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6 **Concise and informative title**: Elaiosome-bearing plants from the Iberian Peninsula and
7 the Balearic Islands

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Abstract

The importance of many mutualistic interactions is poorly understood because information on their frequency and distribution at wide spatial scales is lacking. One such interaction is that between ants and plants bearing diaspores equipped with elaiosomes, which function as a reward for ants in exchange for dispersion. Our aim was to estimate the number of taxa having elaiosome-bearing diaspores in the Ibero-Balearic territory and its relationship to several factors. We estimated that at least 572 species and subspecies, almost one-third endemic, are present, which corresponds to ca. 5.1% of European angiosperms and 9% of Iberian ones. Because this number of elaiosome-bearing taxa is much higher than those given so far for the Northern Hemisphere, the Ibero-Balearic territory should be considered an important center of myrmecochory, with myrmecochorous species richness significantly positively correlated with ruggedness, latitude, and longitude. In contrast to other myrmecochorous territories (Australia and Cape Province), where numerous trees and shrubs develop on acid substrates, most myrmecochores in the Ibero-Balearic area are perennial herbs occupying basic substrates. Such perennial herbs are more frequent in the Eurosiberian floristic region, whereas annuals abound in the Mediterranean region. The enumerated taxa mainly inhabit forests, scrubs, and anthropized sites. Among them, 56.5% carry the elaiosome on seeds (especially strophiole and caruncle types). In 36.7%, the elaiosome is borne on indehiscent fruits, such as achenes in Asteraceae, where they are found either at the base of the style or the basal hilum, and at the base of nutlets (Boraginaceae and Lamiaceae).

Keywords Diaspore. Endemism. Eurosiberian region. Iberian flora. Mediterranean region. Myrmecochory.

1 Introduction

Although mutualistic interactions help shape the structure and function of ecological communities, the degree of this contribution is poorly understood because information on the frequency and distribution of such interactions is generally lacking on wide spatial scales (Vander Wall et al. 2017). Some of these interactions involve ants (Hymenoptera, Formicidae), which are related to plants in various ways (e.g. domatia, pollination, dispersal). Ants may disperse diaspores by dyszoochory or myrmecochory. In dyszoochory seed-eating ants (harvester ants) usually transport diaspores to their nest for consumption, although some diaspores escape predation (Wolff and Debussche 1999; Gorb and Gorb 2003; Barroso et al. 2013; Delgado Santana et al. 2013). Myrmecochory is a mutualistic interaction implying the existence of an appendage, mainly high in fat, in certain diaspores (elaiosome, Sernander 1906). The elaiosome functions as a reward for mutualistic ants and in return, they disperse diaspores. These ants, generally scavengers or omnivores, collect and transport diaspores to their nest; after consumption of the elaiosome by the colony, mostly by the larvae (Fischer et al. 2005), the seeds are discarded, either within or outside of the nest (Wolff and Debussche 1999; Giladi 2006). Nevertheless, the designation of a certain ant species as a mutualist or predator could not always be clearly decided, as the same species can act as a mutualist at one time and as a predator at another time. In some cases, ants may be exploited by cheating, non-rewarding diaspores that mimic elaiosomes by chemical cues (Pfeiffer et al. 2010); however, this exploitation may also occur in diaspores possessing elaiosomes (Turner and Frederickson 2013).

Elaiosomes, which are found on seeds, fruits, and other organs of various angiosperms, vary in morphology, color, hardness and size (Sernander 1906; Gorb and Gorb 2003). Elaiosomes of many European plants are fleshy, soft, and rapidly drying (Mayer et al. 2005; Mayer 2009); this may partly explain their omission from taxonomic and floristic descriptions, as descriptions in some cases are not based on recent herbarium sheets. Considering the size, absolute elaiosome mass and elaiosome/diaspore mass ratio fluctuate within and between species (Gorb and Gorb 2003; Edwards et al. 2006; Levine et al. 2019; Miller et al. 2020).

Elaiosomes are composed mainly of lipids along with varying amounts of starch, proteins, sugars, vitamins, amino acids, and sterols (Sernander 1906; Bresinsky 1963; Lisci et al. 1996; Gorb and Gorb 2003; Gammans et al. 2005; Fischer et al. 2008). The

main lipids are fatty acids (Boulay et al. 2006; Fischer et al. 2008; Pfeiffer et al. 2010; Boieiro et al. 2012). Interspecific differences in the concentrations of individual fatty acids seem to be associated with seed attractiveness to ants (Boieiro et al. 2012; Boulay et al. 2006, 2007; Fischer et al. 2008; Gammans et al. 2005; Miller et al. 2020), with the most attractive species having the highest concentrations of oleic acid. The content of this acid that can vary geographically (Boulay et al. 2007; Boieiro et al. 2012), acts as a behavioural release signal that stimulates ants to pick and carry items to or from the nest (Boulay et al 2006; Pfeiffer et al. 2010; Turner and Frederickson 2013; Miller et al. 2020 and references therein). Also, the metabolic profile of elaiosome phytochemistry can vary interspecifically (Fischer et al. 2008; Miller et al. 2020).

Elaiosomes have a diverse origin (Sernander 1906; Bresinsky 1963; Gorb and Gorb 2003; Mayer et al. 2005; Mayer 2009) and thus constitute a good example of convergent evolution (Gorb and Gorb 2003; Mayer et al. 2005; Lengyel et al. 2009, 2010). Elaiosomes of seeds originate from various anatomical structures. Considering their origins, different types can be distinguished, e.g. aril, arillode, caruncle, strophiole, or even sarcotesta (i.e. an external seed layer, usually soft and sappy, with substances attractive to ants; Bresinsky 1963; Gorb and Gorb 2003). Elaiosomes may also arise from the fruit-derived tissues, the receptacle, floral tube, perigonium, floral bract base, style base, or, in certain grasses, the spikelet (Sernander 1906; Bresinsky 1963; Gorb and Gorb 2003; Mayer et al. 2005; Mayer 2009).

Myrmecochory may occur as the sole dispersal mode (strict, specialized, or pure myrmecochory) either by collecting diaspores directly from the mother plant or by collecting those naturally fallen on the ground (gravity dispersal, or barochory). In other cases, myrmecochory may take place after other types of dispersal (ornitochory, anemochory, autochory), a phenomenon referred as diplochory (Nakanishi 1994; Vander Wall and Longland 2004; facultative myrmecochory according to Gorb and Gorb 2003). In either case, the possession of elaiosomes does not necessarily indicate functional myrmecochory. In this paper, all species that possess some morphological and/or chemical adaptation for dispersal by ants have been considered regardless of whether evidence of direct myrmecochory or diplochory exists.

Plant dependence on ant dispersers corresponds with diaspore morphological, chemical and phenological adaptations that maximize seed attractiveness to the most effective seed-dispersing ants (review in Warren et al. 2014; Miller et al. 2020). The most

important of these adaptations is the presence of elaiosomes. In some cases, seed size is a key character determining the likelihood of seed dispersal (Manzaneda et al. 2009; Miller et al. 2020 and references therein), while elaiosome size and elaiosome/seed size ratios are sometimes important as well (e.g. Oostermeijer 1989; Gorb and Gorb 2003; Levine et al. 2019), but not always (e.g. Boulay et al. 2007; Turner and Frederickson 2013; Miller et al. 2020). Myrmecochorous species exhibit earlier flowering and fruiting than non-myrmecochorous ones in temperate areas (Oberrath and Böhning-Gaese 2002; Gorb and Gorb 2003; Mayer et al. 2005; Servigne 2008; Warren et al. 2014) and some Mediterranean habitats (Guitián and Garrido 2006).

Diaspore-dispersing ants have wide geographical distributions (Beattie 1983; Gómez and Espadaler 2013), performing dispersal on a strictly local scale (Gómez and Espadaler 1998). They can be classified into two behavioral guilds: (1) granivores and (2) scavengers. Granivorous ants (poor-quality dispersers), forage in groups and are predominantly seed predators; they store seeds in nests, where many seeds are consumed regardless of whether an elaiosome is present or not. Dispersal may be effective in some cases. Scavenging ants (high-quality dispersers) forage individually and transport diaspores to the nest. They consume only the elaiosomes and discard the intact seeds from the nest (reviewed in Giladi 2006; Levine et al. 2019); in addition, they transport diaspores further than granivores. Myrmecochory confers selective advantages on plants, such as directed dispersal (to safe sites), dispersal for distance and escape from seed predators (reviewed in Giladi 2006); other advantages in some specific ecosystems include fire avoidance and nutrient limitation (Beattie 1983). Not all mutualistic ants are equally effective partners (Warren and Giladi 2014), however, and only a small subset act as keystone seed dispersers. They tend to be very common in local communities (Gove et al. 2007), although numerically similar to granivores in some systems (Levine et al. 2019). Approximately 100 ant species are estimated to be effective seed dispersers (Warren and Giladi 2014).

Lengyel et al. (2009, 2010) reported that myrmecochory is an evolutionary innovation and global driver of plant diversity present in ca. 11,000 angiosperm species (4.5%), 334 genera (2.5%), and 77 families (17%), and identified at least 101 independent origins of this phenomenon. Geographically, myrmecochory is distributed worldwide and is especially concentrated in the dry heath and sclerophyllous vegetation of Australia (Berg 1975; Beattie 1983; Orians and Milewski 2007), the Fynbos of South Africa (Milewski

and Bond 1982; Bond and Slingsby 1983; Bond et al. 1991), the Mediterranean region (Sernander 1906; Berg 1975; Espadaler and Gómez 1996), the deciduous forests of Europe and North America (Sernander 1906; Beattie 1983; Beattie and Hughes 2002; Lengyel et al. 2010), and tropical ecosystems of South America (Leal et al. 2015). Although general estimates have been made of the number of myrmecochores, the approximate number in certain regions is far from clear; this uncertainty is due not only to a lack of experimental work but also because the floras of some areas are largely summaries and do not always describe elaiosomes. Mayer (2009) reported that ca. 156 myrmecochores belonging to 48 genera and 29 families are present in Central Europe, but no data are available to minimally estimate their representation in the Mediterranean region. Of the above-mentioned geographical areas, Australia, with approximately 1,500 species, is the world's largest myrmecochory territory (Berg 1975), followed by the Cape floristic region (South Africa) with ca. 1,300 species (Bond and Slingsby 1983).

In this study, we focused on the myrmecochorous flora of the Iberian Peninsula and the Balearic Islands, a territory represented biogeographically by two climate types: Mediterranean, which encompasses most of the area (Mediterranean region), and temperate, restricted to the north and northwest (Eurosiberian region) (Rivas Martínez et al. 2004) (Fig. 1-inset). Regarding the first region, the southern area (Baetic System) and the Balearic Islands are recognized as regional hotspots (Médail and Quézel 1999) within the Mediterranean Basin (Myers et al. 2000). In addition, Buira et al. (2017) have shown that the Baetic System is the floristically richest region of the territory. The Iberian flora is one of the richest (5,537 native species and 739 non-natives) in Europa and Mediterranean Basin and has a level of endemism (24%) only surpassed by Turkey (Buira et al. 2017; Aedo et al. 2017).

Our main goal was to provide an estimate of the number of taxa with elaiosome-bearing diaspores in the Iberian Peninsula and the Balearic Islands. Specifically, we analyzed the incidence of myrmecochory based on several ecological factors, such as plant habit, flowering phenology, habitat (including edaphic substrate and elevational range), as well as biogeography and level of endemism; likewise, we calculated the percentage of myrmecochores in the angiosperm flora of the Ibero-Balearic territory, its correspondence at European and world levels, and compared it with that of other territories (e.g. Australia, Cape Province and temperate Europe). In addition, we examined the myrmecochorous flora with respect to diaspore origin (seeds or other

organs); in the case of seeds, we determined the most frequent type of appendage. We also examined, as far as known, the number of myrmecochores *s. str.* vs. diplochores. In this paper we evaluated the following factors: (1) most common habit, (2) floristically richest areas, and (3) predominant ecological environments. Prior to these analyses, we tested the phylogenetic independence of myrmecochores with respect to a sister pool of non-myrmecochores.

Methods

Collection of myrmecochory data

We first developed a database of myrmecochores based on a list of genera and families in Lengyel et al. (2010). We then examined the literature for studies on myrmecochores present in the Ibero-Balearic territory even if the observational or experimental data were derived from other territories (e.g. Sernander 1906; Bresinsky 1963; Pemberton and Irving 1990; Gorb and Gorb 2003; Mayer et al. 2005, etc.), which yielded more than one-third of the myrmecochores recognized in this study. Finally, we consulted *Flora iberica* (Castroviejo 1986–2020), regardless of whether or not the genus or family appeared in Lengyel et al. (2010). We searched for the following keywords: elaiosome, myrmecochory, strophiole, caruncle, aril, arillode, and ant.

After preparing the gross database, we updated the taxa using the families recognized by APG IV (2016). We also annotated each taxon with the following parameters, collected mainly from the mostly online version of *Flora iberica* (www.floraiberica.es): (a) autotroph vs. parasite; (b) habit (annual, biennial, or perennial, the latter divided into (i) herbaceous or slightly woody at base, (ii) woody at the base or suffrutescent, and (iii) completely woody (shrub or tree); (c) native vs. allochthonous or naturalized; (d) habitat, including altitude and substrate type; (e) flowering period; (f) worldwide distribution and distribution in the territory, with an indication, where appropriate, of its endemic nature; (g) Ibero-Balearic provinces inhabited, and (h) biogeographical distribution. In addition, the following features related to the elaiosome and dispersion were added for each taxon: (1) elaiosome type and origin according to consulted authors (or, in a few cases of non-reported but suspected myrmecochory, a confirmatory figure); (2) literature citations for the presence of elaiosomes in the diaspore as well as for field observations and/or experimental confirmation of diaspore transport by ants; and (3) the type of dispersion (myrmecochory *s. str.* vs. diplochory). Because many taxa have been described since the

publication of some volumes of *Flora iberica*, we consulted the original published descriptions in cases of suspected myrmecochores. We also looked for and photographed some types of diaspores in the field and in herbaria (Fig. 2).

To compare myrmecochores (Appendix A, Table S1) and non-myrmecochores in our territory and determine the incidence of myrmecochory among the different analyzed parameters, we created a database of native non-myrmecochores that included the main parameters mentioned above (Appendix A, Table S2). To avoid a phylogenetically-biased representation of the data, the following two criteria were used to select non-myrmecochorous taxa: (1) all non-myrmecochores of each genus with at least one myrmecochorous taxon were included, and (2) all non-myrmecochores of the sister genus (or the closest phylogenetically genus) were included when all the species of that genus inhabiting our territory were or could be myrmecochores. The references used to select the non-myrmecochorous genera appear in Appendix A, Table S2. No sister group was included in the database for nine genera: *Buxus* (Buxaceae), *Myrtus* (Myrtaceae), *Polygala* (Polygalaceae), *Montia* (Montiaceae), *Portulaca* (Portulacaceae), *Arum*, *Biarum*, *Arisarum* and *Helicodiceros* (Araceae) in which all species in the studied territory were considered myrmecochores.

Although our list of myrmecochores included several non-native species, the comparative statistical analysis of myrmecochores vs. non-myrmecochores only considered autochthonous taxa. Two variables –elevation above sea level and flowering period– were divided into categories. In particular, the elevation was divided into four categories: (a) very high (2,551 to > 3,000 m), (b) high (1,701–2,550 m), (c) intermediate (851–1,700 m), and (d) low (< 850 m). The flowering period was divided into four categories: (a) winter (from the beginning of December until the end of February); (b) spring (from the beginning of March until the end of May); (c) summer (from the beginning of June until the end of August); and (d) autumn (from the beginning of September until the end of November); the duration of flowering was recorded as the number of months, and initial and final months of flowering were also noted (January was considered as 1, February as 2 and so on). The type of substrate was divided into acid, neutral, basic, ultra-basic, saline and indifferent edaphic. Taxa were assigned into one of three biogeographic categories: (a) Eurosiberian, (b) Mediterranean, or (c) both, according to Rivas-Martínez et al. (2004). In addition, the presence level per geographic

province was counted. If a taxon fell into more than one category of a given variable, it was assigned to them all.

To identify myrmecochores protected at European or national levels, we consulted the IUCN Red List, the List of Wild Species in Special Protection Regime of Spain, the Spanish Catalog of Endangered Species, and the List and Red Book of Spain. Likewise, we ascertained the invasive nature of each taxon by consulting lists of invasive species of Spain, Portugal, the European Union, and the IUCN.

Finally, we prepared a table of other possibly myrmecochores that could possess elaiosomes but that have not been documented to contain them nor to have diaspores transported by ants.

Statistical analysis

To confirm the correct selection of non-myrmecochores, a Mantel test was carried out with 9,999 permutations in GenAlEx 6.502 (Peakall and Smouse 2012) considering genetic distance among taxa and myrmecochory. Two different matrices based on 1,376 taxa were created: (1) a matrix (called myrmecochory) with myrmecochory codified as binary data (0, both species myrmecochorous or non-myrmecochorous; 1, one species is myrmecochorous and the other non-myrmecochorous) and (2) a matrix of genetic distance among taxa. Because genetic distances between species, genera and/or families were not available for all the selected taxa, we followed the same approach of Oberrath and Böhning-Gaese (2002) to construct the genetic distance matrix considering eight different taxonomic levels (with the assumed distance for each level in parentheses): species (1), genus (2), subfamily or same clade within a family if a phylogeny was available (3), family (4), order (5), same clade within a superorder (6), eudicots (7), and angiosperms (8). For higher taxonomic levels (family and above), we mainly followed APG IV (2016) to select relationships between taxa, while specific references were used for infrafamilial relationships (Appendix A, Table S2). A phylogenetic tree illustrating intergeneric relationships, generated in Mesquite, is shown in Appendix B.

Additional analyses to correlate myrmecochory and characteristics of the taxa can be consulted in Appendix C.

Appendix G (Supplementary file 3) contains the list of myrmecochores and non-myrmecochores and all analyzed variables, characters, and their coding. A linear regression analysis was performed to study the relationship between myrmecochore and non-myrmecochore richness (number of species per geographic province) and the average

altitude, area, and ruggedness ("mountainousness") of each province as well as latitude and longitude (the coordinates of each provincial capital). We only had information for ruggedness, a characteristic related to the irregularity or difficulty of the terrain (Goerlich and Cantarino 2010), for Spain.

A chi-square test was used to analyze the independence of the studied variables relative to their presence in myrmecochorous and non-myrmecochorous taxa and in Mediterranean vs. Eurosiberian regions. As some studied taxa fell into more than one category (for example, a taxon might include annual and perennial individuals), two different methodologies were followed: (a) if all the taxa fell into a single category, the chi-square test was performed normally, i.e., the corresponding variable (biogeographic region, endemism status) was analyzed by including all considered categories; (b) if some taxa fell into more than one category, the test was performed independently for each category of the corresponding variable (life form, habitat, substrate, elevation, and phenological season) and, finally, the P values obtained were adjusted using the false discovery rate.

Differences in flowering phenology were analyzed using a generalized linear model (GLM) fitted to a Poisson distribution with a logarithmic link function. These analyses were carried out in three different frameworks. First, we performed a global analysis of differences between myrmecochores and non-myrmecochores, with elaiosome presence/absence used as the only main factor. Second, we conducted an analysis of differences between myrmecochores and non-myrmecochores, which considered the biogeographic region (Mediterranean vs. Eurosiberian) and used elaiosome presence/absence and biogeographic region as the main factors. Data on taxa inhabiting both regions were not considered. Finally, we carried out an analysis of differences between myrmecochores and non-myrmecochores that considered plant habit (annual, biennial, or perennial) and used elaiosome presence/absence and habit as the main factors. If a taxon fell into more than one category, the flowering data used for the calculation were incorporated into each appropriate category (annual, biennial, and/or perennial).

Finally, a chi-square test was used to compare the frequency of myrmecochores in the studied territory with that of other areas of the world. Specifically, to estimate the percentage of myrmecochores among angiosperms in the study area and allow comparisons with other areas for which published information on the approximate number of myrmecochores was available, we counted the number of angiosperms. These

numbers were obtained from floras of the territories involved in the analysis, when available (Austria, Australia and North America); in the case of the Ibero-Balearic territory, temperate Europe and the Cape Province, the information was extracted from studies on the flora or myrmecochore diversity (see Appendix D).

Results

The Mantel test performed to confirm the phylogenetic independency of myrmecochore and non-myrmecochore databases showed a relationship between genetic distance and myrmecochory (Pxy = 50312.225, r^2 = 0.0043, *P* < 0.001); but only 0.43% of the variability in myrmecochory was explained by genetic distance among taxa. Given that low level of variability (lower than 0.5%), the two databases can be assumed to be independent (Sokal and Rohlf 2012). The constructed databases were thus considered to be adequate for comparative analyses between them.

Taxonomic representation

The presence of an elaiosome in a diaspore suggests that a taxon is morphologically adapted for ant dispersal (Lengyel et al. 2009). Using this criterion, we identified 572 myrmecochorous species and subspecies belonging to 111 genera and 43 families in the studied territory (Appendix A, Table S1). Of these, 28 are allochthonous or naturalized and only two species (*Acacia dealbata* and *Ricinus communis*) are officially recognized as invasive. Only 121 of the 544 indigenous taxa have some degree of legal protection. Among the 572 taxa, 12 are hemiparasites and 2 holoparasites.

The families with the highest number of myrmecochores are Asteraceae, Euphorbiaceae and Fabaceae, which are all eudicots. The most represented monocot families are Amaryllidaceae and Juncaceae. In total, only 99 taxa are monocots, with the number of eudicots being almost five times higher (473) (Table 1). The largest eudicot genera in the database are *Centaurea* (109 taxa) and *Euphorbia* (69), while *Luzula* (19) and *Narcissus* (17) predominate among monocots (Table 1). A total of 47 genera were not cited in Lengyel et al. (2010) (Table 2); they may have gone unnoticed or were perhaps omitted because of nomenclatural transfers (e.g. *Pterospartum* and *Teline*) or lack of information on the existence of elaiosomes. These genera are more fully described in *Flora iberica*.

Comparison with other myrmecochory-rich territories

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Different areas of the world have significantly different frequencies of myrmecochores. The highest percentage of myrmecochores is found in the flora of the South African Cape region, followed by the Ibero-Balearic territory and Australia and then different areas of the Holarctic kingdom (Fig. 3a). If the two largest genera (*Centaurea* and *Euphorbia*) are excluded, the percentage of myrmecochores in the Ibero-Balearic territory is significantly lower from that of Australia, but is twice the percentage in temperate Europe myrmecochores (Fig. 3b).

Life forms

Among the taxa in the myrmecochorous database, 111 are annual (occasionally biennial or rarely perennial), 24 biennial (behaving mostly as annual or perennial herbs), and 473 perennial. Of these, 352 are herbaceous and/or slightly woody at the base, 73 are woody at the base and/or suffrutescent and 59 (9 allochthonous) are completely woody (shrubs and/or trees). Compared with non-myrmecochores, myrmecochores are more frequently perennial and less often biennial (Fig. 4a); when perennials are considered by subtype, the only category in which non-myrmecochores significantly outnumber myrmecochores is in plants that are woody at the base and/or suffrutescent (Fig. 4b). If *Centaurea* and *Euphorbia*, which are overrepresented in our flora, are removed from the database, only completely woody myrmecochores are significantly more frequent than non-myrmecochores ones ($\chi^2 = 10.15$, $P < 0.01$).

Considering both biogeographic regions (Mediterranean vs. Eurosiberian), perennial myrmecochores are significantly better represented in the Eurosiberian region than in the Mediterranean (Fig. 4c,e, Box 1). By contrast, annual myrmecochores are more numerous in the Mediterranean region. In both regions, the pattern exhibited by myrmecochores and non-myrmecochores is similar (perennial the most abundant and biennial the least abundant) but not identical. In the Mediterranean region, percentages of annual and biennial myrmecochores are significantly lower than those of non-myrmecochores, whereas percentages of perennial myrmecochores are higher (Fig. 4c,e). Considering perennial habit subtypes, the distribution of myrmecochores and non-myrmecochores is similar, but myrmecochores that are herbaceous/slightly woody at the base are significantly more highly represented in the Mediterranean region and less represented in the Eurosiberian region compared with non-myrmecochores; the opposite is true for myrmecochores that are woody at the base/suffrutescent (Fig. 4d,f).

Habitat

A total of 234 myrmecochores occupy undergrowth and/or forest edges (171—70 resinous—in evergreen forests and 146 in deciduous forests), while 214 inhabit shrublands and 186 are found in grasslands/meadows. Other habitats include sands and coastal dunes (28), rupicolous environments (124), and more-or-less nitrified environments (ca. 222; e.g. ruderal and roadside plants). All habitat types, except rupicolous environments, have a significant influence on the distribution of myrmecochores vs. non-myrmecochores (Fig. 5a). Nitrophilous environments, shrublands and forests (including riparian forests) significantly present more myrmecochores than non-myrmecochores. By contrast, grasslands/meadows, sands and costal dunes, and wetlands show significantly more non-myrmecochores than myrmecochores. Within forest types, myrmecochores are significantly more frequent in deciduous forests than are non-myrmecochores; by contrast, non-myrmecochores are significantly better represented in resinous forests (Fig. 5b).

Considering the two biogeographic regions independently, myrmecochores of nitrified places and shrublands are significantly more frequent in the Mediterranean region, while those inhabiting grasslands/meadows are more commonly found in the Eurosiberian region (Fig. 5 Box 1, c,d). In contrast, neither biogeographic region is more strongly correlated with myrmecochores inhabiting forests or rocky locations (Fig. 5 Box 1). This last habitat type has no influence on the relative distribution of myrmecochores vs. non-myrmecochores in either region. The same is true for grasslands/meadows in the Eurosiberian region, whereas non-myrmecochores are significantly more abundant in such habitats in the Mediterranean region (Fig 5c,d). Regarding forest type, the only significant correlation is that Mediterranean resinous forests harbor significantly fewer myrmecochores than non-myrmecochores (Fig. 5e,f). In addition, myrmecochores of evergreen forests are significantly more frequent in the Mediterranean region and those from deciduous forests in the Eurosiberian, although only marginally in both cases (Fig. 5 Box 2).

In regard to edaphic pH, our data are incomplete, but 179 myrmecochores grow on basic substrate, 86 prefer acid soils, 87 are edaphically indifferent and only three inhabit saline soils. Except for saline substrate, which supports significantly more non-myrmecochores ($\chi^2 = 9.42$, $P < 0.01$) than myrmecochores, the type of substrate has no influence on the relative distribution of the two groups of taxa (Appendix E, Fig. S1).

In relation to elevation, myrmecochores are found between sea level and 3,350 m (e.g. *Luzula spicata*). A considerable number (127) prefer thermophilic zones (< 850 m), while many range from sea level to 1,700 m (213) or up to 2,550 m (153). Approximately 15 species have a very large elevational distribution from low to very high zones. Only nine species are sometimes found at mountainous elevations higher than 3,000 m (Appendix A). Although both myrmecochores and non-myrmecochores preferentially inhabit low and intermediate areas, the relative percentage of myrmecochores is highest at low elevations and that of non-myrmecochores at high-very high elevations (Fig. 6a). A similar pattern is observed with respect to the two biogeographic regions, except that the highest percentages of both types of plants in the Eurosiberian region are mainly at intermediate elevations (Fig. 6b,c). Regarding the myrmecochores, these are significantly more represented in low-elevation areas of the Mediterranean region and at high to very high elevations of the Eurosiberian region (Fig. 6b,c, Box 1).

Phenology

Both myrmecochores and non-myrmecochores flower during spring and/or summer. Specifically, most myrmecochores (344) bloom exclusively between spring and summer (flowering period: summer, spring and, spring-summer). The flowering time of the remaining myrmecochores takes place in other seasons or, in a minority of cases, extends for more than two seasons (sometimes also including spring and/or summer). Only 29 bloom at any season of the year. The percentage of myrmecochores in bloom is significantly higher than that of non-myrmecochores in spring, autumn and winter, while flowering non-myrmecochores are more frequent in summer (Fig. 7a). In regard to the two biogeographic regions, a similar pattern is observed in the Mediterranean region, whereas myrmecochores and non-myrmecochores are equally distributed in the Eurosiberian region (Fig. 7b,c).

Globally, the flowering duration of myrmecochores is significantly higher than that of non-myrmecochores (4.21 ± 1.94 vs. 3.52 ± 1.57 months, respectively; χ^2 Wald = 40.61, $P < 0.000$). In addition, myrmecochores begin flowering significantly earlier than non-myrmecochores (early April vs. mid-April; χ^2 Wald = 7.01, $P < 0.01$).

Biogeography has a significant influence on all studied parameters (duration, beginning and end of flowering), with Mediterranean taxa having a longer flowering duration (mostly 3-4 months) and earlier flowering start and end than Eurosiberian taxa

(mostly 2-3 months) (Table 3). Similar to biogeography, habit has a significant effect on all studied parameters; the exception is the end of flowering, with perennial taxa having a shorter flowering duration and later flowering start than either annual or biennial taxa (Table 4). By contrast, the interaction of elaiosome presence/absence with either variable (biogeography or habit) has no effect on the three aforementioned parameters (Tables 3 and 4). Differences in flowering between the two regions and among growth habits are therefore not explained by the presence of taxa with or without elaiosomes.

Biogeography

Excluding introduced taxa and those naturalized elsewhere, 95.78% of myrmecochores have a Holarctic distribution. As far as taxa with a wide distribution, only 12 are subcosmopolitan, and one is cosmopolitan (*Fumaria officinalis*). In contrast, 189 (33.04%) are endemic, mostly *Centaurea* (74) and *Euphorbia* (22). In general, most of the endemism is distributed across many families (Table 1). Nevertheless, the endemism percentage among myrmecochores is higher than, but not significantly different from that of non-myrmecochores ($\chi^2 = 3.80$, $P > 0.05$; Appendix E, Fig. S2a).

The distribution of the myrmecochores depends on biogeographic region ($\chi^2 = 10.55$, $P < 0.01$). Non-myrmecochores are significantly more frequent in the Mediterranean region, while myrmecochores are among those species inhabiting both regions (Appendix E, Fig. S2b). If taxa occupying both regions are removed, myrmecochore presence is independent of biogeographic region. Specifically, most myrmecochores (259; 45.28%) are restricted to the Mediterranean region. The Eurosiberian region includes 71 taxa (12.41%), and many taxa (241; 42.13%) are common to both regions. Without considering this biogeographic classification, the geographic provinces with the largest numbers of myrmecochores are located in the Pyrenees, followed by the province of Granada (located in the Baetic System), the Cantabrian mountain range, the Iberian System, the Baetic mountain range and Madrid and Salamanca provinces (Fig. 1).

Considering Spanish provinces only, myrmecochore richness is positively and significantly related with ruggedness (F = 5.810, $R^2 = 0.112$, $P < 0.05$) but not with average provincial altitude (F = 0.271, $R^2 = 0.006$, $P > 0.05$). If the entire Ibero-Balearic territory is considered, myrmecochore richness is positively and significantly related to both latitude (F = 6.016, $R^2 = 0.094$, $P < 0.05$) and longitude (F = 20.841, $R^2 = 0.264$, $P < 0.01$), but not provincial area (F = 1.121, $R^2 = 0.019$, $P > 0.05$).

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Diaspore and elaiosome types

In most taxa, the diaspore is a seed (323) or indehiscent fruit (210) (achene [166], nutlet [43], or drupaceous [1]). The diaspore in the remaining 38 taxa is a spikelet (10), involucel (9), perianth (1), pedicle (5) or utricle (13) (Fig. 2). In most (86.47%) of the 266 taxa for which information is available, the elaiosome is light-colored rather than dark (16.17%). Because the diaspore is usually dark (82.12%), it contrasts with the elaiosome in most (68.67%) of these taxa. Furthermore, the diaspore is pubescent in 46.49% of cases, sometimes surrounding the elaiosome (e.g. *Centaurea* sp.) and/or with some type of ornamentation or rugosity; on the contrary, elaiosome pubescence appears only in 10.34% of the cases. Elaiosome texture (soft vs. hard) is not usually specified in the literature. Although information is lacking for some taxa, the elaiosome morphology is quite varied (Appendix A, Table S1). Only three genera (*Glinus*, *Luzula* and *Danthonia* – Fig. 2g) have diaspores with two elaiosomes.

In seeds functioning as diaspores, the elaiosome is anatomically represented by a strophiole (130 taxa), caruncle (118), aril (8), arillode (1), part of the endosperm or endospermic haustorium (8 hemiparasitic taxa), or simply a funicle (18 taxa); in the latter case, this may be an aril (e.g. in *Acacia*). In other cases (e.g. *Cytisus*), two different terms (aril vs. strophiole) are indicated for several species. In addition, a few species (e.g. *Allium ursinum*) have no elaiosomes; instead, an oily testa (sarcotesta) has the same role. Similarly, the fruit pulp surrounding the seed acts as an elaiosome in *Cytinus hypocistis* and *Cyclamen balearicum*.

In achene-type fruits acting as diaspores, the elaiosome in Asteraceae preferentially occupies two positions, one on the hilum, generally towards the base of the achene, and the other at the base of the style (the upper part of the achene). In contrast, the position of the elaiosome on nutlets in Boraginaceae and Lamiaceae is always basal.

Specialized myrmecochory vs. diplochory

Information on the type of myrmecochory could only be found for 124 of the taxa in our database; in many cases, no experimental studies or extensive observations have been performed (data not shown). Almost half of the 124 taxa are diplochorous. Although questionable in some cases, another 27 taxa are strictly myrmecochorous. Several species are heterocarpous, with different dispersal mechanisms depending on the type of fruit. The most common types of diplochory, in which myrmecochory is the second phase of

diaspore dispersal, are autochory (47 species, many employing ballistic mechanisms involving explosive capsules or legumes), anemochory (7), and endozoochory (5), the latter mainly via birds (e.g. *Myrtus communis*).

Potentially myrmecochorous taxa

In addition to the above-mentioned taxa (Appendix A, Table S1), a considerable number of taxa in *Flora iberica* (73) are possibly myrmecochorous (Appendix F), which seems quite evident in some cases (e.g. *Cytisus decumbens* and different *Centaurea* species). Drawings and/or photographs posted online sometimes show appendices that could act as elaiosomes and resemble those of other myrmecochores.

Discussion

Our work is the first to provide a minimum estimate of the number of probable myrmecochores in southwestern Europe, which is poorly known at European and worldwide levels. The estimated number of myrmecochores (572), which corresponds to almost 5.2% of the worldwide myrmecochorous flora, represents only 0.2% of global angiosperms (287,899 species according to Christenhusz et al. 2017), 5.1% of European angiosperms (11,290 species according to Tutin et al. 1980, 1993), and almost 9% of the Ibero-Balearic angiosperms (Aedo et al. 2013). Although in absolute numbers our estimate is much lower than that reported for Cape Province (South Africa; ca. 1,300 taxa; Bond and Slingsby 1983) or Australia (ca. 1,500; Berg 1975), area must be taken into account: Australia is almost 13 times larger than our studied territory, and the corresponding in the province of El Cabo (89,000 km^2) is 6.7 times smaller. Although the numbers cited for both austral territories are probably now outdated and may be considerably lower than in reality, they are still useful for comparison with our data. When the angiosperm flora of both territories is considered, the Ibero-Balearic territory has the world's second highest myrmecochory percentage together with Australia.

That percentage in our territory, which is lower than that of South Africa, does not surpasses that of Australia if the most represented genera (*Centaurea* and *Euphorbia*) in our flora are eliminated. This ranking should be taken with caution, however, because our data are mainly based on the presence of elaiosomes in diaspores, and plant-ant mutualistic interactions have not been verified in many of the species. In the case of Australia and Cape Province, the estimated number of myrmecochores is based partly on field observations and dispersal experiments of a small selection of species and partly on

morphological information from taxonomic literature and herbarium specimens (Berg 1975; Bond and Slingsby 1983). Nevertheless, our study area should be considered an important center of myrmecochory at European and Holarctic levels. Indeed, our estimate of myrmecochores is much higher than numbers estimated for the Northern Hemisphere (ca. 300 species; Beattie and Hughes 2002), for which the following numbers have specifically been published: ca. 156 in central Europe (Mayer 2009), ca. 89 in Austria (Krückl in Mayer 2009), and ca. 106 in temperate Europe (Servigne 2008). In addition to North America (Vander Wall et al. 2017), these territories are characterized by lower percentage of myrmecochory.

In the present study, we identified 111 myrmecochorous genera and 43 myrmecochorous families, corresponding to 33.2% and 55.8%, respectively, of the world's myrmecochorous flora (Lengyel et al. 2010). Compared with temperate Europe, the Ibero-Balearic territory houses almost twice as many families with myrmecochory (Servigne 2008). As indicated in Appendix F, we have identified 73 additional taxa that are probably myrmecochorous even though no information about elaiosomes in their diaspores has been published. If our hypothesis is confirmed, the myrmecochore number in the Ibero-Balearic territory would be much higher (ca. 645 taxa).

We have included in our database to *Cytinus hypocistis* which has no apparent elaiosome but whose fruit pulp enveloping the seeds serves a similar function (de Vega et al. 2011). *Cyclamen balearicum* is another example (Affre et al. 1995).

Many of the myrmecochores (189) in our database are endemics (14.2% of endemic Ibero-Balearic species; see Buira et al. 2017), especially those in the genera *Centaurea* and *Euphorbia*. This number of endemics represents almost one-third of the estimated Ibero-Balearic myrmecochorous flora, thereby bolstering the myrmecochore richness of the territory. Nevertheless, the percentage of endemism among myrmecochores is not significantly different from that of non-myrmecochores, which indicates that this type of mutualism has not been of great importance in the speciation processes occurring in the studied territory. Australian and Cape Province myrmecochorous floras also have high levels of endemism (Berg 1975; Bond and Slingsby 1983). In contrast, very few taxa are cosmopolitan or multiregional; instead, they are mostly Holarctic in distribution. Of the total, 121 appear in catalogs, lists, and red books of threatened species, and many are vulnerable (e.g. *Anchusa puechii*), endangered (*Cytisus insularis*), or even critical (*Dioscorea chouardii*) according to IUCN criteria.

In regard to the two biogeographic regions present in the territory, most myrmecochores (45.3%) are found in the Mediterranean region, while 12.4% inhabit the Eurosiberian region, and 42.1% are in both. These percentages are unsurprising, as the first region encompasses almost six times more area than the second. Médail and Quézel (1999) recognized the Baetic System and the Balearic Islands as regional hotspots, with the Baetic System shown to be the richest region in the territory (Buira et al. 2017). According to our data, the Baetic System is also effectively a center of myrmecochory, but it lags behind the main center (the Pyrenees) and is similar to Cantabrian and Iberian systems and the provinces of Madrid and Salamanca (Fig. 1). Despite their great floristic diversity, however, the Balearic Islands are not a center of myrmecochory.

Beattie (1983) proposed a latitudinal gradient in which the richness and abundance of myrmecochores increased with decreasing latitude. We uncovered a positive correlation between myrmecochore richness by province and latitude, similar to the situation in North America (Vander Wall et al. 2017). The correlation with longitude is even stronger and is consistent with the greater richness of myrmecochores in the half eastern provinces of the peninsula.

Most Ibero-Balearic myrmecochores are perennials (473). Very few are bushes or trees, which is similar to the situation in the Northern Hemisphere (e.g. 0.4% in North America; Vander Wall et al. 2017) but very different from Cape Province (mostly shrubs; Bond and Slingsby 1983; Bond et al. 1991) and Australia (mostly trees and large shrubs; Berg 1975; Orians and Milewski 2007). The higher frequency of perennial herbs (352) would be consistent with their representation in the Northern Hemisphere (Beattie and Culver 1981; Beattie 1983; Servigne 2008; Vander Wall et al. 2017). After removing the two overrepresented genera (*Centaurea* and *Euphorbia*), however, the completely woody habit appears to be significantly represented among myrmecochores compared with non-myrmecochores. In our myrmecochorous flora, in any case, the percentage of annual herbs is not negligible (19.4%), and they are significantly more frequent in the Mediterranean region provinces. This percentage of Mediterranean annual myrmecochores is significantly lower, although only marginally, than that of non-myrmecochores; therefore, this habit does not appear to have promoted myrmecochory in this region.

The distribution of myrmecochores is significantly dependent of all types of habitats, except rupicolous environments. Anthropized environments, shrublands and forests

present many myrmecochores, whereas grasslands/meadows, sands and costal dunes, and wetlands are significantly preferred by non-myrmecochores. Comparison of the two biogeographic regions provides two insights. First, the first three above-mentioned habitats include many myrmecochores in both regions, whereas grasslands/meadows harbor significantly fewer myrmecochores than non-myrmecochores only in Mediterranean environments. Several authors (Sernander 1906; Bresinsky 1963; Beattie 1983) argued that a considerable percentage of myrmecochores in the Mediterranean basin were ruderal because of prolonged vegetational disturbance over past millennia; although the late Holocene climate change also had an influence in this disturbance (Collins et al. 2012); similar scenario could apply to shrublands. Second, myrmecochores are frequent in forests of both regions, specifically in evergreen forests for the Mediterranean region and in deciduous forests for the Eurosiberian region, which is consistent with the climax vegetation of both regions (Bresinsky et al. 2013). Consequently, none of the analyzed forest types favor myrmecochory over non-myrmecochory; even the Mediterranean resinous forests harbor significantly fewer myrmecochores than non-myrmecochores, an observation in line with Sernander (1906), who indicated that the Aleppo pine forest is poor in myrmecochores.

Most Ibero-Balearic myrmecochores inhabit basic substrates; according to our results, however, this type of substrate does not seem to have exerted selective pressure on myrmecochory. These substrates predominate in many areas of northern, southern, and eastern Spain, where many myrmecochores have been recorded. This relative frequency reflects the typical division between basic and acidic regions of Iberia (east vs. west, respectively) (see also Buira et al. 2017). Interestingly, myrmecochory in other territories (Cape Province and Australia) seems to be largely restricted to nutrient-poor soils (Bond and Slingsby 1983; Bond et al. 1991). In terms of elevation, the abundance of both myrmecochores and non-myrmecochores follows an elevational gradient. However, myrmecochores are favored in low places, as previously indicated by some authors (Bresinsky 1963; Sernander 1906) and are scarcer in high or very high areas compared with non-myrmecochores in both biogeographic regions. The lower incidence of myrmecochores in higher areas may be partly due to low temperatures and wind, the latter being stronger because it is not blocked by the sparse vegetation. In these areas, wind acts as one of the main dispersal vectors, with plants thus having less reliance on biotic vectors, such as ants.

As indicated previously, the Mediterranean region occupies a larger portion of the Iberian Peninsula than does the Eurosiberian region, and the percentage of myrmecochores is thus obviously greater (45.3% vs. 12.4%). The latter region may actually be richer, however, because most of the Eurosiberian provinces contain high numbers of myrmecochores. The highest numbers of myrmecochores (207–239) are found in the Pyrenean provinces, followed by Granada (to the south), provinces located in the main Spanish mountain systems (Cantabrian, Iberian, and Baetic), and the provinces of Madrid and Salamanca. This regional distribution is consistent with the positive correlation between myrmecochore richness and ruggedness. A possible explanation for the observed distribution is that the mostly mountainous topography and high level of precipitation favoring the growth of forests, along with forest edges and grassy clearings, are responsible for the higher myrmecochore richness. However, provinces occupying other mountain systems, such as the Central System (excluding Madrid and Salamanca), Montes de Toledo, Sierra Morena, and the Galician Massif, do not show as much richness. The fundamental difference between the former and latter sets of systems lies in the type of dominant substrate: basic vs. acidic, respectively.

In regard to phenology, most myrmecochores and non-myrmecochores bloom during spring and summer, and usually bear fruits from then until autumn, but the start of the flowering period is significantly earlier in myrmecochores. These results are consistent with the findings of studies on Holarctic species (Oberrath and Böhning-Gaese 2002; Gorb and Gorb 2003; Guitián and Garrido 2006; Servigne 2008; Boulay et al. 2007; Warren et al. 2014), in which the peak of seed release usually coincides with the peak activities of dispersal ants. Regional differences in myrmecochore flowering time (e.g. the later beginning and ending of flowering of Eurosiberian myrmecochores compared with Mediterranean ones) are parallel to those of non-myrmecochores, i.e., plants with elaiosomes follow the flowering pattern typical of their biogeographic region. Servigne (2008) reported that central European myrmecochores have a flowering duration of 2 to 3 months, similar to Eurosiberian taxa in our study. These results are unsurprising, as central Europe and the northern Iberian Peninsula are biogeographically part of the Eurosiberian region. By contrast, however, the statistically significantly shorter flowering duration observed in the Eurosiberian region compared with the Mediterranean region was unexpected. This finding, which is possibly because the methodology used did not consider the simultaneous effect of altitude, latitude, continentality, or other

environmental factors, requires further investigation. In addition, perennial myrmecochores bloom significantly later than annuals. The latter type is abundant in the Mediterranean region and would be expected to take better advantage of spring rains prior to characteristic drought periods than would perennials.

As with other mutualisms, myrmecochory may depend on phenological overlap between mutualistic species and is thus potentially vulnerable to climate change (Gordon et al. 2019). Warmer temperatures could make myrmecochory vulnerable to phenological mismatch if both mutualists respond differently to increasingly early spring periods (Gordon et al. 2019), a trend that is especially evident in the studied territory.

Regarding the type of diaspore, 56.5% of Ibero-Balearic myrmecochores have elaiosomes on seeds, while the elaiosome is present on indehiscent fruits (e.g. achenes and nutlets) in 36.7%; other cases being minority. Most elaiosomes are light-colored and contrast with the darker and sometimes brightly colored diaspore, an observation that has been previously noted (e.g. Sernander 1906; Gorb and Gorb 2003). These characteristics are consistent with those of Australian myrmecochores (Berg 1975), which also lack diaspores that have a sarcotesta functioning as an elaiosome, similar to our case. As mentioned by Sernander (1906), indument is common on or near elaiosomes; this indument and other ornamentation is now generally known to aid the grip of ants to facilitate more effective transport (e.g. Oostermeijer 1989; Gómez et al. 2005; Bas et al. 2007).

The most common type of elaiosome on seeds is a strophiole, followed by a caruncle. Histological and ontogenic studies are required, however, to elucidate the anatomical origin of elaiosomes in controversial cases (e.g. aril vs. strophiole in *Cytisus* and related genera; Rodríguez-Riaño et al. 2006). Such studies are unfortunately tedious and time-consuming; in addition, transitions may occur in certain cases (e.g. aril and sarcotesta; Bresinsky 1963). The origin of the elaiosome is obvious in some other cases. In the Asteraceae, for example, the elaiosome appears on the upper part of the achene after widening of the base of the style or forms on the basal hilum of the fruit (Sernander 1906; Devesa et al. 2014).

Possession of an elaiosome does not necessarily imply that a plant exhibits strict myrmecochory, as other mechanisms may be involved. No studies have been published on the diaspore dispersal of most of the analyzed taxa. Dispersal in 27 cases appears to involve myrmecochory *s. str.*, while approximately 62 taxa exhibit diplochory, that is,

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dispersal in two (or more) phases, the second assisted by ants. This latter dispersal mechanism is surely more common; for example, dispersal in most members of Euphorbiaceae and Fabaceae in the Ibero-Balearic territory probably involves an initial ballistic dispersal phase, as suggested by their fruit types (explosive capsules and legumes, respectively), followed by ant transport. In this sense, Australian and South African floras include many diplochores but few strict myrmecochores (Berg 1975; Bond and Slingsby 1983). According to Vander Wall et al. (2017), the incidence of diplochory with a ballistic-type first phase and a myrmecochorous second phase is low (1.1%) in North America.

Lengyel et al. (2009) have reported that many invasive species are myrmecochorous. In our territory, only two species are officially designated as invasive (*Acacia dealbata* and *Ricinus communis*). Montesinos et al. (2018) have shown that the invasion of *A. dealbata* and *A. longifolia* has affected ant communities and the dispersal of native plants. In highly invaded areas, they found that native plant seed dispersal has suffered a significant reduction, which suggests a possible mechanism for the displacement of native plants.

Finally, we note that our database is only an approximation of potential myrmecochory in southwestern Europe. Although many field investigations carried out in the Ibero-Balearic territory have made important and significant contributions to the study of myrmecochory, most of these studies have focused on a few species as a model (e.g. *Helleborus foetidus*; Garrido et al. 2002; Rey et al. 2006; Boulay et al. 2006, 2007; Alcántara et al. 2007; Manzaneda and Rey 2008, 2009; etc.). Wolff and Debussche (1999) hypothesized that ant-based dyszoochory is a major mechanism of seed dispersal in the Mediterranean region, whereas myrmecochory is apparently underrepresented because of biogeographic factors and lack of strong selective pressure. Given the scarcity of field studies, whether or not the many taxa with elaiosomes in the Ibero-Balearic territory rely extensively on ants for seed dispersal is unknown. If this mode of dispersal is not heavily utilized, one possibility is that our flora is rich in taxa having various vestigial structures identified as elaiosomes that probably play a minor role in attracting legitimate seed-dispersing ants. Therefore, much field observation and experimentation are needed, especially given that the elaiosomes of different species are not equally attractive to ants (Sernander 1906; Bresinsky 1963; Miller et al. 2020). Many factors influence this

attractiveness (see Fischer et al. 2008) and the same diaspore might even be readily dispersed by ants in one population but not in another.

Declarations

Conflicts of interest/Competing interests (include appropriate disclosures): The authors declare that they have no conflicts of interest.

Ethics approval: Not applicable.

Consent to participate: Not applicable.

Consent for publication: Not applicable.

Availability of data and material (data transparency): "Not applicable" for that section.

Code availability (software application or custom code): "Not applicable" for that section.

Authors' contributions: AOO was responsible for the conception and design of this study. Material preparation and data collection was done by AOO with the help of TRR, JL and FJV; statistical analyses and figures design were performed by TRR. The appendix D, the study of the protection level of each taxon and the possible invasive species were carried out by JL. All the photos and the Mantel test were realized by FJV. AOO wrote the first draft of the manuscript, all authors commented and improved it. All read and approved the final manuscript.

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1 **Figure captions**

2 **Fig. 1** Number of myrmecochores in each province of the Ibero-Balearic territory.
3 Provinces are abbreviated according to *Flora iberica* (http://www.floraiberica.es). Lower
4 right inset, location of Eurosiberian (green) and Mediterranean (yellow) regions on the
5 studied territory

6 **Fig. 2** Myrmecochorous diaspores. **a-c**: Seeds (**a** *Euphorbia segetalis*; **b** *Rhamnus*
7 *alaternus*; **c** *Portulaca oleracea* subsp. *oleracea*), **d-f**: Fruits (**d** *Lamium purpureum*; **e**
8 *Nonea vesicaria*; **f** *Silybum marianum*), **g-h**: Spikelets (**g** *Danthonia decumbens* –right
9 inset, detail of palea–; **h** *Melica minuta* subsp. *minuta*). Specimen vouchers: **g** UNEX-
10 8487; **h** UNEX-4605. Scale bar = 2 mm (**e, f, h**), 1 mm (**a, b, g**), 0.5 mm (**c, d**)

11 **Fig. 3** Percentage of myrmecochory for different areas of the world and the results of a
12 Pearson chi-square test comparing them. **a** Considering all taxa. **b** Considering all taxa
13 excepting *Centaurea* and *Euphorbia*. χ^2: ***, $P < 0.001$. Different letters indicate
14 significant differences between territories

15 **Fig. 4** Life form distribution (percentages) of myrmecochores and non-myrmecochores.
16 **a**, **b** Taxa inhabiting the Ibero-Balearic territory (entire territory). **c, d** Taxa exclusively
17 inhabiting the Mediterranean region (MED). **e, f** Taxa exclusively inhabiting the
18 Eurosiberian region (EUR). Each figure shows χ^2 values from comparisons of
19 myrmecochores vs. non-myrmecochores. Boxes 1 and 2 indicate χ^2 values from
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21 0.01; *, $P < 0.05$; ns, not significant. Herb/SWB = herbaceous and slightly woody at base;
22 WB/Suff = woody at base and suffrutescent; CW = completely woody (shrubs and trees)

23 **Fig. 5** Habitat distribution (percentages) of myrmecochores and non-myrmecochores. **a**
24 Habitats considered in the Ibero-Balearic territory (entire territory). **b** Forest habitats
25 considered in that territory. **c, e** Habitats and forest habitats selected of taxa living
26 exclusively in the Mediterranean region (MED) or **d, f** the Eurosiberian region (EUR).
27 Each figure shows χ^2 values from comparisons of myrmecochores vs. non-
28 myrmecochores. Boxes 1 and 2 indicate χ^2 values from comparisons of myrmecochores
29 in MED vs. EUR regions. χ^2: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant.
30 Nit = nitrophilous; Gr/Me = grasslands-meadows; Shr = shrublands; For = forests; Rup =
31 rupicolous; Sa/Du = sands and costal dunes; Rip = riparian; Wet = wetlands

32 **Fig. 6** Elevational distribution (percentages) of myrmecochores and non-myrmecochores.
33 **a** Taxa inhabiting the Ibero-Balearic territory (entire territory). **b** Taxa exclusively
34 inhabiting the Mediterranean region (MED) or **c** the Eurosiberian region (EUR). Each
35 figure shows χ^2 values from comparisons of myrmecochores vs. non-myrmecochores.
36 Box 1 indicates χ^2 values from comparisons of myrmecochores in MED vs. EUR regions.
37 χ^2: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant

38 **Fig. 7** Percentage of myrmecochores and non-myrmecochores considering flowering
39 seasons. **a** Taxa inhabiting the Ibero-Balearic territory (entire territory). **b** Taxa
40 exclusively inhabiting the Mediterranean region (MED) or **c** the Eurosiberian region
41 (EUR). Each figure shows χ^2 values from comparisons of myrmecochores vs. non-
42 myrmecochores. Box 1 indicates χ^2 values from comparisons of myrmecochores in MED
43 vs. EUR regions. χ^2: ***, $P < 0.001$; *, $P < 0.05$; ns, not significant

Table 1 Families and genera with the largest number of myrmecochorous taxa in the studied territory showing numbers of endemic and allochtonous taxa

Family	Genera number	Species/subspecies			Genera	Species/subspecies		
		Total	End	Alloc		Total	End	Alloc
Eudicots	**87**	**473**	**165**	**25**				
Asteraceae	13	140	77	3	*Centaurea*	109	74	3
					Cirsium	9	0	0
Euphorbiaceae	3	77	22	2	*Euphorbia*	69	22	1
Fabaceae	9	64	28	12	*Ulex*	21	16	0
					Cytisus	18	8	0
Boraginaceae	11	23	7	2				
Lamiaceae	7	20	2	0	*Lamium*	10	2	0
Violaceae	1	19	3	1	*Viola*	19	3	1
Polygalaceae	1	16	3	0	*Polygala*	16	3	0
Caryophyllaceae	3	15	10	0	*Petrocoptis*	11	10	0
Rosaceae	1	13	0	0	*Potentilla*	13	0	0
Plantaginaceae	2	11	1	0	*Veronica*	10	0	0
Caprifoliaceae	2	10	3	0	*Knautia*	9	3	0
Papaveraceae	6	10	0	0				
Ranunculaceae	6	9	1	0				
Orobanchaceae	3	8	0	0				
Campanulaceae	1	6	4	0				
Santalaceae	1	5	1	0				
Rhamnaceae	1	4	2	0				
Resedaceae	1	4	1	1				
Others	15	19	0	4	Others	151	29	8
Monocots	**24**	**99**	**24**	**3**				
Amaryllidaceae	6	23	14	0	*Narcissus*	17	13	0
Juncaceae	1	19	2	0	*Luzula*	19	2	0
Araceae	5	13	3	1				
Cyperaceae	1	13	0	0	*Carex*	13	0	0
Poaceae	2	10	1	0	*Melica*	9	1	0
Iridaceae	2	9	3	1				
Liliaceae	2	6	0	0				
Dioscoreaceae	1	2	1	0				
Others	4	4	0	1	Others	41	8	3

End = Endemic taxa; Alloc = Allocthonous taxa
Others: other underrepresented families
Eudicots: Buxaceae, Celastraceae, Cytinaceae, Molluginaceae, Montiaceae, Myrtaceae, Polygonaceae, Portulacaceae, Primulaceae, Rubiaceae, Sapindaceae, Solanaceae, Urticaceae and Zygophyllaceae
Monocots: Asparagaceae, Asphodelaceae, Colchicaceae

Others: other genera with less representation (see Appendix A, Table S1)

Table 2 Genera not listed in Lengyel et al. (2010)

Families	Genera				
		Eudicots			
Asteraceae	*Calendula*	*Cheirolopus*	*Cynara*	*Rhaponticoides*	*Silybum*
	Tyrimnus	*Tussilago*			
Boraginaceae	*Glandora*	*Gyrocarium*	*Lithodora*	*Lycopsis*	*Myosotis*
Campanulaceae	*Jasione*				
Caryophyllaceae	*Petrocoptis*	*Silene*			
Celastraceae	*Maytenus*				
Cytinaceae	*Cytinus*				
Euphorbiaceae	*Ricinus*				
Fabaceae	*Cytisophyllum*	*Erophaca*	*Genista*	*Pterospartum*	*Teline*
Lamiaceae	*Glechoma*	*Nepeta*	*Prunella*		
Molluginaceae	*Glinus*				
Orobanchaceae	*Lathraea*				
Papaveraceae	*Ceratocapnos*	*Platycapnos*	*Sarcocapnos*		
Plantaginaceae	*Lafuentea*	*Veronica*			
Polygonaceae	*Polygonum*				
Portulacaceae	*Portulaca*				
Ranunculaceae	*Ranunculus*				
Rhamnaceae	*Rhamnus*				
		Monocots			
Amaryllidaceae	*Allium*				
Araceae	*Arisarum*	*Arum*	*Biarum*	*Helicodiceros*	*Zantedeschia*
Asphodelaceae	*Simethis*				
Dioscoreaceae	*Dioscorea*				
Iridaceae	*Crocus*	*Hermodactylus*			

Table 3 Flowering phenology (mean ± SD) and the statistical tests comparing myrmecochorous and non-myrmecochorous taxa between Mediterranean and Eurosiberian regions

Flowering variables	Myrmecochores (elaiosome)		Non-myrmecochores (non-elaiosome)	
	Mediterranean	Eurosiberian	Mediterranean	Eurosiberian
Duration (months)	3.80 ± 1.63	3.26 ± 1.57	3.29 ± 1.44	2.93 ± 1.11
Beginning	4.48 ± 2.38	5.33 ± 1.37	4.50 ± 1.73	5.70 ± 1.12
End	6.68 ± 1.91	7.39 ± 1.49	6.68 ± 1.59	7.63 ± 0.92

Main factors	Duration		Beginning		End	
	χ^2Wald	*P*	χ^2Wald	*P*	χ^2Wald	*P*
Presence/absence elaiosome (Myr)	6.145	0.013	0.797	0.372	0.220	0.639
Biogeography (Biog)	7.094	0.008	27.019	0.000	12.519	0.000
Myr x Biog	0.164	0.685	0.608	0.435	0.228	0.633

Beginning and end of flowering: January = 1; December = 12

χ^2 Wald = GLMs fitted to a Poisson distribution with a logarithmic link function

Table 4 Flowering phenology (mean ± SD) and the statistical tests comparing myrmecochorous and non-myrmecochorous taxa with different growth habits

Flowering variables	Myrmecochores (elaiosome)			Non-myrmecochores (non elaiosome)		
	Annual	**Biennial**	**Perennial**	**Annual**	**Biennial**	**Perennial**
Duration (months)	5.18 ± 2.44	5.50 ± 1.91	4.03 ± 1.77	4.21 ± 1.81	4.15 ± 2.01	3.38 ± 1.49
Beginning	3.15 ± 1.40	3.80 ± 1.40	4.51 ± 2.19	3.56 ± 1.42	4.24 ± 1.58	4.85 ± 1.65
End	7.27 ± 2.02	8.25 ± 1.37	7.07 ± 1.83	6.71 ± 1.48	7.40 ± 1.43	7.15 ± 1.55

Main factors	Duration		Beginning		End	
	χ^2**Wald**	**P**	χ^2**Wald**	**P**	χ^2**Wald**	**P**
Presence/absence elaiosome (Myr)	25.883	0.000	4.209	0.040	2.869	0.090
Habit	65.497	0.000	85.188	0.000	4.925	0.085
Myr x Habit	0.958	0.619	0.507	0.776	4.436	0.109

Beginning and end of flowering: January = 1; December = 12

χ^2 Wald = GLMs fitted to a Poisson distribution with a logarithmic link function
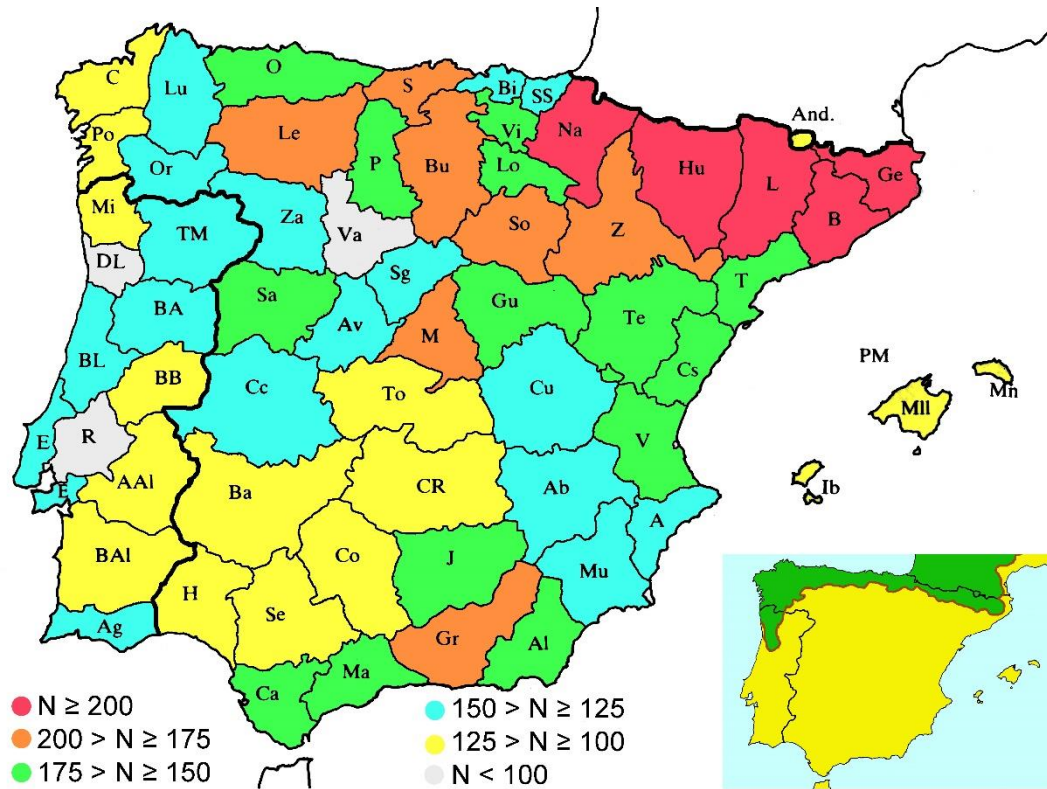
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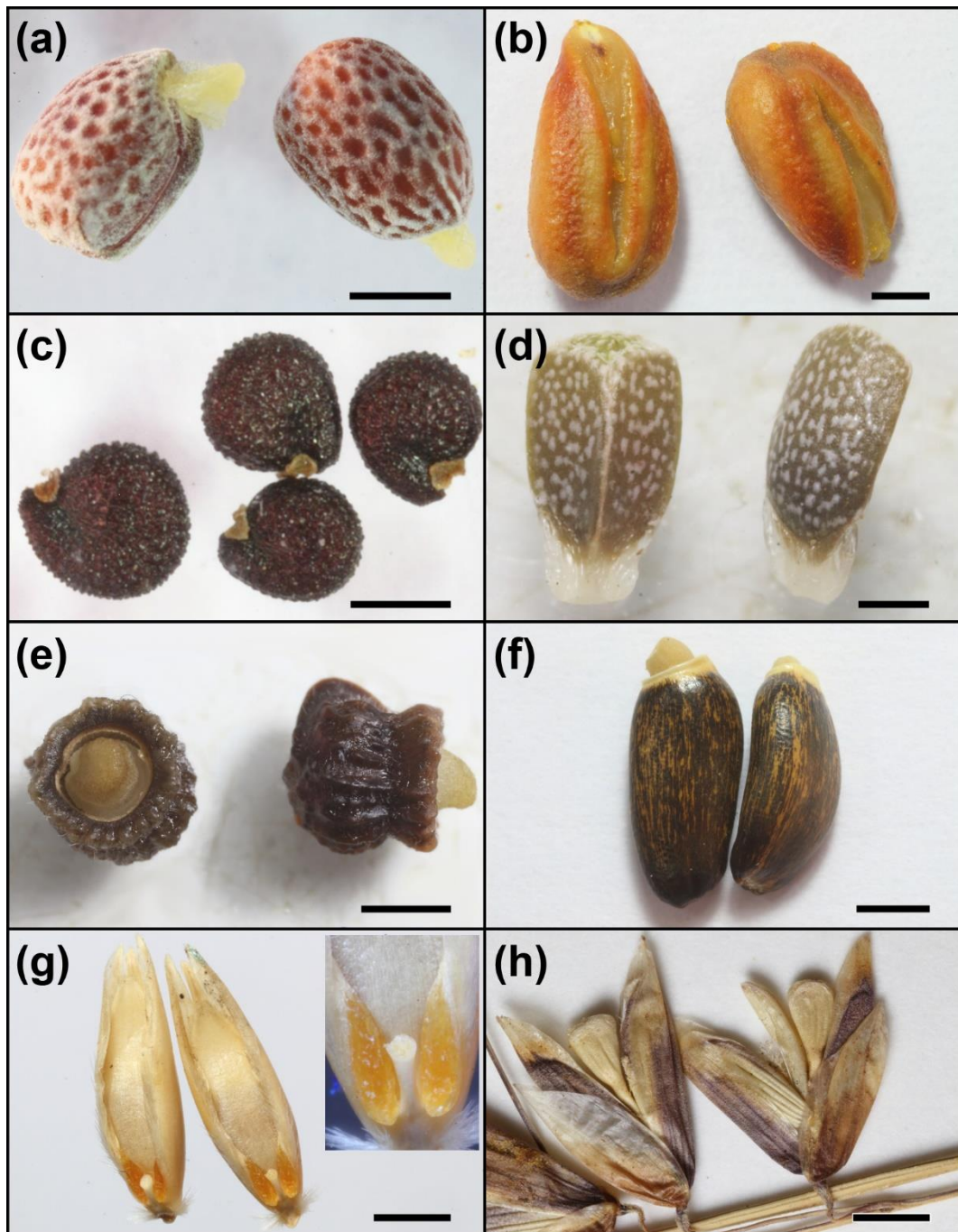
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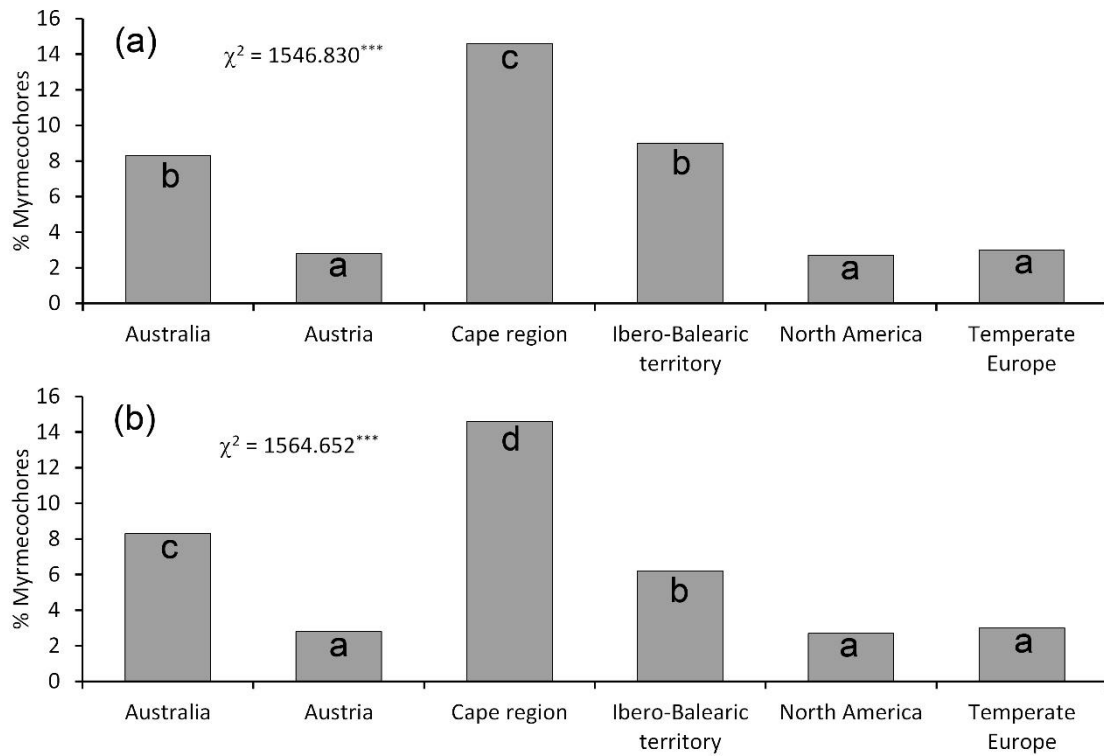
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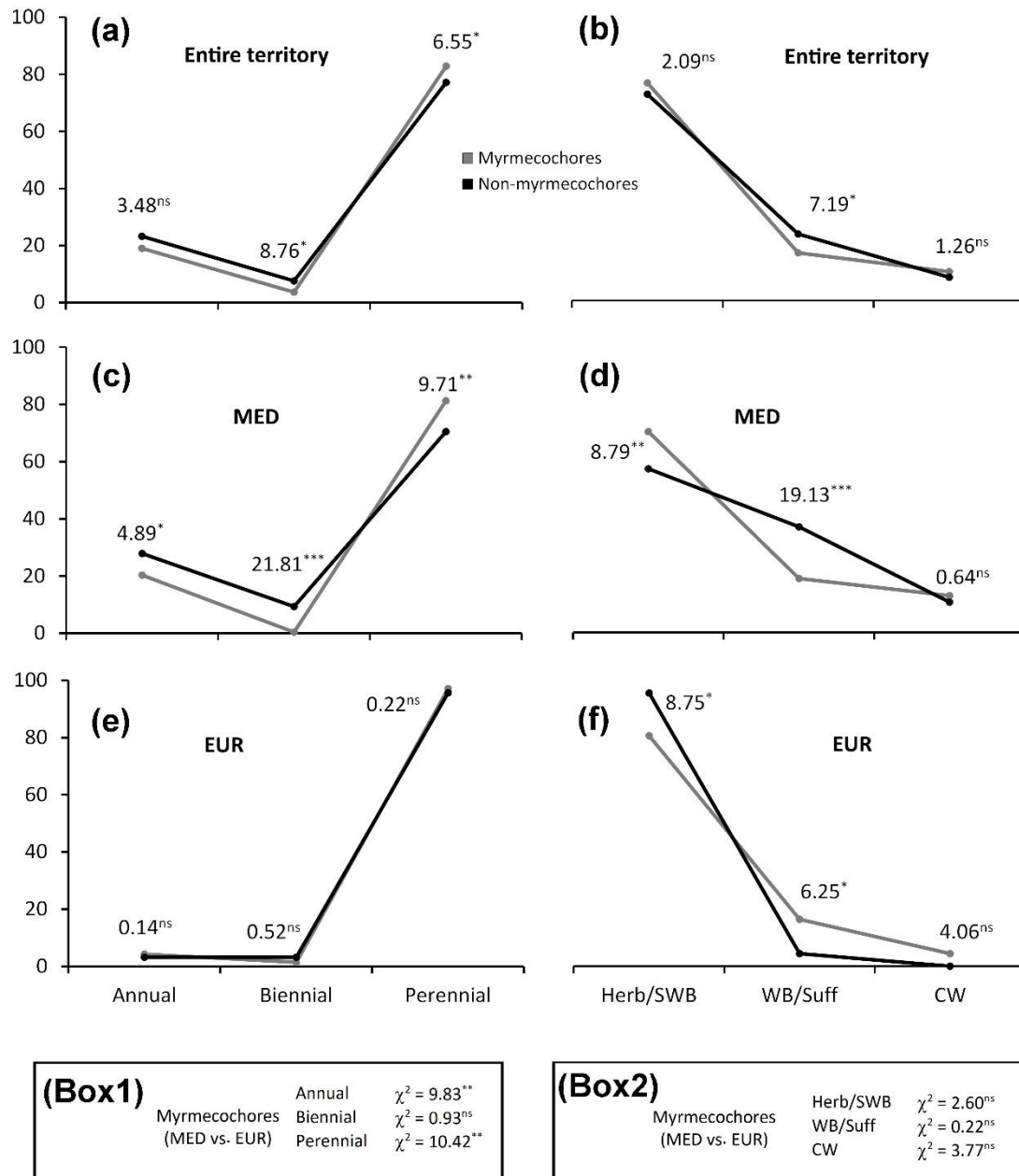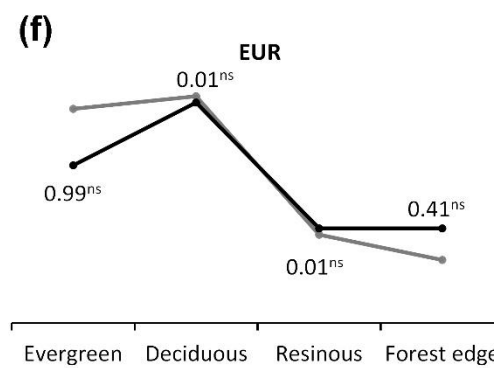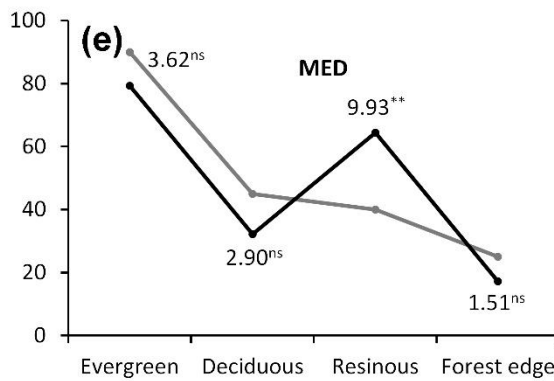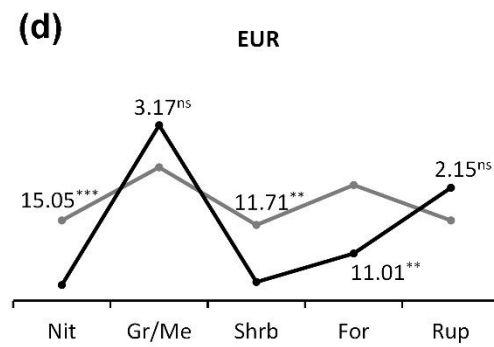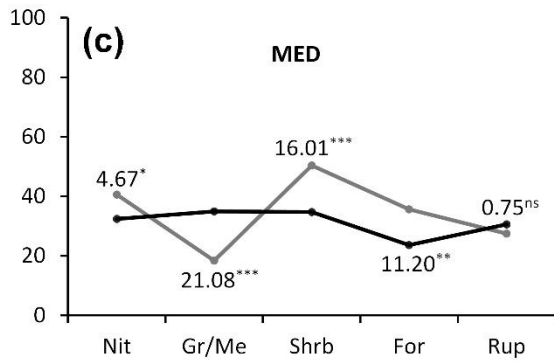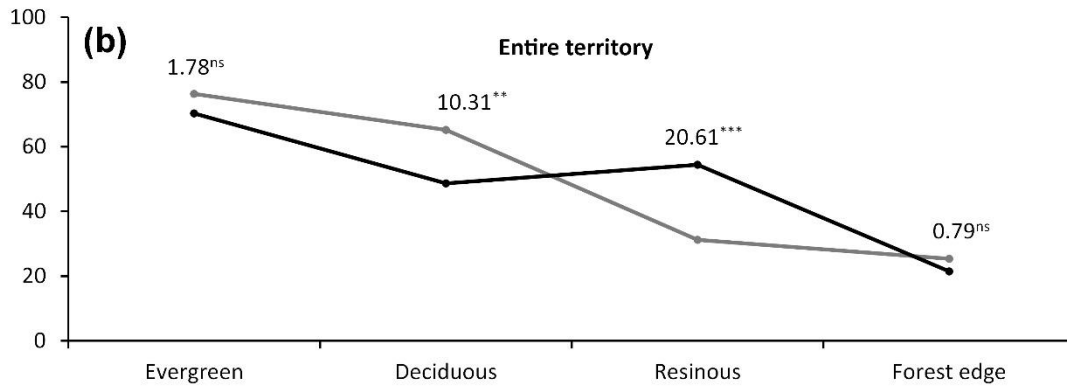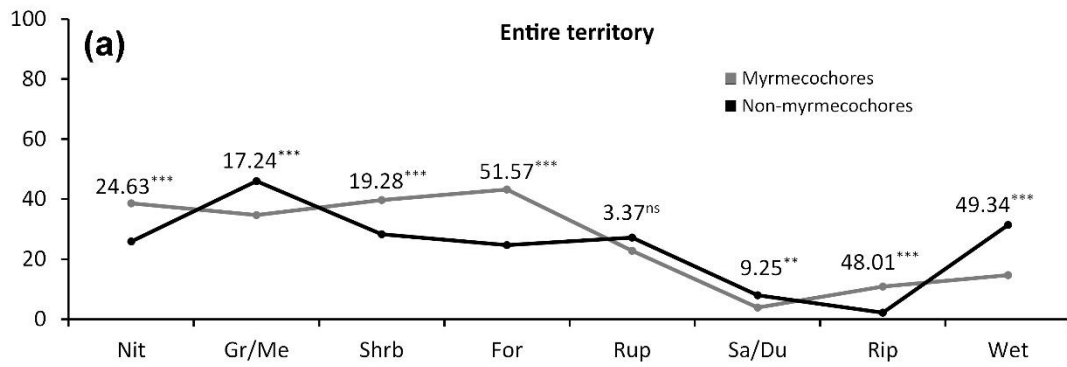
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(a) Entire territory

■ Myrmecochores
■ Non-myrmecochores

24.63*** 17.24*** 19.28*** 51.57*** 3.37ns 9.25** 48.01*** 49.34***

Nit Gr/Me Shrb For Rup Sa/Du Rip Wet

(b) Entire territory

1.78ns 10.31** 20.61*** 0.79ns

Evergreen Deciduous Resinous Forest edge

(c) MED

4.67* 16.01*** 0.75ns
21.08*** 11.20**

Nit Gr/Me Shrb For Rup

(d) EUR

15.05*** 3.17ns 11.71** 2.15ns
11.01**

Nit Gr/Me Shrb For Rup

(e) MED

3.62ns 9.93**
2.90ns 1.51ns

Evergreen Deciduous Resinous Forest edge

(f) EUR

0.01ns 0.41ns
0.99ns 0.01ns

Evergreen Deciduous Resinous Forest edge

(Box 1) Myrmecochores (MED vs. EUR)

Nitrophilous	$\chi^2 = 4.21^*$
Gr/Me	$\chi^2 = 19.92^{***}$
Shrubland	$\chi^2 = 13.31^{***}$
Forest	$\chi^2 = 0.23^{ns}$
Rupicolous	$\chi^2 = 0.01^{ns}$

(Box 2) Myrmecochores (MED vs. EUR)

Evergreen	$\chi^2 = 7.14^*$
Deciduous	$\chi^2 = 5.56^*$
Resinous	$\chi^2 = 1.18^{ns}$
Forest edge	$\chi^2 = 0.26^{ns}$

Fig. 5 Habitat distribution (percentages) of myrmecochores and non-myrmecochores. **a** Habitats considered in the Ibero-Balearic territory (entire territory). **b** Forest habitats considered in that territory. **c, e** Habitats and forest habitats selected of taxa living exclusively in the Mediterranean region (MED) or **d, f** the Eurosiberian region (EUR). Each figure shows χ^2 values from comparisons of myrmecochores vs. non-myrmecochores. Boxes 1 and 2 indicate χ^2 values from comparisons of myrmecochores in MED vs. EUR regions. χ^2: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant. Nit = nitrophilous; Gr/Me = grasslands-meadows; Shr = shrublands; For = forests; Rup = rupicolous; Sa/Du = sands and costal dunes; Rip = riparian; Wet = wetlands
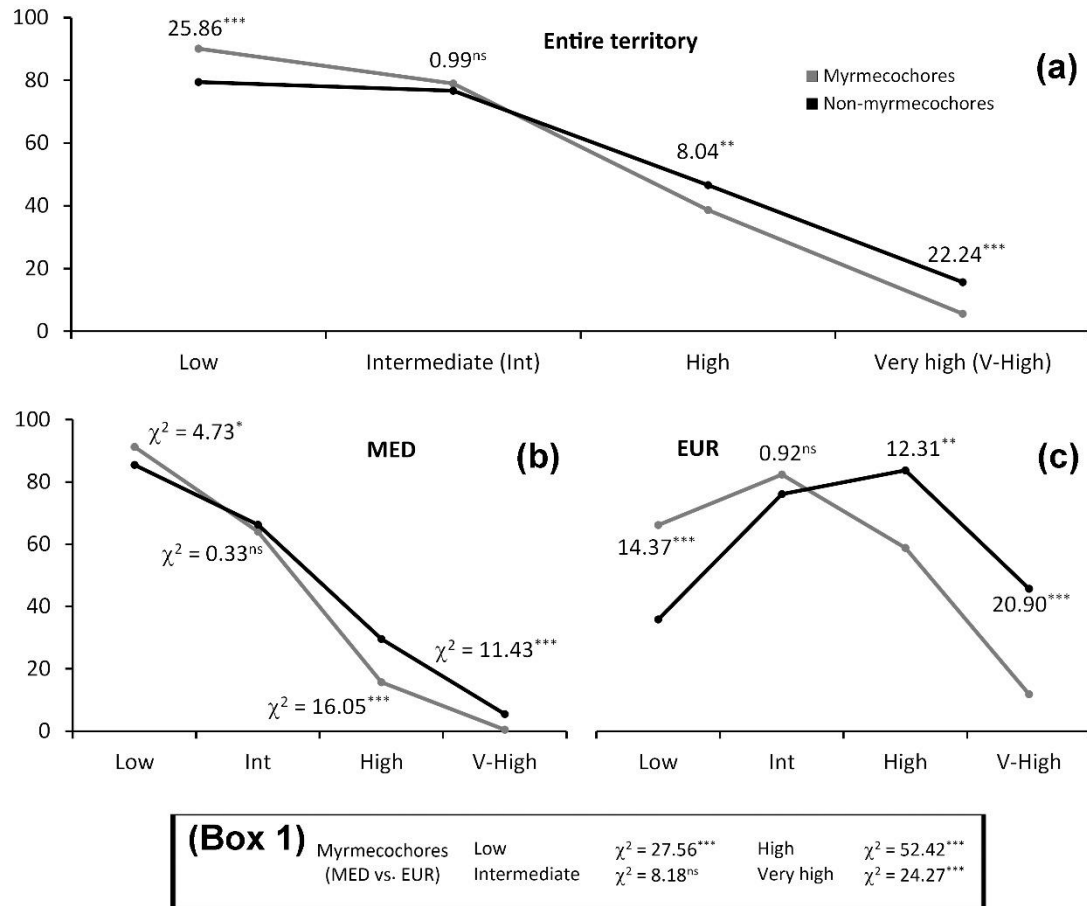
Fig. 6 Elevational distribution (percentages) of myrmecochores and non-myrmecochores. **a** Taxa inhabiting the Ibero-Balearic territory (entire territory). **b** Taxa exclusively inhabiting the Mediterranean region (MED) or **c** the Eurosiberian region (EUR). Each figure shows χ^2 values from comparisons of myrmecochores vs. non-myrmecochores. Box 1 indicates χ^2 values from comparisons of myrmecochores in MED vs. EUR regions. χ^2: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant
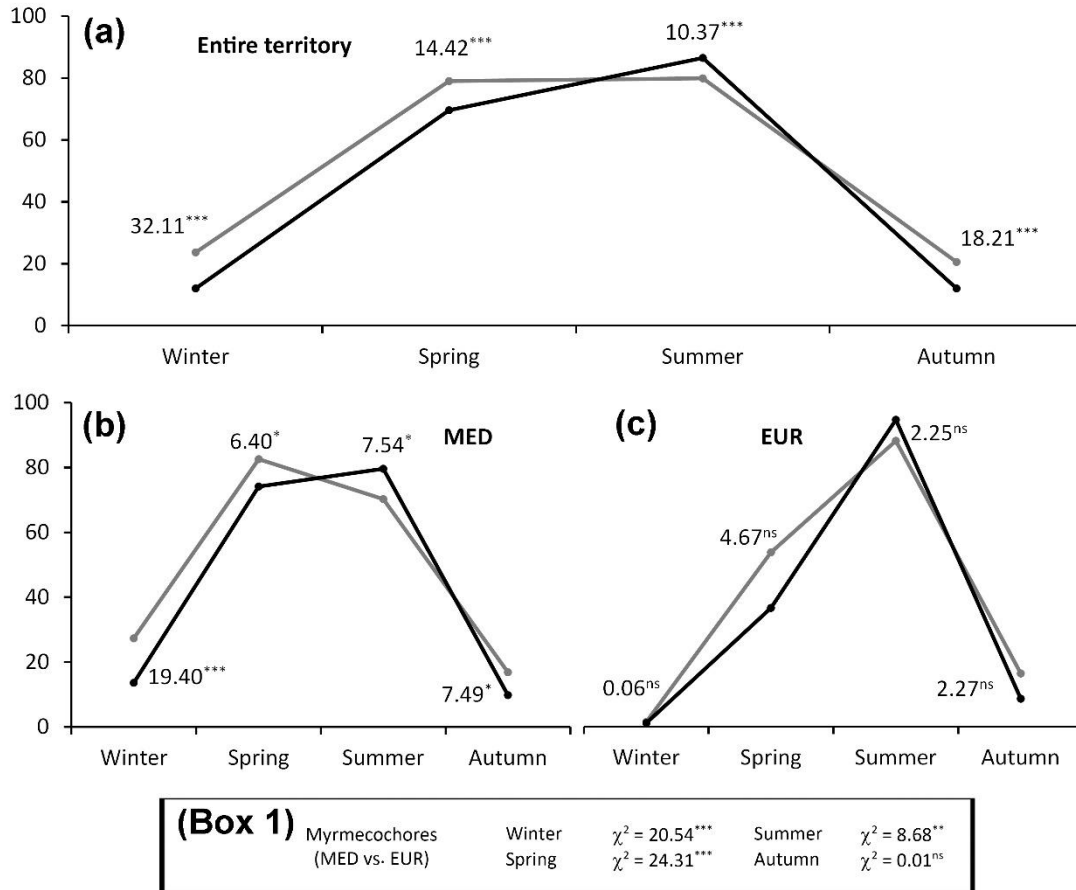
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Supplementary file 1

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