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Zoogeography of the Ants (*Hymenoptera: Formicidae*) of the Segura River Basin

C Catarineu[1], GG Barberá[2], JL Reyes-López[3]

1 - Asociación de Naturalistas del Sureste (ANSE), Murcia, Spain
2 - Department of Soil and Water Conservation, CSIC-CEBAS, Murcia, Spain
3 - Área de Ecología, Universidad de Córdoba, Córdoba, Spain

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Corresponding author
Chema Catarineu
Asociación de Naturalistas del Sureste
Plaza del pintor José María Párraga nº 11
30002, Murcia, Spain.
E-Mail: chema@asociacionanse.org

Abstract

The work submitted in this paper presents the first checklist of the ant species of the Segura River Basin based on a review of specific literature and biological material collected during field work conducted from 2012 to 2016. Our findings recorded 110 species that belong to 30 genera of ants and twenty-two of these species have been recorded for the first time in this area. The zoogeographical composition is dominated by the species of the Mediterranean zone (75.2%), followed by the mixed and deciduous forest zone (19.1%). The most important zoogeographic elements are: Iberian (20%), Holomediterranean (17.1%) and West-Mediterranean (13.3%). There are only six cosmopolitan species (5.71%). There is a greater proportion of species from the mixed and deciduous forest zone in the high-mid altitudes in the Segura River Basin, where the climate is cooler, and more humid. The Euro-Caucasian and Euro-West Siberian elements tend to be more associated to forest with a higher precipitation, whilst the South Palearctic elements seem to be more associated to ecosystems more similar to the forest-steppe zone with intermediate precipitation. The existence of these different zoogeographic origins in this area is probably linked with: the position between Africa and Europe; the complex geotectonic, paleogeographic, and paleoclimatic history during the last 7 My; the complex geomorphology; and the high climate and habitat diversity. Based on ant studies and other taxa, possible explanations of the zoogeographic origin of these ant chorotypes are proposed.

Introduction

The Mediterranean Basin, including the Iberian Peninsula, is one of the most important biodiversity hotspots in the world, with a high level of endemism (Médail & Quézel, 1997; Myers et al., 2000; Gómez & Lunt, 2007; Hewitt, 2011). Médail and Quézel (1997), based on floral endemism, identified ten Mediterranean Basin hotspots, and the Baetic-Rifan complex (including the Baetic ranges), one of them being.

Our study area, the Segura River Basin, is located in the central sector of southeastern Iberian Peninsula (Fig 1) and is representative of the environmental diversity of the area. It is framed in the western border by the Baetic ranges, a result of the convergence between the African and Iberian plates. The Baetic ranges intercept Atlantic cyclones in such a way that at some points of the mountainous area rainfall reaches 900-1,200 mm per year, whilst a rain shadow lies immediately to the east and dominates the region. The Segura River Basin (19,025 km^2) has large orographic variety, with mountains that reach up to 2,000 m.a.s.l., as well as contrasting coastal areas and extensive plains and valleys (Confederación Hidrográfica del Segura, 2017).

Mountain lithology consists of limestone, dolomite and shale, and other metamorphic siliceous materials, whilst the plains and valleys between mountains are usually filled with marls, alluvial, and colluvial quaternary deposits and some volcanic outcrops (Mellado et al., 2002). The territory is very

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singular, both for the Iberian Peninsula and Europe as a whole, and is dominated by a Mediterranean semiarid climate, yet, also presents strong rainfall and temperature gradients (Vidal-Abarca et al., 1987). The vegetation, predominantly xerophytic, is a product of climate aridification during mid-to-late Holocene and human induced degradation (Carrión et al., 2010).

The contrasts in altitude, lithology, precipitation, temperature and also in relation to human occupation, generate a great diversity of environments that allows a high biodiversity. The complex paleogeographic and paleoclimatic history of the area (Carrión et al., 2010) has also contributed to the existence of a rich biodiversity.

The Iberian ant fauna is progressively more widely known, although this knowledge is still very fragmentary and limited to studies of specific areas. There are only a few sub regional checklists of the myrmecofauna in this area (Tinaut, 1981; Ortiz & Tinaut, 1988; Espadaler, 1997a; Espadaler, 1997b; Catarineu & Tinaut, 2012; Del Campo et al., 2014). There are also very few publications focusing on the zoogeography of European ants: northern Europe (Baroni-Urbani & Collingwood, 1977), Greek islands (Collingwood, 1993), Poland (Czechowski et al., 2002; Czechowski et al., 2012), Ukraine (Radchenko, 2011), and Montenegro (Karaman, 2011). Dynamic lists, such as Antmaps (Antmaps.org, 2016), also provide species distribution information. The southeastern Iberian Peninsula is included in only four publications mentioning ant zoogeography, in the Sierra Nevada (Tinaut, 1981), Cabo de Gata (Tinaut et al., 2009), SE-Spain (Piñero et al., 2011), and Región de Murcia (Catarineu & Tinaut, 2012).

The main objectives of this paper are:

1) to compile a checklist of ant species in the Segura River Basin based on a review of the literature and material collected during sampling conducted from 2012 to 2016;

2) to classify the ant species of the Segura River Basin into zoogeographic chorotypes;

3) to analyze if zoogeographic chorotypes are related to climatic gradients in the Segura River Basin.

Material and methods

Ant data sources

The checklist presented is based on three different sources: (i) a literature review (23 papers that cite Southeastern Iberian ants, see Table 1); (ii) systematic sampling of 60 locations spread over ten 10×10 km UTM squares representative of the climatic, geological and geomorphological variation of the region [in each location, a 100-m transect was set up, consisting of 10 pitfall traps separated by 10 metres and open for one week (in July 2014 and July 2015); pitfall traps were polystyrene tubes (2 cm diameter, 10.5 cm long) filled with 5 ml of 50:50 propylene glycol and water solution with a few drops of liquid soap added to reduce surface tension]; (iii) non-systematic sampling by pitfall trapping and hand collecting over the whole region, adding up to 103 different localities during the period 2010-2016 (see Fig 1 for the 163 locations, and Table S1 for the whole information about locations and dates).

All ant samples were sorted and identified to species level using a stereo microscope and Iberian ant taxonomic keys (Hormigas.org, 2016), taxonomic revisions of some ant genera (Seifert, 1988, 1992, 2002), and species descriptions and high-resolution pictures provided by Antweb (2017). It was not possible to identify species of *Leptanilla* Emery*, Proformica* Ruzsky*,* and *Solenopsis* Westwood due to a lack of modern revisions and complete taxonomic keys in these genera. In relation to *Tapinoma* cf *nigerrimum* and *Tetramorium* cf *caespitum*, recently Seifert et al. (2017) and Wagner et al. (2017) confirmed the existence of different cryptic species within these species complexes found in the Iberian Peninsula. Unfortunately, there is not a simple nor precise method for phenotypical species delimitation in these species complex as we have no access to the specific optical equipment required for this task. Identified ants were transferred to vials with ethanol 70º, or were mounted. All specimens are deposited

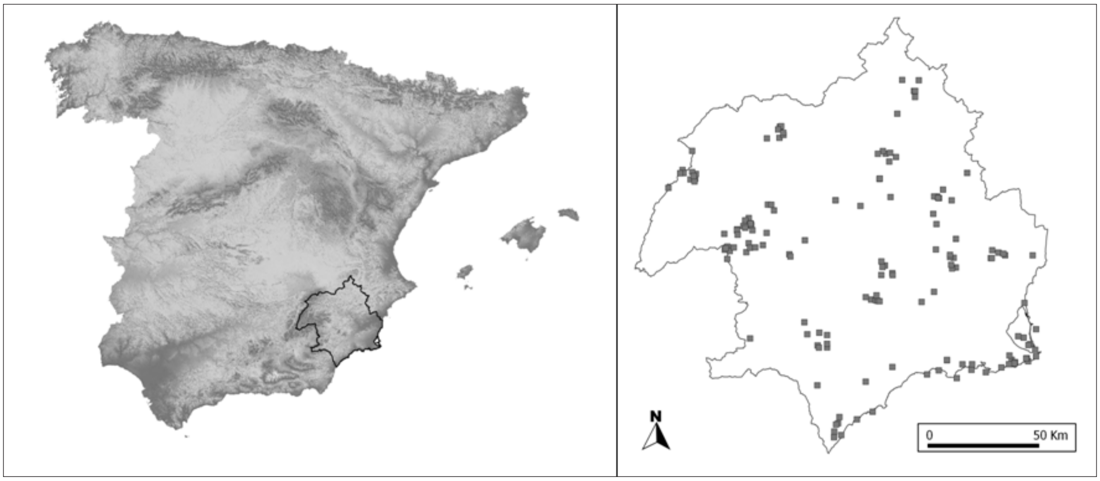

Fig 1. Map of Spain with the Segura River Basin outlined (on the left) and a map of the Segura River Basin with the 163 localities sampled indicated with grey squares (on the right).

in the premises of Asociación de Naturalistas del Sureste (Murcia, Spain) and some duplicates samples in the University of Córdoba (Área de Ecología, Córdoba, Spain).

Zoogeographic categories

A review of the present geographic distribution of the Segura River Basin ants was undertaken, based mainly on the following sources: Czechowski et al. (2002); Glaser (2006); Csösz et al. (2007); Karaman (2011); Czechowski et al. (2012); Seifert (2012a, 2012b); AntArea (2015); Antmaps (2016); Hormigas.org (2016); Janicki et al. (2016); Antweb (2017); and Lebas et al. (2017). Considering their current geographical distribution in the Palaearctic and Saharo-Arabian zoogeographic realms (sensu Holt et al., 2013), the native ant species were classified into two main zoogeographical classes corresponding to the two main Palaearctic vegetation zones, in accordance with Czechowski et al. (2002) and Czechowski et al. (2012): (I) mixed and deciduous forest zone; and (II) the Mediterranean zone sensu lato. Within each zone, species ranges were classified into the following scheme:

Elements represented in the Segura River Basin ants (modified from Czechowski et al., 2012):

I. Mixed and deciduous forest zone.

1) The Central and Southern European element (CSE)- species distributed mainly in Southern and Central Europe.

2) The Central and Southern European/Maghrebian element (CSE/M)- species distributed mainly in Southern and Central Europe and also in the Maghreb.

3) The Eurocaucasian element (EC)- species distributed mainly in the zone of deciduous forest, partly in mixed forest areas within Europe and the Caucasus; possibly reaching Asia Minor and the Near East.

4) The Eurocaucasian/Maghrebian element (EC/M)- Eurocaucasian species also present in the Maghreb.

5) Euro-West-Siberian element (EWS)- species widely distributed in Europe (usually also in the Caucasus) and West Siberia, reaching the east Altai Mts.

6) Euro-West-Siberian/Maghrebian element (EWS/M)- Euro-West-Siberian species also present in the Maghreb.

7) The South-Palaeartic element (SP)- generally Trans-Palaeartic forms, often distributed from the Atlantic to Pacific Oceans, whose ranges cover mainly the southern part of the forest zone and the forest-steppe zone; ecologically associated with dry forest or dry grasslands.

II. Mediterranean zone sensu lato.

8) The Tethyan Element (T)- species with a wide area that includes wholly or at least mostly the Mediterranean region, south of central and eastern Europe, the Caucasus, Asia Minor, the Middle East, Iran, Kazakhstan and Middle Asia.

9) The Holomediterranean element (HM)- species distributed in the European Mediterranean Region, south of central and eastern Europe, North Africa and, in Asia Minor (or in a significant part of this area). They can also occasionally reach Near and Middle East, Central Europe, and the southern part of East Europe.

10) The North-Mediterranean element (NM)- species distributed in the European Mediterranean Region but absent in North Africa.

11) The West-Mediterranean element (WM)- species distributed in the West-Mediterranean Region: Iberian Peninsula, France, the Apennine Peninsula and the Maghreb. In some cases, they are also present in Balearic Islands, Corsica, Sardinia or Sicily.

12) The North-West Mediterranean element (NWM) – species distributed in the Iberian Peninsula and southern France. They can also reach the northern Apennine Peninsula.

13) The Iberian elements (I)- species distributed only in the Iberian Peninsula. We include some Iberian sensu lato species, that can also reach the French Pyrenees or the Balearic Islands.

14) The Iberian/Maghrebian elements (I/M)- species distributed in the Iberian Peninsula and also in the Maghreb.

Relation of zoogeographic chorotypes to environmental variability

Data sources are heterogeneous and the sampling effort was heavily unbalanced across the region. Therefore, we adopted a strategy designed to deal with this problem. Firstly, we resampled data at 10×10 km resolution on the UTM grid in order to obtain a higher number of species by sampling unit and a more homogeneous definition of the *locality* concept. In total there are data from fifty-seven 10×10 km UTM squares. Then, we studied the relationship between the *proportion* of species belonging to the class of mixed and deciduous forests and the precipitation (computed as the mean of the localities sampled within a 10×10 km UTM square) by logistic regression, being the number of *success* the number of species belonging to the class of mixed and deciduous forests, and the number of *trials* the total number of species. The species richness of a particular chorotype is clearly influenced by sampling intensity, however one can expect that the proportion of species in a chorotype is independent of the sampling intensity although values on less sampled areas are not as reliable. Moreover, the Fisher scoring algorithm for logistic regression weighs observations proportional to the number of species, allocating low weights to sampling units with low sampling intensity and high weights to adequately sampled units. Therefore, estimates of parameters is much more influenced by best sampled localities, while marginal information of other areas is not absolutely neglected. Mean annual precipitation and temperature data for the whole basin were obtained from Worldclim 2 (Fick & Hijmans, 2017), and altitude from ASTER satellite imagery. There was a very high correlation (>0.95) between the three variables as a result of the natural correlation of precipitation (positive) and temperature (negative) with altitude in the area, but it was probably exacerbated by the interpolation methodology in Worldclim 2 as altitude is incorporated in the interpolation algorithm. Because of redundancy between the three variables, we chose precipitation as the target climatic predictor variable.

Localities with ant data are a biased sample of the basin. Highest altitudes (>1200 m) are overrepresented in the sample (Fig S1.a) while low-mid altitude (200-1100 m) are in general underrepresented, but lowest altitudes (<200 m) are again overrepresented. Since the correlation between altitude and precipitation (positive) and temperature (negative) is high in the area, this means the coldest and rainiest areas are overrepresented in the sample, while intermediate temperature and precipitation are underrepresented except in the warmest areas (Fig S1b-c). The sampling bias is a consequence of much higher proportion of natural habitats on the mountain ranges than in the inter-range plains and valleys, mostly occupied by agricultural lands (López- Bermúdez et al., 1986) which were rarely sampled.

A second approach to better understanding the relationship between chorotypes and environmental variability was carried out using elements instead of zones as zoogeographic units. At this higher zoogeographic resolution, the number of species per chorotype becomes rather reduced, therefore we used only data obtained from the systematic sampling of ten 10×10 km UTM squares (item ii; Ant data sources). These squares were selected as representing the diversity of climates, lithologies and geomorphology of the basin, after clustering data with those variables using *k*-means method (data not shown). Sampling intensity was exactly the same across the 10 squares and therefore data are strictly comparable. In this analysis, we grouped CSE and CSE/M; EC and EC/M; and CSW and CSW/M (CSE, EC/M and EWS/M had only 1, 1 and 2 species respectively). Then, we calculated the richness per chorotype element (permitting the grouping indicated) and the richness matrix by element by 10×10 km UTM square was submitted to a non-metric multidimensional analysis (NMDS; Bray-Curtis distance; dimensions = 2; stress = 0.13). Coordinates in the NMDS space are represented on the geographic space of the basin and sampling unit coordinates on NMDS axis 1 and 2 were individually regressed on precipitation.

Results

The checklist of the Segura River Basin ants includes 110 ant species from 30 genera of five subfamilies (Dolichoderinae, Formicinae, Leptanillinae, Myrmicinae, and Ponerinae). Two subfamilies were dominant: Myrmicinae with 53 species and Formicinae with 46 species (Table 2). The most represented genera are *Temnothorax* Mayr (19 species), *Camponotus* Mayr (14 species), *Lasius* Fabricius (8 species), *Formica* Linnaeus, and *Plagiolepis* Mayr (6 of each). Twenty two species were recorded for the first time in this area (Table 1).

One species previously reported from the area is excluded: *Lasius niger* L. There are only two records of *L. niger* for the Segura River Basin (Collingwood & Yarrow, 1969; Martínez et al., 2002), and these records possibly correspond to *Lasius grandis* Forel, because the first record was before Seifert (1992) raised *L. grandis* to species, and the second was based on one queen only. Seifert (1992) argues that in most mesophilic areas of Spain *L. niger* is completely displaced by *L. grandis* and our findings appear to support him. One new species was discovered as a result of our field work, *Temnothorax ansei*, recently described by Catarineu et al. (2017).

There are three undescribed species in the checklist: *Camponotus* sp.1 (a parasite of *Camponotus pilicornis* Roger); *Plagiolepis* sp.1 (a parasite of *Plagiolepis schmitzii* Forel); and *Temnothorax* sp.1. *Camponotus* sp.1 and *Plagiolepis* sp.1 are being described by X. Espadaler (X. Espadaler, personal communication); *Temnothorax* sp.1 is being described by A. Tinaut (A. Tinaut, personal communication).

Table 2. The composition of the ant fauna of the Segura River Basin, with species and genus numbers/percentages given for each subfamily.

Subfamily	No. of genera (%)	No. of species (%)
Dolichoderinae	3 (10.0)	6 (5.5)
Formicinae	10 (33.3)	46 (41.8)
Leptanillinae	2 (6.7)	2 (1.8)
Myrmicinae	13 (43.3)	53 (48.2)
Ponerinae	2 (6.7)	3 (2.7)
Total	30	110

Zoogeographical composition

Table 3 shows the zoogeographical composition of the ant fauna in the Segura Basin. For this classification, we consider only 105 species, discarding those not identified as species (*Leptanilla* sp., *Proformica* sp., *Solenopsis* sp., *Tapinoma* cf *nigerrimum* and *Tetramorium* cf *caespitum*). Three quarters of the species (79 spp., 75.2%) are associated with the Mediterranean zone, while nearly a fifth (20 spp., 19.05%) are associated with the mixed and deciduous forest zone. The other species are Cosmopolitan (6 spp., 5.7%), tramp species introduced in this region with larger distribution globally, which on the other hand indicates that 94.3% of the species collected can be considered as native from the Segura River Basin region. The four principal zoogeographical elements are clearly: Iberian (21 spp., 20 %), Holomediterranean (18 spp., 17.1%), West-Mediterranean (14 spp., 13.3%) and North-West Mediterranean (11 spp., 10.5%). Over two-fifths of the Segura Basin ants are also encountered in the Maghreb region (43 spp., 41%).

Chorotypes and environmental variability

There is a clear relationship between the proportion of ant species in the mixed and deciduous zone and precipitation (Fig 2). It is rare to find species of this zone in areas with less than 350 mm of annual precipitation. With rainfall over 450 mm these species were only absent in 10×10 km UTM squares with very low intensity sampling (very low total observed ant richness consequently). With rainfall between 300-400 mm (the most frequent precipitation range in the region, Fig S1.c) there is a considerable spread of the proportion of species in the class. It may be related to the large environmental differences between south and north-face of the mountain ranges, the latter faces being considerably mesic as compared to areas on flat or south-faced slopes, and therefore having denser vegetation, less insolation and higher humidity.

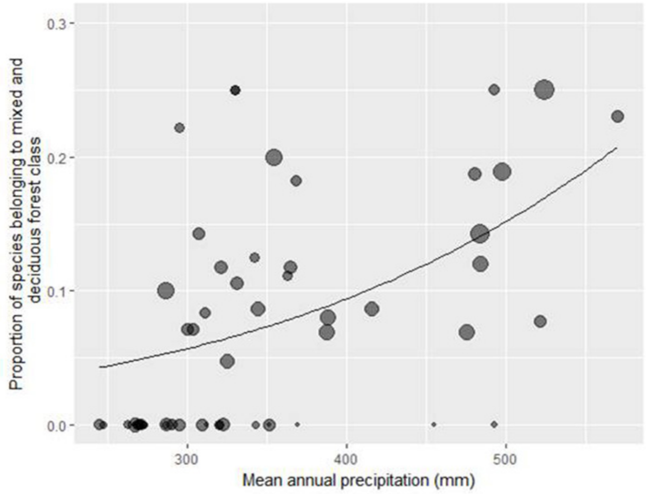

Fig 2. Relationship between proportion of species on the mixed and deciduous forest class and mean annual precipitation. Solid line, logistic regression model expectation. Dots, empirical data grouped on 10×10 km UTM squares. Size of dots is proportional to the total number of ant species recorded on the square. Two squares with one and two species, respectively, are not represented on the figure as they are out of range (proportion of mixed and deciduous forest class 0.5 and 1). Intercept: -4.4427 ± 0.5479, z= -8.108, P=<0.001; Precipitation: 0.0054 ± 0.0013, z= 4.271, P=<0.001.

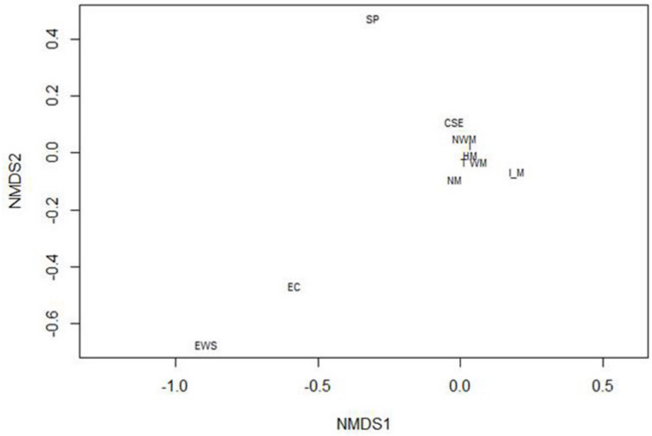

Fig 3. Non metric multidimensional scaling (NMDS) of zoogeographic elements on 10×10 km UTM squares representing the geological, geomorphological and climatic variation of the Segura River Basin. CSE = Central and Southern European, EC = Euro-Caucasian, EWS = Euro-West Siberian, HM = Holomediterranean, I = Iberian, I/M = Iberian/ Maghrebian, NM= North-Mediterranean, NWM = North-West Mediterranean, SP = South-Paleartic, T = Tethyan, WM = West-Mediterranean.

Focusing on elements only for homogeneously sampled 10×10 km UTM squares, the pattern that appears clearly separates most of the mixed and deciduous forest zone elements from the Mediterranean elements (Fig 3).

The first axis (NMDS1) separates Euro-Caucasian (EC + EC/M) and Euro-West Siberian (EWS + EWS/M) elements from the rest. The second axis (NMDS2) clearly separates South Paleartic (SP), EC and EWS elements from the rest, but EC and EWS and SP are on opposite sides of the axis (Fig 3). NMDS1 separates presumably forest associated elements EC and EWS from the rest, while NMDS2 separates clearly SP element more associated to steppe Eurosiberian ecosystems. This is clearer on the geographical representation of the NMDS coordinates of the 10×10 km UTM squares (Fig 4.a-b). The Euro-Caucasian and Euro-West Siberian elements seem to be more associated with subhumid and humid forests on the NW-Segura River Basin mountains. The South Paleartic elements seem to be more associated to the N- Segura River Basin, an area of transition to the central Spain plateau, characterized by mid-height mountains surrounded by relatively high valleys and plains more similar to the forest-steppe zone with more open forests and grasslands (Fig 4a and 4b).

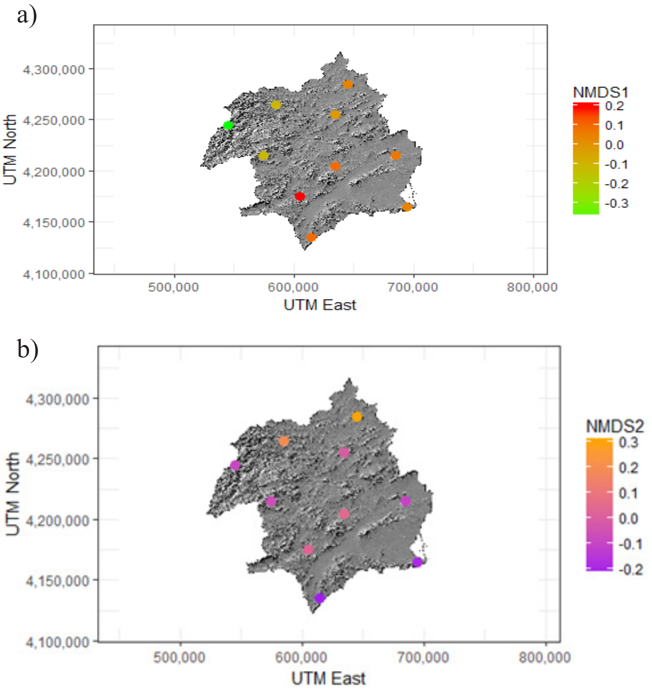

Fig 4. Geographical representation of coordinates of 10×10 km UTM squares of the systematic sampling (see Methods) on NMDS space of Figure 3. (a) Coordinates on axis NMDS1. (b) Coordinates on axis NMDS2.

Both axes have a clear relation with precipitation (Fig 5). Thus, NMDS1 coordinate is linearly negatively correlated with precipitation (P = 0.04; linear regression; R^2 adj = 0.61), while NMDS2 shows a peak at intermediate precipitations which is better fitted by a linear regression with linear and quadratic terms of precipitation as predictors (P = 0.02; R^2 adj = 0.79).

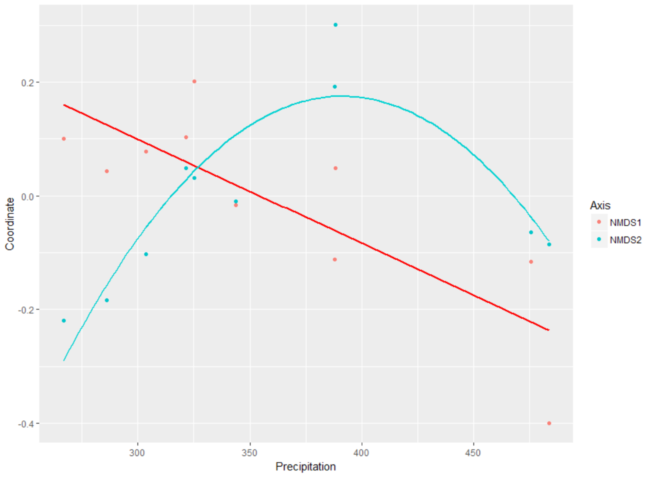

Fig 5. Coordinates of 10×10 km UTM squares of the systematic sampling (see Methods) on NMDS space of Figure 3 against precipitation. Dots, empirical data; lines fitted regression lines between NMDS coordinates in each axis and precipitation (see Methods).

Discussion

At this point 110 ant species belonging to 30 genera and five subfamilies were recorded in the Segura River Basin but the actual species number is undoubtedly higher. A greater sampling effort, the study of hypogaeic species such as Leptanilla spp., the delimitation in the *Tapinoma* cf *nigerrimum* and *Tetramorium* cf *caespitum* species complexes, and the revision of genera such as Proformica or Solenopsis, will increase the inventory of species. Ant diversity in the Segura River Basin seems similar to other Iberian Peninsula regions like the Comunitat Valenciana (108 sps, 23,255 km^2, Mediterranean coast; Del Campo et al., 2014) or Burgos (99 sps, 14,022 km^2, northern plateau in the transition between Mediterranean and Cantabrian ranges with oceanic climate; García & Cuesta, 2017).

The Segura River Basin ant fauna is formed by species with different evolutionary and zoogeographic origins (two zoogeographical zones and 14 zoogeographical elements; Table 3). The existence of these different zoogeographic origins in this area is probably linked with: the position between Africa and Europe; the complex geotectonic, paleogeographic, and paleoclimatic history during the last 7 My; the complex geomorphology; and the high climate and habitat diversity.

Ant species from the mixed and deciduous forest zone

The ant species from the mixed and deciduous forest zone in the Segura River Basin accounted for 19.1% of the species inventoried. These species possibly suffered contraction in their ranges during the ice ages and survived in several southern refuges, such as the Baetic ranges.

The climatic oscillations during the Pleistocene Ice Ages, and particularly over the last 2 My, are known to have had an important influence on the zoogeographic history of Europe driving the repeated contraction/expansion of the

Table 3. Zoogeographical composition of the ant fauna of the Segura River Basin (south-west Spain). It includes only the 105 species in which it has been possible to reach the species level.

Zoogeographical zones	Zoogeographical elements	Acronym	n	%
Zone of the mixed and deciduous forest	Central and Southern European	CSE	1	0.95
	Central and Southern European/ Maghrebian	CSE/M	3	2.86
	Euro-Caucasian	EC	5	4.76
	Euro-Caucasian/Maghrebian	EC/M	1	0.95
	Euro-West-Siberian	EWS	3	2.86
	Euro-West-Siberian/Maghrebian	EWS/M	2	1.90
	South Palearctic	SP	5	4.76
			20	**19.05**
Mediterranean zone	Holomediterranean	HM	18	17.14
	Iberian	I	21	20.00
	Iberian/Maghrebian	I/M	5	4.76
	North-Mediterranean	NM	6	5.71
	North-West Mediterranean	NWM	11	10.48
	Tethyan	T	4	3.81
	West-Mediterranean	WM	14	13.33
			79	**75.24**
Cosmopolitan	Cosmopolitan	C	**6**	**5.71**
Total number of species			**105**	**100.00**

zoogeographical ranges (Hewitt, 2011). The Iberian Peninsula was one of the most important refuges in Europe during the Pleistocene Ice Ages (Hewitt, 2000, 2001, 2011; Gómez & Lunt, 2007). After the last glacial maximum period (20-14 ky BP) some species have expanded their range northward from their Iberian refugia, or tracked suitable habitats higher up along elevation gradients within mountain ranges (Gómez & Lunt, 2007; Hewitt, 2001). The Baetic ranges, where the Segura River Basin is located, were one of the Iberian refugia (Carrión et al., 2003; Gómez & Lunt, 2007, Hewitt, 2011).

Consistent with this, in the NMDS analysis, both NMDS1 and NMDS2 axis are mainly determined by zoogeographic elements of mixed and deciduous forest class (Fig 3). There is a greater proportion of species from the mixed and deciduous forest zone in the high-mid altitudes in the Segura River Basin, where the climate is cooler, the precipitation regime is subhumid or humid, and vegetation is dominated by *Pinus* L. and *Quercus* L. forests (Fig 2, 4 and 5). This happens especially with Euro-West Siberian (EWS + EWS/M) and Eurocaucasian (EC + EC/M) elements. South Paleartic (SP) species have a similar pattern but peaks at intermediated precipitation/elevation and, especially at the transition zone between the Baetic ranges and valleys typical of the Segura Basin and the Central Spain plateau. CSE elements, on the contrary, appear clearly grouped with typically Mediterranean elements. Therefore, the general pattern of the class shows a clear gradient of elements where species are mainly associated to Eurosiberian forests (EC, EWS) than those on the transitional areas forest –steppe (SP) and then transitional to Mediterranean and CSE elements.

Some Euro-Caucasian and Euro-West-Siberian species were recorded only at high altitudes, with more humid climate: *Temnothorax unifasciatus* Latreille (EC/M, 1161 m.a.s.l.); *Polyergus rufescens* Latreille (EWS, 858-1282 m); *Strongylognathus testaceus* Schenck (EWS, 2000 m); *Camponotus fallax* Nylander (EWS/M, 1280-1286 m). Other species classified under the same zoogeographical elements, were regularly collected at high altitudes but also at lower altitudes in humid habitats such as gallery forests or gardens: *Myrmica specioides* Bondroit (EC, 640-1275m); *Temnothorax affinis* Mayr (EC, 640- 1100 m); *Formica rufibarbis* Fabricius (EWS, 40-1359m); and *Camponotus vagus* Scopoli (EWS/M, 640-1356 m). Some SP species were also collected only at high altitudes: *Formica pratensis* Retzius (1208-1280 m); *Formica sanguinea* Latreille (1280 m); and *Lasius carniolicus* Mayr (1563 m).

Global climate change is probably inducing altitudinal shifts of some ant species that will track suitable habitats along elevation, but the ant species currently limited to the mountain-tops have no further elevation range to track habitats with suitable climatic conditions. Talavera et al. (2014), studying a recently described and endemic ant from the Balearic Islands (*Lasius balearicus* Talavera et al., 2014) state that this species, elevationally constrained to island summits, is endangered by climate change and is potentially facing extinction. This could also be the case of species that inhabit only at high altitudes in the Segura River Basin which could be in danger of local extinction, as *F. pratensis* (Tinaut et al., 2011).

Ant species from the Mediterranean zone

The species from the Mediterranean zone accounted for three quarters of the species collected (79 spp., 75.2%), with the Iberian species, the most commonly represented zoogeographical element (21 spp., 20%). The Iberian Peninsula is known to present high endemism of plants (25-30%; Castroviejo et al., 1986), Iberian carabid (43.1 %; Serrano et al., 2003), and other taxa as reptiles, amphibians, mammals, fishes or butterflies (Abellán & Svenning, 2014). Many of these endemic species possibly evolved during the Pleistocene Ice Ages from Tertiary species, when conditions in the different Iberian refugia enabled long periods of allopatry, with speciation occurring as a result of adaptive selection and genetic drift processes (Huseman et al., 2013). Gómez and Lunt (2007) stated that many species and species complex show strong genetic subdivisions in the Iberian Peninsula which provides evidence of their isolation. A Pleistocene origin is also proposed for other endemic taxa as Dytiscidae water beetles: most Iberian endemics have an apparent recent origin, differing less than 2% in mDNA from their sister species, which implies an origin from Middle to Late Pleistocene (Ribera, 2003). A possible example of the Pleistocene speciation may be found in *Cataglyphis* Foerster ants: Villalta et al. (2017) investigated the phylogeography of the *Cataglyphis albicans* group and suggested the existence of at least three clades in the Iberian Peninsula and five in the Maghreb. The three Iberian clades are monophyletic and parapatric, and estimation of divergence times suggests a speciation process initiated after the Messinian Salinity Crisis and the last reopening of the Gibraltar Straits (≈5,33My). Other Iberian ant endemics such as *Aphaenogaster iberica* Emery and *A. dulcineae* Emery could also be derived from a North-African ancestor, bearing in mind that nowadays there are 40 *Aphaenogaster* Mayr native species and morphospecies in Morocco (Antmaps, 2016).

Medail and Quézel (1997) proposed the Baetic Rifan complex, which includes the Baetic ranges, as the most important areas of plant biodiversity inside the Mediterranean Basin Hotspot. Gómez-Campo et al. (1984) state that the Baetic ranges display the highest plant biodiversity in continental Europe with great Iberian endemic species richness, many of which are Baetic ranges endemic species. This high endemism is the result of the long-term survival, genetic divergence and speciation in these refugia (Gómez & Lunt, 2007; Hewitt, 2011). The mountainous geomorphology is particularly important in these processes of isolation, divergence and speciation during the past 3My (Hewitt, 2000). The number of endemic plants in the Baetic ranges is outstanding: 418 taxa (Pérez-García et al., 2012) and these endemics concentrate on highland disjunct areas (Mota et al., 2002). There are also a lot of species of terrestrial animals that are local endemics, as the amphibian *Alytes dickhilleni* Arntzen and García-París or the Spanish lizard *Algyroides marchi* Valverde (Gómez & Lunt, 2007). Piñero et al. (2011) studying the arid areas of south-east Iberian Peninsula found a 8.4% insect and a 9.6% spiders species endemic to this area. In the case of ants, Piñero et al. (2011) report 9.5% of endemic species but, in the Segura River Basin, we found only four endemic ants of the south-east Iberian Peninsula, accounting for 3.6% of the total number of species: *Camponotus haroi* Espadaler, *Goniomma collingwoodi* Espadaler, *Temnothorax ansei* and *Temnothorax cristinae* Espadaler.

Holomediterranean elements account for 17.1% (18 species). These species are possibly Tertiary species that found suitable habitats and survived the Pleistocene Ice Ages in the Iberian Peninsula and other refuges around the Mediterranean Basin. The paleoecological similarities of the Maghreb and Southern Europe have led to a circum-Mediterranean distribution of many taxa (Huseman et al., 2013).

There are 43 species of the Segura Basin ants also present in the Maghreb (CSE/M, EC/M, EWS/M, HM, I/M, T and WM) accounting for 41% of the recorded species. The presence of Ibero-North African species has been reported in other taxonomic groups, for example, the Baetic ranges have the highest values of Ibero-North African plants in the Iberian Peninsula (Gómez-Campo et al., 1984) and this occurrence is also found in spiders and in various insect orders (Piñero et al., 2011). The Maghreb was also an important differentiation and speciation center during the Pliocene and Pleistocene, where many taxa may have evolved or survived and later expanded to the Iberian Peninsula and Europe (Huseman et al., 2013).

Two paleogeographical events allowed the exchange of terrestrial organisms between Africa and the Iberian Peninsula. The first event was the separation of parts of the Baetic region from the Iberian mainland and its connection by the south to Africa during the Baetic crisis 16-14 Mya (Veith et al., 2004). The second event was the closure of the Mediterranean-Atlantic connections due to tectonic processes during the Messinian Salinity Crisis 5.96-5.33 Mya (Veith et al., 2004; Agustí et al., 2006; Hewitt, 2011; Gibert et al., 2013). The Strait of Gibraltar has been an effective barrier to genetic exchange since this event, although there is evidence that some terrestrial reptiles or amphibians crossed during the Pleistocene, possibly with lower sea levels during the glacial maxima (Veith et al., 2004; Hewitt, 2011; Huseman et al., 2013). The I/M and WM ants in the Segura Basin might represent Tertiary species that colonized the Iberian Peninsula, and in some cases southern France, from North Africa during the Messinian Salinity Crisis. There are no ant species in the Segura River Basin also present in the Afrotropical realm. Serrano et al. (2003), studying Iberian Carabidae (Coleoptera), state that the Iberian Peninsula is poor in Afrotropical elements, probably because of the strong isolation derived from the Sahara Desert.

The proportion of species from the Mediterranean zone is greater in the lowland areas, and decreases with the altitude in the Segura River Basin (Fig 2), possibly because they are more thermophilic species. In the NMDS analysis, all the Mediterranean elements are strongly aggregated together and with the Central and Southern European element, only Iberian/Maghrebian elements are lightly separating from the rest (Fig 3).

Cosmopolitan ant species

The cosmopolitan ant species are all introduced tramp species, and account only for 5.7% (6 species). None of them seem to have much ability for invasion in the Segura River Basin. The most widespread, *Linepithema humile* Mayr*,* as well as the scarcer *Pheidole indica* Mayr and *Cardiocondyla mauritanica* Forel are present only in degraded coastal habitats and in anthropogenic environments such as gardens. *Paratrechina longicornis* Latreille was collected at only two sites in urban habitats, while *Strumigenys membranifera* Emery was collected at a single site in a semiarid and altered area. It is likely the harsh conditions of the semi-arid areas of the Segura River Basin are not suitable for the invasion of the exotic species.

Future directions

Unfortunately, zoogeographical studies are so scarce that we are not able to compare the zoogeographical ant composition of the Segura Basin to other Mediterranean regions. Further comparative phylogeographical analyses are needed to elucidate the range changes and the evolutionary history of the myrmecofauna in the Iberian Peninsula during the Cenozoic. There is also further research required on the zoogeographic consequences of the changes we currently face living in the present epoch, the Anthropocene. The Segura River Basin has suffered during thousands of years the effects of deforestation, fire, and pastoralism. During the last decades, the area has suffered dramatic ecosystem changes caused by uncontrolled urban development, expansion of intensive agriculture, abandonment of extensive livestock farming, inadequate reforestations, soil degradation, habitat fragmentation, and a deficiency in the conservation management (Piñero et al., 2011). Climate change is already occurring and, as it progress, it will also cause ecosystem changes with important effects on biodiversity. Some species will suffer a rapid loss of suitable habitat and face extinction (Thomas et al., 2004; Wilson et al., 2005). Other species are less vulnerable or may even be favoured by these changes. The evolutionary origin of species and their elevational distribution seem to be important in determining vulnerability to climate change. Management for biodiversity conservation requires monitoring ecosystem changes and their effects on the biocenosis. For this task, ants could be crucial bioindicators in the coming years.

Table 1. Checklist of the ant species of the Segura River Basin. The list is arranged alphabetically by subfamily, genus and species. Species names in bold characters refer to species recorded for the first time in this area. Zoogeographical classes (ZC) and Zoogeographical elements (ZE) abbreviations: 1 = mixed and deciduous forest zone, 2 = Mediterranean zone, 3 = Cosmopolitan, CSE = Central and Southern European, CSE/M = Central and Southern European/Maghrebian, C = Cosmopolitan, EC = Euro-Caucasian, EC/M = Euro-Caucasian/Maghrebian, EWS = Euro-West Siberian, EWS/M = Euro-West-Siberian/Maghrebian, HM = Holomediterranean, I = Iberian, I/M = Iberian/ Maghrebian, NM = North-Mediterranean, NWM = North-West Mediterranean, SP = South-Palearctic, T = Tethyan, U = Unknown, WM = West-Mediterranean, ? = zoogeographical element questionable. Elevation range units: masl. Bibliographic references are as follows: a = Emery 1924, b = Santschi 1932, c= Collingwood & Yarrow 1969, d = Martínez & Espadaler 1986, e = Cerdá 1988, f = Seifert 1988, g = López et al. 1990, h = López, 1991, i = Seifert, 1992, j = Haro et al. 1995, k = Dahbi et al. 1996, l = Espadaler 1997c, m = Martínez et al. 1997, n = Martínez et al. 2002, o = Morcillo et al. 2006, p = Espadaler et al. 2007, q = Tinaut et al. 2011, r = Catarineu & Tinaut 2012, s = Martínez et al. 2012, t = Arcos et al. 2013, u = Del Campo et al. 2014, v = Asociación Ibérica de Mirmecología 2016, x = Catarineu et al. 2017, y = present paper. For locations, see Table S1.

Subfamily	Scientific valid name	Z.C.	Z. E.	Elevation range	References
DOLICHODERINAE	*Bothriomyrmex meridionalis* (Roger, 1863)	2	WM	275–1,223	r, y
	Linepithema humile (Mayr, 1868)	3	C	1–1,148	c, n, o, r, t, y
	Tapinoma erraticum (Latreille, 1798)	1	SP	2	r
	Tapinoma madeirense Forel, 1895	2	NWM	248–1,429	r, v, y
	Tapinoma cf nigerrimum (Nylander, 1856)	2	?	2–1,507	b, c, r, v, y
	***Tapinoma nigerrimum* (Nylander, 1856)**	2	NWM	339–392	y
FORMICINAE	*Camponotus aethiops* (Latreille, 1798)	2	T	640–1,282	c, r, v, y
	Camponotus cruentatus (Latreille, 1802)	2	WM	858–1,442	r, y
	Camponotus fallax (Nylander, 1856)	1	EWS/M	1,280–1,282	r, v, y
	***Camponotus figaro* Collingwood & Yarrow, 1969**	2	I	858–1,359	y
	Camponotus foreli Emery, 1881	2	I/M	1–1,280	b, m, r, v, x, y
	***Camponotus haroi* Espadaler, 1997**	2	I	484	y
	Camponotus lateralis (Olivier, 1792)	2	HM	51–1,359	r, v, y
	Camponotus micans (Nylander, 1856)	2	WM	286–1,113	b, r, u, y
	Camponotus piceus (Leach, 1825)	2	NM	248–1,507	b, c, r, v, y
	Camponotus pilicornis (Roger, 1859)	2	NM	590–1,442	c, p, r, y
	Camponotus ruber Emery, 1925	2	I/M	15–238	r, t
	Camponotus sp.1 Espadaler in prep.	2	I	1148–1,155	p, r
	Camponotus sylvaticus (Olivier, 1792)	2	WM	1–1,406	b, c, d, n, r, t, v, x, y
	***Camponotus vagus* (Scopoli, 1763)**	1	EWS/M	640–1,356	y
	Cataglyphis iberica (Emery,1906)	2	I	1–1,282	e, j, k, l, m, n, r, t, v, x, y
	Cataglyphis piliscapa (Forel, 1901)	2	NWM	?	c
	***Cataglyphis rosenhaueri* Santschi, 1925**	2	I	905–1,304	y
	Cataglyphis velox Santschi, 1929	2	I	640–1,406	r, v, y
	Colobopsis truncata (Spinola, 1808)	2	HM	1,280–1,282	r, v, y
	Formica cunicularia Latreille, 1798	1	EC	42–1,406	c, r, v, y
	Formica decipiens Bondroit, 1918	2	I	242–1,282	r
	***Formica frontalis* Santschi, 1919**	2	I	1,356	y
	Formica pratensis Retzius, 1783	1	SP	1,077–1,282	q, r, v, y
	Formica rufibarbis Fabricius 1793	1	EWS	42–1,359	r, v, y
	Formica sanguinea Latreille, 1798	1	SP	1,280	v
	***Iberoformica gerardi* (Bondroit, 1917)**	2	I	1,356	y
	Iberoformica subrufa (Roger, 1859)	2	I	15–1,359	b, r, v, x, y
	Lasius alienus (Foerster, 1850)	1	SP	?	c
	Lasius brunneus (Latreille, 1798)	1	EC	1,282	r
	***Lasius carniolicus* Mayr, 1861**	1	SP	1,563	y
	Lasius cinereus Seifert, 1992	2	NWM	640–2,000	i, r, v, y
	Lasius emarginatus (Olivier, 1792)	1	EC	495	r
	Lasius grandis Forel, 1909	2	WM	2–1,307	c, n, r, t, v, y
	***Lasius lasioides* (Emery, 1869)**	2	HM	248	y

Table 1. Checklist of the ant species of the Segura River Basin. The list is arranged alphabetically by subfamily, genus and species. Species names in bold characters refer to species recorded for the first time in this area. (Continuation)

Subfamily	Scientific valid name	Z.C.	Z. E.	Elevation range	References
FORMICINAE	*Lasius myops* Forel, 1894	1	CSE/M	793–1,661	r, y
	Paratrechina longicornis (Latreille, 1802)	3	C	73	r, y
	Plagiolepis grassei Le Masne, 1956	2	NWM	400	s
	Plagiolepis pygmaea (Latreille, 1798)	1	CSE/M	87–1,429	c, n, r, t, v, y
	Plagiolepis schmitzii Forel, 1895	2	HM	2–1,341	n, r, t, v, x, y
	***Plagiolepis* sp.1 Espadaler in prep.**	2	I/M	2–392	y
	***Plagiolepis taurica* Santschi, 1920**	1	SP	437–1,046	y
	Plagiolepis xene Stärcke, 1936	1	CSE	107–1,280	n, r, t, y
	Polyergus rufescens (Latreille, 1798)	1	EWS	858–1,282	r, y
	***Proformica ferreri* (Bondroit, 1918)**	2	I	472	y
	Proformica nasuta (Nylander, 1856)	2	NWM	?	c
	Proformica sp.	?	?	640–923	y
LEPTANILLINAE	*Leptanilla sp.*	?	?	242–1,258	x, y
	Leptanilla theryi Forel, 1903	2	I/M	?	r
MYRMICINAE	*Aphaenogaster dulciniae* Emery, 1924	2	NWM	329–1,155	c, r, y
	Aphaenogaster gibbosa (Latreille, 1798)	2	HM	277–1,492	r, v, y
	Aphaenogaster iberica Emery, 1908	2	I	1–2,000	b, c, l, m, n, r, t, v, x, y
	Aphaenogaster senilis Mayr, 1853	2	WM	15	r
	Cardiocondyla batesii Forel, 1894	2	HM	2–714	c, r, x, y
	Cardiocondyla mauritanica Forel, 1890	3	C	2–10	r
	Crematogaster auberti Emery, 1869	2	WM	1–1,359	a, c, r, t, v, x, y
	Crematogaster laestrygon Emery, 1869	2	HM	2–465	r
	Crematogaster scutellaris (Olivier, 1792)	2	HM	10–1,359	b, r, t, v, y
	Crematogaster sordidula (Nylander, 1849)	2	HM	192–1,359	a, c, r, t, y
	Goniomma blanci (André, 1881)	2	NWM	392–1,280	r, v, y
	***Goniomma collingwoodi* Espadaler, 1997**	2	I	472	y
	Goniomma hispanicum (André, 1883)	2	WM	244–640	r, v, x, y
	Goniomma kugleri Espadaler, 1986	2	I	244–465	x, y
	Messor barbarus (Linnaeus, 1767)	2	WM	1–1,359	b, l, m, n, r, v, x, y
	Messor bouvieri Bondroit, 1918	2	NWM	1–1,313	b, c, r, v, x, y
	Messor capitatus (Latreille, 1798)	2	HM	248–1,442	r, v, y
	Messor structor (Latreille, 1798)	1	T	1,200	c, y
	Monomorium andrei Saunders, 1890	2	I/M	2–192	r, t, y
	Monomorium subopacum (Smith, 1858)	2	HM	1–275	r, y
	Myrmica aloba Forel, 1909	2	NWM	905–1,307	c, f, r, y
	Myrmica specioides Bondroit, 1918	1	EC	248–1,275	v, y
	Oxyopomyrmex saulcyi Emery, 1889	2	WM	198–881	x, y
	Pheidole indica Mayr, 1879	3	C	10–16	r
	Pheidole pallidula (Nylander, 1849)	2	T	1–1,442	a, c, n, o, r, t, v, x, y
	Solenopsis latro Forel, 1894	2	HM	192–793	c, r, t
	Solenopsis sp.	4	U	6–1,359	n, r, v, y
	Strongylognathus caeciliae Forel, 1897	2	I	238	r, x
	***Strongylognathus testaceus* (Schenck, 1852)**	1	EWS	2,000	y
	Strumigenys membranifera Emery, 1869	3	C	154	n
	Temnothorax affinis (Mayr, 1855)	1	EC	640–1,077	v, y
	Temnothorax angustulus (Nylander, 1856)	2	HM	640	v, y

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Subfamily	Scientific valid name	Z.C.	Z. E.	Elevation range	References
MYRMICINAE	*Temnothorax ansei* Catarineu, Barberá & Reyes-López, 2017	2	I	244–591	x,y
	Temnothorax blascoi **(Espadaler, 1997)**	2	I	854–1,339	y
	Temnothorax cristinae (Espadaler, 1997)	2	I	107–787	l, r, t, x, y
	Temnothorax curtulus **(Santschi, 1929)**	2	I/M	1307–1,356	y
	Temnothorax formosus (Santschi, 1909)	2	WM	465–1,359	r, v, x, y
	Temnothorax gredosi (Espadaler & Collingwood, 1982)	2	I	248	r
	Temnothorax kraussei **(Emery, 1916)**	2	HM	1,307	y
	Temnothorax kutteri **(Cagniant, 1973)**	2	NWM	120	y
	Temnothorax luteus (Forel, 1874)	2	NM	79–1,406	c, x, y
	Temnothorax niger (Forel, 1894)	2	NM	2–1,077	r, x, y
	Temnothorax pardoi (Tinaut, 1987)	2	WM	248–1,406	r, v, y
	Temnothorax racovitzai (Bondroit, 1918)	2	NM	79–1,359	r, t, x, y
	Temnothorax recedens (Nylander, 1856)	2	HM	107–1,291	r, t, v, y
	Temnothorax **sp.1 Tinaut in prep.**	2	I	1,231	y
	Temnothorax specularis (Emery, 1916)	2	NM	44–1,359	v, x, y
	Temnothorax unifasciatus **(Latreille, 1798)**	1	EC/M	1,162	y
	Temnothorax universitatis (Espadaler, 1997)	2	I	465	x
	Tetramorium biskrense Forel, 1904	2	HM	88–1,406	v, y
	Tetramorium cf caespitum (Linnaeus, 1758)	4	U	1–2,000	g, h, l, m, r, v, y
	Tetramorium forte Forel, 1904	2	WM	392–1,507	r, y
	Tetramorium semilaeve André, 1883	2	HM	2–1,359	c, g, h, l, m, r, x, y
PONERINAE	*Hypoponera eduardi* (Forel, 1894)	3	C?	?	c
	Ponera coarctata (Latreille, 1802)	2	HM	500	c, r
	Ponera testacea **Emery, 1895**	1	CSE/M	1155–1,280	y

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