

Article

Biogeography of Iberian Ants (Hymenoptera: Formicidae)

Alberto Tinaut  and Francisca Ruano * 

Department of Zoology, University of Granada, Campus de Fuentenueva s/n, 18071 Granada, Spain; hormiga@ugr.es

* Correspondence: fruano@ugr.es

Abstract: Ants are highly diverse in the Iberian Peninsula (IP), both in species richness (299 cited species) and in number of endemic species (72). The Iberian ant fauna is one of the richest in the broader Mediterranean region, it is similar to the Balkan Peninsula but lower than Greece or Israel, when species richness is controlled by the surface area. In this first general study on the biogeography of Iberian ants, we propose seven chorological categories for grouping them. Moreover, we also propose eight biogeographic refugium areas, based on the criteria of “refugia-within-refugium” in the IP. We analysed species richness, occurrence and endemism in all these refugium areas, which we found to be significantly different as far as ant similarity was concerned. Finally, we collected published evidence of biological traits, molecular phylogenies, fossil deposits and geological processes to be able to infer the most probable centre of origin and dispersal routes followed for the most noteworthy ants in the IP. As a result, we have divided the Iberian myrmecofauna into four biogeographical groups: relict, Asian-IP disjunct, Baetic-Rifan and Alpine. To sum up, our results support biogeography as being a significant factor for determining the current structure of ant communities, especially in the very complex and heterogenous IP. Moreover, the taxonomic diversity and distribution patterns we describe in this study highlight the utility of Iberian ants for understanding the complex evolutionary history and biogeography of the Iberian Peninsula.

Keywords: species richness; species occurrence; endemic species; distribution ranges; dispersal routes; centre of origin; refugium areas



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1. Introduction

Ants bring together a number of traits that make up an interesting subject for biogeographical studies: they are conspicuous and one of the most well-known taxa of the terrestrial invertebrates [1], near-ubiquitous in terrestrial ecosystems [2]. They are an ecologically dominant faunal group [3] and highly diverse but still accessible [3] and show an extreme diversity of dispersal strategies although they are sessile superorganisms [4].

Local ant species richness is strongly correlated with temperature, which is the most important factor determining the structure of ant communities [1]. Ants are highly diverse in hot and dry habitats [5] and in low-elevation, low-latitude forests [6]. The latitudinal diversity gradient [6] with an asymmetric northern hemispheric pattern has been detected for ants, which is impossible to explain by only contemporary biotic and abiotic variables [5]. None of the current factors sufficiently correlate to explain current ant diversity [2,5,7]. Moreover, modern ant assemblages suggest a climate-driven past reorganization of the Palaearctic ant fauna [7]. Many ant lineages which previously lived in a warmer Europe, were not able to survive through long-term cooling (Pliocene) and glacial cycles (Pleistocene) but some of them persisted in Indomalayan and Australian regions [7]. Thus, the high extinction pattern in the northern hemisphere appears to have conditioned its marked asymmetric latitudinal diversity gradient [5,7].

Knowledge of the ants found in the Iberian Peninsula (the IP including Andorra, Gibraltar, Portugal and Spain) is still fragmentary [8]. Moreover, there are very few publications treating data regarding their biogeography, and they are limited to some

genera, species or zones [8–13]. The biogeography or philogeography of other Iberian arthropods have been addressed for example for the coleopteran genera *Berberomeloe* [14], *Pimelia* [15], *Blaps* [16], *Cephalota* [17], *Hydraena* [18] and some others cited throughout this article.

The IP forms part of the Mediterranean biodiversity hotspot, unique in the Palaearctic region. It is a threatened area with elevated species richness and a high level of endemism in all the taxa [19–21]. Hewitt [22] established that the IP has an intermediate position as far as species richness and the number of paleoendemic species are concerned, compared to the other two Mediterranean peninsulas (Italy and the Balkans). This high level of diversity within the IP was attributed mainly to its environmental heterogeneity conditioned by its complex orography. The IP mountain ranges are at different latitudes and altitudes with an east-western orientation. These ranges are sometimes permeable, but others act as geographic barriers producing isolated valleys, plateaus and plains. The east-western orientation also permits the establishment of particular and markedly different microhabitats on the southern and northern slopes, which vary depending on the altitude and latitude.

On the other hand, changing paleogeography and paleoclimate in the region favoured the convergence of different lineages, sharing evolutionary history for a long period [23]. Thus, in the early Paleogene (60 mya), the small Iberian plate, fragmented during the Mesozoic (100 mya) and united with the European plate, had a semitropical climate until the end of the Miocene (23–5.3 mya) [24,25] defining similar biomes to the current African savannah. Moreover, in the southern territories a succession of separations and unifications with the African plate continued until the end of the Miocene, closing the IP with Africa during the evaporitic Messiniense [26]. These semi-tropical communities from the Miocene were composed of species of Asiatic and African origin [27]. Later, successive climatic and orographic changes in the Pliocene and Pleistocene produced migrations towards the IP [25,28–30] which led to the formation of a mosaic of fragmented populations that persisted in small refugia throughout the entire Iberian refugium (the “refugia-within-refugium” scenario) [22,31–33] which is very important for the understanding of the diversity and phylogeography of some Iberian taxa [31,32,34]. After the glacial periods the IP played an important role when the Palaearctic peninsulas acted as providers of re-colonizing species to the northern territories [35–37]. These relatively recent biogeographical processes have greatly conditioned the current faunistic composition of the IP.

Thus, to the best of our knowledge, this is the first biogeographic global study on the richness and distribution of the Iberian formicids. We have undertaken this challenge well aware that the knowledge about ant distribution and endemic species in the IP is still incomplete. Our goals have been (1) to analyse the number of ant genera and species in the IP but also to compare them with other Mediterranean countries, especially France (linking the IP with the European Palaearctic) and Morocco (with the African Palaearctic), (2) to take into account the putative refugia within the Iberian refugium, and we propose a subdivision of the IP in refugium areas and attribute a chorological category to each species, and (3) we have defined four different groups of species depending on the different dispersal patterns (centre of origin and dispersal routes) based on biological traits, molecular phylogenies, fossil deposits and geological processes, when available.

2. Materials and Methods

2.1. Species Included in the Study

In this study we have included known species in the IP (Andorra, Gibraltar, Portugal and Spain) and compared them with the species found in nearby countries such as France and Morocco. We have tried to use the most updated published lists in the four countries closely involved adding new citations such as some general reviews [38–40]. Only described and named species are included in our study (those species appearing as “sp.”, species 1, 2, species under description, etc. are not included). Moreover, we have only considered mainland species, avoiding the species which only appear on the islands

belonging to the four countries. In general, we have not undertaken taxonomic problems such as synonyms or misidentifications of species included in the different faunistic lists, assuming as correct the most recent reference. For the nomenclature of the social parasite species of *Temnothorax* and *Tetramorium* we have adopted the criterion of Seifert et al. [41]. With this method of managing citations our final results might show slight differences with some published lists, but this has not affected our main goals.

For the Portuguese species we focused on Sagueiro [42], taking into account previous publications of Collingwood & Prince [43] and later ones such as Boeiro et al. [44] and Gonçalves et al. [45]. We have excluded from our lists *Temnothorax caparica* Henin, Paiva and Collingwood, 2001, which resulted to be a misidentification of *Cardiocondyla mauritanica* Forel, 1890 [46].

For the Spanish species we focused on the list included in Sánchez-García et al. [47] and added some recently described species [48] and some new findings [49].

In the case of Andorra we have used the list of species of Bernadou et al. [50]. For Gibraltar there is no up-to-date catalogue and citations appear in general articles for the Iberian ants, except for some recent records that have been taken into account [51–53].

For the French species we used Casevitz-Weulersse & Galkowski [54] adding some of the variations included in Monnin et al. [55], and Seifert [56] to clarify the status and current distribution of the European *Lasius* species.

The faunistic list of the Moroccan ant species was constructed from the results of Cagniant [57] and also included the additions provided in different publications [53,58–66].

We have also used the available data on the myrmecofauna of most of the other Mediterranean countries (Table 1) permitting us to put the IP ant species into a Mediterranean context.

Table 1. List of Mediterranean countries and number of cited species.

Country/Region	N° Species	Reference
EUROPE	622	[67]
IP	299	present paper
FRANCE	211	present paper
ITALY	187	[68]
BALKANS	319	[69]
ALBANIA	79	[70]
SERBIA	116	[71]
CROATIA	140	[72]
YUGOSLAVIA (former)	171	[69]
MACEDONIA	80	[73]
GREECE	259	[74]
TURKEY	286	[75]
ISRAEL	203	[76]
EGYPT	97	[77]
TUNISIA & ALGERIA	180	[57]
MOROCCO	233	present paper

2.2. Biogeographical Analysis

We undertook three different biogeographical aspects of the Iberian biogeography: 1. Analysis of the chorology of all the species included in the Iberian list; 2. Assessment of the distribution range of these species in the IP, emphasizing the endemic, rare and relict species; 3. To analyse the colonization history of the IP and propose four different ant groups, taking into account their most probable centres of origin and dispersal routes.

2.2.1. Chorology

According to Ribera [78] we established similar chorological categories (categories one to four) but adding three more (five to seven). Specifically, the seven chorological categories we have used are: 1. southern species (S) present in northern Africa and in some

areas of the IP but never extending their distribution beyond the north of the Pyrenees; 2. northern species (N), mostly distributed in the north of Europe, northern Pyrenees and some other northern areas in the IP; 3. Iberian endemic species present only in the IP (X) or extending their distribution to the northern slopes of the Pyrenees or some areas in southeastern France (XS); 4. trans-Iberian species (T) present in the northern Pyrenees, the IP and northern Africa; 5. species living only in the northern Mediterranean basin (MN); 6. species distributed over all the Mediterranean basin (M); 7. introduced species (I).

2.2.2. Distribution Range

We have also aimed to portray the distribution of all the listed species for the IP in as much detail as possible, although the ant distribution and endemic species is still incomplete and the methods and effort sampling were heterogeneous (pitfall traps, visual inspection, etc.) and sometimes unknown to us, such as those taken from bibliography which only report the species occurrence. Therefore, we have defined biogeographical subdivisions following the criteria established in other studies. Arnan et al. [79] established only two subdivisions in the IP, the Atlantic and Mediterranean, but we have subdivided the two biogeographic subregions into eight refugium areas (Figure 1), following Gómez and Lunt's criteria [32] based on general biota occurrence (plants, vertebrate and invertebrates animals). We have limited the refugium areas to mountain ranges which act as borders because ants prefer low altitudes [6]. We considered an Atlantic and a Mediterranean coast refugia, which have been defined as biogeographical areas for butterflies [80] and birds [81]. Some of these areas are supported as refugia such as the southern plateau, Atlantic and south-eastern Mediterranean for *Pimelia* species [15] or the entire Mediterranean during the Pleistocene for *Polyommatus* species [37]. Thus, we have finally defined the following refugium areas (Figure 1): 1. the Cantabric including the Cantabric and Basque ranges and a part of the eastern Galaic mountains; 2. the Pyrenean including all the southern slopes of the Pyrenean range from Navarra to Catalonia; 3. the Mediterranean, including the eastern and south-eastern coasts; 4. the Atlantic including the western Iberian coasts; 5. the northern plateau, bordered to the south by the northern slopes of the Central and Iberic ranges, and to the north by the Cantabric range; 6. the southern plateau, bordered to the north by the southern slopes of the Central and Iberic ranges and to the south by the Sierra Morena range; 7. the Guadalquivir Valley; and 8. the Ebro Valley. The geographical position of the citations has been obtained from the AntMaps.org web page [82], and confirmed with our own data and recent publications and reviews (see Material and Methods 1.1). Moreover, we have analysed the occurrence and the number of species found in every refugium area, as well as the number of refugium areas occupied by each species. We also analysed the endemic species distribution highlighting the rare species and the refugium areas which they inhabit. Finally, we tested the similarity of each of the refugium areas by mean of hierarchical clustering analysis based on Jaccard's index as the association estimate and the paired group algorithm UPGMA (Unweighted Pair Grouping method with Arithmetic Means) procedure [80,83,84] as the agglomeration criterion using PAST program V. 4.04 [85] and excluding ubiquitous species. The significant differences in similarity (Jaccard's Index) have been calculated among all the branches of the cluster [80,86,87].

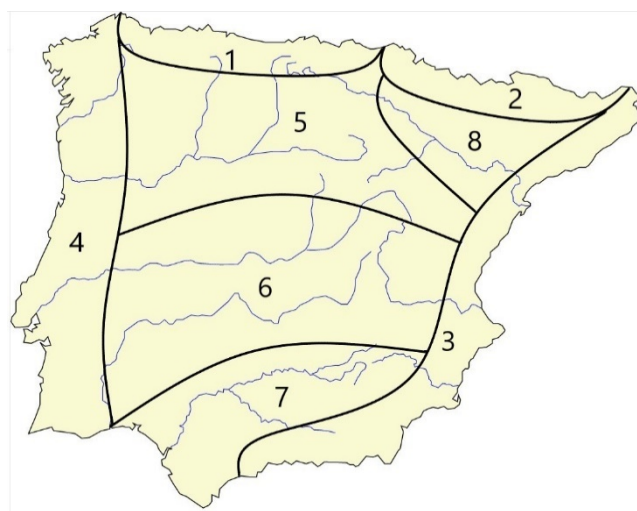


Figure 1. Aprioristic refugium areas considered in the Iberian Peninsula. 1. Cantabric; 2. Pyrenean; 3. Mediterranean coast; 4. Atlantic; 5. Northern plateau; 6. Southern plateau; 7. Guadalquivir Valley; 8. Ebro Valley.

2.2.3. Origin and Dispersal Routes

We collected biogeographical evidence from the bibliography about biological traits, dated molecular phylogenies (with different estimation methods) and fossil deposits of the different ant subfamilies, genera and species when available. We inferred from these data the origin and the most plausible dispersal routes up to the current distribution range, taking into account the most probable geology and climate distribution admitted for each epoch in the bibliography and the comparison results obtained from other taxa.

3. Results

3.1. Taxonomic Richness

The Iberian Peninsula (IP) has 299 ant species, the highest number compared to the French (211) and the Moroccan (233) ant faunistic lists (see Table S1 in Supplementary Material). The Iberian ant richness is only comparable with the 259 ant species of Greece and the 286 of Turkey. To the north the ant richness followed the latitudinal diversity gradient (Belgium 85 species [88], Norway 57 species [89]). Nevertheless, the ratio species richness/surface in the three countries revealed a similar ratio for the IP and Morocco (5.1×10^{-4} and 5.2×10^{-4} species/km² respectively) and much lower for France (3.2×10^{-4} species/km²). Even in a wide view of the Mediterranean context, the ant fauna of the IP is the second in species richness, with only a few species less than the Balkan peninsula but not when the ratio of species/surface is taken into account, where the IP has a higher ratio than France, similar to Morocco, but surpassed by Greece and Israel. The Iberian ant species appear grouped in seven subfamilies (Amblyoponinae, Ponerinae, Proceratiinae, Leptanillinae, Dolichoderinae, Formicinae and Myrmicinae), but Morocco has two more subfamilies (Cerapachyinae and Dorylinae) and France one subfamily less than the IP (Amblyoponinae). The subfamilies Amblyoponinae, Cerapachyinae and Dorylinae, which are widely considered as tropical [90], are absent from France and only the subfamily Amblyoponinae is present in the IP.

The subfamily Myrmicinae had the highest species richness for the three studied areas, 114 species (54% of the total ants) in France, 171 (57%) in the IP and 147 (63%) in Morocco. The subfamily Formicinae has a lower number of species than Myrmicinae in all the three areas: 77 in France (36.5%), 95 species (33%) in the IP and 61 (26%) in Morocco. The subfamily Dolichoderinae appears far below, followed by Dorylinae and Cerapachyinae (see Supplementary material Table S1).

The most diverse genus in the IP is *Temnothorax* (47 species and 16% of the total species richness), followed by *Lasius* (25 species, 8%), *Formica* (23 sp., 8%) and *Camponotus*

(20 species, 7%). *Temnothorax* is also highly diverse in France (28 sp., 13%) and Morocco (39 sp., 17%) but represents a slightly higher percentage of the total species in the latter country. The other most abundant genera in France are *Formica* (13%), *Lasius* (12%) and *Myrmica* (10%) and in Morocco *Messor* (12%), *Aphaenogaster* (11%) and *Cataglyphis* (9%).

Although the total number of endemic species in the IP (72 sp., 24 %) is the highest in the Mediterranean countries (21 endemic ant species in Greece [74]; 25 in Israel [76]; and 56 in Morocco [57]), but again the ratio of endemic species/surface is similar to Morocco (1.25×10^{-4} endemic sp./km²) and surpassed by Greece (1.6×10^{-4} endemic sp./km²) and Israel (12.0×10^{-4} endemic sp./km²). In the IP, the highest number of endemic ants belong to Myrmicinae (41 species) followed by the subfamily Formicinae (25 species, Figure 2). Amongst the Myrmicinae, the genus *Temnothorax* includes the most endemic species (16 species, 22% of the total endemic species and 30% of the full *Temnothorax* species). Nevertheless, the genus *Cataglyphis* is the most proportionally rich in endemic species, all of its 10 Iberian species are endemic. Although a positive correlation exists between the species richness and the number of endemic species within a genus ($R = 0.73$; $F_{(1,28)} = 31.81$; $p < 0.0001$), some genera are especially above the expected number of endemic species, such as *Cataglyphis*, *Temnothorax* or *Goniomma*, and other genera below, such as *Lasius*, *Tetramorium* and *Formica* (Figure 3).

Moreover, the presence of an endemic genus in the IP, *Iberoformica*, with only one living species in the world, *I. subrufa*, is very remarkable. This species extends its distribution to some southern French locations. The exceptional appearance of the genus *Rossomyrmex* in the IP is also noteworthy. This genus has three different species in Asia (the Anatolian plateau, the plains of the Caspian Sea and other regions of Central Asia), which are different to the one in the IP, *R. minuchae* [30,58], the only species of this genus which exists in the full western Palaearctic.

Another interesting group of species because of their natural history are the social parasites of which 43 species appear in the IP, including temporal and permanent parasitism (22 and 21 species). Together they account for 14.4% of the total Iberian species. The number and percentage of parasite species decreased in France (20 temporal + 13 permanent which represent 15.7%), and many more in Morocco (5 temporal + 7 permanent which constitutes 5.2%).

Finally, comparing the shared species belonging to every subfamily amongst the IP, France and Morocco, (Table 2; Table S1) we obtained the highest percentage of overlapping species between the French and the Iberian ant lists (84%). Nevertheless, the IP only shared 59% of its species with the French list. Morocco shared the lowest number of species with France 21%. and the highest with the IP 37% (Table 2). A cluster based on the similarity (Jaccard's Index, Cophenetic correlation index = 0.98) amongst the three areas, grouped France and the IP together (Figure 4) without significant differences between them (Jaccard's Index = 0.52, $p > 0.05$) and showed significant differences between Morocco with France and the IP (Jaccard's Index = 0.12 and 0.19 respectively, $p < 0.01$). Moreover, the replacement of species is more frequent between Morocco and the IP, but the overlapping is mainly between France and the IP (Table S1). For instance, France has three *Bothriomyrmex* species shared with the IP, but only one of the six *Bothriomyrmex* from Morocco appear amongst the four species in the IP. Even more striking is the case of the genus *Cataglyphis*, none of the 22 species in Morocco appear amongst the 10 species in the IP, which moreover are Iberian endemic species. Something similar occurred in other genera, such as *Aphaenogaster*, *Oxyopomyrmex* and *Temnothorax*, although to a lesser extent.

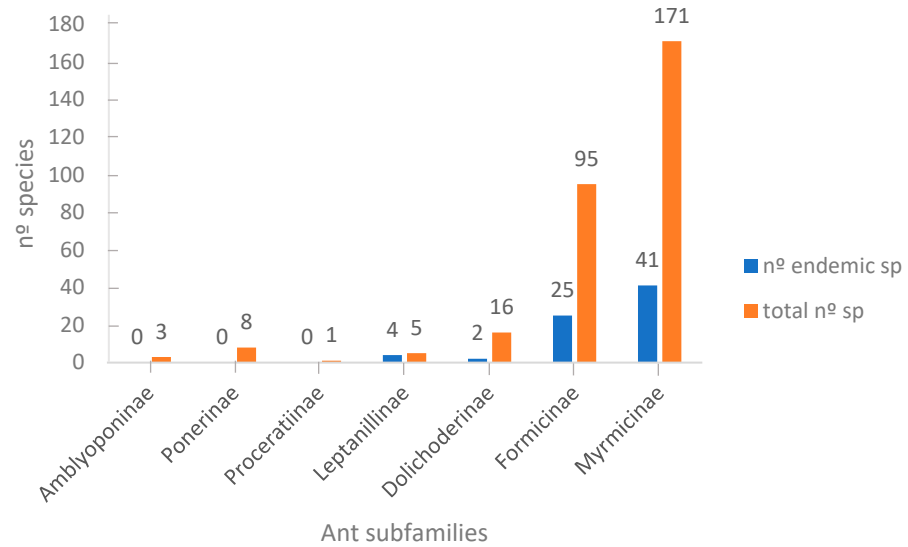


Figure 2. Number of species (orange) and endemic species (blue) belonging to each ant subfamily in the Iberian Peninsula (IP).

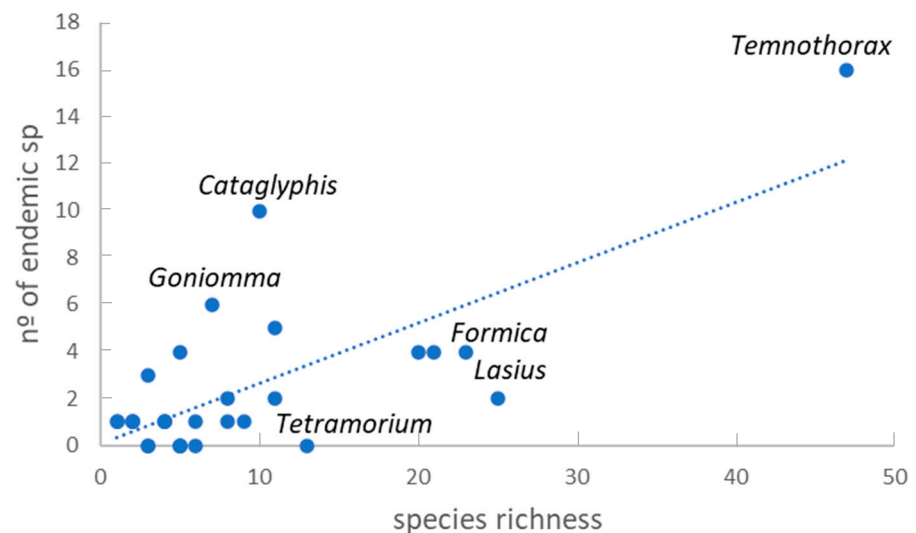


Figure 3. Positive correlation between species richness and the number of endemic species in each genera, including only native species ($R = 0.73$; $p < 0.0001$; $F_{(1,28)} = 33.32$).

Table 2. Total shared and unshared species and percentage amongst France (Fr), Iberian Peninsula (IP) and Morocco (Mo).

Subfamily	Total Shared sp/% Fr-IP	Total Shared sp/% Fr-Mo	Total Shared sp/% IP-Fr	Total Shared sp/% IP-Mo	Total Shared sp/% Mo-Fr	Total Shared sp/% Mo/IP
Amblyoponinae	0/0%	0/0%	0/0%	2/67%	0/0%	2/67%
Cerapachyinae	0/0%	0/0%	0/0%	0/0%	0/0%	0/0%
Dorylinae	0/0%	0/0%	0/0%	0/0%	0/0%	0/0%
Ponerinae	7/87.5%	4/50%	7/87.5%	5/63%	4/80%	5/100%
Proceratiinae	1/100%	0/0%	1/100%	0/0%	0/0%	0/0%
Leptanillinae	1/100%	1/100%	1/20%	1/20%	1/33%	1/33%
Dolichoderinae	10/100%	3/30%	10/62%	4/25%	3/37%	3/37%
Formicinae	69/90%	13/17%	68/72%	19/20%	13/21%	19/31%
Myrmicinae	89/79%	28/25%	89/52%	57/33%	28/19%	45/38%
Total shared species	178/84%	49/23%	176/59%	88/29%	49/21%	87/37%
Total unshared species	33/16%	162/77%	123/41%	211/17%	184/79%	146/63%

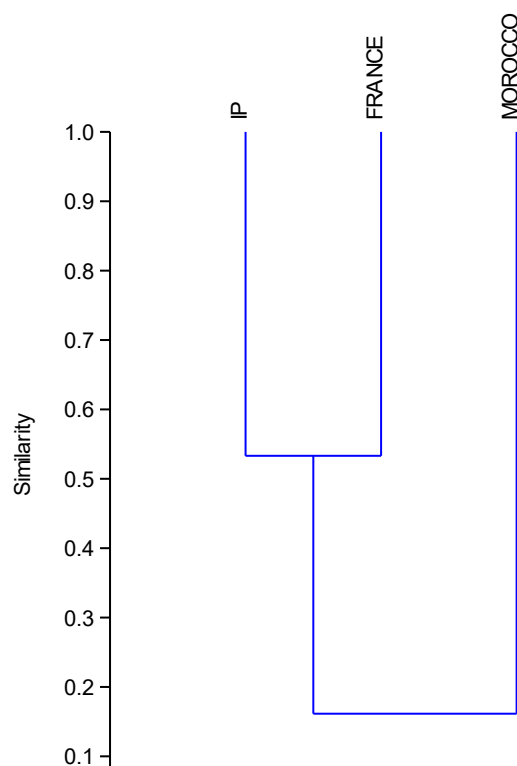


Figure 4. Cluster analysis based on the similarity (Jaccard's Index) of the ant species found in the three adjacent areas (IP, France and Morocco).

3.2. Biogeographical Analysis

3.2.1. Chorology

The most frequent chorological category in the IP was the northern species (N, 30.8%), which together with the trans-Iberian species (T, 11.7%) are 42.5% (Figure 5). On the other hand, the Mediterranean species, including the northern Mediterranean (MN, 6.7%), all the Mediterranean basin (M, 6.7%), the southern Mediterranean (S, 12%), and the Iberian endemic species (X + XS, 24.1%) represented 49.5% of the total species. The lacking percentage corresponded to the introduced species (I, 8%) (Figure 5). Amongst the ant subfamilies, the northern species (N) are clearly more abundant in Formicinae and Myrmicinae (Figure 6). In the latter subfamily the “endemic species” is the next most abundant chorological category (Figure 6). Nevertheless, the percentage of endemic species is similar for Formicinae and Myrmicinae (26% and 25%). The next most abundant category in Myrmicinae is the southern species (S), contrarily under-represented amongst the Formicinae ants (Figure 6).

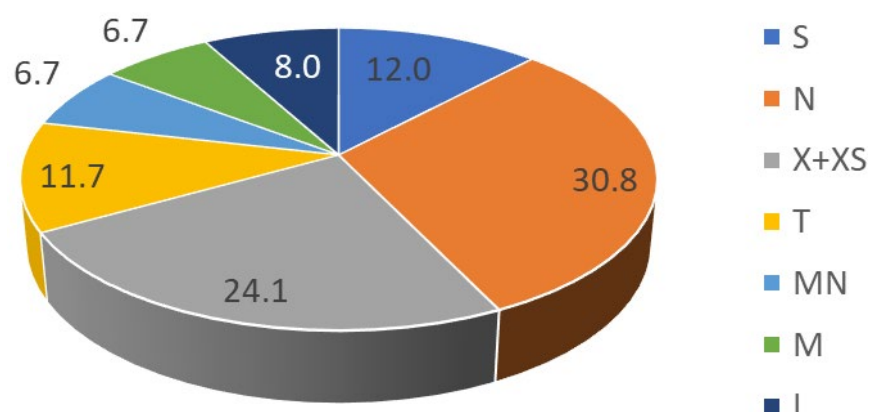


Figure 5. Percentage of species pertaining to the different chorological categories (S: Southern; N: Northern; X + XS: Endemic; T: Trans-Iberian; MN: Northern Mediterranean; M: Mediterranean; I: Introduced).

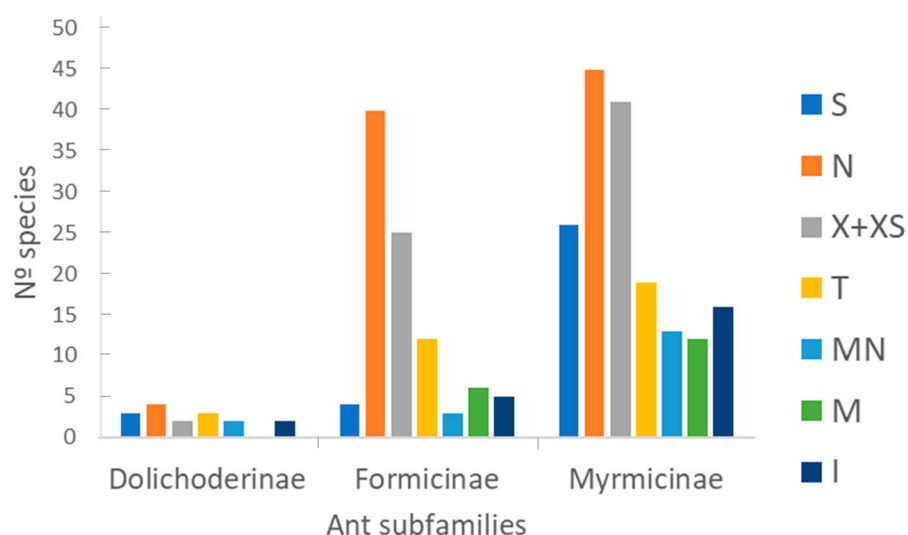


Figure 6. Chorological composition of the three more abundant subfamilies. (S: southern species, N: northern species, X + XS: endemic species, T: Trans-Iberian species, MN: north Mediterranean species, M: Mediterranean and I: introduced species).

3.2.2. Distribution Range

We have evaluated the importance of every refugium area harbouring ant species richness (see Supplementary material Table S2). We found that all the aprioristic defined refugium areas presented significant differences in similarity (Jaccard's index, $p < 0.01$) with respect to the others (Table 3). Those refugia with the high similarity index were the northern plateau, the Guadalquivir Valley and the southern plateau (Jaccard's index = 0.4; Table 3, Figure 7).

The refugium area with the highest number of ant species is the Mediterranean (144 species), followed by the Guadalquivir Valley (118 species) (Figure 8). These two refugium areas also contain the highest number of endemic species, followed by the northern plateau and the Pyrenees. The Atlantic and the southern plateau refugia contain an intermediate number of species, and the Cantabric together with the Ebro Valley present a similarly low number. The number of ubiquitous species, occurring in all the eight refugium areas was relatively low with only 46 species.

Many of the Iberian ant species appeared exclusively in one of the Iberian refugium areas (86 species, 29%) and may be considered as rare species, although they are not always endemic. Progressively a lower number of species occupied more refugium areas, with only a final increase for ubiquitous species (Table 4). The 21 endemic species which appear in only one refugium area are shown in Table 5.

Analysing the most diversified or peculiar ant genera (see Annex S2, Supplementary Material), we found the genus *Lasius* (25 species) to be the most widely distributed across all the IP and, when local, generally appear in the northern half of the IP and frequently in the Pyrenees, the Ebro Valley and the Mediterranean refugia. There are only two endemic species in this genus that are widely distributed (*L. cinereus* and *L. piliferus*). The genus *Formica* is composed of 23 species, the majority appearing in the Pyrenees (14 species) or the Mediterranean (9 species) refugia. Twelve *Formica* species of the IP belong to the *rufa* group; again, the majority of these latter species (7 of them) were present in the Pyrenean refugium and only 3 in the Guadalquivir Valley. The genus *Camponotus* is composed of 20 species, of which 16 are widely distributed in the IP. Nevertheless, the only two strictly endemic species (X chorological category) belonging to this genus (*C. haroi* and *C. amaurus*) presented a narrow distribution linked to the Mediterranean coast and the northern plateau. In the case of the genus *Cataglyphis*, 10 species are represented in the Iberian myrmecofauna, all of which are endemic (nine strictly X and one shared with France XS). Species from this genus have never been found in the most northern zones (Cantabric or Pyrenees) and principally were present in the southern areas (southern plateau, the Guadalquivir Valley and on the Mediterranean coast). Four of the endemic *Cataglyphis* species (*C. floricola*, *C. gadeai*, *C. humeya* and *C. tartessica*) are exclusively distributed in either the Guadalquivir Valley or the Mediterranean refugium areas. The genus *Temnothorax*, includes 47 species in the IP, 16 of which are endemic. Twenty-five percent of the *Temnothorax* species are distributed in only one refugium area, and the areas with the most *Temnothorax* species are the northern plateau, the Mediterranean coast and the Guadalquivir Valley. The refugium area with the lowest number of *Temnothorax* species is the Cantabric. Finally, the genus *Stigmatomma* is composed of only three species, with a narrow distribution, in only one or two refugium areas, thus in the Guadalquivir Valley we found the three species and one of them also on the Mediterranean and Atlantic coasts. In fact, the Guadalquivir Valley is the refugium containing the highest number of ant species linked with tropical environments, such as *Stigmatomma emeryii*, *S. impressifrons*, and the Ponerinae *Anochetus ghilianii* and *Chryptopone ochracea*.

Table 3. Jaccard's Index (black numbers) and probability associated to significant differences (blue numbers) amongst the occurrence of species in paired refugium areas of the IP.

	Cantabric	Pyrenees	Mediterranean	Atlantic	Northern Plateau	Southern Plateau	Guadalquivir Valley	Ebro Valley
Cantabric	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Pyrenees	0.28	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Mediterranean	0.11	0.26	1	<0.01	<0.01	<0.01	<0.01	<0.01
Atlantic	0.12	0.25	0.33	1	<0.01	<0.01	<0.01	<0.01
Northern plateau	0.23	0.32	0.35	0.36	1	0.01	<0.01	<0.01
Southern plateau	0.1	0.22	0.3	0.37	0.4	1	<0.01	<0.01
Guadalquivir Valley	0.1	0.21	0.4	0.35	0.4	0.4	1	<0.01
Ebro Valley	0.1	0.25	0.09	0.17	0.21	0.2	0.15	1

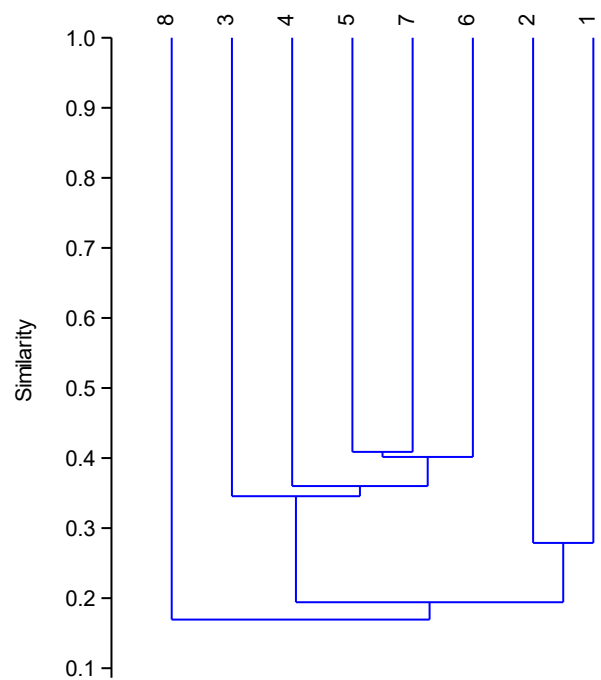


Figure 7. Cluster analysis based on the similarity of ant species occurrence (Jaccard’s Index) in the eight refugium areas of the IP, all of them showing significant differences ($p \leq 0.01$; Refugium areas 1. Cantabric; 2. Pyrenean; 3. Mediterranean coast; 4. Atlantic; 5. Northern plateau; 6. Southern plateau; 7. Guadalquivir Valley; 8. Ebro Valley).

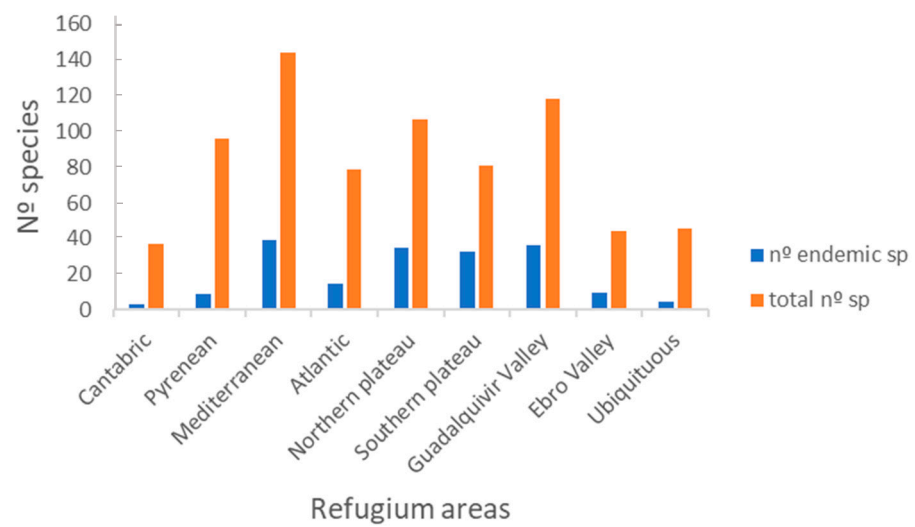


Figure 8. Number of species (orange) and endemism (blue) in the different refugium areas of the IP.

Table 4. Number of ant species occupying an increasing number of refugium areas.

Nº Occupied Refugium Areas	1	2	3	4	5	6	7	8
Nº species	86	46	35	32	31	16	6	46
Nº endemic sp	24	12	10	10	10	2	0	5

Table 5. List of 21 endemic species appearing in only one refugium area in the IP.

Pyrenean Area	
Myrmicinae	-
<i>Myrmica lemasnei</i>	Bernard, 1967
Mediterranean Area	
Leptanillinae	-
<i>Leptanilla theryi</i>	Forel, 1903
Formicinae	-
<i>Camponotus amaurus</i>	Espadaler, 1997
<i>Cataglyphis gadeai</i>	De Haro & Collingwood, 2003
<i>Cataglyphis humeya</i>	Tinaut, 1991
Myrmicinae	-
<i>Goniomma collingwoodi</i>	Espadaler, 1997
<i>Goniomma compressisquama</i>	Tinaut, 1994
<i>Messor timidus</i>	Espadaler, 1997
<i>Teleutomyrmex kutteri</i>	Tinaut, 1990
<i>Temnothorax ansei</i>	Catarineu, Barberá & Reyes-López, 2017
<i>Temnothorax crepuscularis</i>	(Tinaut, 1994)
Northern Plateau Area	
Leptanillinae	-
<i>Leptanilla charonea</i>	López, Martínez & Barandica, 1994
Myrmicinae	-
<i>Aphaenogaster ulibeli</i>	Gómez & Espadaler, 2018
<i>Myrmoxenus bernardi</i>	(Espadaler, 1982)
Southern Plateau Area	
Leptanillinae	-
<i>Leptanilla plutonia</i>	López, Martínez y Barandica, 1994
Myrmicinae	-
<i>Crematogaster fuentei</i>	Menozzi, 1922
<i>Oxyopomyrmex magnus</i>	Salata & Borowiec, 2015
Guadalquivir Valley Area	
Formicinae	-
<i>Cataglyphis floricola</i>	Tinaut, 1993
<i>Cataglyphis tartessica</i>	Amor & Ortega, 2014
Myrmicinae	-
<i>Goniomma baeticum</i>	Reyes & Rodríguez, 1987
Ebro Valley Area	
Myrmicinae	-
<i>Temnothorax caesari</i>	(Espadaler, 1997)

4. Discussion

4.1. Taxonomic Richness

Ants showed a higher number of species in the IP (299 species), compared with the adjacent Mediterranean countries, with only a few species less than the Balkan Peninsula. A similar number of species is found in Greece and Turkey [74,75] (Table 1). Following the expected latitudinal diversity gradient there is a decrease in species richness to the north [88,89]. Although the IP has a higher ant species richness than Morocco [5,91,92], the last has two more subfamilies than the IP and three more than France, which follows the latitudinal diversity gradient. These results varied when the area surface is taken into account, the ratio is similar between the IP and Morocco, being higher than in France and much lower than other Mediterranean countries such as Israel.

With respect to the richness of the endemic species the same pattern occurred. The IP shows the highest number (72 endemic species), compared with other Mediterranean countries such as Greece, (21 species [74]); Israel (25 species [76]) or Morocco (56 species [57]),

but when the surface areas are considered, a similar ratio between the IP and Morocco again occurred, but this was much higher in the eastern Mediterranean.

Nevertheless, not only the number of species and endemic taxa in the IP are remarkable but also the singularity of the Iberian myrmecofauna including one endemic genus (*Iberoformica*), with only one endemic species *I. subrufa* and the fossil of its probable ancestor *I. horrida* [93]. Moreover, the IP is the only place in Europe where the genus *Rossomyrmex* is located outside Asia. The presence of these two exclusive genera highlights the importance of the IP as a refugium. At least for *Rossomyrmex*, there is evidence that have been several episodes of extinction of this genus between the nearest geographical point (Turkey) and the IP. This genus has survived in the IP and not in other nearby countries, as have other emblematic animals such as the *Lynx* or the Azure-winged magpie [94].

The presence of these two ant genera as well as the low number of Iberian ant species shared with Morocco (29%) and with France (59%), while France shares with the IP 84%, and Morocco 37% with the IP, indicates that the IP harbours a unique and fairly exclusive ant fauna and functions as a "cul de sac" of ant species [94].

Several factors are responsible for the high ant biodiversity in the IP, as mentioned in the introduction, derived from the highly complex Iberian orography and convulse geological and climatic history. Another factor affecting the Iberian ant diversity is the peninsular effect, which explains the increase in diversity near the isthmus [95,96], assessed in the IP for birds [97] and butterflies [98]. Moreover, the role of the Palaearctic peninsulas during the Quaternary glaciations, as refugia for biota and centres of speciation [36], together with the Iberian complex orography producing "refugia-within-refugium" effect that has been assessed for different animal groups, contributed to increase the Iberian biodiversity [14,99].

Analysing the contribution in the IP ant diversity of the most relevant worldwide genera according to Wilson (1976 in Pie & Feitosa, [100]), only *Camponotus* make an important contribution to Iberian biodiversity, whilst *Pheidole* and *Crematogaster* had few species represented. This phenomenon is common to all Europe [69]. In the IP, the genus that we can consider "to have conquered the world" following Wilson's criteria must be *Temnothorax*, the most diverse Iberian genus (47 Iberian species) with the highest number of Iberian endemic species (16). This is an abundant genus in all the IP habitats, except in the high mountains above 2,700 m a.s.l., reflecting a high plasticity and adaptation ability. Probably its small size and its mode of mate location behaviour, by means of female pheromones, act as a speciation driver in this genus. Nevertheless, other diverse genera such as *Lasius*, *Formica* or *Camponotus* have a much lower number of endemic species than expected. Again, the mating behaviour by mass nuptial flights, which facilitates the populations mixing at a landscape level, might influence the lower rates of speciation in these genera. Moreover, other genera, such as *Cataglyphis* or *Goniomma*, showed a higher number of endemic species than expected. Other factors, probably linked with the biogeography, biotic traits and plasticity of the genera, may be responsible for this high level of endemism.

All these data contribute to highlight the singularity of the Iberian myrmecofauna and its relevance in the Mediterranean region, placing the IP in a similar position to the Balkan Peninsula as a centre of ant diversification.

4.2. Biogeographical Analysis

4.2.1. Chorology

The chorological analysis showed two groups of ants, one widely distributed in the northern half of Iberia, sharing species with the western Palaearctic region but sometimes extending up to northern Africa, (N + T chorological categories), and the other group, mainly including species belonging to the Mediterranean basin and northern Africa (S + MN + M + X + XS chorological categories). This result is congruent with those obtained for aquatic coleopterans [78] and showed the IP acts as a transitional element between Europe (north Palaearctic) and north Africa (south Palaearctic).

This north-south distribution pattern is shown at different taxonomic levels (ant genera and species), thus we can find genera preferentially distributed in the north of the IP, such as *Formica*, *Lasius*, *Myrmica* and *Leptothorax* and others in the southern half, such as *Cataglyphis*, *Proformica*, *Stigmatomma*, *Anochetus*, *Messor*, etc. At species level, we can find the same pattern, with some typically northern species such as *Lasius fuliginosus*, most of the *Formica rufa* group, *Camponotus herculeanus*, *C. ligniperda*, *Tapinoma pygmaeum*, the three *Leptothorax* species, and more examples included in the Supplementary Material (Annex S2). In the same way, a similar number of species could be considered as southern, such as some of those included in the genus *Cataglyphis* (*C. humeya*, *C. floricola*, *C. tartessica*), *Goniomma* (*G. collingwoodi*, *G. compressiquama*), *Messor timidus*, *Aphaenogaster striativentris*, the three species of the genus *Stigmatomma*, or *Anochetus ghilianii*, amongst others (see Table S2).

4.2.2. Distribution Ranges

The complex orography of the IP produced not only a north-south division of species distribution, but even in the eight proposed refugium areas, we can find a significantly different ant fauna. This result supports the fact that similar processes affected all the biota, with common patterns emerging, although some slight differences in shape probably depend on biotic traits of the studied species such as dispersal ability [32,80,81,84,101]. Most of the proposed biogeographical subdivisions of the IP established between five (Mollusca: Pulmonata [101]) to eleven zones (birds [81]). Our proposal is closer to that of vascular plants and vertebrates [32,81,84]. The social character of ants does not appear to alter the biogeographical pattern followed for the general biota, except for their presence in the high mountains. Amongst the IP refugia the most similar for occurrence of ants (high Jaccard's diversity Index) are the northern plateau, the Guadalquivir Valley and the southern plateau. From the analysis of the species occurrence within each refugium areas, we have proved that the Mediterranean and Guadalquivir Valley refugia show the highest species richness and number of endemic species, highlighting their importance for ant conservation. In fact, Andalusia is considered the Iberian region with the highest general biodiversity [21] where both refugium areas are represented. In the Guadalquivir Valley refugium, we can find some special habitats such as the prequaternary forest with relict plant species located near the Straits of Gibraltar [102]. In this habitat we can also find the very few semitropical ant species appearing in the IP, which belong to the subfamilies Amblyoponinae together with some Ponerinae such as *Anochetus ghilianii*.

The Pyrenean and the northern plateau are the following refugium areas in biodiversity importance. The Pyrenean range is in the isthmus, concentrating the peninsular effect, which together with the high heterogeneity derived from the altitudinal variation and its west-east position, produced an important climatic variability, responsible for the species richness in this refugium. Nevertheless, the number of endemic species is not very high (10 species), pointing to the possibility of gene flow between the Pyrenean and the European populations, diluting speciation possibilities. The northern plateau is the oldest region of the IP, including the Hercynian plate; its age may be the cause of the increment in biodiversity in this refugium.

Most of the species are distributed in more than one refugium area, but about a third is found in only one IP refugium (86 species). On the other hand, only 46 species are ubiquitous in all the IP.

Similarly, from analysing the distribution of endemic species in the different refugium areas, we have been unable to find a clear pattern, finding 21 endemic species limited to only one refugium and only five endemic species being considered ubiquitous. These results are congruent with those found by different authors [78,99] pointing to different causes for the absence of clear patterns of endemism in the IP, including sampling artifacts.

On the other hand, although mountain ranges promoted species richness and endemism [103], this pattern is not detectable for the Iberian and Palaearctic formicids. Only one ant species is exclusive to high mountains: *Proformica longiseta* (between 1800 and

3000 m a.s.l. in the Sierra Nevada mountains [104] and the Baetic range [13]). According to these findings, the majority of the Iberian ant endemic species are related with semiarid habitats with scarce vegetation at low altitudes, such as some of the species pertaining to the genus *Temnothorax*, as *T. ansei*, *T. blascoi*, *T. caesari*, *T. crepuscularis* [105]. Another important number of endemic species are found in medium altitude mountain ranges, such as *Teleutomyrmex kutteri* (1700–2250 m a.s.l. in different Baetic ranges [106,107]), *Temnothorax gredosi* or *T. conatensis* (900–1500 m a.s.l. [108,109]).

Whereas the rare species, i.e., those found in only one or two refugium areas, include for instance the social parasite ant species, where their way of life makes them difficult to find. These are known in very few and sometimes very distant areas, such as *Rossomyrmex minuchae* [12,110], *Myrmoxenus bernardi* [111] or *Anergates atratulus* [112]. Another example of a rare species is *Aphaenogaster cardenai*, an Iberian endemic species of relatively wide distribution [113], but living in scarcely sampled habitats (the mesovoid shallow substratum, shallow caves and mines [114]).

4.2.3. Origin and Dispersal Routes

Other different causes responsible for the high ant biodiversity in the IP are related with the centre of origin and dispersal routes of the ancestors of the current ant fauna. In agreement with Blaimer et al. [115] the origin of formicids probably occurred during late Cretaceous (104–117 mya), but the rise of the modern ant fauna probably occurred during the early Cenozoic and continued until the present day. There are signs that all the genus-level taxa appeared from the first 50–60 mya are now extinct in the western Palaearctic [7]. Blaimer et al. [115] gave the estimated time of divergence for several genera from the subfamily Formicinae, thus, the clade giving place to the tribe Formicini, appeared 60 mya, and the most probable ancestral range was the Palaearctic region. These data are congruent with the estimated age of *Cataglyphoides constrictus*, a probable ancestor of the genus *Cataglyphis* (but see [116]), or *Formica horrida*, probably a species belonging to the current genus *Iberoformica* [93]. Both fossils were found in the Baltic amber (middle to late Eocene 37–42 mya) [117]. According to Blaimer et al. [115] the *Formica/Iberoformica* clade appearance is dated to 50 mya, the clade of *Rossomyrmex*, *Cataglyphis/Bajcaridris*, *Proformica* diverged in 45 mya, *Bajcaridris/Proformica* in 20 mya and finally *Rossomyrmex/Cataglyphis* in 15 mya, which are in agreement with the results of Guenard et al. [7].

The genus *Temnothorax*, which belongs to the subfamily Myrmicinae, showed its centre of origin in the Palaearctic region during the Eocene-Oligocene transition (38–33 mya) [118]. The genus *Myrmica* appeared to diversify following drastic climatic cooling in the same epoch (34 mya), and its most probable centre of origin is central or south-eastern Asia [119]. The genus *Stenamamma* shared its time of origin with the previous genera but the centre of origin is estimated in the Nearctic region, and two dispersal waves to the Palaearctic were detected, the first in early Oligocene (30 mya), leaving in the Iberian myrmecofauna the species *S. striatulum*, and the second at late Pliocene (about 3 mya) with *S. debile* [120]. Undoubtedly posterior dispersals have occurred, as has been demonstrated for other insects such as the butterfly *Parnassius apollo* with a recent (late Pleistocene) colonization of most of their range [121].

With this retrospective view, we know that most of the current extant ant genera inhabited the Palaearctic region 15 mya (Middle Miocene), but the question is whether they inhabited the IP at the same time.

From the Cenozoic (60 mya), the Iberian plate was fused with the European plate [95]. Unfortunately, the ant fossil data from this time are scarce and, in some cases, too ancient to resolve the question [122,123]. We only have some scarce data from recent periods, thus, the existence of the genera *Camponotus*, *Dolichoderus*, *Iridomyrmex*, *Lasius* or *Formica*, *Liometopum* and *Messor*, in the Middle and Late Miocene of the IP has been reported (13 to 7 mya) [124,125]. The paleoclimate and paleoenvironments of the Miocene (23 mya) have been recreated more accurately through the coral reef and mammal fossils [24,29,30,126]. During this period the IP climate was semitropical and the biota was equivalent to the

current African savannah [127], including important Asian and African components [27]. Nevertheless, from the Miocene until the Pliocene (5.33 mya) the biogeography of the IP was quite convulsed, especially on the southern extreme, frequently joined and separated with the African plate [26]. Moreover, the climate was cooling which finally provoked the substitution of the semitropical fauna for others better adapted to temperate or cool climates [7].

In this situation, some ant genera may have inhabited the Iberian savannah from the Miocene and later the steppes from the Pliocene and Pleistocene [7,115]. This dynamic process of sequenced colonization, extinction and diversification did not stop. Thus, during the transition Pliocene-Pleistocene, the effect of Quaternary glaciations on these Asian and African fauna dispersed to the IP, giving way to the current myrmecofauna. This view is reinforced with data on radiation of the *Formica* genus and the *Formica rufa* group species, dated in the Middle Pliocene and Pleistocene [128,129], and this was similar for other insects, as has been proved by means of molecular analyses in different coleoptera [14–18]) and in plants [130,131], pointing to a general process for all the biota of the IP.

In our analysis of the origin and dispersal routes which shaped the Iberian ant myrmecofauna, we can differentiate four groups of dispersal patterns:

Relict Species

From the middle to late Eocene (34–42 mya) [117] the climate was semi-tropical and the ant fauna known from the Baltic amber was very diverse including extant genera or their ancestors [132,133]. Some of them, such as *Formica* or *Aphaenogaster*, which nowadays have reached a high diversity, must have previously adapted to semi-tropical warm environments that were predominant when they were trapped by the amber. Later they were able to adapt to the cooling produced from the end of the Miocene and have survived until now. Nevertheless, both genera do so in different ways, one adapting to temperate or cool habitats (*Formica*, now more diversified to the north of the IP) and the other to temperate or warm habitats (*Aphaenogaster*, currently more diversified in the south of the IP). Nevertheless, some other genera were unable to adapt to the changing conditions and disappeared from the western Palaearctic [7], such as the fossils of the genera *Pachycondyla* from Denmark, preceding the Paleocene-Eocene transition (55 mya) [134]. In some rare cases, semitropical ant species such as *Anochetus* and *Stigmatomma*, found in Santo Domingo amber (16–19 mya) [117,135] and the Baltic amber [133] respectively, and currently well distributed in tropical and semitropical regions, were able to remain in some restricted locations of the IP surrounding the Straits of Gibraltar [136,137], an exceptional zone also inhabited by paleoendemic plant species [102,138]. Although Jowers et al. [9] concluded that *Anochetus ghilianii* is a recent invader of the IP, we think that the coincidence in this area of botanical paleoendemic species together with different semitropical ants (*Anochetus* and *Stigmatomma* species), it must be the result of a similar biogeographical process acting on them. Anyway, *A. ghilianii* should be considered as a relict Moroccan species and its presence in the IP is noteworthy.

Asian-IP Disjunct Species

In the Pliocene (5.33 mya) the Mediterranean Sea reopened through the Straits of Gibraltar and the climate was cooling, favouring the substitution of the existing semitropical fauna for one better adapted to temperate climates. This temperate fauna proceeded principally from Central Asia, reaching the IP as confirmed by fossil deposits [25,28–30]. The Asian colonizing waves have occurred repeatedly during the transition Pliocene-Pleistocene (2.6, 2.5 and 1.7 mya) [25] even during the late Pleistocene [139] and later. The migrant mega-fauna must have been dispersing together with invertebrates, among them obviously ants, sharing the same origin and similar ecological requirements. These Asiatic and African faunas from the later Pliocene, evolved under glacial and interglacial periods during the Pleistocene, and many of these species became extinct or remained isolated in some refugia throughout the entire Iberian refugium, setting up the current

myrmecological fauna [22,31–33]. Some of these species continued isolated and now have a narrow distribution range, as is the case of the slave-making ant *R. minuchae* in Spain, and the other three species of the genus, which are dispersed, although with a wider distribution range in Asia. The genus *Rossomyrmex* can be considered as a relict in the IP. On the other hand, the species of the genus *Proformica*, the host of *Rossomyrmex*, with a probable centre of origin in Central Asia [11], were able to recolonize wide distribution ranges both before and after glacial periods, occupying all the southern Palaeartic from Central Asia to the IP. This genus, more diversified in the western Mediterranean, specifically in the IP, is not distributed in Morocco, where it has been replaced by the close genus *Bajcaridris* [11,115,140]. This fact suggests the hypothesis of a frequent dispersal route on the two sides of the Mediterranean (Figure 9) with speciation concluding in different genera (*Proformica* and *Bajcaridris*). An opposite direction of the dispersal route (from western Mediterranean to Asia) has been suggested for *Rossomyrmex* [11] as occurred, for example, with the plant genus *Odontites* [130].



Figure 9. Suggested dispersal routes affecting the myrmecofauna of the IP. (Base map obtained from <https://laboratorioriediam.cica.es/VisorRediam/> (Accessed on 2 December 2020)). Junta de Andalucía. Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible (ámbito de Desarrollo Sostenible).

Another genus offering interesting disjunct distributions is *Cataglyphis*, specifically the species group *altisquamis* shows two different and discontinuous distribution ranges: one group of five species distributed from Central Asia to the western Mediterranean and the other nine species distributed in the western Mediterranean (IP and Morocco) [141] (Figure 11). This second group of species is absent from Turkey to France, by the northern route, and from Egypt and Libya, by the southern route, due to extinction processes in the intermediate points. The age of the entire genus and its high diversity in Asia point to a Central Asian origin. Three different dispersal routes are possible from Asia to the western Mediterranean: 1. the simultaneous dispersal route via the two sides of the Mediterranean, 2. the dispersal by the northern Mediterranean side across to the Balkan region, and 3. the dispersal only by the southern Mediterranean side (Figure 9). The three are possible but until now only the southern route (3) has been suggested for the *Cataglyphis albicans* group [10]. Nevertheless, the three dispersal routes from Asia have also been proposed for the genus *Cephalota* (Coleoptera: Cicindelidae) [17] and may be more frequent dispersal patterns than had generally been considered. An extension of the phylogenetic study on *Cataglyphis* including middle-west distributed species should produce a wide and accurate view for the biogeography and dispersal patterns of these species.

The genera *Goniomma* and *Oxyopomyrmex*, both endemic of the Mediterranean basin, also show disjunction between the eastern and western Mediterranean distributions [142, 143] (Figure 10). Their centre of origin is unknown, although they probably appeared in the Miocene (12 mya) [90]. A similar distribution pattern is found in the coleopteran species of the genus *Pimelia* [15], *Berberomeloe* [14] and the plant genus *Odontites* [130].

Another example of current Iberian fauna showing Asian-IP disjunct distribution is the Iberian azure-winged magpie [144] or amongst the insects, the lepidopteran *Pseudochazara wiliamsi* or the coleopteran of the subgenus *Parentius* (see [145]), and together with these, we find many other species adapted to arid or semi-arid environments such as Monegros (Zaragoza) or Guadix-Baza (Granada) [146,147] or to mountain ranges [148]. Thus, all these examples reinforce the importance of Asia as a centre of origin for the Iberian fauna.



Figure 10. Disjunct distribution range of the species belonging to genus *Goniomma*. Note the presence of one species in Israel (citations from [71] are included; base map as in Figure 9).

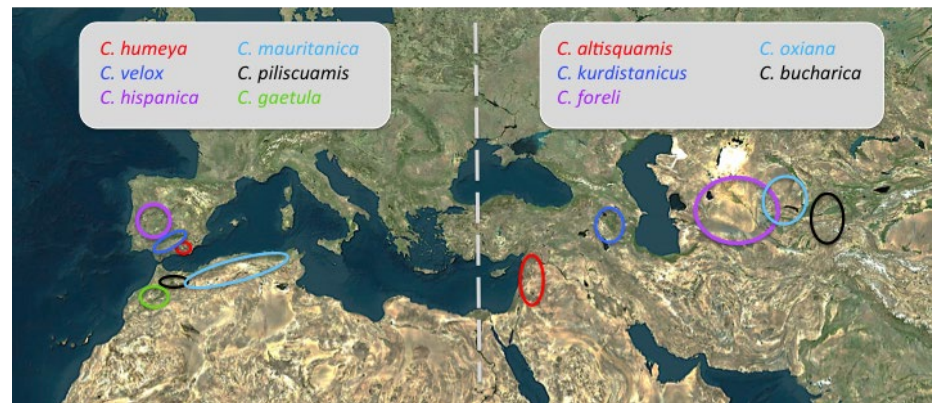


Figure 11. Disjunct distribution of the species belonging to the *Cataglyphis altisquamis* group (modified from [149]; base map as in Figure 9).

Baetic-Rifan Species

This dispersal pattern includes the shared species between the south of the IP and the north of Africa. Within this group, the ants with apterous or brachypterous females, such as *Monomorium algiricum*, *A. ghilianii*, *Stigmatomma* species or *Aphaenogaster senilis* group, gain biogeographical relevance, due to their handicap for flight dispersal across the Mediterranean Sea. One plausible explanation for this kind of distribution comes from the geological history of this territory. South-western Iberia and the north of Morocco share stratigraphic deposits, forming the Baetic-Rifan territories [150] derived from the Miocene island of Alborán, emerged in the western Mediterranean 16 mya [126]. This island was united with Morocco until 8 mya when it again became disconnected and isolated until 5.9 mya. After this, it was again partially united with the IP until 5.3 mya. At this time, the Straits of Gibraltar reopened, dividing the territories of the Miocene island of Alborán between the IP and Morocco. The existence of this island may explain the relatively high presence of apterous species in this zone, because apterism is one of the known island syndromes. This effect is known in the Baetic-Rifan territories not only for ants [151] but also for *Pimelia* and *Blaps* Tenebrionid [15,17] and Meloid (*Berberomeloe* group)

coleoptera [14], both of them apterous. The existence of this island is more extended in geological time than the habitually invoked desiccation of the Mediterranean during the Messiniense (late Miocene) to explain the shared presence of species between the IP and northern Africa.

Alpine Species

Another important and more recent dispersal route is related with the Pleistocene glaciations, the last occurring 10,000 years ago. Many northern species survived and took refuge in the southern Palaeartic peninsulas, and during interglacial periods returned to the north and/or the populations climbed the slopes of the mountains [37]. One good example of this group is the pair of Iberian endemic species *Formica frontalis*/*F. dusmeti*, very close phylogenetically to *F. truncorum*, distributed in northern Europe ([129], unpublished data). Probably the presence of *T. kutterii* in the south of the IP and *T. schneideri* in the northern IP and in the Alps is likely to have had this similar origin. Some species of *Myrmica*, *Temnothorax*, *Lasius*, etc, may belong to this group of alpine species, but this should be confirmed by phylogenetic molecular studies on the Mediterranean species.

5. Conclusions

The taxonomic diversity and distribution patterns we have presented in this study highlight the importance of Iberian ants for a better understanding of the complex evolutionary history and biogeography of the IP. Moreover, we have tried to show the importance of biogeography driving the structure of the current ant communities, ecological interactions, such as hierarchic competence and biotic factors, only explain a part of their structure [152]. Our results on ant biogeography support the hypothesis that the centre of origin of the species and their dynamic processes (dispersal, vicariance, speciation and extinction) are the missing link to fully explain and understand the evolution and the structure of these ant communities [2,5,7]. We hope the hypothesis and proposals put forward in this study will promote new biogeographical, phylogenetic and evolutionary studies about the ant fauna of the Mediterranean Basin and produce a wide and accurate view of the centre of origin and the dispersal patterns of Iberian ants.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/2/88/s1>, Table S1. Ant species list of France, Morocco and the IP. Table S2. List of Iberian ant species and their occurrence in the refugium areas.

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