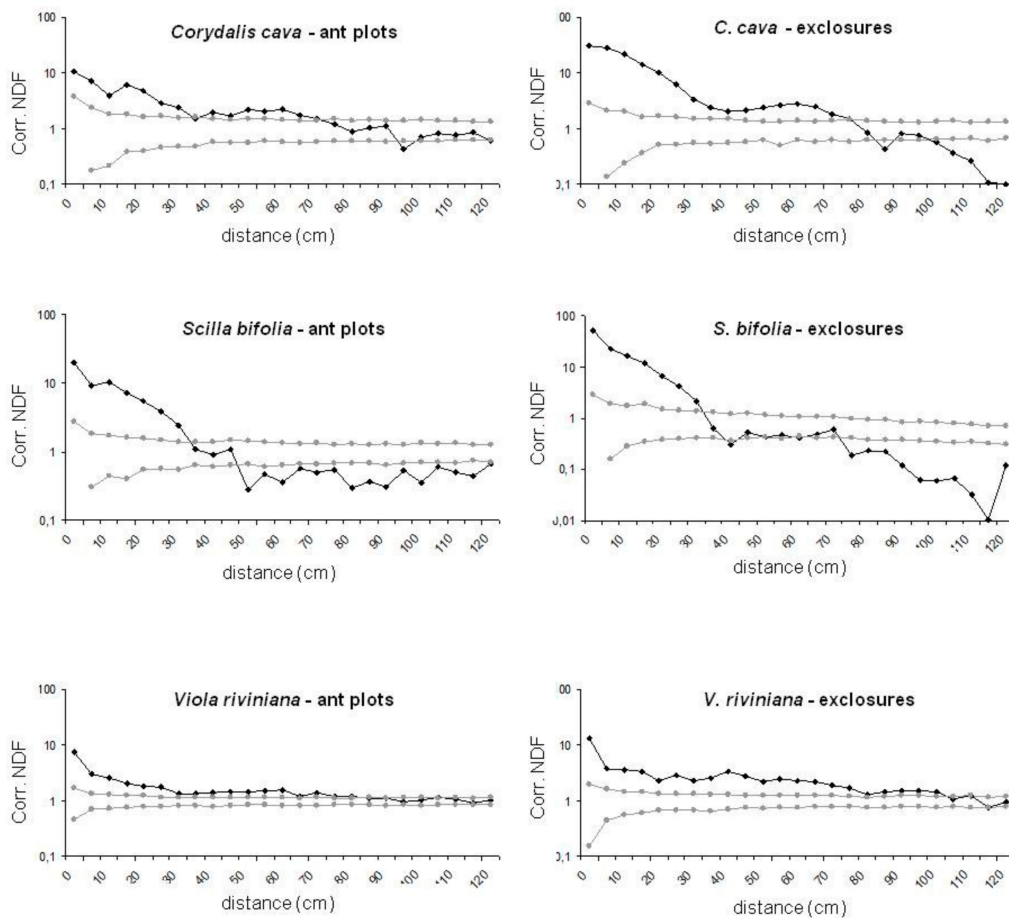


Figure 4. Corrected neighborhood density function (NDF) of *Corydalis cava*, *Scilla bifolia*, and *Viola riviniana* in ant plots and in exclosures. The black line represents the corrected NDF dependent on distance and the grey lines represent the 99% confidence interval for random distribution.

3.2. *Scilla bifolia*

Myrmica ant workers were seen carrying *Scilla bifolia* seeds to their nest and several seedlings emerged in more than 50 cm distance from the mother plants, with 322 cm as the highest dispersal distance of a seedling (Figure 3). As in *C. cava*, the spatial distribution of *S. bifolia* showed a highly scattered pattern of dispersed seedlings in ant plots, but at least three of these seedlings grew nearby the nest (see Figure 2). The mean nearest neighbor distance of *S. bifolia* seedlings without ants was non-significantly smaller than in ant plots (14.35 ± 9.34 cm vs. 16.56 ± 5.10 cm). The NDF shows high aggregation levels at small distances with a maximum of 52.1 in exclosures versus 7.4 in ant plots (Figure 4). With no difference between treatments, 70% of seedlings survived the first year and could be rediscovered in 2006.

3.3. *Veronica hederifolia*

Except for three presumably ant-dispersed outliers with a maximum distance of 258 cm, all *V. hederifolia* seedlings appeared in a radius of 68 cm around their mother plants (Figures 2 and 3). The mean nearest neighbor distance was 16.90 ± 7.13 cm in ant plots and 10.97 ± 2.54 cm in exclosures (Mann–Whitney $U = 12.0$; $p = 0.58$) with no significant difference between the treatments.

3.4. *Viola riviniana*

V. riviniana seedlings reached high dispersal distances in all plots with a maximum of 324 cm in ant plots and 241 cm in exclosures (Figure 3). Five apparently ant-dispersed seedlings appeared directly at the

nest, between the wooden branches. Although there was no significant difference between the treatments considering a 50 cm radius around the initial mother plants, the numbers of seedlings exceeding a distance of 200 cm showed a highly significant differentiation between ant plots and exclosures (see Table 2). The mean nearest neighbor distance was 18.75 cm with *Myrmica* and 23.88 cm without ants, was not significantly different between the treatments (Mann–Whitney $U = 12.0$; $p = 0.337$), and the NDF shows slightly higher values of aggregation up to a 100 cm distance in exclosure plots (Figure 4).

4. Discussion

4.1. Spatial Seed Dispersal Pattern and Distances

Myrmica ants had a substantial influence on the seedling distribution of most study plant species and they increased the dispersal distances of all four species. In the following section, we discuss the dispersal patterns and distances for the single plant species.

4.1.1. *Corydalis cava* and *Scilla bifolia*

Seedlings of the bulb geophytes, *Corydalis cava* and *Scilla bifolia*, showed a relatively randomized seed dispersal pattern and estimated by nearest neighbor distances, ant-dispersed individuals of these species had more free space unoccupied by conspecifics around them. Derived by the need of nutrients for colony development in spring, ants are reliable dispersal vectors when the seeds of spring geophytes ripen [30], so that those myrmecochorous bulb geophytes may have evolved the closest adaptation to myrmecochory. Without ants, these plant species might only gain considerable dispersal distances by rare endozoochorous transport events which may have taken place during Holocene immigrations to Central Europe [31,32].

4.1.2. *Veronica hederifolia*

Since most *V. hederifolia* seedlings emerged in the vicinity of the mother plants, myrmecochory is probably not as important for this species. The species is also dispersed nautochorously, epizoochorously, and endozoochorously [33,34]. For *V. hederifolia*, the costs for the development of elaiosomes in thickened cell walls can be supposed to play a minor role compared to *Scilla* or *Corydalis* bearing large elaiosomes so that this annual species may gain a positive net benefit even in the face of the apparently smaller dispersal benefit. Moreover, annual species do not suffer from intraspecific competition with mother plants but actually have to replace them for sustaining the population. In addition, for successful distance dispersal, the elaiosome could also optimize seed taste for animals favoring endozoochorous dispersal.

4.1.3. *Viola riviniana*

Viola riviniana exhibits capsules with a ballistic mechanism for autochorous seed dispersal. Nevertheless, there was an increase in dispersal distance due to the presence of *Myrmica* ants. Thus, *V. riviniana* can be clearly referred to as a diplochorous species producing seeds that are primarily dispersed ballochorously (seed dispersal by explosion) and that might occasionally be picked up and carried by ants afterwards [35]. The genus *Viola* comprises a set of myrmecochorous species with large elaiosomes, comparable to *Scilla* or *Corydalis* in our study, and a set of ballistic diplochorous species with rather small elaiosomes, like the Northern American Common Violet (*Viola papilionacea* Pursh [36]), or our Central European *Viola riviniana*.

4.2. Dispersal Distance

An increase in dispersal distances was apparent in all plant species during our experiments, whereas a decreased mortality could not yet be assured. However, the general decrease of aggregation and the increase of nearest-neighbor distance for ant-dispersed seedlings (significant in *Corydalis cava*) suggest a benefit in favoring the establishment and reproductive success of myrmecochorous plants. Myrmecochory thus gives the opportunity for seeds to escape from the mother plant including the

spatial growth of a population [37]. Those ant dispersed plants may thus suffer less from intraspecific competition while growing and the availability of a free sunlight gap could hence influence the chance of young *C. cava* and *S. bifolia* plants to develop into successful reproductive individuals in the following years.

The observed dispersal pattern in our experiment also suggests an improved genetic diversity of natural myrmecochorous plant populations through dispersal since the undirected relocation of seeds may reduce the proportion of having a sibling as nearest neighbor in a seed aggregation [38]. Already, Horvitz and Le Corff [39] showed that if spatial scale is ignored, ant-dispersed plants even show less clumped dispersion patterns than bird-dispersed species.

Considering distance dispersal in cultural landscapes, there is a severe lack of dispersal vectors in intensified environments only harboring a poor ant fauna, so that the annual migration rates of myrmecochorous plants may become extremely low. For another *Corydalis* species (Fumewort, *C. solida* (L.) Clairv.), Petersen and Philipp [40] found a migration rate of only 0.7 m per year in a new forest on former arable land, which is much lower than in our experiment. World-wide studies on ant invasions in natural communities have also shown that pest ants like the Argentine ant (*Linepithema humile* Mayr) can disrupt most myrmecochorous processes, causing a shift in natural plant communities which may involve the loss of large seeded myrmecochores [41,42]. Thus, nature conservation practices have to consider the maintenance of diverse ant communities, e.g., if endangered central European species such as Spring Pheasant's Eye (*Adonis vernalis* L.), Crested Cow-wheat (*Melampyrum cristatum* L.) or Narrow-leaved Lungwort (*Pulmonaria angustifolia* L.) shall be supported. *S. bifolia*, too, is locally declining due to climate change, eutrophication, and forestry [43]. For those plant species, a successful (re)-colonization of habitats will always require the abundance of suitable ants.

4.3. Directed Dispersal

In our study, about one fourth of *C. cava* seedlings were dispersed beyond 50 cm, resembling the observations of Ohkawara et al. [44] who counted that 11% of *Corydalis ambigua* Cham. & Schltdl. seeds dispersed from mother plants by different ant species in a Japanese forest. The same study also lists a proportion of 46% of seeds recovered in ant nests. This pattern was not found in our study system as we observed a highly scattered seedling distribution of *C. cava* seeds with *Myrmica*, and we could not find any remaining seeds in the nests. However, seeds may have been stored or buried in the nests without the chance to germinate, so that those seeds would have lost their germinability as the germination capacity of large seeds decreases rapidly with time [45].

The scattered pattern of seedlings in our ant plots could be caused by the dropping of seeds (ants that lose or leave seeds on the foraging trail [46]) but also by the secondary deposition of seeds from the nest [16]. In a dispersal study of *Carex pilulifera* with *Myrmica ruginodis*, only 16%–20% of collected seeds had obviously been relocated away from the nest, thereby being dropped along the path between nest and foraging area [16]. Only molded seeds had been relocated by *M. rubra* L. workers in a feeding experiment in which we provided dry and apparently unaffected nest sites to the colonies. Fokuhl et al. [5] suggested that the fraction of relocated seeds may depend on the hygienic state of seeds and nest sites. Also contrasting with the “directed dispersal hypothesis” [13,20] could not show any relationship between ant nest and plant distribution, which they discussed as consequence of the high turnover of ant nests in dunes or as a cause of a restricted seedling establishment. For the Northern American species, *Myrmica discontinua* Weber, Turnbull [47] did not find a spatial association between seedlings and ant nests, and for *Myrmica punctiventris* Roger, Banschbach and Herbers [48] reported nest movements within one year to be more common than perennial nest sites. Altogether, benefits through nutrient-enriched microsites—nest sites or garbage dumps—might rather be the exception for myrmecochorous plants dispersed by *Myrmica* ants [49].

5. Conclusions

Our results on the four plant species studied in *Myrmica* mesocosms confirm a strong dependence of myrmecochorous plants on ants if a species relies on only one dispersal vector, namely myrmecochory [50], while the diplochorous *Viola riviniana* uses a mixed dispersal strategy being able to spread their seeds without ants, too. Subsequent analyses of nearest-neighbor distances and the neighborhood density function indicated less aggregated seedling patterns around mother plants and higher convergence towards random seedling distributions.

Thus, our results validate the dependence on ants regarding the formation of dispersal patterns for myrmecochorous plants with distance dispersal as the major benefit (Table 3) through this mutualism.

Table 3. Benefits for study plants. Benefits for myrmecochorous plants in our experiments are indicated by ‘+’ for positive trends and by ‘++’ for significances, while absent differences are indicated as ‘○’.

Plant species	Distance dispersal	Directed dispersal	Establishment success	Dispersal vectors
<i>Corydalis cava</i>	++	○	○	ants only
<i>Scilla bifolia</i>	++	+	○	ants only
<i>Veronica hederifolia</i>	+	○	○	ants and animals
<i>Viola riviniana</i>	++	○	○	autochory (ballistic dispersal) and ants

Interestingly, slugs were also recently discovered to disperse the myrmecochorous herbs of central European forests [51] which is opening a new dimension in the discussion on whether myrmecochorous plants may be rather “slugichorous” [52].

Overall, the approach of studying myrmecochory (but also “slugichory”) in mesocosms provides a powerful set of opportunities for further research on invertebrate seed dispersal.

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