



Effects of increasing red deer density on ant communities in a Mediterranean Ecosystem

Master's degree in Terrestrial Ecology and Biodiversity Management
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COMPONENTS OF THE STUDY	STUDENT CONTRIBUTION
Project design	C
Data collection	C
Data processing	A
Statistical analysis	A
Writing	A

(A) Entirely performed by the student; (B) Partially performed by the student; (C) Entirely performed by others.

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SUMMARY

1. Land use changes along with the intense hunting of large predators have favoured the increase of large herbivore populations in the northern hemisphere. This increase in ungulate populations has consequences on ecosystem structure affecting other plant and animal organisms. Ants, insects that rely on landscape structure, are prone to be affected by such herbivore increases. Experimental studies in this sense, however, are scarce.

2. We conducted a BACI (Before/After and Control/Impact) experimental design, in which we simulated three scenarios of contrasted red deer (*Cervus elaphus*) density namely Control, without deer, High density (35 deer/ km²), and Hyper-density (62 deer/ km²) in two different habitats: shrub and forest, to explore whether ungulates affect ant communities in a Mediterranean environment in Central Spain. We presumed to detect more changes in ant communities as deer density was higher, expecting the changes to be greater in ant communities within the Hyper-density treatments. Furthermore, we believed that these changes would be more prominently manifested in the composition of ant communities found in the shrub, due to the natural attributes of the forest that make it more stable against herbivory.

3. Surprisingly, shifts in ants' community composition decreased at the highest deer density (Hyper-density) shrub enclosure. We suggest that a deer overabundance maintained open spaces in the shrub preserving favourable ecological conditions for ants, whereas, in areas with fewer deer (High density), the environment was capable of recovering itself leading to compositional changes. In the case of deer absence (Control) in the shrub enclosure, we suggest that shifts in ant community composition were likely driven by environmental changes associated with the potential habitat recovery, leading to the restoration of its vegetation. Our findings revealed alterations in the composition

of ant communities within the shrub habitat while maintaining stability in the forest, which supports that the relationship between deer and ants depends largely on the features of the habitat in which they coexist. Given the intriguing results obtained, a more extensive and prolonged research effort would be necessary to gain a deeper understanding of the dynamics observed.

Keywords: ants, *Cervus elaphus*, composition, forest, overabundance, shrub.

1 | INTRODUCTION

Megafauna, those vertebrates over 44 kg (Martin & Steadman, 1999; Hansen & Galetti, 2009), have shaped terrestrial ecosystems since the last glacial period (Galetti et al. 2018). Game hunting management, the intensification of agriculture, and the near annihilation of large predators have favoured the increase of large herbivore populations (Jefferies, 1999; Côté et al. 2004; Simard et al. 2013) in developed countries of northern latitudes, resulting, in many cases, in an overabundance (Redford, 1992; Ripple et al. 2015). Since herbivores such as ungulates can feed on a wide range of plant species (Clauss et al. 2013; Forbes et al. 2019), move along large geographic areas, transporting nutrients through defecation and urination (Wolf, Doughty & Malhi, 2013; Forbes et al. 2019), and modifying soil structure through trampling and digging (Beck, Thebpanya & Filiaggi, 2010; Long et al. 2017; Pringle, 2008; van Klink et al. 2015; Forbes et al. 2019), their influence on both vegetation and soil affect other organisms (Philpott et al. 2010), but in particular those with limited mobility such as terrestrial invertebrates (Sierszen, Peterson & Scharold, 2006; Stenroth et al. 2008; Gibb & Johansson, 2011).

Overabundant ungulates such as cervids (red deer –*Cervus elaphus*–, roe deer –*Capreolus capreolus*–...) alter the population and community composition of many invertebrates, birds, and small mammals (Côté et al. 2004), for these species can directly affect primary consumers by removing their food resources and triggering a reduction of secondary consumers that prey on them (Allombert, Stockton & Martin, 2005). For instance, browsing limits the regeneration of tree species (Rooney & Waller, 2003) as well as reduces vegetation cover and complexity in the understory, which often reduces the habitat's availability for animals like invertebrates (McShea & Rappole, 1997; Miyashita, Takada & Shimazaki, 2004; Côté et al. 2004). Although the main impact of grazing is a result of foliage removal, only the presence of the animal itself has other effects on the

vegetation, through trampling, which damages plant populations by causing seedling mortality and harming adult plant canopies (Huntly 1991; Seifan & Kadmon, 2005), and through the modification of soil stability and compaction, altering interactions between plant species (Seifan & Kadmon, 2005). Through all of these impacts, high deer densities appear to alter biological communities (Rooney & Waller, 2003), such as insects (Blakley & Dingle, 1978; Rooney & Waller, 2003) like ants.

Ants are a particularly prominent invertebrate group (Hoffmann, 2010) and important components of nearly every terrestrial ecosystem (Hölldobler & Wilson, 1990; Tillberg et al. 2006). They are the most diverse group of social insects (Bolton et al. 2007; Ward, 2010; Del Toro, Ribbons & Pelini, 2012), and trophically speaking, the family Formicidae is remarkably rich in species (Hirosawa, Higashi & Mohamed, 2000; Blüthgen, Gebauer & Fiedler, 2003; Davidson et al. 2003; Tillberg et al. 2006). The characterization of the feeding habits of ants can be difficult to approach because they can utilize a large variety of food sources and, therefore, have a broad dietary niche, added to their sociality (Feldhaar, Gebauer & Blüthgen, 2010). However, it is always necessary to consider that an ant colony's dietary input is the result of several eusocial variables (Tillberg et al. 2006). For instance, ants' colonies are characterised by having overlapping generations, behavioural specialization, food-sharing among the nestmates (Børgesen, 2000; Tillberg et al. 2006), and differing dietary requirements between workers and larvae (Lee Cassill & Tschinkel, 1999; Tillberg et al. 2006). Some ant species are predators, omnivores, herbivores (Hirosawa et al. 2000; Blüthgen et al. 2003; Davidson et al. 2003; Tillberg et al. 2006), scavengers (Cerdà & Retana, 1998), granivores and nectarivores.

Ants are considered particularly useful for monitoring since they are ubiquitously abundant and important in terrestrial ecosystems, easily sampled, and have community dynamics that vary predictably concerning environmental stress and disturbance (Majer,

1983; Greenslade & Greenslade, 1984; Andersen, 1990; Hoffmann, 2010), which make them sensitive to changes in habitat (Lassau & Hochuli, 2004; Stuble et al. 2013; Mahon, Campbell & Crist, 2019). Moreover, ants are important functionally at many different trophic levels and play critical ecological roles in soil turnover and structure (Humphreys, 1981; De Bruyn & Conacher, 1994; Underwood & Fisher, 2006), nutrient cycling (Levieux, 1983; Lal, 1988; Underwood & Fisher, 2006) plant protection, seed dispersal (Ashton, 1979; Beattie, 1985; Christian, 2001; Underwood & Fisher, 2006), pollination (Peakall, 1989; Rostás & Tautz, 2011; Del Toro et al. 2012), and regulation of animal community structure (Hölldobler & Wilson, 1990; Del Toro et al. 2012).

Either domestic or wild large herbivores are known to coexist with ants in some terrestrial ecosystems, which can lead to synergistic effects on litter decomposition (Li et al. 2021), and benefit plants by helping them shift their resource allocations when needed (Zhong et al. 2021). However, the way that large herbivores affect ants' communities may vary; for instance, some ant species may increase in open habitats resulting from the large herbivores' overgrazing effect (Hutchinson & King, 1980; Andersen, 1991; Read & Andersen, 2000) since it can improve their microclimate favourability (Read & Andersen, 2000). Palmer et al. (2008) studied the impact of herbivore browsing on ant communities, comparing patches with and without large herbivore access. With the absence of all wild herbivores (>15%), *Acacia drepanolobium* trees decreased their investment toward supporting symbiotic ants, which caused marked shifts in the community of these ants, turning into an increase of the dominant species and the reduction of the more specialists due to the lack of feed.

Conversely, it has been documented that large herbivores can impact negatively ground-dwelling insects by altering their habitat (e.g., the soil structure), and by the intense browsing of understory vegetation (Rooney & Waller, 2003; Foster, Barton &

Lindenmayer, 2014; Record et al. 2018). As evidenced in some studies, changes in ecosystems may even lead to a modification in ants' diet (Gibb & Johansson, 2011). For instance, Read & Andersen (2000) studied the effects that cattle grazing had on ant communities, by comparing control and experimental treated grazing sites. The ant communities experienced a difference in composition since some of their species suffered a reduction in their population due to their preferences for old-growth vegetation.

Our study aims to assess the ant communities' response to the deer overabundance in the following distinct habitats from a Mediterranean ecosystem: **shrub** and **forest**. Given that most of the related studies have been conducted in similar habitats (mostly savannas), our study aims to assess the ant communities' response to the deer overabundance in shrub and forest habitats. By arranging different enclosures in both habitats, we simulated three scenarios of contrasted herbivory pressure (deer density treatments) called Control (with no deer), **High deer density**, and **Hyper deer density**, following a **BACI** experimental design (Before/After and Control/Impact) (Underwood et al. 1992), between 2021 and 2022. In 2021, we established transects in every enclosure of each habitat and introduced the deer in spring. Then, we i) took samples (both in 2021 and 2022) of ants by using pitfall traps distributed in each deer density treatment within the two distinct habitats, ii) identified the species of ants as well as their community composition, iii) analysed the results among habitats and deer density treatments between the two years and determined if changes in ant communities' composition were found. **We hypothesized that changes in deer density, particularly in enclosures exhibiting an overabundance of deer, would notably influence the ant community compositions in both habitats, through reductions in vegetation and litter biomass, exhibiting greater variation from one year to the next, when contrasted with the other treatments.** Furthermore, we believed that these **changes would be more pronounced in the shrub**, since previous studies have evidenced that forest

attributes might enhance understorey herbs' resistance against deer overabundance since persistent seed banks in forests are scarce (Bierzychudek, 1982; Whigham, 2004; Schäfer et al. 2019), and many herbaceous species are dispersal-limited (McEuen & Curran, 2004; Schäfer et al. 2019) and rely on dispersal by large herbivores (Sorensen, 1986; Heinken, 2000; Schäfer et al. 2019).

Additionally, in Mediterranean ecosystems, shrubs are characterized by plant communities growing within a matrix of herbaceous plants, mainly annuals (Zohary, 1962; Seifan & Kadmon, 2006), whose spatial pattern depends on both their vegetative growth and seed dispersal (Seifan & Kadmon, 2006). Given that these factors are highly perturbed under conditions of deer overabundance, leading to shifts in the spatial distribution of herbaceous communities, it follows that such changes could consequently impact severely the composition of ant communities. Hence, we examined these dynamics in both the shrub and forest habitats, allowing us to conclude about the impact of deer density on ant communities across these two distinct habitats.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in a Mediterranean environment of Spain, located in the south-central: Quintos de Mora (Toledo) (Fig. 1) of the country.

Quintos de Mora ($39^{\circ} 26' 45.9''$ N, $4^{\circ} 05' 56.4''$ W) is a completely enclosed extension of 6.864 ha (San Miguel, Rodríguez-Vigal & Perea, 2001) located within Los Yébenes (Toledo), with an altitude range between 800-1235 m (Notario et al. 2007). Its climatology is Mediterranean with a Continental thermal regime, with an annual mean temperature of 13°C , and pluviometry of 622 mm (San Miguel, Rodríguez-Vigal, & Perea

2011). The lithology is dominated by slate and quartzite (Fernández-Olalla et al. 2006). Soils are acidic and poor in nutrients on the slopes whereas, in the valley bottoms, the soil turns more developed and richer in organic matter on the superficial horizons which constitutes a humic cambisol (León Gómez et al. 1981; San Miguel et al. 2011). Regarding its vegetation, two distinct plant communities dominate: forests situated in the valley bottoms and shrubs on the hills and more sun-exposed areas. Forests are dominated by *Quercus pyrenaica* and *Q. faginea* subsp.. *broteroi*. Other woody species such as *Q. ilex* subsp. *ballota*, *Arbutus unedo* L., *Erica scoparia* L., *E. arborea* L., *E. australis* L., *Phillyrea angustifolia* L. and *Rosmarinus officinalis* L. are also present, followed by herbaceous species like *Bromus* spp., *Cynosurus*, *Festuca* spp. And *Vulpia* spp., *Geranium* sp. pl. Second, the shrub comprises as dominant species *Cistus ladanifer* L., *Rosmarinus officinalis*, and *Erica* sp. pl. Other woody species such as *Thymus mastichina* (L.) L., *Cistus populifolius*, and small-sized individuals of *Pinus pinaster* and *Q.ilex ballota* coexist. The herbaceous layer comprises numerous taxa like *Tuberaria guttata* (L.) Fourr., *Crepis*, *Trifolium*, *Filago*, *Galium*, and *Vulpia*.

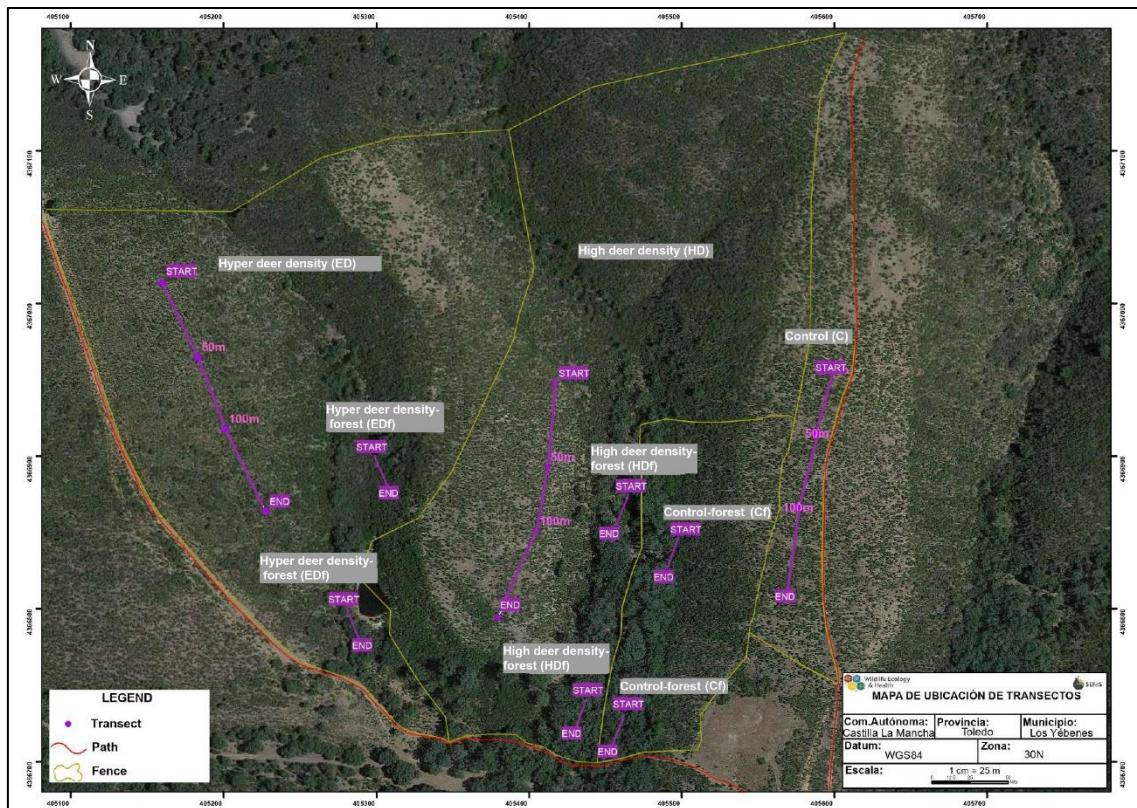


Figure 1. Study site of Quintos de Mora (Toledo). Purple lines correspond to every transect divided by each experimental deer density treatment. Shrub enclosures are divided into Control (C), High deer density (HD) and Hyper deer density (ED), while forest enclosures are divided into Control-forest (Cf), High deer density-forest (HDF), and Hyper deer density-forest (EDf).

2.2 | Experimental design and sampling details

We recreated three scenarios of contrasted herbivory, one per plot (hereafter treatments), namely: Control (no deer), High density (7 female deer, 95 young female deer/km², equivalent to 63 deer/km²) and Hyper-density (12 female deer, 169 young female deer /km², equivalent to 113 deer/km²) in two habitats: shrub and forest (see Fig. 1). Enclosure areas were 2.6 ha, 7.1 ha, and 7.4 ha, respectively. The aim was to analyse whether the overabundance of deer would lead to higher changes in ant communities when compared to the other deer density treatments, and if these changes would be more pronounced in

the shrub. 2021 corresponded to the “Before” part of the experiment and 2022 to the “After”, following a BACI experimental design.

In 2021, we placed 12 pitfall traps along 160 m transects within three distinct shrub enclosures: Control (C), High deer density (HD) and Hyper deer density (ED as ‘Extreme Density’, to differentiate it from HD treatment’ abbreviation), and 3 pitfall traps along 30 m transects within three distinct forest enclosures (two transects per enclosure): Control-forest (Cf), High deer density-forest (Hdf), and Hyper deer density-forest (Edf). We replicated the procedure in 2022. It should be noted that all the samples collected were from June 2021 and June 2022.

The content inside the pitfall traps was composed of propylene glycol at 50%, and a detergent drop. The pitfall traps used in this study were set at intervals of 13 m to guarantee the samples’ independence since ants can individually move within a radius of 10 m around their nest to search for food (Fourcassié & Oliveira, 2002). All the pitfall traps were placed at the end of June, when Mediterranean ants’ activity is high (Cros, Cerdà & Retana, 1997), and were opened a week after to avoid *digging-in* effects (Majer, 1978). We let them active for five days. After this period, all of the content stored inside each pitfall trap was placed in plastic tubes.

Once all of the samples were taken to the laboratory. We first added ethanol at 96% to the plastic tubes with the pitfall trap content until we obtained a concentration of ethanol at 70%. Then, all of the samples were preserved (at 25°C) until sample processing.

For ant species identification, we were assisted by an expert in the field of myrmecology.

2.3 | Data analyses

To analyse all the samples, we worked with the following data: 2 Habitats (shrub and forest), 2 Years (2021 and 2022), 3 Deer density treatments in the shrub (Control, High deer density and Hyper deer density), and 3 Deer density treatments in the forest (Control-forest, High deer density-forest, and Hyper deer density-forest).

To assess the changes in ants' community composition depending on the deer density treatments, our sampling unit was the composition distance obtained between the related pitfall traps between 2021 and 2022. Subsequently, we analysed whether these distances varied depending on the deer density treatment. It should be noted that the analyses were performed separately for each habitat.

Before conducting every statistical model, all variables were tested for normality and homoscedasticity using the Shapiro-Wilk and Levenne's tests respectively. If significant differences were found after conducting every statistical model, we ran a pairwise posthoc test to analyse the differences between each pair of all groups tested by following a Tukey method, if possible.

All statistical analyses were conducted in the R software 4.3.1 version (R Core Team, 2023).

2.3.1 | Ant communities

We first created a matrix where each row corresponded to an observation (pitfall), each column a variable (ant species), and each cell constituted the abundance of individuals per species. To visualize patterns in community composition among treatments, we generated a Non-Metric Multidimensional Scaling (NMDS) based on a Bray-Curtis dissimilarity index.

To assess ant communities' composition change over the two years studied, we first divided our study depending on the habitat (shrub and forest). Then, we compared every related ant community sample (pitfall traps) depending on each deer density treatment. To analyse the changes, we performed a Bray-Curtis dissimilarity index to obtain a composition distance between every related pitfall (2021-2022) depending on the "Deer density treatment". The variable "Distance" encompassed all the distances obtained. For both shrub and forest habitats, we conducted a Linear Model (LM), considering "Distance" as the dependent variable of the "Deer density treatment", and tested its significance through a one-way Analysis of Variance (ANOVA) test to analyse if there were any significant differences between distances depending on each "Deer density treatment".

If significant differences between distances depending on each "Deer density treatment" were found, we would evaluate the effect of these treatments separately, to assess whether the effect of each treatment on ant community composition also differed between years, by performing a Permutational Multivariate Analysis of Variance (PERMANOVA), with a Pairwise test to analyse differences between each pair of related treatments among years. To determine which species were contributing significantly to these composition differences among all of the pitfalls for each pair of related treatments compared, we followed a Similarity Percentage Analysis (SIMPER).

If changes in the compositions were detected, we analysed other more specific bioindicator parameters that determine the ant community composition, such as the ants' abundance (I), composed by the total number of individuals per pitfall; species richness (II), composed by the total number of species found per pitfall; Shannon's diversity index (III):

$$H = -\sum (p_i * \log_2(p_i))$$

where p_i is the proportion of each species in the pitfall; and species evenness (IV), by analysing the Hurlbert's Probability of Interspecific Encounter (PIE):

$$\text{PIE} = N/(N-1) * (1 - p_i^2)$$

where N is the total number of individuals in the pitfall and p_i is the relative abundance of species in it. To analyse these changes, we would first obtain the distances between every corresponding parameter value between each related pitfall (2021-2022) and encompass them in the variable "Distance" for the four parameters. For the ants' abundance, we conducted a GLM with a Gaussian distribution and ran an ANOVA where we compared the model with a null model to test if the "Distance" variable was influenced by the "Deer density treatment". For species richness, Shannon's diversity index and species dominance we followed an LM and tested its significance through a one-way Analysis of Variance (ANOVA) test to analyse if there were any significant differences between distances depending on each "Deer density treatment". In all cases considering "Distance" as the dependent variable of the "Deer density treatment".

3 | RESULTS

A total of 40 ant species were found: 31 in the shrub, and 26 in the forest (see Appendix).

A difference between the ant communities depending on the habitat type (shrub and forest) was evident (Fig. 2). The most predominant and representative ant species found in the shrub habitat in both years (2021-2022) were *Cataglyphis hispanica*, *Iberoformica subrufa*, and *Cataglyphis iberica*. In Control, *C. iberica* and *C. hispanica* predominated, while *C. hispanica*, *I. subrufa* and *C. iberica* did it in High deer density treatment, and *I. subrufa*, *Pheidole pallidula* and *C. hispanica* did it in Hyper deer density treatment. In the forest, the most predominant and representative ant species found in both years (2021-2022) were *P. pallidula* and *Camponotus cruentatus*. In Control *Crematogaster*

scutellaris and *Lasius grandis* predominated, while *C. cruentatus*, *P. pallidula* and *Formica fusca* did it in High deer density treatment, and *P. pallidula* did it in Hyper deer density treatment.

Treatment (deer density) influenced ant communities change (Bray-Curtis distances) in the shrub enclosures ($F_{2,33} = 8.34, p = 0.001$), with differences between Hyper deer density and Control ($t = -0.48, p = 0.004$), and Hyper deer density and High deer density ($t = 0.720, p = 0.002$) treatments. Only High deer density and Control did not differ significantly ($t = 0.061, p = 0.98$). Concerning forest habitat, no significant differences between deer density treatments were found ($F_{2,15} = 0.70, p = 0.53$) (Fig. 3).

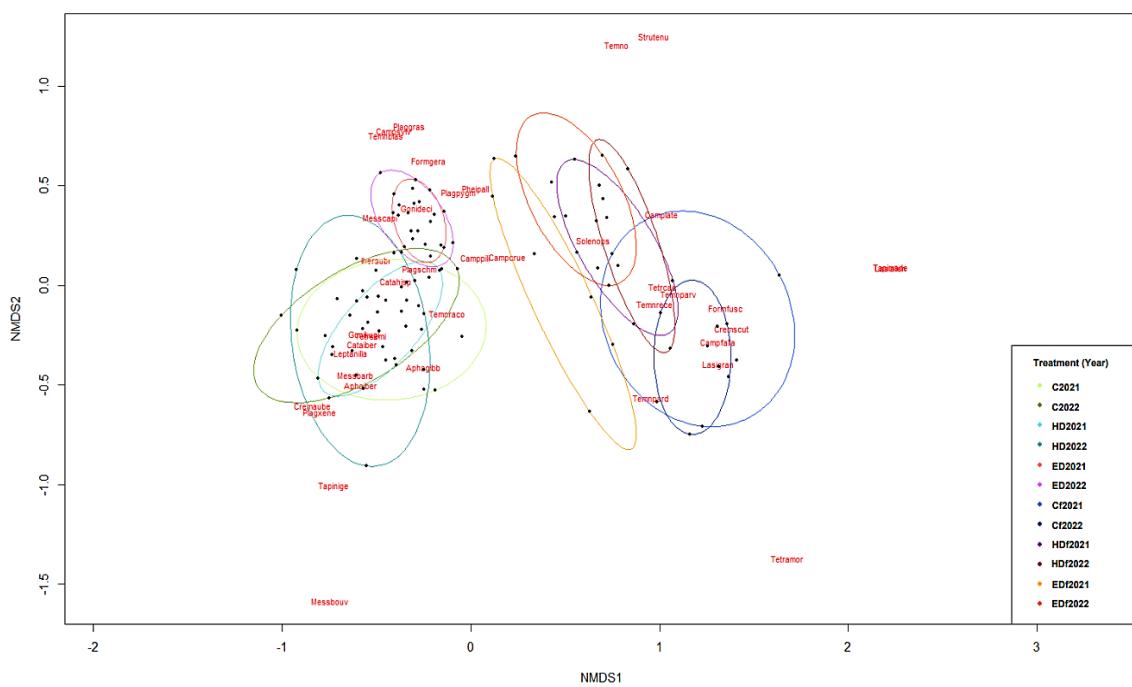


Figure 2. Non-metric multidimensional scaling (NMDS) of the ant communities' composition, depending on each deer density treatment (divided into shrub treatments corresponding to Control (C), High deer density (HD), and Hyper deer density (ED), and forest habitat as Control-forest (Cf), High deer density-forest (HDf), and Hyper deer density-forest (EDf)). Black points correspond to each pitfall, plotted in two years (since the samples were taken in 2021 and 2022), and represent their ant community. Ant species

are abbreviated (see Appendix) in red and indicate their influence on ant communities by appearing near the respective pitfalls they characterize notably.

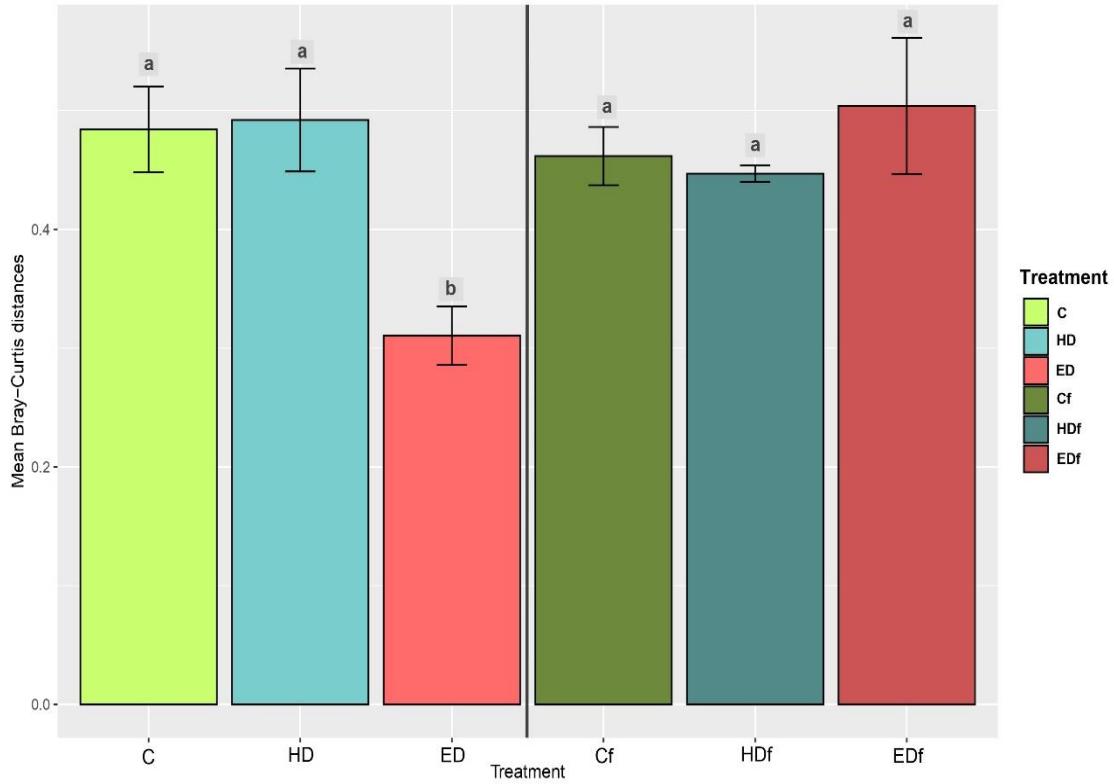


Figure 3. Bray-Curtis distances of ant community (mean \pm SE), depending on each deer density treatment (divided into shrub habitat corresponding to Control (C), High deer density (HD), and Hyper deer density (ED), and forest habitat as Control-forest (Cf), High deer density-forest (HdF), and Hyper deer density-forest (EdF). Different letters indicate significant differences between deer density treatments ($p < 0.05$).

Since significant differences were found in ant communities present in the shrub habitat, we kept analysing the ant community composition for this site. Treatment effects on the ant community composition differed between years ($F_{5,66} = 5.72, p < 0.001$) yet only ant communities of Control significantly changed between 2021 and 2022 ($F_1 = 2.23, p = 0.03$), in contrast, High deer density 2021-2022 and Hyper deer density 2021-2022 did not differ significantly ($F_1 = 1.60, p = 0.10$; $F_1 = 0.41, p = 0.91$, respectively). Finally, a

total of 4 ant species' changes in their abundance contributed significantly to dissimilarities in the ant community composition among years in the Control, and Hyper deer density treatments, while the decrease of 1 species did it in the High deer density treatment (Table 1).

Table 1. Species whose contribution to dissimilarity changed over the years in each deer density treatment situated in the shrub. Results from SIMPER analysis are shown as percentage contributions. The fourth and fifth columns show the ants' abundance change (in square root and normal units, respectively), while the last column shows each ant species' feeding habit.

Pair of treatments	Ant species	Percentage of contribution to dissimilarity	Abundance's change (in sqrt)	Abundance's change	Feeding habit
C 2021 – C 2022	<i>Tetramorium semilaeve</i>	13.2%	(2.12-0.74)	- (4.5-0.54)	Omnivores (Retana, Cerdà & Espadaler, 1992)
	<i>Cataglyphis hispanica</i>	9.2%	(2.70-3.65)	+ (7.29-13.32)	Scavengers (Gonçalves et al. 2017), carnivores (Galkowski & Wegnez, 2017)
	<i>Crematogaster auberti</i>	8.1%	(0.80-0.93)	+ (0.64-0.86)	Omnivores (Galkowski & Wegnez, 2017), Scavengers (Eubanks, Lin & Tarone, 2019)
	<i>Camponotus pilicornis</i>	5.7%	(0.60-0.66)	+ (0.36-0.44)	Omnivores (Galkowski & Wegnez, 2017)
HD 2021 – HD 2022	<i>Aphaenogaster iberica</i>	3.3%	(0.51-0.12)	- (0.26-0.01)	Omnivores (Galkowski & Wegnez, 2017), Scavengers (Gaytán et al. 2021)
ED 2021 – ED 2022	<i>Camponotus sylvaticus</i>	7.3%	(0.60-1.04)	+ (0.36-1.08)	Omnivores (Galkowski & Wegnez, 2017), sugary liquids (Retana, 1988)
	<i>Formica gerardi</i>	6.7%	(0.50-0.98)	+ (0.25-0.96)	Omnivores (Galkowski & Wegnez, 2017)
	<i>Plagiolepis pygmaea</i>	3.5%	(0.17-0.43)	+ (0.03-0.18)	Omnivores (Galkowski & Wegnez, 2017)
	<i>Temnothorax blascoi</i>	2.5%	(0.20-0.17)	- (0.04-0.03)	Omnivores (Espadaler & Reyes-López, 1997)

We also evaluated changes (distances) in abundance, richness, diversity, and evenness depending on deer density shrub treatments (Fig. 4), but no differences were found for any of them (ants' abundance: χ^2_2 ($n= 36$) = 2.28, $p = 0.24$; richness: $F_{2,33} = 0.34$, $p = 0.71$; Shannon's diversity index: $F_{2,33} = 2.60$, $p = 0.08$; evenness: $F_{2,33} = 2.41$, $p = 0.10$).

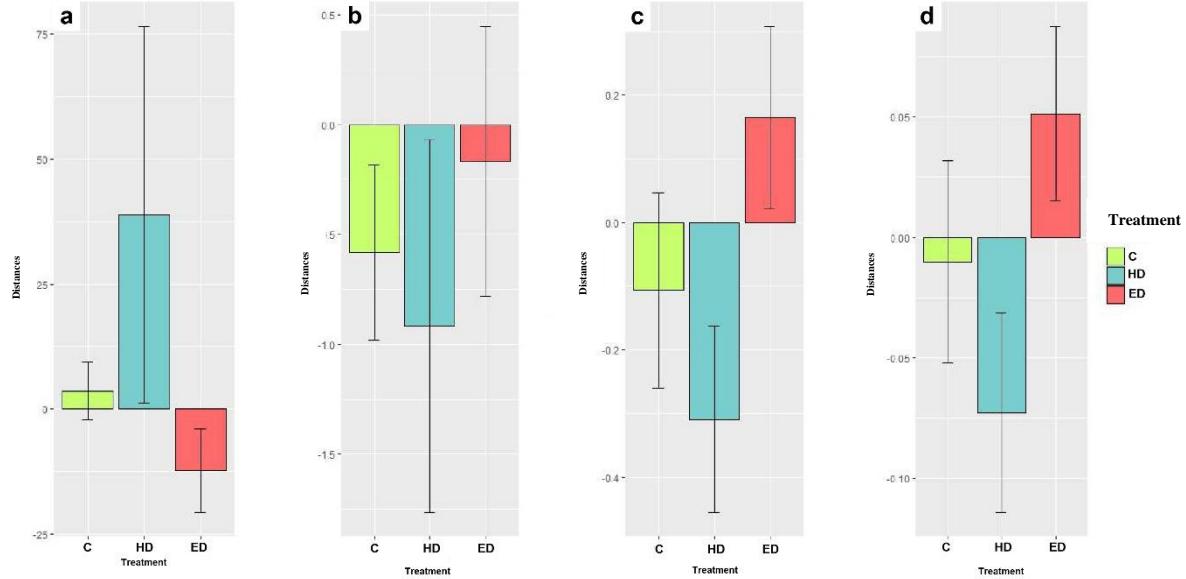


Figure 4. Distances of a) ants' abundance, b) species richness, c) Shannon diversity index and d) species evenness (mean \pm SE) between years, depending on each deer density treatment (Control (C), High deer density (HD), and Hyper deer density (ED)) situated in the shrub.

4 | DISCUSSION

4.1 | Ant communities

Unexpectedly, we found that the composition of ant communities found in the shrub exhibited more stability when the overabundance of deer was higher, as more changes occurred in Control and High deer density treatments (Fig. 3). Contrary to the model studied by Seifan & Kadmon (2006), in which they concluded that the effect of the intense herbivory varies the spatial pattern of shrubs, and thus, in our case, we expected that a

deer' overabundance would have led to bigger shifts in the ant communities composition, the changes that we found did not fit this pattern.

Deer can benefit ants by providing more open habitats (Hutchinson & King, 1980; Andersen, 1991; Read & Andersen, 2000), and supporting symbiotic relations (Palmer et al. 2008). Conversely, deer can also exert detrimental effects on ants through intense browsing and grazing (Read & Andersen, 2000) that change the conditions of the habitat (Mahon et al. 2019) through the soil compaction caused by the trampling or by the reduction of feeding resources due to the decrease in vegetation coverage (Fernández, 2001; Rivas-Arancibia et al. 2014), negative disturbances that compromise the ant community, impoverishing it with a few dominant species of more generalist feeding habits (Carrol & Risch, 1983; Perfecto & Vandermeer, 1996; Rivas-Arancibia et al. 2014). Contrary to our findings, a similar study carried out by Mahon et al. (2019), concluded that variation in ant species composition was lower in plots without deer than in plots with deer due to changes in microhabitat caused by their presence. Hence, our results diverge from the previously mentioned studies, as well as from the old-time belief that complex and diverse habitats tend to stabilise their ecological communities (Kovalenko, Thomaz & Warfe, 2012; Blake, Duffy & Richardson, 2014; Hyman et al. 2019).

In Hyper deer density shrub enclosure, deer appeared to preserve favourable ecological conditions for ants (e.g., solar radiation received, temperature, feeding resources,...). For instance, since most of the ant species found in that treatment followed an omnivorous and scavenger diet, the effects of the reduction in vegetation caused by the heavy browsing did not probably suppose a crucial factor in their survival. In our study, the reduction of woody and herbaceous plant cover has been significant, especially in the Hyper deer density enclosures (Cuerdo et al. 2022; del Olmo et al. 2022). Such reduction

of the vegetation cover might have allowed the stabilization of the coexistence of ant species when in a more complex habitat (shadier, for instance) could have resulted in composition changes facilitating the increase in dominant species since they tend to be heat-intolerant, a common pattern in the Mediterranean ants (Retana & Cerdà, 2000). In this line, Retana and Cerdà (2000) concluded that the Mediterranean ground ants community's composition of open habitats was mainly regulated by thermal variations and less by biotic interactions.

Conversely, fewer deer could have led to ecosystem recovery and greater variations in both ecosystem dynamics and ants' community composition. With fewer deer, the system may have been able to recover itself (Akashi, 2009), leading to compositional changes of determined species, as some studies have evidenced in which moderate deer density scenarios lead to shifts in species composition due to the heterogeneity induced by intermediate browsing levels (Ripple & Beschta, 2003; Parker, Salminen & Agrawal, 2010; Royo et al., 2010). The significant temporal changes (2021-2022) in ant community composition in the Control enclosure (I.e. without deer) might be due to environmental changes associated with the potential habitat recovery in the absence of deer, leading to the restoration of its vegetation (Wills, Retallick & Bennett, 2003) and, therefore, changes in the ant's community composition over the years.

Thus, ant communities' composition in Control shrub enclosure differed over the years, while High deer density and extremely Hyper deer density treatments did not, and had a lower percentage of ant species' contribution to changes in community composition (Table 1). If we look at the species that contributed the most (>5%) to the composition differences found in each shrub treatment over the years, regarding the Control shrub enclosure, the increase of species such as *Cataglyphis hispanica*, *Crematogaster auberti* and *Camponotus Pilicornis* explained 23% of the ant communities' composition

dissimilarities found. *Tetramorium semilaeve* decrease contributed as well to these changes. The subordinate *Cataglyphis hispanica*, whose genus is thermophilous but highly adaptable (Boulay et al. 2017) despite preferring nesting under temperate weather, tends to be found in Mediterranean oak groves (Galkowski & Wegnez, 2017). *Crematogaster auberti*, an opportunist species with a broad habitat range (Carpintero, Reyes-Lopez & Reyna, 2004) which is mainly nocturnal and hygrophilous (Bernard, 1968; Lapeva-Gjonova, 2011), appears to live in well-preserved shrubs (González-Robles et al. 2020) as well as showing resistance against the abundant growth of other dominant species (Carpintero et al., 2004). *Camponotus pilicornis*, which is a subordinate species (Carpintero & Reyes, 2008) and mainly nocturnal (Cammell, Way & Paiva, 1996) tends to be more abundant in recovered lands (Azcarate & Peco, 2012). The crepuscular and nocturnal (Retana et al. 1992) especially during summer (Cros et al. 1997), *Tetramorium semilaeve*, which is a small mass recruitment species (Cerdà, Retana & Cros, 1997), lives in xerophilous habitats (Galkowski & Wegnez, 2017). Considering the similarities in their biology (eg. diet), and their daily rhythm preferences, the reduction of *Tetramorium semilaeve* species could be linked to the interspecific competition, even though it is a dominant species. Given that the Control shrub enclosure was characterised by the lack of deer and, therefore, the growth of its vegetation was not limited, this pattern observed could have been accompanied by a possible increase in local humidity (Valenti et al. 1999). We suggest this idea because the increment of species well adapted and flexible to temperate environments (whether it is for living or nesting) together with the decrease of the xerophilic *Tetramorium semilaeve*, have constituted the highest percentage contributors to the changes in ant community composition in the Control shrub enclosure.

Regarding the Hyper deer density shrub enclosure, the increment of *Camponotus sylvaticus*, and *Formica gerardi* species explained 14% of the ant communities'

composition dissimilarities. Considering the effects of the deer overabundance, it is consistent to have found *Camponotus sylvaticus* species increase since it is frequent in zones with scarce vegetation. Notwithstanding its diet is narrow, consisting almost exclusively of sugary liquids, nectar, and flowers, it has been documented that it can feed on animal faeces, despite it seldom occurs. Finally, it is also reasonable to have found the omnivorous (Galkowski & Wegnez, 2017) and generalist predator (Martínez-Ferrer & Campos-Rivela) *Formica gerardi* to increase in this treatment since it is a thermophilic species that habits in the Mediterranean forests clearings, despite being dependent on shaded areas (Gómez et al. 2018), suggesting that the level of browsing was not yet too intense, with enough vegetation to provide shade.

Despite no significant changes being found, a trend in Control and High deer density shrub enclosures suggested conversion of their ant communities to slightly less diverse communities, by an increase of specific ant species' dominance (Fig. 4), resulting in a reduction in diversity and evenness of their communities (Retana & Cerdà, 2000) and an increase of species that possess greater adaptability and flexibility in response to environmental changes (Smart, Hatton & Spence, 1985; Hobbs & Huenneke, 1992).

Concerning the ant species that predominated in each habitat (shrub and forest), given that browsed areas such as shrub enclosures with deer presence are more open, resulting in a higher abundance of dead insects due to greater sun exposure, it is logical to have observed a higher abundance of *Iberoformica subrufa* since it forages upon these resources. The same pattern as *Pheidole pallidula* (Retana et al. 1992; Arnan et al. 2015; Vidal-Cordero et al. 2022), which despite being found in the forest, was predominant in enclosures with deer presence. *Cataglyphis iberica* and *Cataglyphis hispanica*, known for inhabiting open and arid habitats (Boulay et al. 2017; Galkowski & Wegnez, 2017), were found to be predominant in shrub enclosures and the High deer density forest enclosure.

As expected, changes in ant communities were more pronounced in the shrub than in the forest (in fact, no changes were found in the second). Our results support that the relationship between deer and ant communities varies depending on the habitat features, given that the environment strongly influences a community's composition (Seoane et al. 2021). Red deer is a mixed-feeder (leaves of trees and shrubs, forbs, seeds and fruits, grasses and sedges) and adapts its diet to the feeding resources of the habitat (Gebert & Verheyden-Tixier, 2001). Then, deer were able to adapt their feeding regime in both the forest and the shrub, thus impacting on the same level. What must have made the difference, however, were the attributes of the habitat to resist such herbivory. Despite understory herbs are also vulnerable to ungulate browsing as they never grow large enough to escape browsing impacts (Rooney & Waller, 2003), forest attributes might have compensated the effects of the deer overabundance by enhancing understorey herbs' reliance on the seed dispersal by deer (Sorensen, 1986; Heinken, 2000; Schäfer et al. 2019), given that persistent seed banks in forests are scarce (Bierzychudek, 1982; Whigham, 2004; Schäfer et al. 2019), and many herbaceous species are dispersal-limited (McEuen & Curran, 2004; Schäfer et al. 2019), showing no significant effects of its overabundance in this habitat and neither in ant communities composition.

5 | CONCLUSIONS

Contrary to our expectations, ants' community composition remained more stable in the Hyper deer density shrub enclosure than in the others, suggesting that a deer overabundance could have maintained open spaces preserving favourable ecological conditions for ants, whereas, in areas with fewer deer, the environmental dynamics could have led to habitat variations and consequent variability in the ants' communities composition, with a trend to poorer communities in that case. That tendency was also observed in the Control shrub enclosure where, in addition, ants' community composition

appeared to vary significantly over the years. Since there was an absence of deer in that enclosure, we propose that environmental changes associated with the potential habitat recovery led to the restoration of its vegetation favouring the adaptation of certain well-adapted species while disadvantaging others.

Additionally, the ant species that contributed the most to the composition differences among each deer density treatments found in the shrub, and their trends of change observed were in harmony with the deer's overabundance scenario, given that their biology (e.g., diet, habitat preferences) could have allowed them to keep habiting in an environment characterised by scarce vegetation caused by the intense browsing, resulting in more open spaces. Furthermore, our study's findings supported that the relationship between deer and ant communities varies depending on the habitat attributes, influencing the extent of deer overabundance's impact on ants' community composition. In our study, forest features appeared to be unaffected in an overabundance of deer scenario, in contrast to the shrub habitat.

Given the interesting results that we have achieved, a more extensive and prolonged research effort would be necessary to better understand the dynamics observed in the present study.

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APPENDIX

Table 2. Ant species collected in pitfall traps, with their corresponding abbreviated names. The third column shows the habitat where they were found: shrub (S) and forest (F). The fourth indicates the deer density treatment. For shrub: (Control (C), High deer density (HD), Hyper deer density (ED), and for forest: Control-forest (Cf), High deer density-forest (Hdf), and Hyper deer density-forest (EDf).

Ant species' full name	Abbreviation	Habitat	Treatment
<i>Aphaenogaster gibbosa</i>	Aphagibb	S, F	C, Cf, HD, Hdf
<i>Aphaenogaster iberica</i>	Aphaiber	S	HD
<i>Camponotus cruentatus</i>	Campcrue	S, F	C, Cf, HD, Hdf, ED, Edf
<i>Camponotus fallax</i>	Campfalla	F	Cf, Edf
<i>Camponotus lateralis</i>	Camplate	F	Cf, Edf
<i>Camponotus pilicornis</i>	Camppili	S, F	C, HD, Hdf, ED, Edf
<i>Camponotus sylvaticus</i>	Campsylv	S	ED
<i>Cataglyphis hispanica</i>	Catahisp	S, F	C, Cf, HD, Hdf, ED, Edf
<i>Cataglyphis iberica</i>	Cataiber	S, F	C, HD, Hdf, ED
<i>Crematogaster auberti</i>	Cremaube	S	C, HD
<i>Crematogaster scutellaris</i>	Cremscut	F	Cf, Hdf, Edf
<i>Formica fusca</i>	Formfusc	S, F	Cf, HD, Hdf, Edf
<i>Formica gerardi</i>	Formgera	S, F	Hdf, ED, Edf
<i>Goniomma decipiens</i>	Gonideci	S	ED
<i>Goniomma kugleri</i>	Gonikugl	S	C, HD, ED
<i>Iberoformica subrufa</i>	Ibersubr	S, F	C, HD, ED, Edf
<i>Lasius alienus</i>	Lasialien	F	Cf
<i>Lasius grandis</i>	Lasigran	S, F	C, Cf, Hdf, ED, Edf
<i>Leptanilla sp.</i>	Leptanilla	S	C, HD
<i>Messor barbarus</i>	Messbarb	S	HD
<i>Messor bouvieri</i>	Messbouv	S	C, HD
<i>Messor capitatus</i>	Messcapi	S	ED
<i>Pheidole pallidula</i>	Pheipall	S, F	C, Cf, HD, Hdf, ED, Edf
<i>Plagiolepis grassei</i>	Plaggras	S	ED
<i>Plagiolepis pygmaea</i>	Plagpygm	S, F	HD, ED, Edf
<i>Plagiolepis schmitzii</i>	Plagschm	S, F	C, HD, Hdf, ED, Edf
<i>Plagiolepis xene</i>	Plagxene	S	HD
<i>Solenopsis sp.</i>	Solenops	S, F	C, Hdf, ED, Edf
<i>Strumigenys tenuipilis</i>	Strutenu	S	Edf
<i>Tapinoma madeirensse</i>	Tapimade	F	Cf
<i>Tapinoma nigerrimum</i>	Tapinige	S	HD
<i>Temnothorax blascoi</i>	Temnblas	S	ED
<i>Temnothorax pardoi</i>	Temnpard	S, F	C, Cf, Hdf, ED, Edf

Ant species' full name	Abbreviation	Habitat	Treatment
<i>Temnothorax parvulus</i>	Temnparv	F	HDf
<i>Temnothorax racovitzai</i>	Temnraco	S, F	C, HD, HDf, ED
<i>Temnothorax recedens</i>	Temnrece	S, F	CF, HDf, EDf
<i>Temnothorax sp.</i>	Temno	F	HDf
<i>Tetramorium caespitum</i>	Tetrcae	F	EDf
<i>Tetramorium semilaeve</i>	Tetrsemi	S, F	C, Cf, HD, ED
<i>Tetramorium sp.</i>	Tetramor	F	Cf