

# Plant-ant interaction in xerophilous ephemeral vegetation of S.E. Sardinia

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## Abstract

Frequency and abundance of annual plants have been measured in 40 square plots, 0.36 m<sup>2</sup> each, settled in an area of approximately 5 ha at the foothill of the Sarrabus massif, in S.E. Sardinia. 20 plots were randomly distributed at less than 5 m from the ant nests, further 20 at more than 30 m from the ants nests. The results showed a significantly lower plant density next to the ant nests, together with a higher species richness. Far from the nests, plots resulted dominated by relatively few species with a patchy distribution, while next to the nests the distribution of frequencies resulted more homogeneous. It is suggested that harvesting ants may contribute to the small-scale regulation of frequency and abundance of annual species and therefore contrast the natural tendency towards increasing the spatial order (and reducing the plant diversity) by the formation of patches. Being ants nests more frequent on secondary vegetation linked to a slight grazing-pressure, such traditional land-use might benefit indirectly the spatial heterogeneity and diversity of plant communities dominated by annuals.

**Key words:** Mediterranean region, ants, *Tuberarietea guttatae*.

## 1. Introduction

The coevolution of angiosperms and ants spans over the last 80 millions yrs and is documented by several examples of symbioses (surveys in: BUCKLEY 1982, BEATTIE 1985, HÖLLEDOBLER & WILSON 1990, HUXLEY & CUTLER 1991). All over the world, several angiosperms accomplish the seed dispersal through myrmecochory, that is the employment of elaiosomes that induce the ants to transport the seeds without arming the embryo or the endosperm. Many ant species use to eat elaiosomes before abandoning the seeds in the field or on heaps of refuges next to the nests.

Providing seeds with elaiosomes involves a metabolic cost that is the more difficult to sustain the more the allocation of water and nutrients is unfavourable for the plant growth (HUGHES et al. 1993). On the other hand, in dry environments with relatively poor soils, ants often do not eat just the elaiosome but feed on the whole seed (O'DOWD & HAY 1980, ARONNE & WILCOCK 1994). Correspondently, the selectivity of ants becomes lower and the seed predation focuses prevalently on the most abundant seeds, with no matter on the occurrence of elaiosomes (DAVIDSON et al. 1980, HAHN & MASCHWITZ 1985, CERDAN et al. 1986). All other things being equal, some seed-predating ants exhibit anyway a certain degree of selectivity towards some plant species (MOTT & MCKEON 1977, WHITFORD 1978, DAVIDSON 1982, RISCH & CARROL 1986, JOHNSON 1991, FEWELL & HARRISON 1991), but the basis of this selectivity is substantially unknown (HÖLLEDOBLER & WILSON l.c.).

Most of the seed-predating ants, also called harvesting ants, belong to the subfamily *Myrmicinae* and chiefly occur in subtropical dry environments, where they are particularly abundant in grasslands and shrublands linked to mediterranean or subdesertic climates. Although seed predating ants destroy a relevant part of the collected seeds, they also contribute to the seed dispersion by losing a part of seeds along the way, or discarding them by accident in the nest.

There are several studies dealing with the foraging behaviour and performances of harvesting ants (reviews in: HÖLLDOBLER & WILSON l.c, HUXLEY & CUTLER 1991), but relatively few focus on their effects on vegetation. Studies about this subject have been carried out in North America (BROWN et al. 1979 a,b, RISSING 1986, RISCH & CARROL 1986, MULL & MCMAHON 1996, BROWN & HUMAN 1997), South Africa (BOND & SLINGSBY 1983) and Australia (ANDERSEN 1987). As concerns the Mediterranean region, even if seed-predating ants were already mentioned in the Book of Solomon and in several ancient Greek and Roman writings (WILSON 1984), at the begin of the twentieth century harvesting ants were still considered a very occasional agent of seed dispersal (SERNANDER 1927, MULLER 1933). Up to now there is a clear lull in the study of the ecological role of harvesting ants in the Mediterranean region and most of the data collected by scientists in other areas of the world still need to be verified for this region. Nearly all the available data deal with the seed predation of some Mediterranean shrubs and phorbs (WILCOCK & DE ALMEIDA 1988, DANIN & YOMTOV 1990, PACINI 1990, THANOS 1992, ARONNE & WILCOCK l.c., LISCI & PACINI 1977, VIEGI et al. 2003), or with the autoecology of Mediterranean harvesting ants (WARBURG & STEINBERGER 1997).

The Mediterranean flora turns out to be one of the richest in annual plants, not only because of the number of species, but also because of the abundance of such species. Therophytes occur nearly everywhere in the Mediterranean region, and for harvesting ants it is a clear advantage to live in a place where so many plants rely on their seeds to avoid the warmest and driest months of the year. In the frame of a research about the therophytic flora and vegetation of Sardinia, we tried to recognize some of the effects of harvesting ants in xerophilous and acidophilous vegetation dominated by therophytes belonging to the phytosociological class *Tuberarietea guttatae*.

## 2. Study area

The field data were collected from an area of approximately 5 hectares located at the foothill of the Sarrabus massif, in South-Eastern Sardinia. The study site is a gently sloping hillside, facing southwards, at 160 m a.s.l.

According to the bioclimatic classification of RIVAS-MARTÍNEZ (1997) the climate of the study site is thermo-mediterranean with a subhumid ombrotype, having an av. annual rainfall of 810 mm and an av. annual temperature of 16,2 °C.

The soil is a fairly homogeneous mixture of crumbling granitic boulders overlaid by finer particles (*Dystric xerorthents*, according to the U.S.D.A. Soil Taxonomy), potentially good for cork-oak woods (*Cytiso villosi-Quercetum suberis*) or acidophilous mediterranean maquis (*Erico-Arbutetum unedonis*).

Sheep grazing, together with periodical fires, transformed this area in an open acidophilous garigue dominated by *Cistus monspeliensis* and *Lavandula stoechas*. The grazing pressure on the study site was ranging from 3 to 5 sheeps per hectare, but in the last two years livestock have been excluded from the whole area. In winter and spring, the good water availability leads to the development of a thick layer of small annual plants, on average 15-20 cm high, which grow in between the perennial plants. Ants belonging to the genus *Messor* are very common in this mosaic of *Cisto-Lavanduletea* and *Tuberarietea guttatae* elements, with an average density of 19 nests/ha.

Annual and perennial plants occur together in the same microenvironment and coexist in the soil seed bank, so ants gather seeds from both. It was decided to focus our investigation on annual plants because their abundance and distribution can be measured accurately in small squares and the number and frequency of annual species are much more sensible to the seed predation than the perennial ones (GUO et al. 2000).

### 3. Data sampling and analysis

40 square plots, each 0.36 m<sup>2</sup> in area, have been settled in the study site. 20 plots were distributed at less than 5 m from the ant nests, 20 were distributed at more than 30 m from the nests, considering that the density of foraging ants decreases exponentially with the distance from the nest exit, with few if any foragers ranging beyond 15 m from the nest (DE VITA 1979, LÉVIAUX 1979). The spatial coordinates of each plot have been randomly generated, basing on the localisation of ant nests recorded in the field. Each plot was subdivided in a grid of 36 square decimetres and the census of annual species have been taken only in those cells where the ground was free of stems of perennial plants. Prostrate therophytes, such as *Scorpiurus muricatus* and *Medicago* species have been counted as many times as many cells were occupied by their vegetative apparatus, even if the creeping branches were belonging to the same individual. The eventual occurrence of microgeophytes, such as *Romulea requienii*, ending their vegetative cycle before the blossom of therophytes, has been disregarded. The positioning of a plot was discarded if the censusable cells were less than 26.

At this level, a first difference was noted: the 20 plots far from the nests have been settled in 27 attempts, while to settle down the plots next to the nests it was necessary to generate 36 spatial coordinates. Although this difference has no statistical meaning, it matches the observation of COFFIN & LAUENROTH (1989) that the density of perennial plants next to the ant nests is higher than in the vicinity.

The number of individuals per species has been recorded on each square decimeter. The census was conducted between the end of April and the begin of May, during the period of peak flowering for therophytes. All the spatial measurements were approximated to the cm and to the sexagesimal degree. The nomenclature of plants follows PIGNATTI (1982).

The census far from the nests included 657 cells, 188 of which shadowed by the canopy of shrubs, whereas the census next to the nests included 596 cells, 261 of which shadowed by the shrubs. To ensure the same size to the two data sets, the data analysis was performed on 523 cells per set, 188 of which shadowed by the shrub layer.

To verify eventual differences in the spatial micropatterns of the therophytic layer, per each of the two sets of data it was evaluated the frequency and abundance of each recorded species. The frequency was characterized by the percent number of cells where the species was present, the abundance by the mean density of a species in all the cells, therefore including the value of zero in the calculation of the average total abundance.

The patchiness of the therophytic layer was evaluated by the Shannon-Wiener index:

$$H = - \sum_{i=1}^n p_i \log p_i$$

where  $p_i$  is the relative abundance of the species  $i$  measured as the decimal fraction of the total plant number for the considered surface (WHITTAKER 1972, 1979).

### 4. Results

The evaluation of the frequency and abundance of species showed a significantly lower plant density next to the ant nests, together with a higher species richness (Tab. 1). Among the 49 censused species, 12 were found significantly more abundant in the plots far from the nests (Tab. 2).

Tab. 1: Species and plant densities in the two data sets (average, standard deviation, 95% confidence interval. P values according to the Student's test).

	Species/m <sup>2</sup> (P <sub>1</sub> = 0,015)			Individuals/m <sup>2</sup> (P <sub>1</sub> = 0,064)		
	Av.	S.D.	95% c.i.	Av.	S.D.	95% c.i.
NEXT	21	5.47	±4.79	787	73.65	±64.55
FAR	17	4.73	±4.15	852	87.29	±76.51

Tab. 2: Species significantly (P<sub>1</sub> < 0,05) more abundant in the plots far from the nests (frequency/plot; average number of individuals/plot).

	NEXT		FAR	
	v /plot (%)	ind./plot	v /plot (%)	ind./plot
<i>Vulpia ciliata</i>	100	43	100	66
<i>Plantago lagopus</i>	100	25	100	37
<i>Plantago bellardi</i>	100	19	100	30
<i>Bromus scoparius</i>	85	18	95	35
<i>Brachypodium distachyum</i>	85	17	100	32
<i>Trifolium stellatum</i>	90	14	85	19
<i>Briza maxima</i>	70	12	70	31
<i>Avena barbata</i>	55	10	85	29
<i>Silene gallica</i>	50	6	35	11
<i>Ornithopus compressus</i>	30	5	20	7
<i>Biserrula pelecinus</i>	25	3	50	9
<i>Ononis reclinata</i>	0	-	25	5

Most of these species belong to the families *Poaceae* and *Fabaceae*. Further 10 were significantly more abundant in the plots next to the nests (Tab. 3). In this case, more families are represented and within the species there are some with large seeds or indehiscent fruits which are not predated by the ants (*Scorpiurus muricatus*, *Medicago truncatula*, *Hymenocarpus circinnatus*, *Lupinus micranthus*) and some others whose tiny seeds might escape predation by falling amongst the soil particles. Most of these species have also a very small size or a prostrate growth form and they might benefit of the lower plant density next to the ant nests.

Tab. 3: Species significantly (P<sub>1</sub> < 0,05) more abundant in the plots next the nests (frequency/plot; average number of individuals/plot).

	NEXT		FAR	
	v /plot (%)	ind./plot	v /plot (%)	ind./plot
<i>Aira cupaniana</i>	100	59	95	27
<i>Tuberaria guttata</i>	95	31	55	14
<i>Filago gallica</i>	85	23	55	19
<i>Asterolinon linum-stellatum</i>	65	19	25	10
<i>Euphorbia exigua</i>	45	13	15	4
<i>Scorpiurus muricatus</i>	50	10	20	7
<i>Tolpis umbellata</i>	55	9	25	6
<i>Hymenocarpus circinnatus</i>	35	8	20	3
<i>Lupinus micranthus</i>	35	7	15	2
<i>Medicago truncatula</i>	55	5	15	4

Within the 27 left species, many were too sporadic to show any significant difference. Some others, although more abundant, have either wind dispersed seeds (*Trifolium arvense*, *Lagurus ovatus*, *Hypochoeris achyrophorus*, *H. glabra*) or seeds provided with awns and bristles that fix diaspores to the soil surface (*Aegylops geniculata*, *Stipa capensis*, *Hordelimum caput medusae* ssp. *crinitus*, *Erodium cicutarium*).

In both data sets, a significant positive relationship has been observed between frequency and the log-transformed abundance of species, although the correlation resulted lower for the data sets next to the nests (Fig.1). Such difference in correlation can be explained by observing the frequency distribution of species across the two data sets: even if the density of annual plants resulted higher in the plots far from the nests (Tab.1), most species had there quite a limited distribution (Fig. 2), with relatively few species occurring on most plots. On the contrary, next to the ant nests the density was lower, but species were more distributed along the plots (Fig. 2).

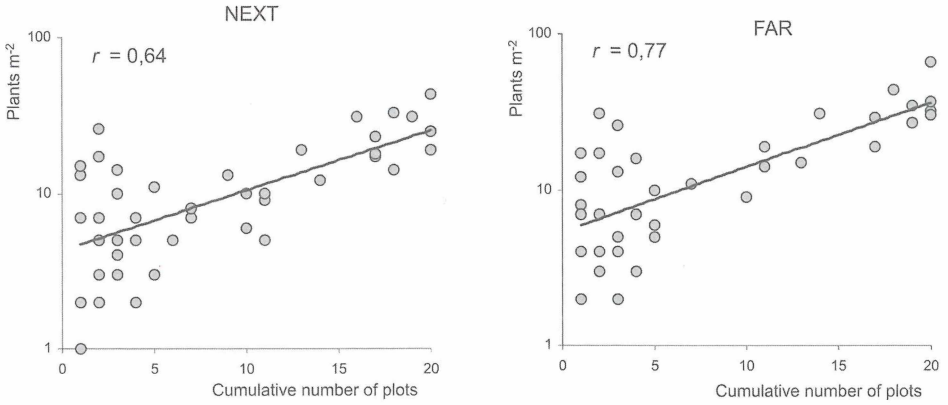


Fig. 1: Relationship between abundance and distribution of plants recorded in the sample plots of the two data sets. Each point represents one species.

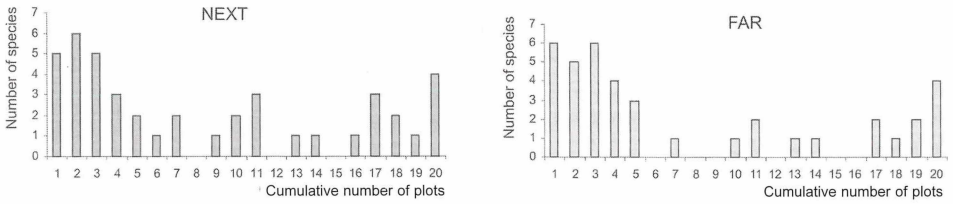


Fig. 2: Frequency distribution species/plot for the two data sets.

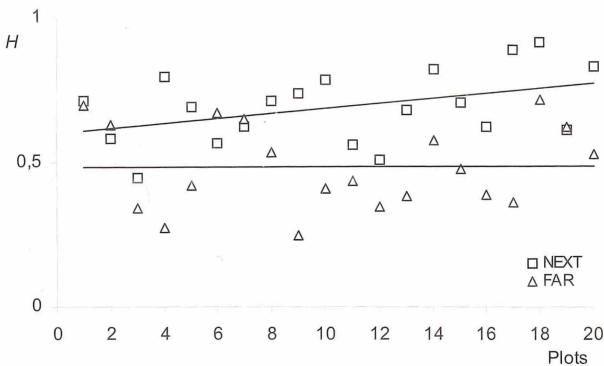


Fig. 3: Distribution of the values assumed by the Shannon-Wiener index in each of the sampled plots.

The patchiness have been evaluated on two spatial scales (plots and cells) and in both cases we found a significantly ( $P_t < 0,01$ ) higher value of  $H$  for the data sampled next to the ants nests (Fig. 3). This matches the difference shown in Fig. 2, as the Shannon-Wiener index does not emphasize the role of the most abundant species but gives more weight to the intermediate species and to the homogeneous distribution of frequencies (WHITTAKER l.c.).

## 5. Discussion

It is difficult to ascertain how much of the observed differences is really due to the foraging activity of ants and not to the higher frequency of perennial plants next to the ant nests. As well, the higher density of perennial plants next to the nests might not be a result of the occurrence of the ant colonies, being the lifetime of the perennial plants probably longer or directly comparable to that of the ant colonies. It is more likely that the probability of success for an ant colony increases where the cover of perennial plants lets to the sunrays to warm up the nests (ensuring the metabolic efficiency of ants) but not to totally dehydrate them during the dry season.

Anyway, being the comparison of our data based on the same number of shadowed and sunny cells, it is likely that, at least at the small scale of the experiment, harvesting ants were partially responsible for the observed differences.

To support this conclusion, a feeding-trials experiment was set up, by means of samples containing a mix of 20 seeds per each species found either significantly more or less abundant next to the nests. Seeds were spread on a 10 x 20 cm sand-paper and put across a foraging trail, next to the entrance of a nest. The experiment was repeated three times and every time foragers showed a clear preference for the seeds of plants, which resulted to be less abundant next to the nests (Fig. 4).

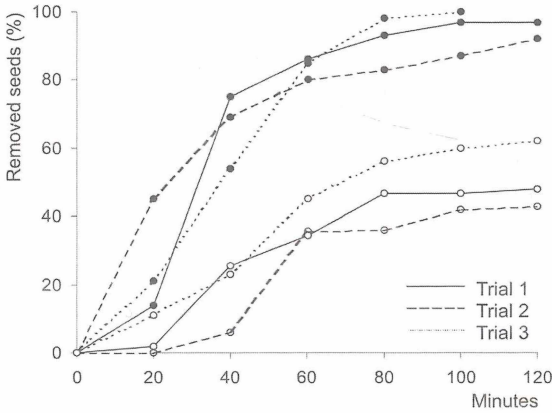


Fig. 4: Cumulative percentage of seeds collected by foraging ants over two hrs after the begin of the feeding trials. Black dots refer to the seeds of the species in Tab. 2 and white dots refer to the seeds of the species in Tab. 3.

It is therefore likely that harvesting ants, by depleting the soil seed bank year after year, contribute to the regulation of frequency and abundance of the studied plant community in the following ways:

- 1) they reduce the seed density, and therefore increase the probability of success of the less competitive species, which, due to their very small size, might be affected by an high density-dependent mortality,

- 2) they rearrange the distribution of seeds on the ground, and therefore contrast the natural tendency of vegetation towards increasing the spatial order (and reducing the plant diversity) by the formation of patches (DHILLION-SHIVCHARN 1999),
- 3) they carry seeds beyond the distance normally covered by the non-anemochorous annual plants, and therefore contribute to the spreading of species and reduce the probability of inbreeding.

## 6. Conclusions

*Tuberarietea*-vegetation has a similar ecology and life history all over the Mediterranean basin, consequently the patterns observed in the present study should be true for the whole Mediterranean region. Being harvesting ants particularly abundant in secondary vegetation linked to a slight grazing-pressure (CRIST & WIENS, 1994), it is likely that such traditional land-use might indirectly benefit the spatial heterogeneity and diversity of plant communities dominated by annuals.

Twelve thousand years of land exploitation greatly contributed to the spreading of annual plants throughout the Mediterranean region, but this cannot explain the exceptional richness in annual species of the Mediterranean flora in comparison with the other regions of the world having a mediterranean climate (MEUSEL 1969, RAVEN 1973). Being the time-scale of the natural evolution not comparable to the time-scale of the human cultural evolution, only in few cases (such as the allopoliploids *Poa annua* *Veronica persica* and *V. hederifolia*) the human activity might have favoured the appearance of new species.

The above mentioned richness in therophytes of the Mediterranean flora could be more probably an effect of the Messinian age (from 5,8 to 5,4 millions yrs b.p.): in that time, the cyclic sea regressions opened new ecological niches and set free broad extensions of land suitable for plant colonisation (BOCQUET et al. 1978). In the struggle to achieve the evolutionary success, the true winners have been those genera who managed to increase as much as possible the seed production and to shorten as much as possible their generation time. It is likely that the tight relationship between harvesting ants and annual species began to evolve during the Messinian age. The progressive increase of the climatic drought happened in the Mediterranean region after the Messinian events (PONS 1984), imposed a selective pressure that favoured dry-fruited and small-seeded species, therefore reinforcing the plant-ant mutualism in the Mediterranean region and making it similar to that of other dry environments of the world. The relatively young age of the eu-Mediterranean flora and climate could give a possible explanation not only to the still in act evolution, observed in several Mediterranean shrubs, from fleshy fruits dispersed by birds and mammals to dry dehiscent fruits dispersed by ants (WILCOCK & DE ALMEIDA, l.c., TEBAR & LLORENS, 1993 ARONNE & WILCOCK 1992, 1994, 1997), but also to the number of genera and species of harvesting ants, that in the Mediterranean region still remains lower than in the other Mediterranean regions of the world (HÖLLDOBLER & WILSON, l.c.).

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