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# Effect of ants (Hymenoptera: Formicidae) on the floristic composition in a Mediterranean habitat complex

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## Abstract

With establishment of their nests, ants change the soil surface and the structure of the underground by modification of physical and chemical soil parameters. Moreover, ants influence the original vegetation of their habitats. We compared the flora on ant nests with the flora in the nest vicinity in a Greek habitat complex. The study included nests of *Aphaenogaster*, *Messor*, *Tapinoma* and five other genera in phrygana sites, pseudomaquis and ruderal pastures. The results of the study indicate a considerable influence of ants on the vegetation and their important role as seed dispersers. A total of 22 plant species (28.2 % of the recorded species number) occurred in significant higher numbers on or near the ant nests than in the environment. Seeds of further 13 plant species were recorded on refuse piles of the ant mounds or their seeds were transported by ants. We conclude that there is a similar large portion of ant-benefiting plants in the European Mediterranean region as in Mediterranean-type habitats of South Africa and Australia. The Greek sites are characterized by a low number of specialized myrmecochorous plants having seeds with elaiosomes. In contrast, there occurs a large number of dyszoochorous (often combined with hemerochorous) plant species. Dyszoochory by harvester ants of the genus *Messor* is significant in pastures and ruderal places. But several plant species appeared more frequently in the nest area of *Aphaenogaster ovaticeps*, *Tapinoma* spp or *Camponotus* spp as well. *A. ovaticeps* dominates the pseudomaquis sites and influences their floristic composition in a similar way as *Messor* species do in pastures. The large portion of dyszoochorous plants distinguishes the Greek sites from ant dominated habitat types in Southern Africa or Australia. We attribute the large portion of dyszoochorous and hemerochorous dispersal strategies to the enduring anthropogenous influence in the Mediterranean region over a long historical period.



## Zusammenfassung

Ameisen verändern mit ihrem Nestbau durch Modifikation bodenphysikalischer und -chemischer Parameter die Bodenoberfläche und die Bodenstruktur. Darüber hinaus beeinflussen sie die ursprüngliche Vegetation. Wir untersuchten die Flora auf bzw. neben Ameisennestern mit der Flora in der Umgebung. Die Untersuchung schloß Nester von *Aphaenogaster*, *Messor*, *Tapinoma* und fünf anderen Ameisengattungen in Phrygana, Pseudomacchie und ruderalen Weiden ein. Die Ergebnisse belegen einen erheblichen Einfluß von Ameisen auf die Vegetation und eine große Rolle bei der Ausbreitung von Samen. Es wurden 22 Pflanzenarten (28,2 % der insgesamt nachgewiesenen Artenzahl) signifikant häufiger auf dem Nest als in der Umgebung gefunden. Samen weiterer 13 Pflanzenarten wurden auf ‚Abfallhaufen‘ der Ameisen gefunden oder durch Ameisen aktiv zum Nest transportiert. Daraus folgern wir, daß im europäischen Mittelmeerraum eine ähnliche hohe Zahl an Pflanzenarten von Ameisen profitiert, wie es aus Lebensräumen des mediterranen Typs in Südafrika und Australien bekannt ist. Allerdings weisen die griechischen Untersuchungsflächen eine auffallend niedrige Zahl an spezialisierten Mymekochoren, deren Samen Elaiosomen besitzen, auf. Vielmehr wurde eine hohe Zahl an dyszoochoren Pflanzen, oft kombiniert mit Hemerochorie, gefunden. Dyszoochorie durch die Ernteameisen der Gattung *Messor* ist besonders häufig auf den Weiden und Ruderalplätzen. Eine Reihe von Pflanzenarten war jedoch häufiger auf Nestern omnivorer Ameisen wie *Aphaenogaster ovaticeps*, *Tapinoma* spp. oder *Camponotus* spp zu finden. *A. ovaticeps* dominiert die Pseudomacchie und beeinflußt dort die floristische Zusammensetzung in ähnlicher Weise wie *Messor* auf den Weiden. Der große Anteil dyszoochorer Pflanzen unterscheidet die griechischen Gebiete von Ameisen-dominierten Lebensraumtypen in Südafrika und Australien. Wir führen den hohen Anteil von dyszoochorer und hemerochorer Ausbreitung auf die seit

historischer Zeit wirksame anthropogene Landnutzung im europäischen Mittelmeergebiet zurück.

**Key words:** Mediterranean region, maquis, phrygana, myrmecochory, vegetation, *Messor, Aphaenogaster*, *Tapinoma*, *Camponotus*

## Introduction

Ants (Formicidae) belong to those organisms which control or change their environment notably: ants influence their ecosystems both top-down and button-up (PLATNER 2004).

With establishment of their nests, ants change the soil surface, the structure of the underground and the original vegetation by modification of physical and chemical soil parameters. Dependent from their way of life and given environmental conditions the water infiltration rate, oxygen contents and concentration of phosphate as well as potassium are increasing near ant nests (BEATTIE 1985, CZERWIŃSKI et al. 1971, CULVER & BEATTY 1983, DEAN & YEATON 1993, LOBRY DE BRUYN & CONACHER 1990, MACMAHON et al. 2000, OOSTERMEIJER 1989, WAGNER 1997). Therefore ant nests may serve as safe sites.

Furthermore, ants are able to remove parts of the vegetation from the nest or nest vicinity probably to avoid strong shadow (ARNDT & SCHNEEMANN, unpubl., see Fig. 6). However, the most important influence of ants on vegetation seems to be myrmecochory, the dispersal of plants by active transport of their propagules. Though myrmecochory is regarded as dispersal type over low distances, the dispersal rate of propagules increases and density dependent (negative) effects, such as competition, predation, or influence of parasites decreases (WILSON & TRAVSET 1992, WOLFF & DEBUSSCHE 1999). Also genetic regression by autogamy can be minimized (MANZANETA et al. 2005, LEINS 2000).

In our opinion, the term "myrmecochory" includes both types of seed of dispersal by ants: dyszoochory and synzoochory. The transport of seeds by granivorous ants (harvester ants) is an aspect of dyszoochory. It often occurs in semiarid regions with dry seasons. Harvester ants, especially those of genus *Messor*, represent together with birds and small mammals the most important seed predators of arid regions influencing the structure and composition of plant communities noticeably (AZCÁRATE et al. 2005, HENSEN 2002, MACMAHON et al. 2000, SCHRÖDER 1998). But seeds rich in lipids, proteins and carbon hydrates also form an additional source of food for several omnivorous ant species in periods of low availability of animal prey (SEIFERT 2007).

Though an important portion of the seeds will be eaten, these plants benefit from ants. Several seeds are lost during transport combined with dispersal over several metres (RETANA et al. 2004, HENSEN 2002, SCHNEEMANN & ARNDT 2007, WOLFF & DEBUSSCHE 1999). Some of the transported seeds will not be eaten, but replaced by other seeds and deposited in waste chambers or waste places (GUARINO et al. 2005, HENSEN 2002, MACMAHON et al. 2000, RETANA et al. 2004). Therefore, plant species benefit even by harvester ants not only from dispersal but also from good conditions for germination.

Synzoochory (or "specialized myrmecochory" in the sense of GORB & GORB 2003) is the second type of myrmecochory. Synzoochorous plants provide an elaiosome attracting especially omnivorous species (SERNANDER 1906, ULBRICH 1939, OOSTERMEIJER 1989, HUGHES & WESTOBY 1992, BONN & POSCHLOD 1998, GAMMANS 2005, ÖZLANT 2005, GILADI 2006). They only use the elaiosome for feeding and deposite the undamaged seeds after transport outside the nest. The specialised myrmecochorous plants avoid see predation by mammals (GORB & GORB 2003) and have a much higher germination rate in comparison with dyszoochorous plants. Therefore, the main differences between dyszoochory and synzoochory concern the involved ant species (genera) and foraging behaviour.

Myrmecochory is a global phenomenon (LENGYEL et al. 2010), but it is particular widely distributed among geophytic herbs of temperate deciduous forests (BEATTIE & CULVER 1981, GORB & GORB 2003, HANDEL et al. 1981) and in the vegetation of some Mediterranean-type regions. A great importance of ants as plant dispersers was shown in open and xerothermic shrub habitat types of South Africa and Australia (BOND et al. 1991, BUCKLEY 1982, WESTOBY et al. 1991). In contrast, myrmecochory is widely lacking in Californian charrapal (MOONEY & HOBBS 1994) and it is still

Fig. 1. Map of Greece with the position of the study area.

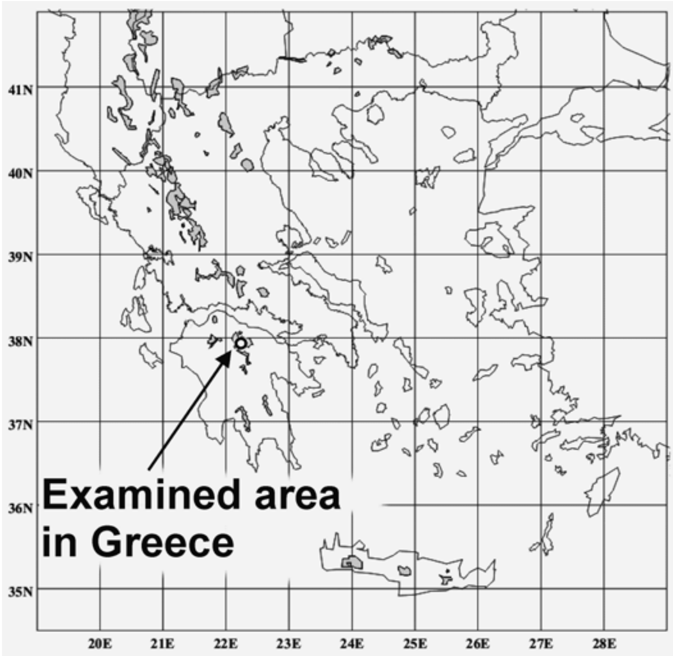


Fig. 2. Part of the study area in northwestern Peloponnisos (April 2006, photo: E. Arndt).

unclear if ants have the same importance as ecosystem engineers in the Mediterranean area as they do in the South African or Australian regions.
Studies on myrmecochory in the Mediterranean area started with Müller-Schneider (1933) but mainly concern a certain plant species or group of few species (Affre et al. 1995, Aronne & Wilcock 1994, Baiges et al. 1991, Espadaler & Gómez 1997, Garrido et al 2002, Li Vigni et al. 2001). Ecosystem effects of ants in the Mediterranean area are confirmed by examinations of seed predation and distribution by *Messor barbarus* (Azcárate & Peco 2003, Azcárate et al. 2005, Reyes-López & Fernández-Haeger 2002, Sanchez et al. 2006) and the study of Wolff & Debussche (1999) in a fallow land. But the number of known myrmecochorous species in the Mediterranean area is by far not as high as in South Africa and Australia. A total of 128 plant species with elaiosome or other ant attracting seed structures (fatty seed coat of pedicellus) are actually known from the European Mediterranean area (Schneemann & Arndt 2007).

The aims of the present paper are (i) to examine the influence of ants on the vegetation in a Mediterranean habitat complex, and (ii) to determine plant species which benefit by ant behaviour and/or environmental conditions on ant nests.

## Material and methods

The vegetation was analysed at 91 study sites with ant nests in a Mediterranean habitat complex near Feneós (Greece, NW Peloponnisos, 37°55'03, 22°17'41; altitude around 900m NN; Figs 1, 2). The main annual temperature of Feneós is between 12 and 14°C, the annual rainfall averages 900mm, 350mm at winter and 25mm at summer (Spyridion 1981). The study included the habitat types phrygana (28 sites), pseudomaquis (in the sense of Adamovic 1909, see also Dafis 1975, Horvat et al. 1974; 14 sites) and ruderal pastures (49 sites) covering a total area of about 15 ha. The field work was carried out between March–August of 2006. There were examined 55 nests of *Messor* sp. [*M. meridionalis* (André), *M. structor* (Latreille)], 17 of *Aphaenogaster ovaticeps* (Emery), and 9 of *Tapinoma* sp. [(T. *erraticum* (Latreille), *T. simrothi phoeniceum* (Emery)]. A few nests of *Camponotus aethiops* (Latreille) (3 nests), *C. gestroi* (Emery) (1), *Crematogaster sordidula* (Nylander) (2), *C. ionia* (Forel) (1), *Formica fusca* (Linné) (1), *Pheidole pallidula* (Nylander) (1) and *Tetramorium semilaeve* (André) (1) were also examined but excluded from the statistical analysis. The two species of *Messor* and of *Tapinoma* respectively were combined in the statistical analysis, because the species pairs are apparently very similar in terms of nest building and food recruitment.

Each study site covered 5 $m^2$ (Fig. 3). In order to analyse the vegetation and to compare the plant community in the immediate nest environment with the plants in the vicinity, squares of $1m^2$ were marked out. The minimum distance between recorded ant nests of the mentioned species was 8 m. The recorded ant nest was situated in the middle of the central square. Two adjacent squares were analysed each in a north-eastern and south-western direction of the central square. The individuals of all plant species were counted in each of the squares not regarding them as ramet or gamet. However, in the case of tussock-forming plants, only the tussocks were counted (e.g. *Aegilops triuncialis*, *Anthoxanthum odoratum*, *Dactylis glomerata* and *Vulpia myurus*).
Moreover, we searched for transport of seeds around each ant nest. Over a period of 30 minutes we counted the number of seeds transported by worker ants into the nest and determinate the plant species of these seeds. Additionally, the seeds on the refuse piles (in direct vi-

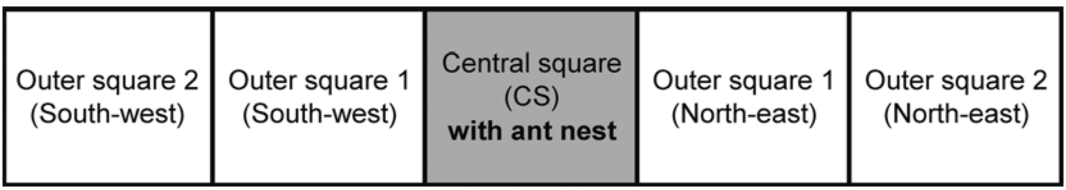


Fig. 3. Arrangement of examined squares (1 $m^2$) at each study site.

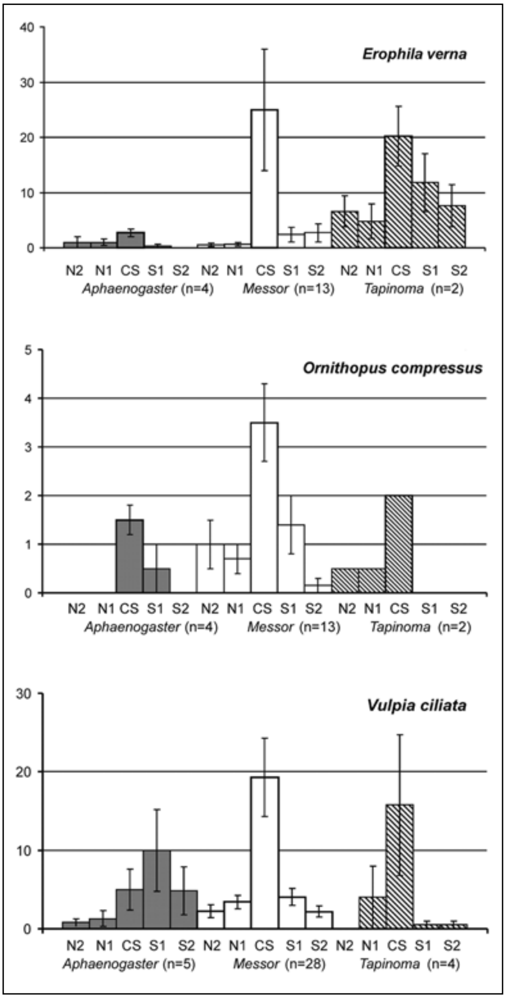


Fig. 4. Average and SD of individuals of *Erophila verna*, *Ornithopus compressus* and *Vulpia ciliata* in central squares (CS) and adjacent northeastern (N1, N2) and southwestern squares (S1, S2) of nests of 3 different ant genera. The plant individuals of *E. verna* and *V. ciliata* are significantly increased in CS of *Messor* and *Tapinoma*, those of *O. compressus* are significantly increased in CS of *Messor* and *Aphaenogaster* (compare Fig. 3 and Table 1).

cinity of ant nests) were counted and determined. The refuse piles were always located in the central square. They are located on or at the margin of the nests.

The decrease or increase of the number of each plant species from the nest (central square) to the more distant environment of the nest (outer squares) was analysed using simple Pearson correlations.

Fig. 5. Open soil surface and extent of a typical nest of *Messor meridionalis* in the study area in early April (beginning of the study period; photo: E. Arndt).

## Results

A total of 78 plant species was found at the 91 study sites (Tabs 1, 2). Many of these plants (46 species) occurred more frequently around the nest in the central square than in outer squares in at least one of the ant species. However, a significantly higher abundance in the central square than in the vicinity was found in 22 plant species (28.2 %). Seeds of additional 13 plant species were transported by ants. So we can conclude that at least 44.9 % of plant species in the studied Mediterranean habitat complex may benefit from ants. This number may be much higher, because several plants were more abundant in central squares as well, but failed statistical significance (see Tab. 1).

A separate analysis of nests of the three examined ant genera *Aphaenogaster*, *Messor* and *Tapinoma* allows a more differentiated insight. A total of 8 plant species occurred in a significantly increased number in the central squares of two different ant genera (Tab. 1): *Aegilops triuncialis*, *Crepis hellenica*, *Erophila verna*, *Ornithopus compressus*, *Poa timoleontis*, *Sanguisorba* *minor*, *Sphenopus divaricatus* and *Vulpia ciliata*. These plants benefit not only from harvester ants but also from active distribution by omnivorous ant species. As an example, Fig. 4 shows the distribution of *Erophila verna*, *Ornithopus compressus* and *Vulpia ciliata* over the nest gradients in *Aphaenogaster*, *Messor* and *Tapinoma* species. Transport of seeds was observed in nearly all of these plants. *Poa timoleontis* was the only plant species with significantly increased numbers on nests of a *Camponotus* species (*C. aethiops*, not included in Tab. 1).

The majority of study sites concerned characteristic Mediterranean habitat types: dry grassland (BRACHYPODIIO-TRIFOLIETUM STELLATI, HORVAT et al. 1974); phrygana (ASTRAGALO-SACROPPTERIETUM SPINOSI, OBERDORFER 1954), pseudomaquis (QUERCETUM COCCIFERAE, DAFIS 1975) and open ruderal places.

We investigated the highest concentration of ant nests in ruderal places. There were found 37 plant species, 16 (43.2 %) of which appeared in a significant higher number near the ant nests. The transport of seeds was recorded for 26 plant species.

The concentration of ant nests in dry grassland was lower than in the ruderal places, nevertheless there were recorded 48 plant species on ant mounds, 19 (39.6 %) in a significant higher number than in the vicinity. Seeds of 25 plant species of the dry grassland were transported or found on refuse piles respectively. A high number of ant nests was examined in the phrygana as well, but these sites were distributed over a larger area. We found 55 plant species in the examined phrygana sites, 20 (36.4 %) of which appeared in a significant higher number near the ant nests. Seeds of additional 9 species were transported by different ants. The pseudomaquis sites produced comparable results. A total of 35 plant species were recorded, 14 (40.0 %) with a significantly higher abundance in the central square and seeds of three further plants were actively distributed by ants.

The pseudomaquis sites were dominated by *A. ovaticeps*, the phrygana by *A. ovaticeps* as well as by *Messor* spp, and ruderal places and pastures were clearly dominated by *Messor* spp. Our results show that *Aphaenogaster* have a similar strong influence on flora and vegetation of (pseudo)maquis than *Messor* species in open habitats. The number of examined nest mounds of other and especially of smaller ant species (e.g. *T. erraticum*, *T. simrothi*, *C. ionia*) was too low to estimate their influence on the floristic composition. However, increased plant numbers on these nests, observations of transported seeds and recorded seeds on their refuse piles (Tab. 2) indicate their possible influence on distribution of plant species.

**Discussion**

The extraordinary role of ants as dispersers of plants in Mediterranean-type vegetation is well known from South Africa and Australia. COWLING et al. (1992, 1994) estimate the portion of all myrmecochorous species in the Cape fynbos to about 30 % and the portion of a typical local fynbos flora more than 25 %. A similar situation is known from Mediterranean Australia (MILEWSKI & BOND 1984).

The results of our study indicate that ants may play an important role in the floristic composition of the European Mediterranean area, too. In our study, at least 44.9 % of plant species benefit from ants. This high portion of ant-benefiting plants may be caused partly by competition advantages on ant mounds instead of direct ant dispersal. The plants find a low number of competitive species there (Fig. 5). Several authors report an increased concentration of nutrients on ant hills (CZERWIŃSKI et al. 1971, DEAN & YEATON 1993, PLATNER 2004) supporting germination and plant growth.

The analysis of our results allows us to assume that the increased frequency of a large number of plant species in the ant nest area is not due to the effects of simple competition or better conditions for germination due to the large portion of ground free of vegetation. More probably ants support such plants actively by dispersal. This is confirmed by observations of many different transported seeds (see Tab. 2 and SCHNEEMANN & ARNDT 2007 for details), but also by AZCÁRATE et al. 2005 and WOLFF & DEBUSSCHE 1999. Germinable seeds are deposited on refuse piles (Tab. 2), but sprouting plants are not equally handled by the ants. At least harvester ants cut certain plants such as large-leafed Asteraceae probably to avoid too much shadow or overgrowth (ARNDT & SCHNEEMANN unpubl., Fig. 6). On the other side, plants which serve feeding are obviously planted by ants on or near the nest. E.g. we could observe in the direct nest area of a *M. meridionalis* more than 350 specimens of *Erophila verna* or 65 specimens

Fig. 6. *Messor meridionalis* cut a large plant and remove it from their nest (April 2006, photo: E. Arndt).

of *Capsella bursa-pastoris* though these plants were apparently lacking in the environment (Fig. 7).

One characteristic of the vegetation in the examined Mediterranean habitat types is the large proportion of dyszoochorous plants and the small number of elaiosome bearing species. *Polygala monspeliaca* is the only species in our study with known elaiosome (Ulbrich 1939). This characteristic makes the difference between the examined Mediterranean area and those in Southern Africa or Australia. We attribute this large portion of dyszoochory to the enduring anthropogenous influence in the Mediterranean region. The several thousand-year old anthropogenous influence is specially related to man-made habitat types like phrygana, pseudomaquis and ruderal places. Consequently, there are dominating plant species which also benefit by human activities. An analysis of distribution vectors confirms that most of recorded plant species in the study area (i) are multichorous and (ii) have adopted the hemerochorous dispersal strategy (Schneemann & Arndt 2007). Specialized myrmecochorous plants as *Carex* spp, *Euphorbia* spp, *Luzula* spp, *Melica* spp, *Polygala* spp, *Veronica* spp or *Viola* spp were under-represented or lacking in examined sites.

However, the distribution ecology and seed morphology of many Mediterranean plants are still less known. Further examinations should focus on the development of elaiosomes in ant-distributed Mediterranean plants. It also should be tested if the distribution strategy “hemerochory + dyszoochory” dominates naturally in Mediterranean habitats or if it results from long-standing human activities.

Fig. 7. Nest of *Messor meridionalis* with numbers of individuals of *Capsella bursa-pastoris*. This plant species occurred exclusively on ant mounds in a large part of the study area (April 2006, photo: E. Arndt).

## Acknowledgements

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## Tables

**Table 1.** List of recorded plants with number of nests where they occurred in the central square (CS: nest or direct nest vicinity). Columns 3-5 ("Increased abundance") indicate whether the number of plant individuals increases from the outer square to the CS with nest (PEARSON correlation, only the three most abundant ant genera are shown). Abbreviations: n.incr. - abundance not increased in CS; n.s. – abundance increased, but not significantly; trend - significance ($p \leq 0.05$) hardly failed.

| Plant species | CS | Increased abundance in CS | | |
|---|---|---|---|---|
| | | *Messor* nests (n=59) | *Aphaenogaster* nests (n=17) | *Tapinoma* nests (n=9) |
| *Aegilops geniculata* | 2 | n.s. | - | - |
| *Aegilops neglecta* | 2 | n.s. | - | - |
| *Aegilops triuncialis* | 28 | p=0.00124 | p=0.00812 | n.incr. |
| *Anthemis segetalis* | 16 | n.incr. | n.incr. | n.incr. |
| *Anthoxanthum odoratum* | 20 | p=0.00572 | n.incr. | n.incr. |
| *Arenaria leptoclados* | 12 | p=0.00048 | - | - |
| *Avena fatua* | 1 | - | n.s. | - |
| *Brachypodium sylvaticum* | 2 | n.incr. | - | - |
| *Briza maxima* | 3 | n.incr. | n.s. | - |
| *Bromus madritensis* | 7 | n.incr. | trend n.s. | - |
| *Capsella bursa-pastoris* | 29 | p<0.0001 | n.incr. | n.incr. |
| *Cardamine hirsuta* | 32 | p<0.0001 | n.s. | n.s. |
| *Carex flacca* | 1 | - | n.s. | - |
| *Centaurea raphanina* | 1 | n.s. | - | - |
| *Cerastium glomeratum* | 29 | p=0.01133 | n.s. | n.incr. |
| *Cerastium semidecandrum* | 3 | n.s. | - | - |
| *Cistus parviflorus* | 18 | n.incr. | n.incr. | n.incr. |
| *Cistus salviifolius* | 2 | - | n.incr. | - |
| *Convolvulus althaeoides* | 1 | n.incr. | - | n.incr. |
| *Crepis hellenica* | 27 | p<0.0001 | p=0.02063 | n.incr. |
| *Crepis neglecta* | 3 | n.incr. | n.incr. | - |
| *Cynosurus echinatus* | 9 | n.incr. | n.s. | n.incr. |
| *Dactylis glomerata* | 34 | n.s. | n.incr. | trend n.s. |
| *Daucus carota* | 1 | - | n.s. | - |
| *Dorycnium hirsutum* | 1 | - | n.incr. | - |
| *Erophila verna* | 28 | p=0.00083 | n.s. | p=0.00287 |
| *Eryngium campestre* | 10 | n.incr. | n.incr. | n.incr. |
| *Filago gallica* | 4 | trend n.s. | n.incr. | - |
| *Helictotrichon convolutum* | 3 | n.incr. | n.s. | - |
| *Hippocrepis unisiliquosa* | 2 | n.s. | n.s. | - |
| *Hordeum murinum* | 3 | n.incr. | - | n.incr. |
| *Hymenocarpus circinnatus* | 2 | n.incr. | - | n.incr. |

| Plant species | CS | Increased abundance in CS | | |
|---|---|---|---|---|
| | | *Messor* nests (n=59) | *Aphaenogaster* nests (n=17) | *Tapinoma* nests (n=9) |
| *Knautia integrifolia* | 1 | n.incr. | - | - |
| *Linaria pelisseriana* | 5 | n.incr. | n.incr. | - |
| *Linum trigynum* | 12 | n.incr. | p=0.01017 | - |
| *Lotus angustissimus* | 6 | n.incr. | n.incr. | n.incr. |
| *Lotus ornithopodioides* | 0 | n.s. | - | - |
| *Medicago aculeata* | 0 | n.incr. | - | - |
| *Medicago minima* | 3 | n.s. | - | n.incr. |
| *Medicago orbicularis* | 4 | n.incr. | - | - |
| *Medicago polymorpha* | 17 | n.s. | n.incr. | n.incr. |
| *Micromeria nervosa* | 2 | - | - | n.incr. |
| *Minuartia globulosa* | 0 | n.incr. | - | - |
| *Onobrychis caput-galli* | 6 | p=0.00225 | n.s. | - |
| *Ononis spinosa* | 1 | n.incr. | - | - |
| *Ornithopus compressus* | 22 | p<0.0001 | p<0.0001 | n.incr. |
| *Parentucellia latifolia* | 10 | p=0.00028 | n.incr. | - |
| *Petrorhagia glumacea* | 14 | p=0.00693 | trend n.s. | n.s. |
| *Phleum pratense* | 6 | p=0.00046 | - | n.incr. |
| *Phlomis fructicosa* | 1 | n.incr. | - | - |
| *Picris hieracioides* | 1 | - | - | n.incr. |
| *Plantago lanceolata* | 18 | n.s. | n.incr. | n.incr. |
| *Poa timoleontis* | 54 | p<0.0001 | trend n.s. | n.incr. |
| *Polygala monspeliaca* | 8 | n.incr. | n.incr. | n.s. |
| *Potentilla reptans* | 1 | n.incr. | - | - |
| *Prunella laciniata* | 13 | n.incr. | n.incr. | - |
| *Quercus coccifera* | 1 | n.incr. | n.incr. | n.incr. |
| *Quercus frainetto* | 3 | - | n.incr. | n.incr. |
| *Sanguisorba minor* | 18 | p=0.00016 | p=0.0105. | n.incr. |
| *Scorzonera laciniata* | 6 | n.incr. | n.incr. | n.incr. |
| *Sedum ochroleucum* | 7 | n.incr. | trend n.s. | n.incr. |
| *Sideritis romana* | 5 | n.s. | n.s. | n.incr. |
| *Spartium junceum* | 3 | - | n.incr. | - |
| *Sphenopus divaricatus* | 24 | p<0.0001 | p=0.00026 | n.s. |
| *Trifolium angustifolium* | 13 | n.incr. | n.incr. | n.incr. |
| *Trifolium arvense* | 9 | n.incr. | n.incr. | - |
| *Trifolium campestre* | 23 | n.incr. | trend n.s. | n.incr. |
| *Trifolium nigrescens* | 1 | n.incr. | - | n.s. |
| *Trifolium repens* | 3 | n.incr. | - | - |
| *Trifolium scabrum* | 14 | n.incr. | n.s. | n.incr. |
| *Trifolium stellatum* | 16 | n.incr. | n.incr. | n.incr. |
| *Tuberaria guttata* | 13 | n.s. | p=0.00812 | - |
| *Vulpia ciliata* | 38 | p<0.0001 | n.incr. | p=0.00323 |
| *Vulpia myuros* | 3 | p=0.0121 | - | - |

**Table 2.** Number of recorded nests with seed transport or seeds in the refuse piles (number of observed ant nests in parentheses). Note that records of transport reflect only a 30 min observation per nest.

| Plant species | *Messor* spp | *Aphaenogaster ovaticeps* | *Tapinoma erraticum* | *Camponotus aethiops* | *Crematogaster ionia* |
|---|---|---|---|---|---|
| *Aegilops triuncialis* | refuse (2) | | | | |
| *Anthemis segetalis* | transport (1)<br>refuse (1) | | | | |
| *Anthoxanthum odoratum* | transport (7)<br>refuse (8) | | refuse (1) | | |
| *Arenaria leptoclados* | transport (4)<br>refuse (1) | | | | |
| *Avena barbata* | transport (1) | | | | |
| *Briza maxima* | transport (2)<br>refuse (1) | | | | |
| *Bromus madritensis* | transport (2)<br>refuse (2) | transport (1) | refuse (1) | | |
| *Capsella bursa-pastoris* | transport (7) | transport (1)<br>refuse (1) | | | |
| *Cardamine hirsuta* | transport (1)<br>refuse (1) | transport (1) | | | |
| *Carex flacca* | transport (1) | | | | |
| *Centaurea raphanina* | transport (1)<br>refuse (1) | | | | |
| *Cerastium glomeratum* | transport (8)<br>refuse (5) | | transport (1) | | |
| *Cerastium semidecandrum* | transport (1) | | | | |
| *Convolvulus althaeoides* | transport (1) | | | | |
| *Crepis hellenica* | transport (7)<br>refuse (5) | transport (1) | | transport (7)<br>refuse (5) | |
| *Crepis neglecta* | transport (1) | | | | |
| *Dactylis glomerata* | transport (1) | | | | |
| *Daucus carota* | refuse (1) | | | | |
| *Erophila verna* | transport (2) | | refuse (1) | | |
| *Eryngium campestre* | transport (1) | | | | |
| *Filago gallica* | transport (2) | | | | |
| *Hippocrepis unisiliquosa* | transport (1) | transport (1) | | | |
| *Hordeum murinum* | transport (1) | | | | |
| *Linum trigynum* | transport (3)<br>refuse (1) | transport (1) | | | |
| *Lotus ornithopodioides* | refuse (1) | | | | |
| *Medicago aculeata* | transport (3)<br>refuse (1) | | | | |
| *Medicago minima* | transport (1)<br>refuse (1) | transport (1) | | | |
| *Medicago orbicularis* | transport (3)<br>refuse (2) | | | | |
| *Medicago polymorpha* | transport (5)<br>refuse (8) | | refuse (1) | | |
| *Onobrychis caput-galli* | transport (1)<br>refuse (5) | refuse (1) | | | |
| *Ononis viscosa* | transport (1) | | | | |
| *Ornithopus compressus* | transport (4)<br>refuse (12) | transport (1)<br>refuse (1) | | | |

| Plant species | *Messor* spp | *Aphaenogaster ovaticeps* | *Tapinoma erraticum* | *Camponotus aethiops* | *Crematogaster ionia* |
|---|---|---|---|---|---|
| *Parentucellia latifolia* | transport (1)<br>refuse (2) | transport (1) | | | |
| *Petrorhagia glumacea* | transport (2)<br>refuse (7) | transport (1)<br>refuse (1) | | | |
| *Phleum pratense* | transport (1) | | | | |
| *Picris hieracioides* | transport (1) | | | | |
| *Plantago lanceolata* | transport (1) | | | | |
| *Poa timoleontis* | transport (16)<br>refuse (4) | | transport (1)<br>refuse (1) | | |
| *Polygala monspeliaca* | transport (3) | | | | |
| *Sanguisorba minor* | | transport (1) | | transport (1) | |
| *Scorzonera laciniata* | refuse (1) | | | | |
| *Sedum ochroleucum* | refuse (1) | | | | |
| *Sideritis romana* | refuse (2) | transport (1)<br>refuse (1) | | | refuse (1) |
| *Sphenopus divaricatus* | transport (1) | | | | |
| *Trifolium angustifolium* | transport (2) | | | | |
| *Trifolium arvense* | transport (2) | | | | |
| *Trifolium campestre* | transport (8)<br>refuse (2) | transport (3) | | transport (1) | |
| *Trifolium scabrum* | transport (4)<br>refuse (2) | transport (1) | transport (1) | | |
| *Trifolium stellatum* | transport (6)<br>refuse (2) | | transport (1) | | |
| *Tuberaria guttata* | transport (2)<br>refuse (3) | transport (1)<br>refuse (1) | | | |
| *Vulpia ciliata* | transport (13)<br>refuse (4) | transport (1) | | | |
| *Vulpia myuros* | transport (1)<br>refuse (2) | | | | |

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