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Research Article

Areas of Endemism and Biogeographic Regionalization of the Iberian Peninsula Based on Ants (Hymenoptera: Formicidae)

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Based on the distribution of 275 species of ants native to the Iberian Peninsula (IP), we identified areas of endemism (AE) within its geographical limits and present a biogeographic regionalization using two complementary methods and two types of operational geographical units. For endemicity analysis (EA), we used a $100 \, km^2$ grid cell, and for parsimony analysis of endemicity (PAE), we used hydrological basins as natural units. The EA revealed twelve areas of endemism that were grouped into five consensus areas. These are the Northeastern area, South plateau, Guadalquivir Valley, Baetic System, and Iberian Peninsula (whole). PAE resulted in a cladogram that classified hydrological basins into at least two successively nested subsets: an Atlantic group that is more related to northern European fauna and an Iberian subset that is well supported by synapomorphies. The Iberian subset was differentiated into four main areas: (a) a Northeastern area formed by the Pyrenees and the Catalan Coastal Range, (b) a mainland area containing the Central System and Guadiana and Tajo valleys, (c) a Southern area consisting of the Guadalquivir Valley and the Baetic System, and (d) a Northern coastal area. The results showed congruence between the two methods since many of the synapomorphies are shared among the diagnostic and IP endemic species of the EA. Both EA and PAE showed the relevance of the heterogeneous peninsular orography that combines mountainous regions with valleys and plateaus, which have acted as historical barriers or corridors. The presence of numerous endemic species, particularly in the southern third of the IP, suggests that several Iberian refuges for ants originated during glacial periods. These areas constitute priority sites for the conservation of ants in particular and biodiversity in general on the IP and allow further research about the processes that generated these distributional patterns.

1. Introduction

The recognition of areas of endemism (AE) is important for conservation biology and biogeographic regionalization [1] and is essential for subsequent cladistic biogeographic analyses [2]. The definition given by Platnick [3] and supported through the years by numerous studies (v. gr. [4, 5]) presents an area of endemism as a congruent distributional area of two or more taxa that are spatially restricted to it. AE are "areas of non-random distributional congruence" [4] because it is assumed that they were shaped by the same ecological and evolutionary processes. In this context, endemism is both restricted distribution and sympatry [6].

In conservation biogeography, endemic taxa have been used as surrogates for biodiversity conservation (v. gr. [7–9]) and many biodiversity hotspots have been described based on them [10]. However, the most important application of areas of endemism is as the basis for biogeographic regionalization [11]. The origins of biogeographic regionalizations are in the manuscripts of de Candolle [12], Sclater [13], and Wallace [14]. Recently, in the Palearctic region, some modern regionalizations have been reconsidered based

on endemicity as defined by these authors. For example, Escalante [15] found that the Palearctic region was divided into two clades (Europe and Mediterranean) but could not be identified by mammals as a monophyletic area; in addition, an area of endemism in Uzbekistan was discovered. For plants, Hurdu et al. [16] identified four areas of endemism in the Southeastern Carpathians. This suggests that more detailed studies using these and other taxa should be performed to evaluate whether the Palearctic constitutes a region and to propose subregions, dominions, and provinces within it.

On the Iberian Peninsula (IP), most of the studies that use fauna to search for AE or attempt biogeographic regionalizations have focused on vertebrates: including fishes [17, 18], amphibians and reptiles [19, 20], and mammals (rodents [21], insectivores [22]). The biogeography of invertebrate fauna has also received some attention, although little effort has been dedicated to the identification of areas of endemism. Puente et al. [23] identified five biogeographical areas on the IP based on the distribution of Helicoidea snails using cluster analysis. Iberian aquatic Coleoptera allowed Ribera [24] to recognize five main geographical regions based on geological and topographical criteria. The geographical distribution of dung beetles (Coleoptera, Scarabaeoidea) was used by Verdú and Galante [25] to describe some patterns of endemism in the IP and the Balearic Islands. García-Barros et al. [26] included Coleoptera (Curculionoidea), Collembola, and Lepidoptera (Noctuidae, Lycaenidae, and Nymphalidae) among other animal and plant taxa, finding up to thirty-six areas of endemism through PAE in the Ibero-Balearic territory. Hortal et al. [27] did an IP regionalization based on Coleoptera (Scarabaeinae), and more recently, Romo and García-Barros [28] used distribution data for Iberian butterflies to propose seven biogeographical regions.

Ants are a well-studied taxon in the Western Palearctic region and an especially diverse group on the Iberian Peninsula, which make them a particularly suitable study subject for this matter [29]. Previous biogeographical studies on ants by Tinaut and Ruano [30] include the recognition of eight refugium areas on the IP and the identification of endemic species based on this concept. The proposed sectorization of the IP in terms of refugia is an excellent context from which to highlight the importance of the peninsular orography to explain the pattern of endemism. This concept is a good starting point for the biogeographical knowledge of the ants of this territory, but it does not consider a systematic analysis of endemisms. Therefore, the aim of this work is to contribute to the knowledge of the biogeography of ants on the IP using the methods of endemicity analysis (EA) and parsimony analysis of endemicity (PAE), focusing on the identification of areas of endemism (AE) and allowing the IP regionalization.

2. Material and Methods

2.1. Study Area.
The ant distribution limits used in this work were assigned according to the continental boundaries of Spain, Portugal, and Gibraltar on the IP. The Balearic Islands were therefore not included, as they do not form a biogeographical unit with mainland Iberia. To establish the north-south division of the Pyrenees, we used the geopolitical/natural border between Spain and France (we included Andorra since it is located at this border).

2.2. Data Records.
Georeferenced records of the Iberian ant fauna were obtained from public databases (http://www.antmaps.org [31]), http://www.antweb.org and http://www.GBIF.org (occurrence download [32]), original articles, and personal records. The records underwent a screening process to ensure data quality, resulting in a total of 12,602 georeferenced distribution records (the number of occurrences of each species can be consulted in Table S1). The identity of certain species was updated to the most recent nomenclature following Bolton [33] (http://www.antcat.org). A filtering based on the criteria of Guénard et al. [31] was used to determine the native set of Iberian ants, excluding the categories "exotic," "indoor introduced," "needs verification," and "dubious," although some exceptions were made based on the taxonomic context and the uncertain status of several ant species in the IP. The final database included 275 native species of Formicidae (Table S1), belonging to 39 genera, 16 tribes, and 7 subfamilies.

2.3. Data Analysis.
Areas of endemism were identified using two complementary methods based on the concept of Platnick [3] and two types of operational geographical units (OGUs). Endemicity analysis (EA) [2, 4] was applied to a grid cell of $100\,km^2$ (resulting in 76 valid cells), which has proven useful in previous biogeographic studies in the IP [26]; and parsimony analysis of endemicity (PAE) [4, 34, 35] was performed using hydrological basins as natural units, which were useful for regionalization. River basins have been used as biogeographical units in several studies [18, 36–38] since they may reveal the complex orography of the IP territory. Hydrological basins reflect the alternation of valleys and mountains, which can act both as barriers and corridors for species and are determinants of evolutionary processes such as vicariance, local extinctions, and dispersal. At the same time, these basins act as proxies for environmental variables such as water availability, soil, and vegetation, which are determinants of ecological processes like dispersion. In particular, the Garona river basin was included even though it is located mostly in France because it marginally overlaps in several locations with the IP at the Pyrenean border. Shapefiles were obtained from the *Global Runoff Data Centre* [39].

EA was performed in NDM/VNDM v. 3.1 [40] using the default parameters, setting a minimum species score of 0.5 and 80% of unique species to keep overlapping subsets. We selected a fill size of 20 and assumed radius size of 40 to increase the inference capability of points near the edge of a cell. The number of repetitions was 50, changing the random seed sequentially from "1" to "50." The scores of all sets and their endemic taxa were analysed for the comparison, and consensus areas were finally obtained with a 50% of

similarity in species against any of the other areas in the consensus.

For PAE, we built a binary matrix in which the presence of a given species (columns) was coded as "1" and its absence in an area unit (rows) as "0." An initial row coded with zeros was included in the matrices to root the cladograms. In addition to the 275 native species, the supraspecific taxonomic levels of 39 genera, 16 tribes, and 7 subfamilies were included as additional columns to overcome the lack of phylogenetic information (except for monotypic taxa) [41–43]. The matrix of 314 taxa and 13 basins was analysed applying the new technology algorithm implemented in TNT software v. 1.5 [44]. We found the minimum length five times and saved 999 trees, using the default options for sectorial search, ratchet, and drift. In order to penalise homoplasy, we applied implied weighting with $k = 0.997$ [15, 45–47], using the setK.run script written by J. S. Arias, based on Goloboff et al. [48]. A strict consensus cladogram was calculated in TNT and visualised in WinClada v. 1.00.08 [49]. Uninformative species were deactivated, and fast optimization was used to prioritise reversions over homoplasy in the consensus to calculate the tree statistics (longitude (L), consistency index (CI), and retention index (RI)) in WinClada.

Maps representing areas of endemism and regionalization using hydrological basins limited to IP boundaries were generated in QGIS v. 3.20.3 [50].

3. Results

3.1. Areas of Endemism in NDM. In NDM, the random seed "1" was selected because all random seeds contained the maximum number of sets available. The analysis led to twelve sets (for candidate areas of endemism, see Figures 1(c)–1(g)), and six consensus areas of endemism (named CA#) were obtained once the consensus was applied, with maximum scores between 2.0 and 27.56 (Table 1). The species resulting from the endemicity analysis (EA species; Table 1 and Table S2 for full names) were divided into EA "diagnostic species" and IP "endemic species" in order to distinguish the strictly endemic species to the IP, from other native species with marginal or wider distribution in the IP that were detected by the EA.

Consensus area 0 (see AE in Figure 1(c)) comprised the whole Iberian Peninsula. This may be a methodological artifact due to the geographic scale and cannot be considered an AE, but rather a spurious area [51]. For that reason, only four CA of endemism were finally selected (Figure 1). They are as follows:

CA1—Northeastern area: built from two AE (Figure 1(d)) and consists of five grid cells that encompass several geographical locations within the Catalan Mediterranean System: southeastern Pyrenees mountains, Catalan Pre-Coastal Range, and Catalan Coastal Range. This area is defined by the congruence of 10 EA diagnostic species: *Aphaenogaster ichnusa* Santschi, 1925; *Formica clara* Forel, 1886; *Formica paralugubris* Seifert, 1996; *Formica pressilabris* Nylander, 1846; *Myrmica lobulicornis* Nylander, 1857; *Myrmica martini* Seifert et al., 2014; *Myrmica vandeli* Bon-

droit, 1920; *Stenamma striatulum* Emery, 1895; and *Tapinoma pygmaeum* (Dufour, 1857) and *Temnothorax stumperi* (Kutter, 1950).

CA2—South plateau: formed by one AE (Figure 1(e)) and corresponds to a more restricted area in Ciudad Real province that covers two grid cells, belonging to the Guadiana River depression. It includes only 1 EA diagnostic species and 1 IP endemic species: *Messor sordidus* (Forel, 1892) and *Crematogaster fuentei* Menozzi, 1922, respectively.

CA3—Guadalquivir Valley: composed of three AE (Figure 1(f)) and covers seven grid cells that correspond to the Guadalquivir Valley, the Gulf of Cádiz, and the Serranía de Ronda. This area encompasses 4 EA diagnostic species, *Colobopsis imitans* Schifani et al., 2022; *Messor marocanus* Santschi, 1927; *Stenamma punctiventre* Emery, 1908; and *Strongylognathus afer* Emery, 1884, and 3 IP endemic species, *Cataglyphis douwesi* De Haro & Collingwood, 2000; *Cataglyphis floricola* Tinaut, 1993; and *Cataglyphis tartessica* Amor & Ortega, 2014.

CA4—Baetic System: formed by four AE (Figure 1(g)) and comprising seven grid cells that cover the whole Baetic System and surrounding territories including the northwest side of the Guadalquivir Valley and the Eastern Andalusian coastline. A total of 12 species contribute to the endemicity score of this CA. There are 5 EA diagnostic species, *Crematogaster laestrygon* Emery, 1869; *Lepisiota frauenfeldi* (Mayr, 1855); *Monomorium algiricum* (Bernard, 1955); *Temnothorax algiricus* (Forel, 1894); and *Temnothorax cagnianti* (Tinaut, 1983), and 7 IP endemic species, *Cataglyphis humeya* Tinaut, 1991; *Goniomma collingwoodi* Espadaler, 1997; *Goniomma compressisquama* Tinaut et al., 1995; *Messor timidus* Espadaler, 1997; *Temnothorax alfacarensis* Tinaut & Reyes-López, 2020; *Temnothorax crepuscularis* (Tinaut, 1995); and *Tetramorium kutteri* (Tinaut, 1990).

3.2. Areas of Endemism and Regionalization under PAE. PAE resulted in a cladogram with a length (L) of 625, a consistency index (CI) of 0.50, and a retention index (RI) of 0.56. The cladogram was completely resolved, and seven synapomorphies showed that all basins of the IP are monophyletic (Figure 2). Almost all of the clades were supported by two or more synapomorphies, showing a nestedness topology of areas of endemism from north to southeast. The total number of autapomorphies in the cladogram was 46, where the highest number (16) corresponds to the Southern Mediterranean Sea basin. These autapomorphies may be synapomorphies at smaller scales and were named as characteristic taxa by Escalante et al. [41]. We refer here to these synapomorphies or characteristic taxa as PAE species (autapomorphies) in order to distinguish diagnostic species from IP endemic species detected by the PAE (Table 2). PAE diagnostic species are native to the Iberian Peninsula although their distribution may extend beyond the study area. Their marginal distribution in this territory adds great value to the regionalization process, as it allows for a more precise division of the territory by taking into account the distributional limits of the species. IP endemic species are found exclusively in the Iberian Peninsula.
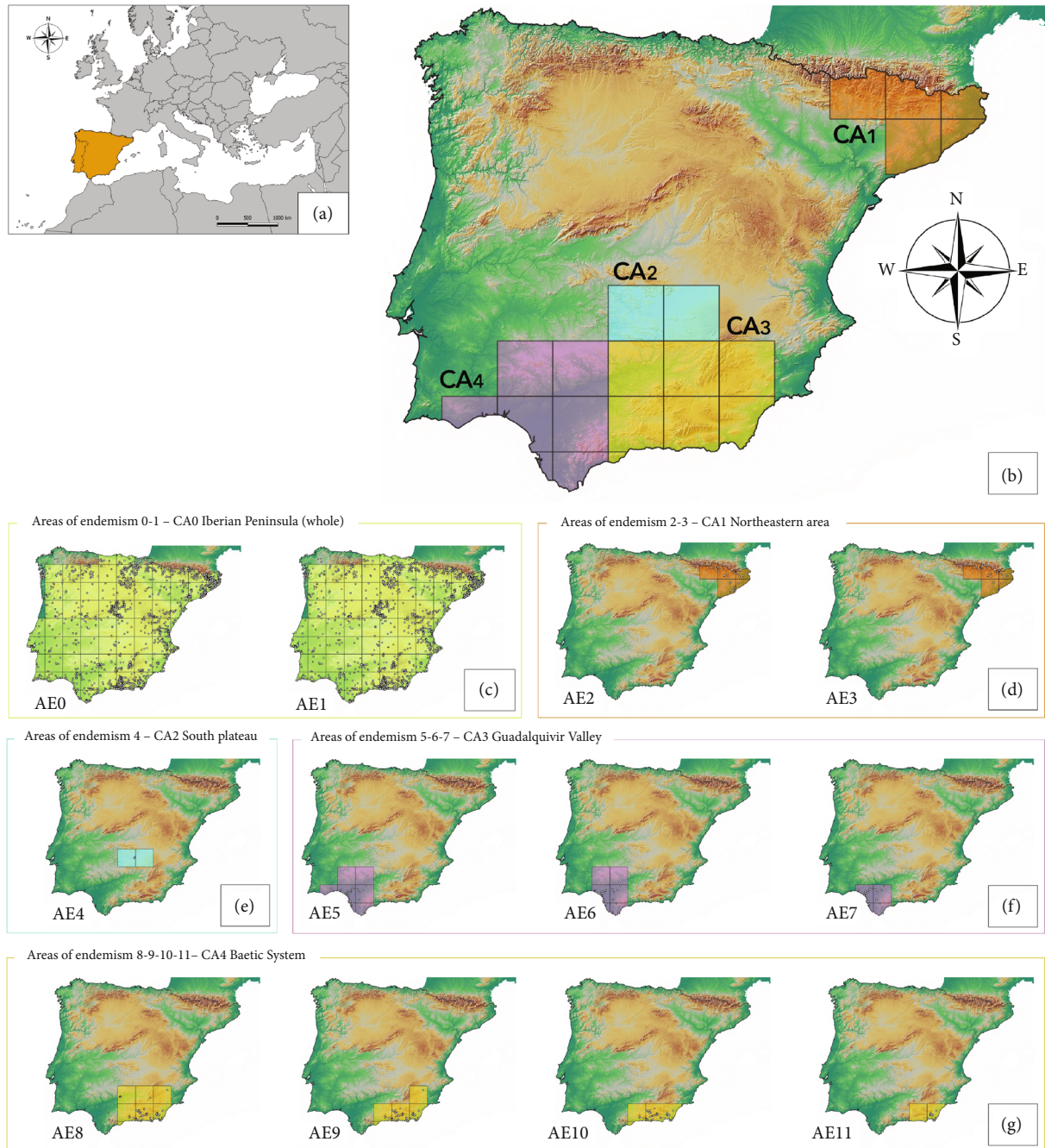
FIGURE 1: (a) Study area corresponding to the Iberian Peninsula highlighted in orange. Limits stablished according to the continental boundaries of Spain, Portugal, Gibraltar, and Andorra. (b) Four consensus areas of endemism (CA) for the Iberian Peninsula based on the geographical distribution of native Iberian ants as a result of the endemicity analysis (EA) using NDM/VNDM. (c) Areas of endemism (AE) corresponding to CA0 (whole Iberian Peninsula). Not considered in (b). (d) AE of CA1—Northeastern area. (e) AE of CA2—South plateau. (f) AE of CA3—Guadalquivir Valley. (g) AE of CA4—Baetic System. Notes for (b)–(g): distances correspond to the grid cell of $100\,km^2$. North arrow applies to all maps. Base map: Iberian Peninsula MDT25 Topography © Cartography Service of the Autonomous University of Madrid (SCUAM). Altitude data: IGN Spain, IGN France, SRTM and others.

The first three areas correspond to the Northern coastline of the IP which comprise the following basins: Garona River, Miño and Limia rivers, and Bay of Biscay (Cantabrian Sea). This group of basins, although paraphyletic, share an Atlantic region affinity. The rest of basins in the cladogram are monophyletic. This clade was supported by 26 synapomorphies and is more linked to the Mediterranean zone.

The Upper and Middle West coast basin presents only one autapomorphy followed by a group consisting of the Southwest coast and Guadiana Valley basins, though this last group lacked synapomorphies. The next branch places the Duero Valley basin between this last group and another branch composed of the Ebro Valley and Northern Mediterranean Sea basins. Finally, the Tajo Valley basin is sister to

TABLE 1: List of consensus areas of endemism (CA) for the Iberian Peninsula based on the geographical distribution of native Iberian ants.

CA	AE	Max. score	EA species (ID number)	Geographical location
0	0-1	27.56	4-18-21-22-23-27-29-30-31-34-45-51-52-55-62-64-68-93-95-96-106-112-128-129-130-165-167-200-204-214-254-265-267-275	Iberian Peninsula (whole)
1	2-3	6.46	6-61-73-77-150-151-160-187-205-256	Pyrenees mountains, Catalan Pre-Coastal and Coastal Range
2	4	2.25	53-137	Guadiana River basin
3	5-6-7	3.94	40-41-48-50-136-186-192	Guadalquivir Valley, Gulf of Cádiz, Serranía de Ronda
4	8-9-10-11	7.99	44-54-86-87-120-138-139-209-210-220-226-272	Penibaetic and Subbaetic System

Areas of endemism (AE) included in the consensus areas are indicated along with the maximum score given by the EA (endemicity analysis) species (EA diagnostic species and IP endemic species) that contribute a high endemicity score to the AE. The main geographical location associated with the CA is pointed out. EA species names appear on areas of endemism in NDM in Results and Table S1.
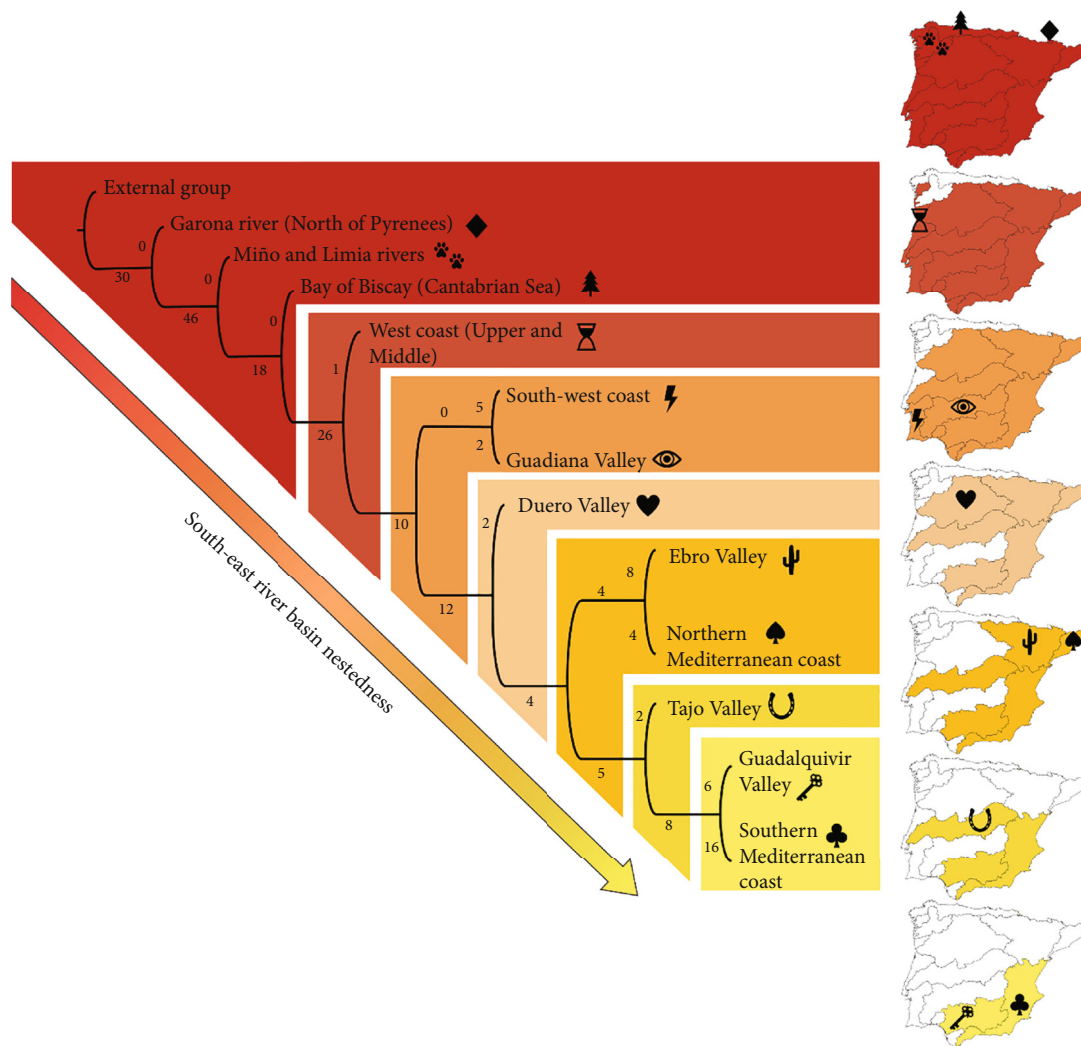

FIGURE 2: Cladogram and maps representing the regionalization of the Iberian Peninsula using the main hydrological basins as natural units for the PAE (parsimony analysis of endemicity). Tree parameters: length = 625, consistency index = 0.50, and retention index = 0.56. The small numbers indicate the number of autapomorphies or synapomorphies.

TABLE 2: Biogeographic regionalization and biogeographical areas of the Iberian Peninsula based on PAE (parsimony analysis of endemicity) of native ant distributions. Overlapping or similar areas proposed in the literature as part of other schemes of biogeographic regionalization are indicated, as well as the AE (area of endemism) that overlaps or is proximate to the biogeographical provinces.

Biogeographical subregion	Biogeographical provinces	Hydrological basin (OGU)	SR	G	A	D	PAE diagnostic species	E	IP endemic species
Atlantic EEA [63] Europe [15] Europe (E3) [29]		Garona River (North of Pyrenees) ◆	32	10	—	—	—	—	—
	Northern coastal area	Miño and Limia rivers ❀	63	18	—	—	—	—	—
		Bay of Biscay (Cantabrian Sea)	74	24	—	—	—	—	—
Mediterranean [61, 62, 15] EEA [63] Western Mediterranean [29]	Mainland IP and Atlantic influence area EA: CA2 and 3	Atlantic coast — West coast (Upper and Middle)	104	28	1	1	*Solenopsis oraniensis*	—	—
		Guadiana Valley and South Portugal plains — Southwest coast ⚡	102	28	5	4	*Cardiocondyla nigra*, ***Stenamma punctiventre***, *Tapinoma magnum, Temnothorax atlantis*	1	***Cataglyphis douwesi***
		Guadiana Valley ◉	89	25	2	1	***Messor sordidus***	1	***Crematogaster fuentei***
		Northern plain — Duero Valley ♥	132	28	2	1	*Lasius bicornis*	1	*Formica bruni*
	Northeastern IP area (Eastern Pyrenees, and Catalan Coastal Range) Northeast [22] Pyrenean [26] EA: CA1	Ebro Valley	176	34	8	8	*Formica selysi, Myrmica karavajevi,* ***Formica paralugubris***, *Myrmica lemasnei,* ***Myrmica martini***, *Temnothorax caesari, Temnothorax conatensis, Tetramorium pyrenaeicum*	—	—
		Northern Mediterranean coast ♣	149	32	4	4	***Aphaenogaster ichnusa, Formica clara, Tapinoma pygmaeum, Temnothorax stumperi***	—	—
		Tajo Valley ∪	151	34	2	1	*Temnothorax clypeatus*	1	*Leptanilla charonea*
	Southern Mediterranean IP area (Tajo Valley, Guadalquivir Valley, Baetic System and Southern Levante) Central (c, d, e) [26] EA: CA3 and 4	Guadalquivir Valley ⚷	166	33	6	3	*Temnothorax curtulus, Temnothorax naeviventris,* ***Strongylognathus afer***	3	***Temnothorax alfacarensis, Temnothorax crepuscularis, Tetramorium kutteri***
		Southern Mediterranean coast ♣	202	36	16	9	*Bothriomyrmex atlantis, Bothriomyrmex communista,* ***Lepisiota frauenfeldi,*** *Leptanilla theryi,* ***Temnothorax algiricus***, *Temnothorax convexus, Temnothorax flavispinus, Tetramorium exasperatum, Stigmatomma emeryi*	7	*Camponotus amaurus, Cataglyphis gadeai,* ***Goniomma compressisquama, Messor timidus,*** *Temnothorax ansei, Temnothorax cristinae, Monomorium schelii*

The following is included: the hydrological basin (OGU) occupied (code from GRDC, [39]; symbols correspond to clades of Figure 2), species richness (SR), number of genera (G), number of autapomorphies (A), diagnostic species (D), and IP endemic species (E) supporting each clade (diagnostic species may present a marginal distribution in the IP but are determinant for the regionalization of the territory; IP endemic species support the regionalization through the endemism pattern). Diagnostic and endemic species that coincide with those from the EA (endemicity analysis) are pointed out in bold letters. The symbols relate each OGU to its geographic representation in Figure 2.

the most distal clade, formed by the Guadalquivir Valley and Southern Mediterranean Sea basins.

Based on the parsimony relationships obtained in the PAE and supported by the areas of endemism from both analyses, a set of biogeographical areas can be proposed: one as a division at the subregion level and a second division at the province level as part of a regionalization of the IP (Table 2). We identified four natural biogeographical areas: (1) Northeastern IP area, which contains the Eastern Pyrenees and the Catalan Coastal Range; (2) Mainland IP and Atlantic influence area, which covers the whole western and central part of the IP; (3) Southern Mediterranean IP area, formed by the Guadalquivir Valley, Baetic System, and Southern Levante; and (4) Northern coastal area, from the Bay of Biscay to the Miño and Limia river basins.

The basin with the highest species richness was the Southern Mediterranean coast with 202 species belonging to 36 genera (Table 2). The Southern Mediterranean coast, along with the Guadalquivir Valley (166 species, 33 genera) and Tajo Valley (151 species, 34 genera), forms the biogeographical province with the most diverse OGUs, which is the Southern Mediterranean IP area. This area also contains the highest number of PAE diagnostic and IP endemic species. Together, they comprise 24 PAE species, with 11 of them being endemic to the PI. The Northeastern IP area is also formed by OGUs with high species richness: Northern Mediterranean coast (149 species) and Ebro Valley (176 species). Although they present several PAE diagnostic species (4 and 8, respectively), they are not characterised by IP endemic species. The lowest number of species was in the Northern coastal area, with 32 species in Garona River (North of Pyrenees), 63 species in the Miño and Limia river basins, and 74 in the Bay of Biscay (Cantabrian Sea) basin, with no diagnostic or IP endemic species detected by the PAE. The rest of river basins, corresponding to the Mainland IP and Atlantic influence area, gather a relatively homogeneous number of species (from 89 to 132) and genera (from 25 to 28), but only 3 IP endemic species are present.

4. Discussion

4.1. Areas of Endemism. Our results show some interesting patterns of endemism based on the detection of areas of nonrandom distributional congruence related to causal processes that shaped the distribution of ants on the IP. The concept of AE used in this work is based on the exclusive occurrence of two or more species in the same area, which allows to detect the pattern of endemism in a territory [2–6]. By having the whole set of native species limited to this territory (IP), the EA and PAE highlight species with restricted distributions in the IP, including diagnostic and endemic species.

In biogeographic analyses, the selection of appropriate OGUs for the study area has been a widely discussed topic [2, 4, 5, 52]. For example, the use of large grid cells could lead to the agglutination of data, which makes it difficult to recognize small areas of endemism [53] or interpret the results [54]. However, García-Barros et al. [26] also mention the use of large cells as a conservative measure, given the

lack of knowledge about the fine distribution of some taxa (here, the distribution of several Iberian species). Although other geographical units could be analysed, the ones selected for this work were useful for obtaining areas of endemism at region, subregion, and province levels in the biogeographical hierarchy. Moreover, the AE consisting of the whole IP could be an effect of the grid size adopted and is considered a spurious area at this scale [51]. At the same time, it could be an indication of larger areas of endemism at the subregion, region, or realm levels in the biogeographic regionalization (e.g., within the Western Palearctic). On the other hand, the use of natural units for the PAE could reinforce the results obtained by the grids.

Some of the areas of endemism identified in this work overlap with large mountain ranges on the IP, but for ants, this is not a pattern as clear as was seen for butterflies [26] and other taxa [38], where the endemic species could have originated during periods of climatic changes [55]. In fact, most of the species identified as endemisms in the present work prefer low altitude habitats, a common trend in ants, as pointed out by Tinaut and Ruano [30]. Here, EA and PAE results showed how the spatial arrangement of the areas of endemism (Figure 1) and biogeographical areas (Figure 2) is influenced by the heterogeneous peninsular orography, as indicated by other authors [26, 38]. The combination of mountainous zones such as the Pyrenees, the Central System, Sierra Morena, and the Baetic System, with areas of valleys and plateaus, such as the South plateau or the Guadalquivir Valley, may have driven the high number of endemisms. These geographical features could act as historical barriers or corridors, supporting the idea of the occurrence of several Iberian refugia for a range of flora and fauna that could have originated during glacial periods in the Pleistocene Ice Ages [4, 30].

The fact that seven AE belong to the Southern IP and four of them exclusively to the Baetic System (Figures 1(f) and 1(g)) underlines the biogeographical importance of this territory on the IP as pointed out by several authors [22–24, 30, 34], in the form of historical and evolutionary processes that have gathered a high number of endemic species and that can be interpreted as a biodiversity hotspot [8]. Consensus area 3 (Guadalquivir Valley) contains species adapted to open spaces with scarce vegetation and sandy soils present at low altitudes like *C. douwesi*, *C. floricola*, *C. tartessica*, or *M. marocanus*. Consensus area 4 (Baetic System) results from a combination of species typical of lowland Mediterranean habitats as *C. humeya*, *G. collingwoodi*, *G. compressisquama*, *M. timidus*, or *T. crepuscularis*. The Southern Mediterranean IP biogeographical area resulting from the regionalization also supports the importance of the southern IP territories for ant endemism, since it contains up to 16 species detected by the PAE, 7 of which are IP endemisms, including distinctive Ibero-Mediterranean species like *Camponotus amaurus* Espadaler, 1997 and *C. gadeai* or *Temnothorax ansei* Catarineu et al., 2017.

On the other hand, CA1 (Northeastern area) has a clear set of diagnostic species to the studied territory typically adapted to the medium and high altitudes of the Pyrenees and the Catalonian Coastal range and forest, mountain

meadow, or humid habitats, like *A. ichnusa*, *F. clara*, *F. paralugubris*, *F. pressilabris*, *M. lobulicornis*, *M. martini*, or *M. vandeli*. PAE also allows us to differentiate a Northeastern IP area, with species belonging to genera typical of mountain forests and humid environments: *Formica*, *Myrmica*, and *Temnothorax* (see Table 2 for complete list). An example is *T. stumperi*, a social parasitic species found in colonies of the mountainous species *Temnothorax tuberum* (Fabricius, 1775) [56]. Although not endemic to the IP, this interesting species brings a point of complexity to the myrmecofauna and ecological interactions. In fact, none of these species are endemic to the PI, but they have a marginal distribution in this territory. In general, these species are more closely related to a northern European fauna, both from a geographical and ecological point of view, due to their widespread distribution in the western Palearctic and their adaptation to colder and wetter environments. It is in this sense that *Messor erwini* Orou et al. [57] stands out because it was recently discovered in a Mediterranean shrubland within this area. New detections may broaden its distribution in the westernmost part of the Palearctic, but the Mediterranean climatic and related ecological conditions become significant in defining the pattern of endemism in the IP.

The only representative near the peninsular center (CA3—South plateau) does not receive a high endemicity score since it is defined by only two species, *C. fuentei* and *M. sordidus*, whose distribution and biology are, in fact, poorly known. This situation, together with the fact that only 16% of the cells (21 out of 76) were detected as valid AE, highlights two aspects. Firstly, the uncertain status of some species needs to be addressed when specifying the pattern of endemism. Resolving the taxonomic status and clarifying the presence of certain species may reveal new areas of endemism in other parts of the IP. Secondly, there is a clear tendency for endemism to be concentrated in the southern third of the IP, which highlights this area's undisputed biogeographical and conservation significance.

4.2. Regionalization of the IP. The IP belongs to the Palearctic region and Mediterranean subregion *sensu* Wallace [14], which comprises Southern Europe and Northern Africa (including the extratropical portion of the Sahara and Egypt to about the first or second cataracts) and eastward through Asia Minor, Persia, and Cabul, to the deserts of the Indus, being the transition to the Ethiopian region. The European subregion of Wallace [14] borders the northern Mediterranean subregion. Recently, Morrone and Ebach [58] recognized the names of the two subregions of Wallace [14] as valid and defined the Pyrenees as the boundary between them, although it is unclear to which region the Pyrenees belong (for Wallace, the Mediterranean subregion comprises "all the countries south of the Pyrenees", p. 200). The Pyrenees could act as a transition (intergradation or contact) zone in the sense of Thorpe [59] between the European and Mediterranean terrestrial faunas. In fact, Wallace [14] mentioned that the Pyrenees form a barrier for migration. Although nomenclaturally, the transition zones are not recognized by the International Code of Area Nomenclature [60], transition zones could exist at all scales and ranks of

the regionalization. However, more evidence would be necessary to propose the Pyrenees as a transition zone.

Escalante [15] found two different clades dividing PI at 42° latitude, named as Europe (north) and Mediterranean (south) for the mammals of the world. This matches with the regionalization proposed in the present work, showing how the Northern coastal area (belonging to a more central-northern European region) is separated from a more Southern Mediterranean territory, with the Pyrenees as a possible transition zone. In fact, Wang et al. [29], by means of a hierarchical clustering analysis based on ant regional lists, showed evidence of a separation between the central-northern Europe and the Western Mediterranean in a similar way, highlighting the importance of the Pyrenees as a geographical barrier that could shape the fauna composition of the PI. This also coincides with the "sectoral patterns" presented by Udvardy [61] and Sanchíz [62] for the Atlantic (northwestern) and Mediterranean (southeastern) IP zones and follows the latest proposal of the European Environment Agency for the biogeographical delimitation of Europe, which considers an Atlantic and a Mediterranean region [63].

In general terms for the IP, some patterns have been found with both a strong longitudinal and latitudinal component. The first one establishes a Cantabrian, Atlantic, and Mediterranean watershed division as shown by Vargas et al. [18] for inland fishes and Rivas-Martínez [64] for flora. García-Barros et al. [26] also found a three-part longitudinal division of the Ibero-Balearic territory based on the distributions of several flora and fauna species, consisting of a Balearic-Pyrenean and an Eastern and a Western sector. They note a clear distinction between the Atlantic watershed and the northwestern part of the IP (including the Pyrenees), which is similar to the results of the present work in which a Northeastern IP area is delimited within the Mediterranean region and does not appear close to the Northern coastal area in the cladogram. On the other hand, the latitudinal division consists of northern and southern territories, as found in amphibians [19] and rodents [21], adding a third smaller region in the northeastern part of the peninsula in the case of insectivores [22]. Ribera [24] also found this north-south division in the case of water Coleoptera, defining a Cantabrian-Pyrenean-Central IP group and a southern complex formed by the Baetic range, Guadalquivir Valley, and Southern Portugal.

The phylogenetic relationships among the taxa used and the different scales and methodologies make it difficult to compare these studies with our present results. Our results fit more closely with the latitudinal pattern, although the hierarchical structure of PAE classification is better explained by a nested pattern towards the Southeast river basins of the IP. Other examples such as the regionalizations presented by Hortal et al. [27] for Iberian beetles or the butterfly-based regionalization by Romo and García-Barros [26] also reflect how both latitudinal (primary pattern) and longitudinal components shape the general pattern.

4.3. Endemism and Conservation Biogeography. Identification of areas of endemism requires that all of the species

present in a given territory be taken into account in order to detect areas of high value for the conservation of the taxa studied. The pattern of endemism found is related to the taxonomic richness in that the most nested area—comprising the Guadalquivir Valley and the Southern Mediterranean coast (Figure 2)—contains the highest richness of genera and species (166 and 202 species, respectively; Table 2). The Southern Mediterranean IP area alone contains 24 PAE diagnostic species, 8 of which coincide with the EA diagnostic species. This constitutes further evidence of the biogeographical importance of this peninsular territory with regard to refugia conservation as pointed out by Tinaut & Ruano [30] and follows a pattern consistent with other taxa [18, 27], where the Southeastern IP exhibits a high species richness and a significant number of endemic species.

The Northeastern IP area also has high diversity compared to other areas and is represented by up to 12 and 10 diagnostic species according to the PAE and the EA, respectively, which makes it a key point for the conservation management of Iberian biodiversity.

The observed pattern of endemism can be explained by a number of processes. Firstly, the peninsular orography has played a key role in speciation processes that could lead to the appearance of endemic species, like vicariance or local extinctions, acting as filters or ecological traps. Secondly, climate changes and Pleistocene glaciations have led to population reorganisations, extinctions, recolonizations, etc. The Iberian Peninsula has been the scenario for the movement of species, which could search for suitable habitats in glacial periods, ascending and descending in the latitudinal range, or the altitudinal one, moving up mountains and crossing valleys searching for climatic stability [55] what led to the refugia phenomena [38]. Thirdly, human impact due to agriculture and livestock farming for millennia could have led to the confinement of species to more natural areas such as the mountain ranges [25]. Fourthly, other factors such as the peninsular effect could have resulted in a concentration of species near an isthmus or a transition zone, the distribution of emerged land areas during the Eocene–Oligocene [18], or the presence of North-African vicariant fauna in southern Iberia [20].

In conclusion, the identification of up to twelve areas of endemism, assembled in four main consensus areas located throughout the Iberian Peninsula shows the great importance of this territory for biodiversity conservation. Despite the ecological differences with the taxa traditionally studied and the methodologies used, our biogeographic regionalization based on ants is congruent with other proposals and allows the detection of areas at the biogeographical province level. Areas of endemism are priority areas for conservation not only because of their associated biodiversity but also because of the idea of conserving genetic lineages and environmental characteristics that are unique to the planet, which have led to the settling of rare, endemic, or restricted distribution species. This is particularly relevant for the Southern Mediterranean IP biogeographic area, which contains a large number of endemic species. Although ants have not been commonly considered as a working group in biogeography, their potential for conservation planning is evident.

Ants are a group that can be used as a proxy for other taxa with similar terrestrial ecologies and environmental constraints, and areas of endemism can help to reinforce land management plans for conservation. In addition, ants have allowed us to establish a regionalization of the Iberian Peninsula based on systematic methods, which can surely be extended to other territories of the Mediterranean or the Western Palearctic to further unravel the evolutionary and biogeographical processes that have shaped the biodiversity present today.

Data Availability

The georeferenced data and presence-absence matrices for PAE used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

Supplementary Materials

Table S1: list of Iberian native species used for the EA (endemicity analysis) and PAE (parsimony analysis of endemicity). The identification number and the number of occurrences (georeferenced distribution records) for each species are included. Table S2: list of species from each consensus area and value of each EA (endemicity analysis) diagnostic species (∗) and IP endemic species that contributes to the endemicity score of the AE (area of endemism) and corresponding AE. EA diagnostic species may present marginal distribution in IP or have a predominant distribution outside IP. (*Supplementary Materials*)

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