Ecological revision of *Pachymerium ferrugineum* (C.L. Koch, 1835) (Chilopoda: Geophilomorpha: Geophilidae) in the Iberian Peninsula and the Balearic Islands

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Abstract

New population data for *Pachymerium ferrugineum* (C. L. Koch, 1847) from the Iberian Peninsula and the Balearic Islands are provided. Inland specimens had 49-55 leg-bearing segments (LBS) and 17-45 mm length while coastal specimens had 51-59 LBS and 28-60 mm length. Due to overlapping values in the number of leg-bearing segments, climatic and edaphic variables from the Ibero-Balearic region were studied. None of the tested ecological variables seemed to explain the differences in the number of leg-bearing segments or body length between inland and coastal populations. Nevertheless, the presence of coastal forms and 55 LBS inland specimens may be explained by the continental indicators BIO2 (mean of diurnal range) and BIO7 (temperature annual range). Additionally, specimens with the highest number of leg-bearing segments and the longest bodies were only detected in coastal hypersaline environments. Morphological and ecological differences between inland and coastal populations of the Iberian Peninsula and the Balearic Islands are discussed in depth.

Key words. Body length, coastal, cryptic species, forms, inland, latitudinal cline, leg bearing segments.

Introduction

Pachymerium C. L. Koch, 1847 is a diverse genus of chilopod myriapods belonging to the order Geophilomorpha and the family Geophilidae. It includes 22 valid species widely distributed throughout the world, with the exception of Australia and the Antarctic (Bonato *et al*., 2016). Nevertheless, most of them are only known from their type localities. *Pachymerium ferrugineum* (C.L. Koch, 1835) is one of the better-known species in this genus. This Palearctic species has been reported from European, Asian and North African regions and introduced to America (Nefediev *et al*., 2017; Barber *et al*., 2020; Cassar & Zapparoli, 2021; Dyachkov & Nedoev, 2021). Currently, *P. ferrugineum* is one of the most widely distributed *Pachymerium* species due to its dispersal by anthropochory, ecological tolerance and capability to colonise new environments (Bonato *et al*., 2005; Volkova, 2016; Nefediev *et al.*, 2017; Barber *et al.*, 2020). In the Iberian Peninsula, *P. ferrugineum* inhabits shrublands, grasslands, agricultural fields and forests (Carballo *et al.*, 1986; Carballo & Daza, 1991; Daza *et al.*, 1991; García-Ruiz & Santibáñez, 1995; García-Ruiz, 1999, 2003, 2009; Sammler *et al.*, 2006; Cabanillas, 2021). It is a frequent species in humid environments such as riparian forests and lagoons (Serra, 1978; Carballo *et al.*, 1986; Daza *et al.*, 1991; García-Ruiz & Santíbañez, 1995; García-Ruiz & Serra, 2003; Cabanillas, 2021). *P. ferrugineum* is also considered a synanthropic species, with records in urban parks and city gardens (García-Ruiz, 2009). Additionally, some authors reported the species in peninsular and insular coastal areas of Spain, for example in beaches and salt marshes (Negrea & Matic, 1973; Carballo & Daza, 1991; Sammler *et al.,* 2006). *P. ferrugineum* is one of the few centipede species able to tolerate sea water submersion (Schubart, 1929; Suomalainen, 1939; Lewis, 1981; Barber, 2011; Barber *et al.*, 2020). This suggests the existence of additional ways of dispersal in *P. ferrugineum* by floating trunks or plant remains (Barber *et al.,* 2020).

In the early 20th century, *Pachymerium ferrugineum insulanum* Verhoeff, 1902 was described from Bosnia-Herzegovina, Croatia, several Greek islands, Tunisia and Turkey. This subspecies is characterised by living in coastal environments and having higher numbers of teeth and fimbriae in the medial and lateral sides of the labrum, 49-61 leg-bearing segments (LBS) and a large body with yellowish tonalities. These criteria were followed by many authors in subsequent publications (Verhoeff, 1902, 1925, 1951; Manfredi, 1953; Kanellis, 1959; Kaczmarek, 1969; Negrea & Matic 1973; Simaiakis & Mylonas, 2003; Simaiakis *et al*., 2004; Sammler *et al*., 2006) but others questioned the validity of *P. f. insulanum* and listed it as a minor synonym of *P. ferrugineum* (Matic, 1972; Zapparoli, 1991, 1994, 2002; Vadell & Pons, 2009). *P. f. insulanum* was officially synonymized by Bonato & Minelli (2014) due to difficulties in detecting not-overlapping diagnostic characters between both subspecies. Other authors firmly support the hypothesis of the occurrence of two distinct forms in *P. ferrugineum* due to non-overlapping values of leg-bearing segments between inland and coastal specimens. In Crete, Simaiakis & Mylonas (2003) and Simaiakis *et al*. (2004) reported a short form with 41-47 LBS from inland environments and a long form with 55-59 LBS from coastal habitats and small satellite islands. An inland short form with 41-49 LBS and a coastal large form with 51-57 LBS are known from France (Blower, 1987; Iorio & Tiberghien, 2007; Barber *et al.*, 2020). Recently, a 57 LBS specimen was reported in a coastal environment of the Channel Islands (Barber *et al.*, 2020), a 57 LBS specimen was detected from a beach of Comino island and two 49 LBS specimens were reported from inland forests in Malta (Cassar & Zapparoli, 2021). Nevertheless, a short form with 41-45 LBS is known from coastal sites in mainland Britain (Lewis, 1960; Barber, 2009). Barber *et al.* (2020) also reported differences in the body length between the short and long form: typically 30-35 mm for the short form and 60 mm for the long form. Summarily, short forms usually occur in inland habitats and have 41-49 LBS, while long forms are frequently found in coastal environments and have 51-59 LBS (Barber *et al.*, 2020).

The Iberian Peninsula represents a suitable territory for the evaluation of both forms due to its location in the extreme south-west of Europe and the existence of both inland and coastal environments. Nevertheless, previous records of *P. ferrugineum* in the Iberian Peninsula and the Balearic Islands are ambiguous or do not provide reliable data about the number of leg-bearing segments. The main aims of this work are to compile previous records of *P. ferrugineum* and to provide new population data from inland and coastal environments of the Iberian Peninsula and the Balearic Islands. Additionally, some ecological variables that might determine the number of leg-bearing segments and body length between the Ibero-Balearic populations are assessed.

Material & Methods

Bibliographical revision

Published records and supplementary data of *P. ferrugineum* previously reported from the Iberian Peninsula, Balearic and Canary Islands were compiled (see Appendix 1). Localities, habitats and the number of leg pairs (when provided) were used to revise the ecology of the species.

Material examined

Surveys were undertaken in coastal and inland environments of the Iberian Peninsula from 2017 to 2021. Inland specimens were searched for underneath rocks, debris, leaf-litter or within soil in grasslands, forests and synanthropic environments. Coastal specimens were searched for beneath stones, pebbles and stranded logs in the supralittoral zone of sand beaches, coves and cliffs. Specimens were hand collected, killed by freezing and then fixed in ethanol 70%. Additionally, some colleagues kindly provided specimens for this study: Francisco Rodríguez-Luque (Almería), Joan Díaz-Calafat and Sebastià Jaume-Ramis (Mallorca) and Daniel Rojas (Cádiz). A binocular stereo microscope model AmScope SM-1TSZZ-144S-10M-3PL (3.5-180x) was used to determine the identity of specimens. Works on the morphology and taxonomy of *P. ferrugineum* and *P. f. insulanum* were consulted (Verhoeff, 1902, 1924; Bonato & Minelli, 2014; Bonato *et al*., 2014; Iorio & Labroche, 2015; Barber *et al*., 2020). Specimens are kept in the first author's collection. Additionally, photographs archived on the image database 'Biodiversidad Virtual' (https://www.biodiversidadvirtual.org/) were thoroughly reviewed. A useful character to distinguish *P. ferrugineum* from other Iberian Geophilidae is the presence of numerous small coxal pores on the ultimate coxae, although most photographs were not adequate for seeing this feature. The following morphological criteria were used to distinguish *P. ferrugineum* from other Iberian Geophilidae: antennae length (less than 4 times as long as breadth of head), head colour and shape (brownish red, almost rectangular and up to 1.4 times as long as broad), forcipules surpassing the cephalic plate, forcipular tergite shape (sides strongly convergent anteriorly), ultimate leg pair length (less than twice the length of the penultimate leg pair) and number of leg-bearing segments (41-59 LBS). Only specimens clearly showing this set of characteristics were considered for ecological tests.

Ecological revision

In order to detect patterns of distribution of the two forms of *P. ferrugineum* in the Ibero-Balearic region, ecological maps with climatic and edaphic variables were consulted. The interval of maximum and minimum values was set according to the climatic and edaphic characteristics of that region. All records were considered to assess the general ecology of the species. Only records with precise coordinates and number of leg-bearing segments per specimen were used to detect patterns of distribution in inland and coastal forms. The following variables were tested: mean diurnal range (BIO2), maximum temperature of warmest month (BIO5), minimum temperature of coldest month (BIO6), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), mean temperature of warmest quarter (BIO10), mean temperature of coldest quarter (BIO11), annual precipitation (BIO12), precipitation of wettest quarter (BIO16), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18), precipitation of coldest quarter (BIO19), organic carbon content in the top soil (soil_oc), pH in the top soil (soil_ph), presence of brackish or salty soils (soil_salt), silt content in the top soil (soil_silt) and annual mean soil moisture index (BIO28). Maps were generated with ArcGis Desktop 10.8.1. Data on climatic and edaphic variables were obtained from WorldClim 2.1 for the 1970-2000 period (http://www.worldclim.org, see Fick & Hijmans, 2017) and the European Soil Data Center (https://esdac.jrc.ec.europa.eu/) at 30-second resolution (~1x1 km at the equator).

Abbreviations: *leg*. = *legit* (collector), LBS = leg-bearing segments, *phot*. = *photographavit* (author of the photograph), spec. = specimen (s). Authors: APF - Alejandro Pérez Ferrer, AR - Antonio Robledo, CE - Constantino Escuer, DG - Daniel García, FAE - Francisco Arnau Esbrí, FM - Fani Martínez, FRL - Francisco Rodríguez-Luque, JDC - Joan Díaz-Calafat, JM - Josefina Miralles, LF - Luis Fernández, MT - Mikel Tapia, MY - Miguel Yuste, SJR - Sebastià Jaume-Ramis, TR - Thomas Rickfelder. * = previously unreported.

Results

Pachymerium ferrugineum (C.L. Koch, 1835)

Material examined: Spain - Alicante*: Finestrat, Puig Campana - 1 spec. (DG *phot*.), 20/04/2013, in a shrubland (30S 742913 4275056). **Almería*:** El Ejido, Almerimar, Punta Entinas-Sabinar - 1♀ with 59 LBS and 45 mm, 1♀ with 59 LBS and 47 mm (FRL *leg*.), 14/12/2017; 1 spec. with 57 LBS (FRL *phot*.), 15/12/2017; 1♀ with 59 LBS and 33 mm (FRL *leg*.), 27/02/2019; 1♂ with 57 LBS and 30 mm

(FRL *leg*.), 22/03/2019; 1♀ with 57 LBS and 31 mm (FRL *leg*.), 18/07/2020, under rocks on a sand beach (30S 526926 4059879). El Ejido, Los Artos - 1♂ with 49 LBS and 30 mm, 1♂ with 51 LBS and 32 mm, 1♂ with 51 LBS and 34 mm (FRL *leg*.), 08/02/2019; 1 spec. with 49 LP (FRL *phot*.), 09/02/2020, under rocks near greenhouses (30S 518037 4067759). Roquetas de Mar, Aguadulce, Puerto Deportivo - 1♂ with 53 LBS and 28 mm, 1♀ with 59 LBS and 60 mm (FRL *leg*.), 03/12/2020, under a rock in a littoral plateau (30S 539776 4074774). Vícar - 1 spec. with 55 LBS (FRL *phot*.), 12/01/2017, under a rock in an abandoned crop field (30S 529519 4074423); 1 spec. with 53 LBS (FRL *phot*.), 04/02/2019, under a rock in a shrubland (30S 534399 4074615). **Asturias***: Villaviciosa, Selorio, Playa de Misiego - 1 spec. with 53 LBS, 24/09/2020, under the bark of a stranded log on dunes with rock sea-lavender (*Limonium binervosum* (G.E.SM.) C.E. Salmon) (30T 307679 4821644). Gozón, Llodero, Playa de Xagó - 1♀ with 55 LBS and 47 mm, 1♀ with 57 LBS and 41 mm, 1♀ with 57 LBS and 47 mm, 1♀ with 57 LBS and 55 mm, 10/10/2020, under stranded logs on a sand beach with sand couch-grass (*Elymus farctus* (Viv.) Runemark Ex Melderis) (30T 264632 4832194). **Balearic Islands:** Mallorca, Inca - 1♀ with 51 LBS and 45 mm (SJR *leg*.), 20/12/2021, under a garden tile near a vegetable growing patch (31S 492806 4396833). Mallorca, Marratxí - 1♀ with 51 LBS and 41 mm, 1♀ with 53 LBS and 43 mm (JDC & SJR *leg*.), 22/12/2021, under a rock in an urban Aleppo pine forest (*Pinus halepensis* Mill.) (31S 477758 4385688). **Barcelona*:** Manresa, Canyet - 1 spec. (APF *phot*.), 25/02/2021, in crop fields (31T 402545 4623396). Terrassa - 1 spec. (JM *phot*.), 31/03/2013, under a stone in a private garden (31T 417358 4601756). **Cádiz:** Puerto Real, Salina de San Pedro y San José-la Covacha - 1♀ with 51 LBS and 35 mm (DR *leg*.), 15/11/2020, under a rock near an abandoned salt pan (29S 750185 4045797). **Cantabria*:** Piélagos, Dunas de Liencres - 1 spec. (TR *phot*.), 18/02/2011, in maritime dunes (30T 421647 4810613). **Castellón*:** Alcossebre, Platja de Ribamar - 1 spec. with 55 LBS, 09/05/2021, under a rock on a pebble beach (31T 271177 4460862). Peníscola, Serra d'Irta - 2 spec. with 57 LBS (FAE *phot*.), 29/11/2021, in a sand and pebble beach (31T 272766 4462137); 1 spec. with 53 LBS (FAE *phot*.), 04/12/2021 and 1 spec. with 57 LBS (FAE *phot*.), 29/12/2021, in a sand and pebble beach (31T 272766 4462137). Torreblanca, Torrenostra, Turbera del Prat de Cabanes - 1 spec. with 53 LBS, 11/05/2021, under a rock near a bog shore (31T 262637 4453132). **Madrid:** Alcalá de Henares, Parque de los Cerros de Alcalá - 1♂ with 53 LBS and 26 mm, 18/11/2019, under an ornamental rock in a suburban park near a river (30T 455565 4463974). Madrid, Centro - 1 spec. with 55 LBS (MY *phot*.), 26/03/2011, in an urban garden (30T 440583 4474243). Madrid, Ciudad Lineal, Calle Idioma Esperanto - 1♀ with 49 LBS and 45 mm, 01/11/2018, under debris in urban grassland (30T 446813 4474443). Madrid, Ciudad Lineal, Parque El Sitio - 1 juvenile with 51 LBS and 17 mm, 23/03/2019, in soil in a holm-oak plantation (*Quercus ilex* L.) of an urban park (30T 446612 4474276); 1♀ with 51 LBS and 32 mm, 1♀ with 51 LBS and 43 mm, 29/03/2019, under a stone in an urban park with holm-oak and mimosa (*Acacia dealbata* Link) (30T 446520 4474182); 1♀ with 53 LBS and 32 mm, 29/03/2019, under debris in an urban grassland with Siberian elm (*Ulmus pumila* L.) (30T 446414 4474186). Rivas-Vaciamadrid, Soto de las Juntas - 1♀ with 55 LBS and 27 mm, 03/12/2016, under debris in a grassland between the rivers Manzanares and Jarama (30T 455565 4463974). San Fernando de Henares - 1 spec. with 51 LBS, 07/01/2017, under decaying wood in a riparian forest (30T 456729 4473760). Valdeolmos-Alalpardo, Alalpardo - 1♀ with 53 LBS and 45 mm, 24/10/2019, under a stone in an abandoned crop field near a stream (30T 460564 4497951). Valdeolmos-Alalpardo, Valdeolmos- 1♀ with 53 LBS and 29 mm, 08/01/2020, under a stone in an abandoned crop field (30T 461658 4498978). **Murcia*:** Cartagena, Cabo de Palos, Playa de la Calafría - 1♀ with 59 LBS and 34 mm, 06/12/2021, under a rock near the supralittoral line of a pebble and sand beach (30S 703844 4167633). Murcia, Cartagena, Rambla de Cobaticas - 1 spec. with 57 LBS (LF *phot*.), 23/12/2012, in a dry riverbed near the coast (30S 698552 4163942). Murcia, Cresta del Gallo - 1♀ with 53 LBS and 42 mm, 07/11/2021, under a rock in an Aleppo pine forest (30S 667682 4201357). Murcia, El Caracolero, Sierra de los Villares - 1 spec. with 51 LBS (AR *phot*.), 26/12/2012, in a shrubland (30S 666323 4194362). **Navarra:** Villafranca - 1 spec. with 51 LBS (MT *phot*.), 20/02/2010, underneath the bark of a poplar tree in an urban garden (30T 603318 4681425). **Sevilla:** Sevilla, Universidad Pablo de Olavide: 1♂ with 51 LBS and 30 mm, 26/02/2021, inside a decayed olive trunk (*Olea europaea* L.) in a grassland (30S 239429 4138444). **Valencia*:** Canals - 1 spec. with 51 LBS (FM *phot*.), 18/02/2011, in agricultural fields (30S 710115 4313860). **Zaragoza:** Perdiguera - 1 spec. (CE *phot*.), 09/10/2008, under a rock in crop fields (30T 696899 4625138).

Distribution and habitat preferences

P. ferrugineum was previously recorded in the Portuguese districts of Coimbra and Porto (Machado, 1952) and the Spanish provinces of Navarra (Salinas, 1990), Huesca and Zaragoza in Aragón (Serra, 1978), Ciudad Real, Cuenca and Toledo in Castilla-La Mancha (Brolemann, 1920; Attems, 1927; García-Ruiz & Santibáñez, 1995; García-Ruiz, 1999, 2003; García-Ruiz & Serra, 2003), Madrid (García-Ruiz, 2009; Cabanillas, 2021) and Cádiz, Granada, Huelva and Sevilla in Andalucía (Attems, 1927, 1952; Carballo *et al.*, 1986; Carballo & Daza, 1991; Daza *et al*., 1991). Additionally, *P. ferrugineum* was reported from insular Spain in Ibiza and Mallorca in the Balearic Islands (Verhoeff, 1924; Negrea & Matic, 1973; Sammler *et al*., 2006; Vadell & Pons, 2009) and Lanzarote in the Canary Islands (Machado, 1953). Regarding the material examined in this study, *P. ferrugineum* was found both in temperate and Mediterranean inland areas of the Iberian Peninsula, with records from the Cantabric region and Pre-pyrenean areas to the Meseta Central and the southern Iberian Peninsula. Additionally, *P. ferrugineum* was found in a previously unreported inland locality of the island of Mallorca (Balearic Islands). It is also present in Atlantic and Mediterranean coastal localities, apparently well-established from the northwestern to the southwestern Iberian coasts. An updated map of the known distribution of *P. ferrugineum* in the Iberio-Balearic region is given in Fig. 1. Iberian populations of *P. ferrugineum* can be found in a wide variety of habitats (Fig. 2A-B). Inland records include grasslands, shrublands, holm oak groves, pine forests and agricultural fields. Inland specimens are particularly common near streams, lagoons and synanthropic environments. Coastal records include hypersaline habitats such as pebble and sand beaches, dune systems, salt marshes and salt pans.

Inland and coastal forms

Most authors did not report any morphological or ecological data in their studies from Spain (see Appendix 1) but some of them did provide the number of leg-bearing segments. Iberian specimens with known ranges of leg-bearing segments were reported from the Portuguese districts of Coimbra and Porto (41-57 LBS, habitat unspecified) (Machado, 1952) and the Spanish provinces of Navarra (45-53 LBS, verified inland environments) (Salinas, 1990) and Madrid (49-53 LBS, verified inland environment) (Cabanillas, 2021). Balearic specimens were originally reported as belonging to the subspecies *P. f. insulanum* (53-57 LBS, habitat unspecified) (Verhoeff, 1924). Sammler *et al*. (2006) also reported *P. f. insulanum* specimens ranging from 53-55 LBS, both from inland and coastal habitats. Vadell & Pons (2009) identified as *P. ferrugineum* an inland specimen with 55 LBS from the island of Mallorca. Regarding the material examined in this study, inland specimens had 49-55 LBS, frequently 51 and 53 LBS (males 49-53 LBS, females 49-55 LBS) and body length 17-45 mm. Apparently, populations with 55 LBS specimens are uncommon in inland localities but may occur in certain continental sites. These specimens were found in synanthropic open areas of Madrid (Central Iberian Peninsula), namely in an agricultural field, a garden and a grassland with presence of construction debris. On the other hand, there is an apparent increase in the number of leg-bearing segments and body length in coastal specimens. These had 51-59 LBS, frequently 57 and 53 LBS (males 53 and 57 LBS, females 51 and 55-59 LBS) and body length 28-60 mm. Regarding the body colour (*in vivo*), inland specimens were commonly reddish brown or dark brown while coastal specimens were mostly yellowish-orange and often paler than inland forms (Fig. 2C-D).

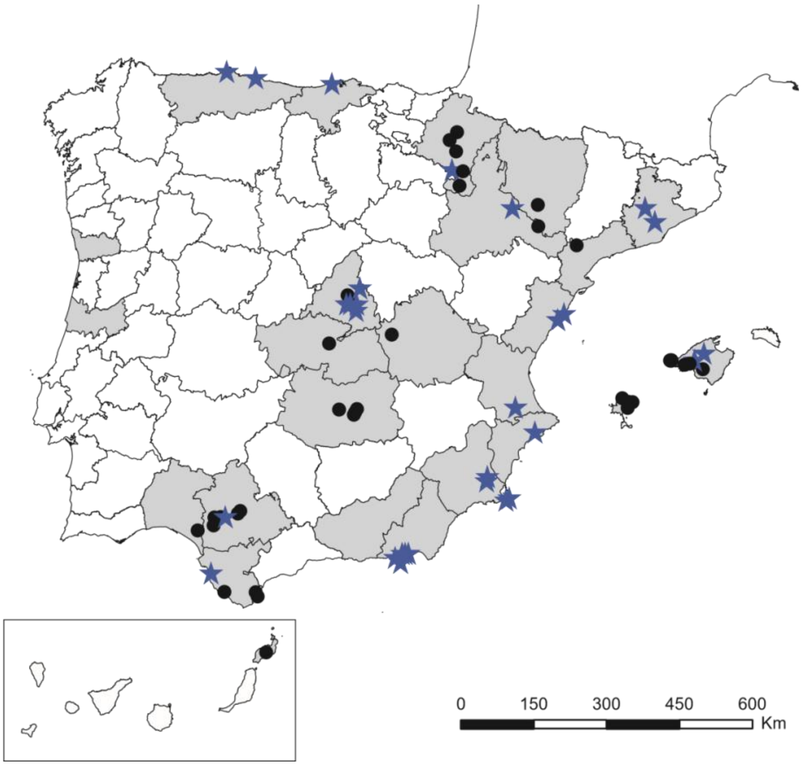

Figure 1: Records of *Pachymerium ferrugineum* in the Iberian Peninsula, Balearic and Canary Islands. (●) Bibliographic records. (★) New records.

Figure 2: Habitats and colour patterns of *Pachymerium ferrugineum*. A) Riparian forest in the central Iberian Peninsula. **B)** Sand and pebble beach in the eastern Iberian Peninsula. **C)** Typical *habitus in vivo* of inland specimens. **D)** Typical *habitus in vivo* of coastal specimens. Authors: A - Bernardo García Medrano, B & D - Francisco Arnau Esbrí, C - David Cabanillas.

Climatic and edaphic variables

The presence of *P. ferrugineum* is apparently not influenced by soil humidity, pH, amount of organic matter or silts. It lives in both coastal and continental sites, under climates with sub-zero temperatures or exceeding 40ºC. It is present in mild areas with high rainfall values (even in the driest season) but also in xeric areas. Regarding the tested climatic variables, the continental indicators BIO2 (mean diurnal range) and BIO7 (temperature annual range) may explain the presence of inland and coastal forms of *P. ferrugineum* in the Iberian Peninsula (Fig. 3A-B). Coastal forms occur in mild areas where annual and day-night temperature oscillation is smaller. This is particularly the case of the 55 LBS specimens from the central Iberian Peninsula and the 55 LBS inland specimen from Mallorca (Vadell & Pons, 2009), since they were found in an area with a mild climate and low values of BIO2 and BIO7 (Fig. 3C-D). The other climatic variables, for example temperatures and rainfall rates, do not seem to condition the number of leg-bearing segments or body length between inland and coastal populations (Appendix 2). Regarding the tested edaphic variables, the amount of organic matter, silt content, soil humidity or pH do not seem to explain the morphological differences between inland and coastal specimens (Appendix 2). Nevertheless, "long forms" of *P. ferrugineum* are only present in soils with high salt concentration (coastal sites), with the exception of the 55 LBS specimens from inland environments. Summarising, none of the tested variables seem to play a decisive role in the number of leg-bearing segments and body length between inland and coastal forms. Maps with edaphic and climatic tests are provided in Appendix 2.

Discussion

The present work represents a breakthrough in the ecological knowledge of *P. ferrugineum* in the Iberio-Balearic region. Although this centipede is a well-known species in Europe (Barber *et al.*, 2020), records from the study area were scarce and did not provide adequate morphological and ecological information. Previous studies on European populations of *P. ferrugineum* (Simaiakis & Mylonas, 2003; Simaiakis *et al.,* 2004; Simaiakis & Mylonas, 2006; Iorio, 2014; Simaiakis *et al.*, 2010; Barber *et al.,* 2020; Iorio *et al.*, 2020) make it possible to discuss in depth some ecological and morphological questions. The existence of two distinct forms of *P. ferrugineum* has been a matter of discussion in the last two decades. *P. f. insulanum* (closely related to the long form) was officially synonymized by Bonato & Minelli (2014) because consistent diagnostic characters could not be found to distinguish *P. f. insulanum* from the nominotypical subspecies. Nevertheless, several authors have reported non-overlapping ranges in the number of leg-bearing segments and differences in the maximum body length between inland and coastal populations (Barber *et al.*, 2020), with the exception of the British specimens (Lewis, 1960; Barber, 2009). Data from the Iberian Peninsula deserve a careful interpretation since they could result in a confirmation bias for both theses.

On the one hand, results from the Iberian Peninsula do not show two distinct forms of *P. ferrugineum* due to overlapping values in the number of leg-bearing segments. The previous European ranges were set between 41-49 LBS for the short form and 51-59 LBS for the long form (Barber *et al.*, 2020). Inland specimens from the Ibero-Balearic region have 45-55 LBS, frequently 51-53 LBS but reaching 55 LBS in certain localities of the central Iberian Peninsula and the Balearic Islands. The Iberian "short form" is longer than expected and frequently overlaps with the minimum number of leg-bearing segments of the long form (51-59 LBS), both in males and females. Additionally, none of the tested climatic and edaphic variables seemed to explain the distribution of inland and coastal forms in the Ibero-Balearic area (Appendix 2). Nevertheless, the continental indicators suggest a possible effect on the distribution of both forms (Fig. 3). *P. ferrugineum* populations with a higher number of leg-bearing segments were mostly found in both inland and coastal areas where annual and day-night temperature oscillation is smaller and almost constant during the year. European populations with the highest number of leg-

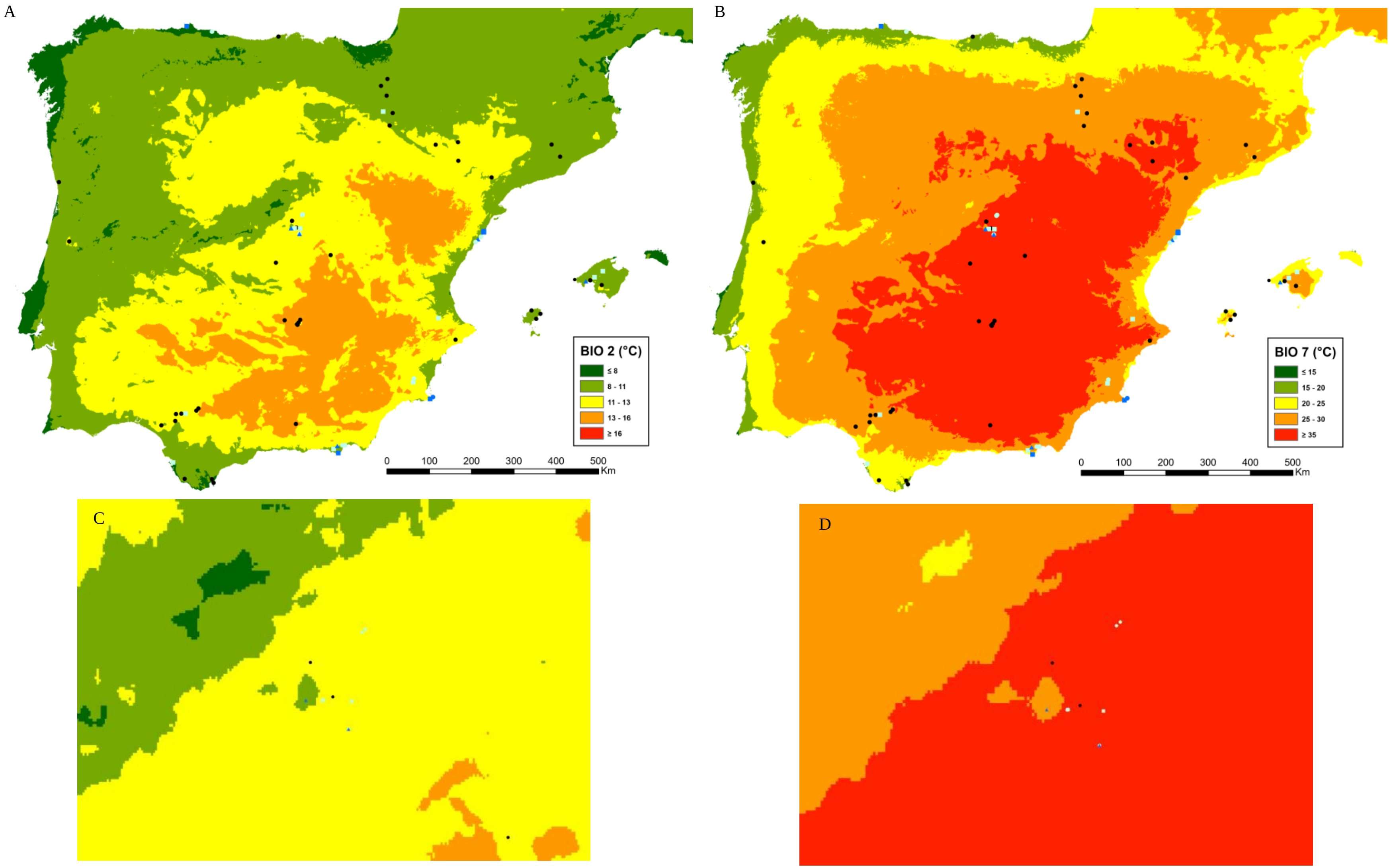

Figure 3: Climatic map with continental indicators in the Iberio-Balearic area. A) Mean diurnal range (BIO2). **B)** Temperature annual range (BIO7). **C)** Highlighted central area for the indicator BIO2. **D)** Highlighted central area for the indicator BIO7. Number of leg-bearing segments: 49 (■), 51 (▲), 53 (●), 55 (■), 57 (▲), 59 (●), unknown leg-bearing segments per specimen or imprecise coordinates (●)

bearing segments have been reported from coastal environments where temperatures are softened influence of the nearby sea (Simaiakis & Mylonas, 2003; Simaiakis *et al*., 2004; Barber *et al*., 2020; Iorio *et al*., 2020, Cassar & Zapparoli, 2021). This has previously been suggested by some authors to explain the pattern of distribution of certain species in the Iberian Peninsula (Cabanillas *et al.*, 2020). Edaphic tests need to be carefully interpreted. The scale used (1 km^2 resolution) could have interfered with the expression of patterns of distribution since microenvironmental edaphic conditions are known to condition the presence of certain centipede species (Fründ, 1991; Dunxiao *et al*., 1999). Maps with higher resolution, for example at 1 m^2 scale, could provide valuable data to better interpret the influence of soil variables. Salinity indicator by itself seems not to be conditioning the number of leg-bearing segments or body length in *P. ferrugineum* populations. Nevertheless, specimens with a higher number of leg-bearing segments were only found in hypersaline soils of coastal areas. The possibility exists that increasing the number of leg-bearing segments may be a physiological response to exposure to hypersaline conditions. Other processes could be taking place since specimens with 55 LBS were also detected in non-saline inland environments of the central Iberian Peninsula and the Balearic Islands.

On the other hand, several facts seem to support the hypothesis of the existence of two forms of *P. ferrugineum* in the Ibero-Balearic area. Geographical differences in the number of leg-bearing segments are well-known to occur in *P. ferrugineum* (Meinert, 1870; Attems, 1902, 1929; Brölemann, 1930; Barber, 2009; Simaiakis *et al.*, 2010). According to Eason (1979), Geophilomorpha centipedes from colder regions usually have lower number of leg-bearing segments than those from warmer regions. Some authors have suggested that a temperature latitudinal cline could condition the number of leg-bearing segments in European *P. ferrugineum* populations (Simaiakis *et al.*, 2010). Apparently, there is also a gradient in the number of leg-bearing segments from northwestern to southwestern inland populations. French inland specimens have 43-49 LBS (Iorio & Tiberghien, 2007; Barber *et al*., 2020), populations from inland environments of the Ibero-Balearic region have 45-55 LBS (Salinas, 1990; Vadell & Pons, 2009; Cabanillas, 2021; present work) and African inland specimens from the High Atlas have 51-53 LBS (Brolemann, 1924). Conversely, coastal forms do not seem to be affected by this temperature latitudinal cline. The number of leg-bearing segments of coastal forms varies from 51-59 LBS at a local scale in every country (Iorio *et al*., 2020; Barber *et al*., 2020; present work), with the exception of the British specimens where the total numbers of specimens recorded are small (A. Barber pers. comm.) This suggests the existence of two ecotypes which, apparently, are not affected by the same ecological factors. The possibility exists that habitat segregation from inland to hypersaline environments could have led to the diversification of *P. ferrugineum* into two lineages ecologically independent. Several Geophilomorpha species are known to be restricted to littoral habitats since they have adapted to live exclusively under saline conditions (Barber, 2011). This may be the case of the coastal form of *P. ferrugineum*. Additionally, differences in body size between inland and coastal populations were also detected in the Iberian Peninsula and the Balearic Islands. Inland specimens had 17-45 mm body length while coastal specimens were usually longer (up to 60 mm), as reported by Barber *et al.* (2020) for the long form from the Channel Islands. Differences in body colour (*in vivo*) could also be detected (Fig. 3C-D). Coastal specimens were yellowish-orange and clearly paler than inland specimens, as reported by Verhoeff (1902) for the subspecies *P. f. insulanum*.

Summarily, this study provides data about an inland form of *P. ferrugineum* with 49-55 LBS (males 49-53 LBS, females 49-55 LBS) and up to 45 mm and a coastal form with 51-59 LBS (males 53 and 57 LBS, females 51 and 55-59 LBS) and up to 60 mm. Morphology and ecology are directly involved in this taxonomical issue and currently there are two theses, both supported by valid arguments. In our opinion, differences in habitat selection are consistent with the potential existence of two ecotypes in *P. ferrugineum*. Further studies should be focused on performing molecular analyses in order to end the debate about the two forms of *P. ferrugineum* in the myriapodological community.

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Appendix 1. Compilation of records of *Pachymerium ferrugineum* in the Ibero-Balearic and the Macaronesian Region.
IB - Islas Baleares (Balearic Islands), IC - Islas Canarias (Canary Islands), LBS - leg-bearing segments, POR - Portugal, pers. comm. - personal communication, SPA - Spain.

Country	District/Province	Municipality	Habitat	Sex	LBS	Body Length	Reference
POR	Coimbra	-	-	-	41-57	-	Machado (1952)
POR	Porto	-	-	-	41-57	-	Machado (1952)
SPA	Alicante	Finestrat	Shrubland	-	-	-	Present work
SPA	Almería	Roquetas de Mar	Littoral plateau	♂	53	28	Present work
SPA	Almería	Roquetas de Mar	Littoral plateau	♀	59	60	Present work
SPA	Almería	El Ejido	Shrubland	♂	49	30	Present work
SPA	Almería	El Ejido	Shrubland	-	49	-	Present work
SPA	Almería	El Ejido	Shrubland	♂	51	32	Present work
SPA	Almería	El Ejido	Shrubland	♂	51	34	Present work
SPA	Almería	El Ejido	Sand beach	♂	57	30	Present work
SPA	Almería	El Ejido	Sand beach	♀	57	31	Present work
SPA	Almería	El Ejido	Sand beach	-	57	-	Present work
SPA	Almería	El Ejido	Sand beach	♀	59	33	Present work
SPA	Almería	El Ejido	Sand beach	♀	59	45	Present work
SPA	Almería	El Ejido	Sand beach	♀	59	47	Present work
SPA	Almería	Vícar	Shrubland	-	53	-	Present work
SPA	Almería	Vícar	Crop field	-	55	-	Present work
SPA	Asturias	Gozón	Sand beach	♀	55	47	Present work
SPA	Asturias	Gozón	Sand beach	♀	57	41	Present work
SPA	Asturias	Gozón	Sand beach	♀	57	47	Present work
SPA	Asturias	Gozón	Sand beach	♀	57	55	Present work
SPA	Asturias	Villaviciosa	Dunar system	-	53	-	Present work
SPA	Barcelona	Manresa	Crop field	-	-	-	Present work
SPA	Barcelona	Terrassa	Garden	-	-	-	Present work
SPA	Cádiz	La Línea de la Concepción	Crop field	-	-	-	Carballo & Daza (1991)
SPA	Cádiz	San Roque	Grassland	-	-	-	Carballo & Daza (1991)

SPA	Cádiz	Vejer de la Frontera	Shrubland	-	-	-	Carballo & Daza (1991)
SPA	Cádiz	Puerto Real	Salt pan	♀	51	35	Present work
SPA	Cantabria	Piélagos	Maritime dunes	-	-	-	Present work
SPA	Castellón	Alcossebre	Pebble beach	-	55	-	Present work
SPA	Castellón	Peníscola	Sand and pebble beach	-	53	-	Present work
SPA	Castellón	Peníscola	Sand and pebble beach	-	57	-	Present work
SPA	Castellón	Peníscola	Sand and pebble beach	-	57	-	Present work
SPA	Castellón	Peníscola	Sand and pebble beach	-	57	-	Present work
SPA	Castellón	Torreblanca	Bog shore	-	53	-	Present work
SPA	Ciudad Real	"Calatrava"	-	-	-	-	Attems (1927)
SPA	Ciudad Real	Pozuelo de Calatrava	-	-	-	-	Brolemann (1920)
SPA	Ciudad Real	Moral de Calatrava	Kermes oak grove	-	-	-	García-Ruiz (1999)
SPA	Ciudad Real	Moral de Calatrava	Shrubland	-	-	-	García-Ruiz (2003)
SPA	Ciudad Real	Moral de Calatrava	Pine forest	-	-	-	García-Ruiz & Santibáñez (1995)
SPA	Ciudad Real	Moral de Calatrava	Riparian forest	-	-	-	García-Ruiz & Santibáñez (1995)
SPA	Ciudad Real	Moral de Calatrava	Shrubland	-	-	-	García-Ruiz & Santibáñez (1995)
SPA	Cuenca	Uclés	-	-	-	-	Attems (1927)
SPA	Granada	-	-	-	-	-	Attems (1927)
SPA	Huelva	Hinojos	Salt marsh	-	-	-	Carballo & Daza (1991)
SPA	Huesca	Sariñena	Saline lagoon	♂+♀	49-51	-	Serra (1978), pers. comm.
SPA	IB - Ibiza	Ibiza	Coastal plateau	-	53-55 (?)	-	Sammler *et al*. (2006)
SPA	IB - Ibiza	Ibiza	Maquis shrubland	-	53-55 (?)	-	Sammler *et al*. (2006)
SPA	IB - Ibiza	Ibiza	Maquis shrubland	-	53-55 (?)	-	Sammler *et al*. (2006)
SPA	IB - Ibiza	Ibiza	Pine forest	-	53-55 (?)	-	Sammler *et al*. (2006)
SPA	IB - Ibiza	Ibiza	-	-	-	-	Verhoeff (1924)
SPA	IB - Mallorca	Calvià	Ravine	-	55	-	Vadell & Pons (2009)
SPA	IB - Mallorca	Inca	Garden	♀	51	45	Present work
SPA	IB - Mallorca	Llucmajor	Coastal area		-	-	Negrea & Matic (1973)
SPA	IB - Mallorca	Marratxí	Pine forest	♀	51	41	Present work
SPA	IB - Mallorca	Marratxí	Pine forest	♀	53	43	Present work
SPA	IB - Mallorca	Palma	-	-	53-57	-	Verhoeff (1924)

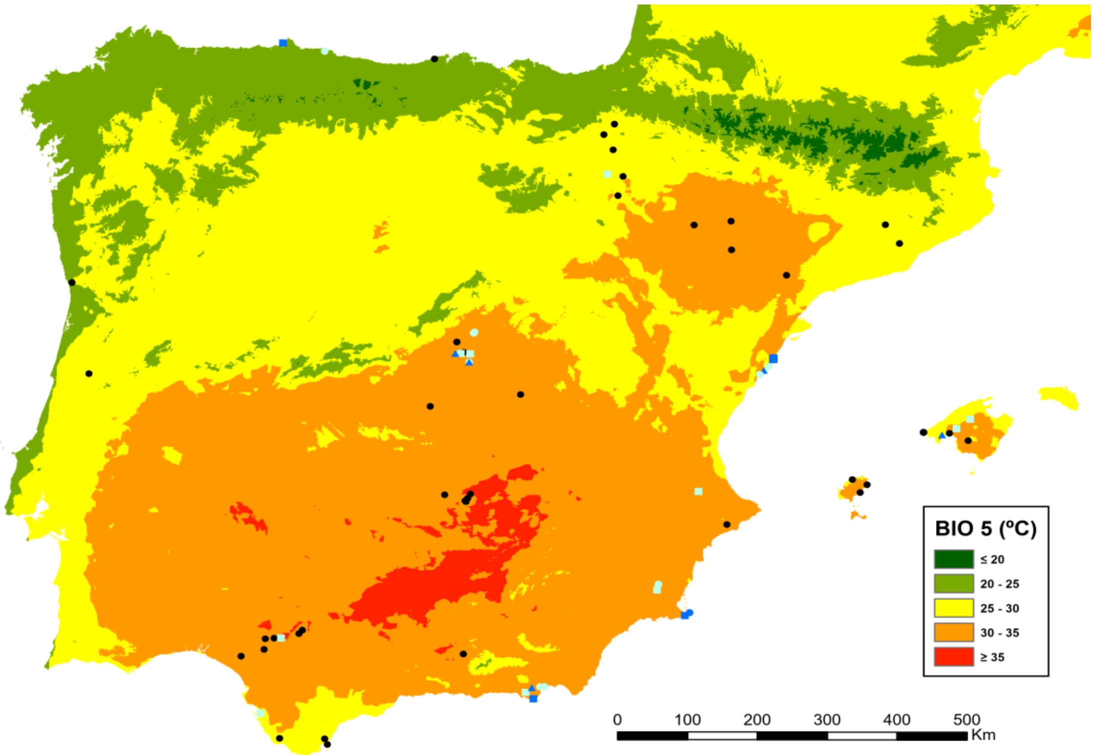
SPA	IB - Sa Dragonera	Andratx	Coastal cavity	-	-	-	Negrea & Matic (1973)
SPA	IC - Lanzarote	-	-	-	-	-	Machado (1953)
SPA	Madrid	Alcalá de Henares	Urban park at riverside	♂	53	26	Present work
SPA	Madrid	Madrid	Urban grassland	♀	49	45	Present work
SPA	Madrid	Madrid	Urban park	-	51	17	Present work
SPA	Madrid	Madrid	Urban park	♀	51	32	Present work
SPA	Madrid	Madrid	Urban park	♀	51	43	Present work
SPA	Madrid	Madrid	Urban park	♀	53	32	Present work
SPA	Madrid	Madrid	Urban garden	-	55	-	Present work
SPA	Madrid	Madrid	Holm oak grove	-	-	-	García-Ruiz (1999)
SPA	Madrid	Madrid	Pine forest	-	-	-	García-Ruiz (1999)
SPA	Madrid	Madrid	Grassland	-	49-53	-	Cabanillas (2021)
SPA	Madrid	Rivas-Vaciamadrid	Grassland	♀	55	27	Present work
SPA	Madrid	San Fernando de Henares	Riparian forest		51	-	Present work
SPA	Madrid	Valdeolmos-Alalpardo	Crop field	♀	53	29	Present work
SPA	Madrid	Valdeolmos-Alalpardo	Crop field	♀	53	45	Present work
SPA	Madrid	-	Built-up areas	-	-	-	García-Ruiz (2009)
SPA	Madrid	-	Grassland	-	-	-	García-Ruiz (2009)
SPA	Madrid	-	Suburban pine forest	-	-	-	García-Ruiz (2009)
SPA	Madrid	-	Urban park	-	-	-	García-Ruiz (2009)
SPA	Murcia	Cartagena	Dry riverbed near coast	-	57	-	Present work
SPA	Murcia	Cartagena	Pebble and sand beach	♀	59	34	Present work
SPA	Murcia	Murcia	Shrubland		51	-	Present work
SPA	Murcia	Murcia	Pine forest	♀	53	42	Present work
SPA	Navarra	Cendea de Galar	-	-	45-53	-	Salinas (1990)
SPA	Navarra	Obanos	-	-	45-53	-	Salinas (1990)
SPA	Navarra	Tafalla	-	-	45-53	-	Salinas (1990)
SPA	Navarra	Tudela	-	-	45-53	-	Salinas (1990)
SPA	Navarra	Valtierra	-	-	45-53	-	Salinas (1990)
SPA	Navarra	Villafranca	Urban garden	-	51	-	Present work
SPA	Sevilla	Bollullos de la Mitación	Stream	-	-	-	Daza *et al.* (1991)

SPA	Sevilla	Carmona	Olive grove	-	-	-	Carballo *et al*. (1986)
SPA	Sevilla	Carmona	Olive grove	-	-	-	Daza *et al*. (1991)
SPA	Sevilla	El Viso del Alcor	Grassland	-	-	-	Daza *et al*. (1991)
SPA	Sevilla	La Puebla del Río	Rice paddy	-	-	-	Carballo *et al*. (1986)
SPA	Sevilla	San Juan de Aznalfarache	Rice paddy	-	-	-	Daza *et al*. (1991)
SPA	Sevilla	Sevilla	Urban grassland	♂	51	30	Present work
SPA	Sevilla	-	-	-	-	-	Attems (1952)
SPA	Tarragona	Flix	-	-	-	-	Attems (1927)
SPA	Toledo	Toledo	Riparian forest	-	-	-	García-Ruiz & Serra (2003)
SPA	Valencia	Canals	Crop field	-	51	-	Present work
SPA	Zaragoza	Bujaraloz	Saline lagoon	-	47-49	-	Serra (1978), pers. comm.
SPA	Zaragoza	Perdiguera	Crop field	-	-	-	Present work

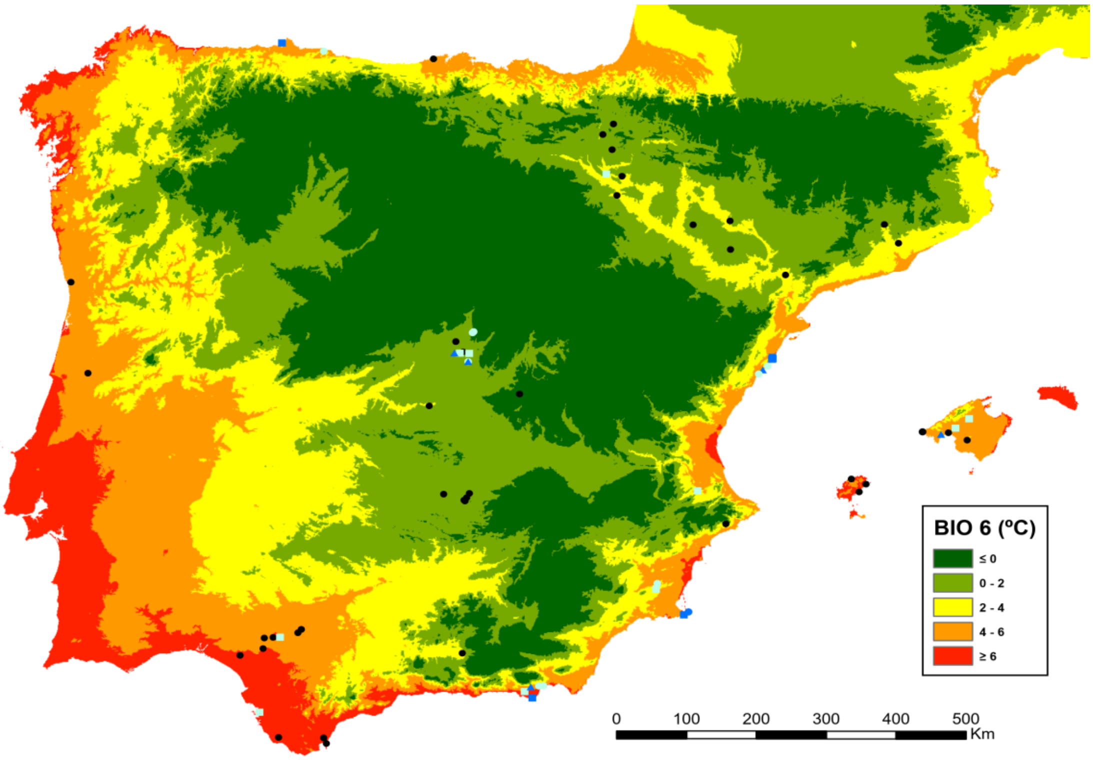
Appendix 2: Ibero-Balearic maps with climatic and edaphic indicators.

Number of leg-bearing segments: 49 (■), 51 (▲), 53 (●), 55 (■), 57 (▲), 59 (●), unknown leg-bearing segments per specimen or imprecise coordinates (●).

A

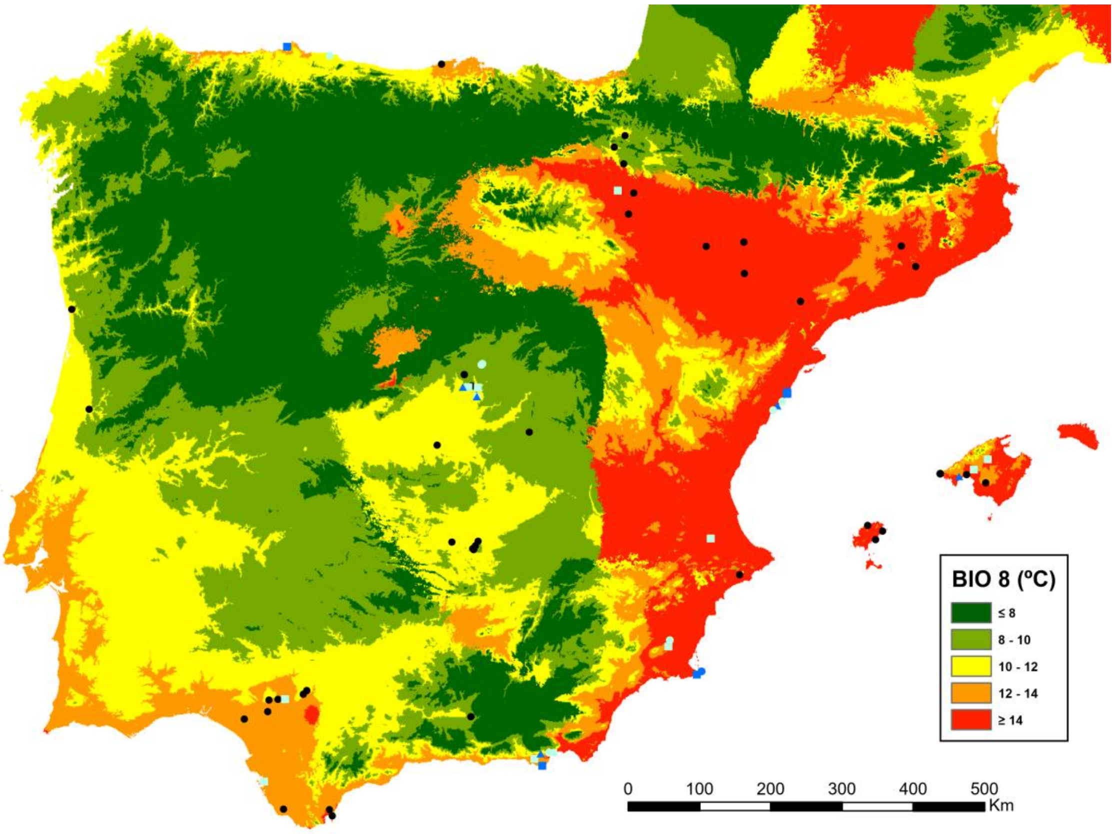


B

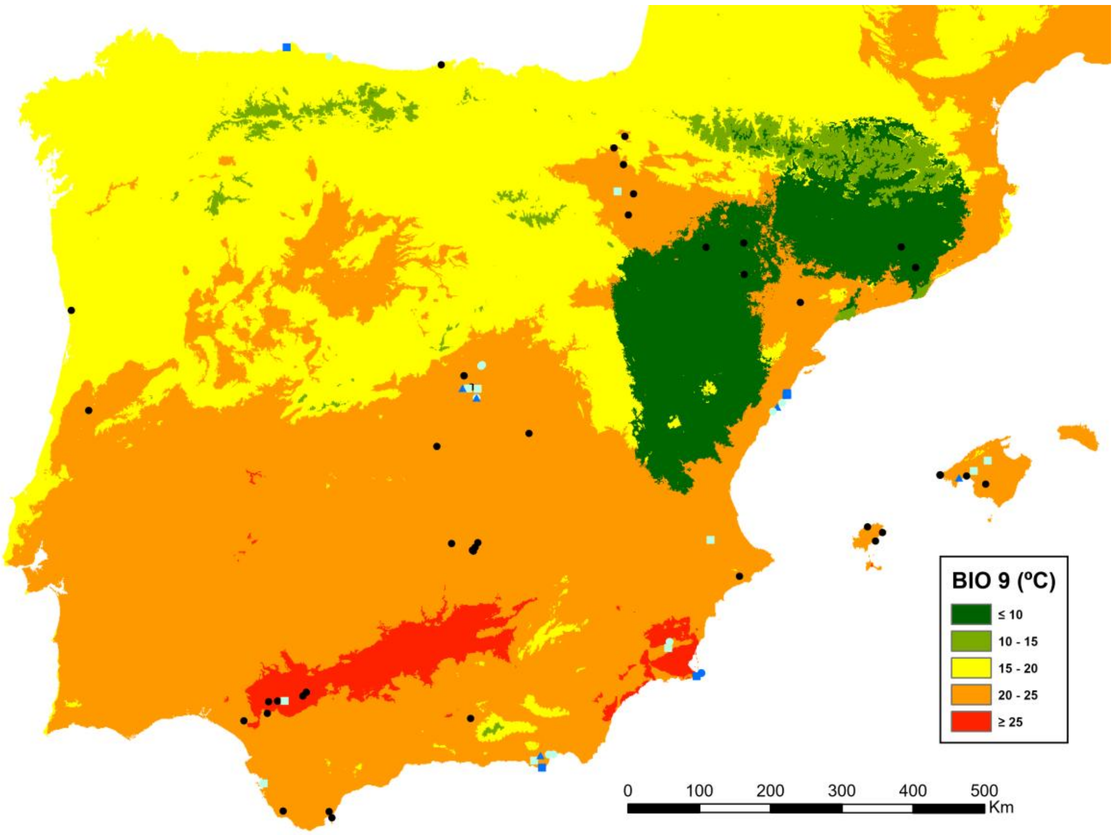


2.1: A) Maximum temperature (º C) of warmest month (BIO5). B) Minimum temperature (º C) of coldest month (BIO6).

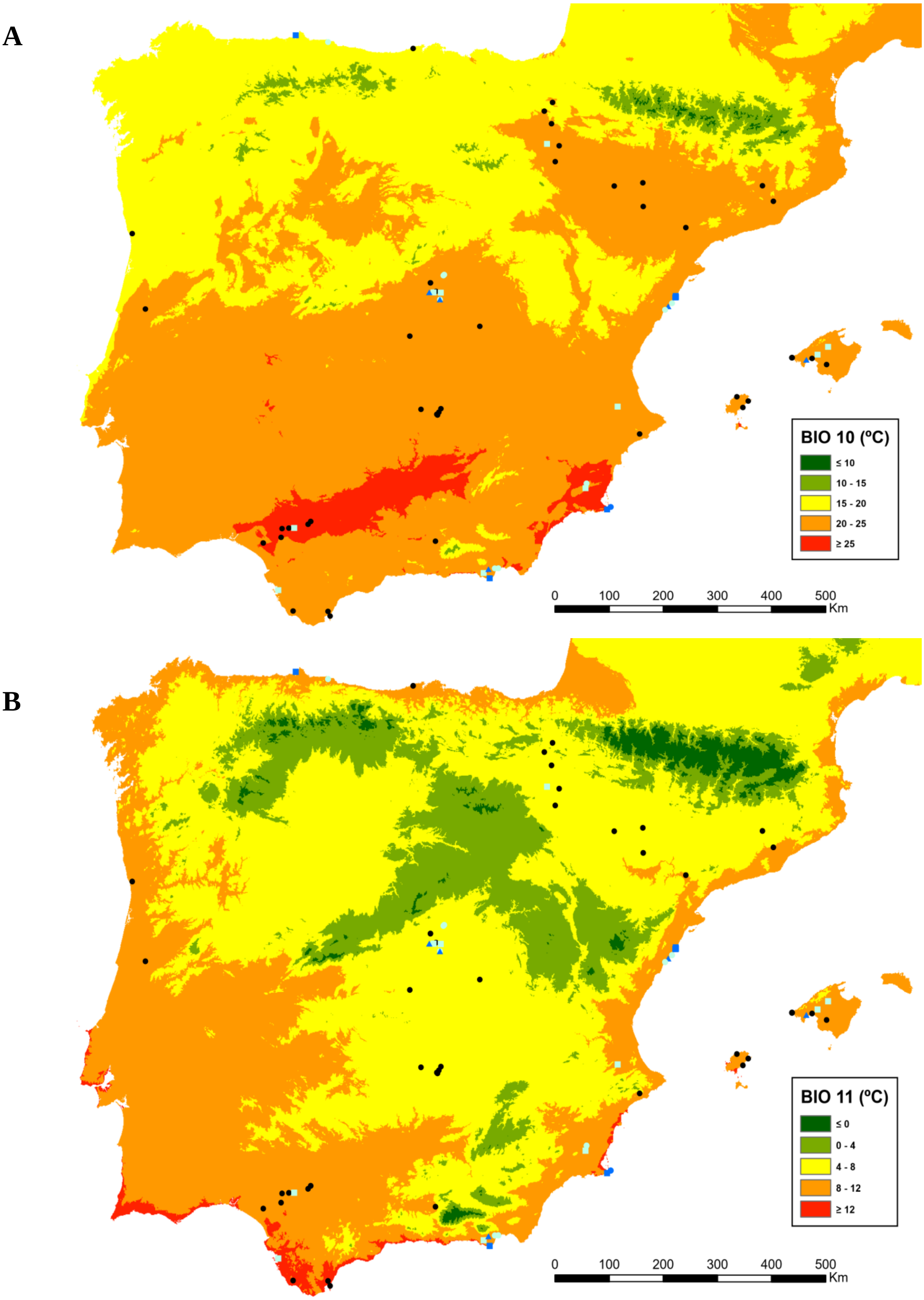
A



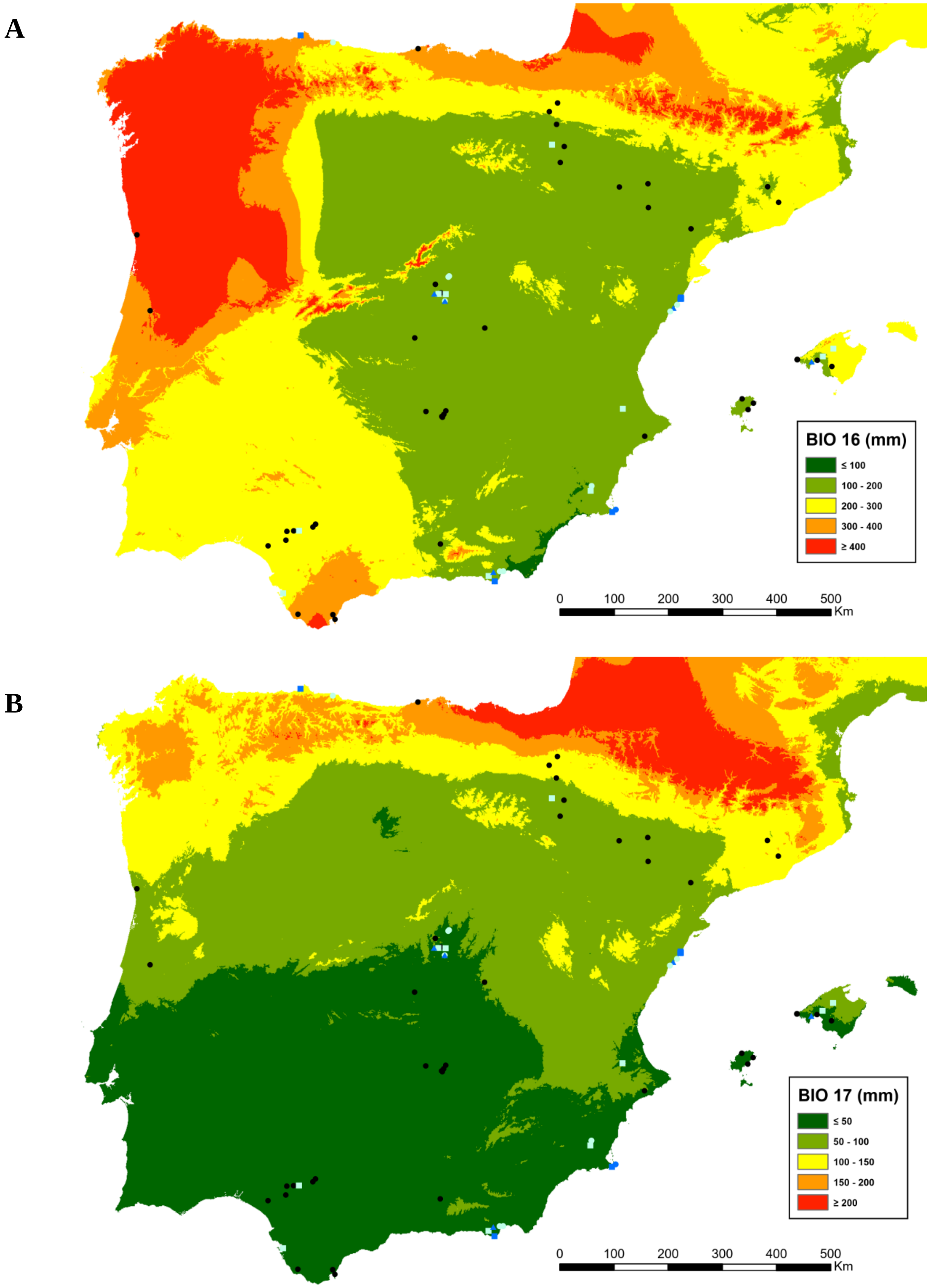
B



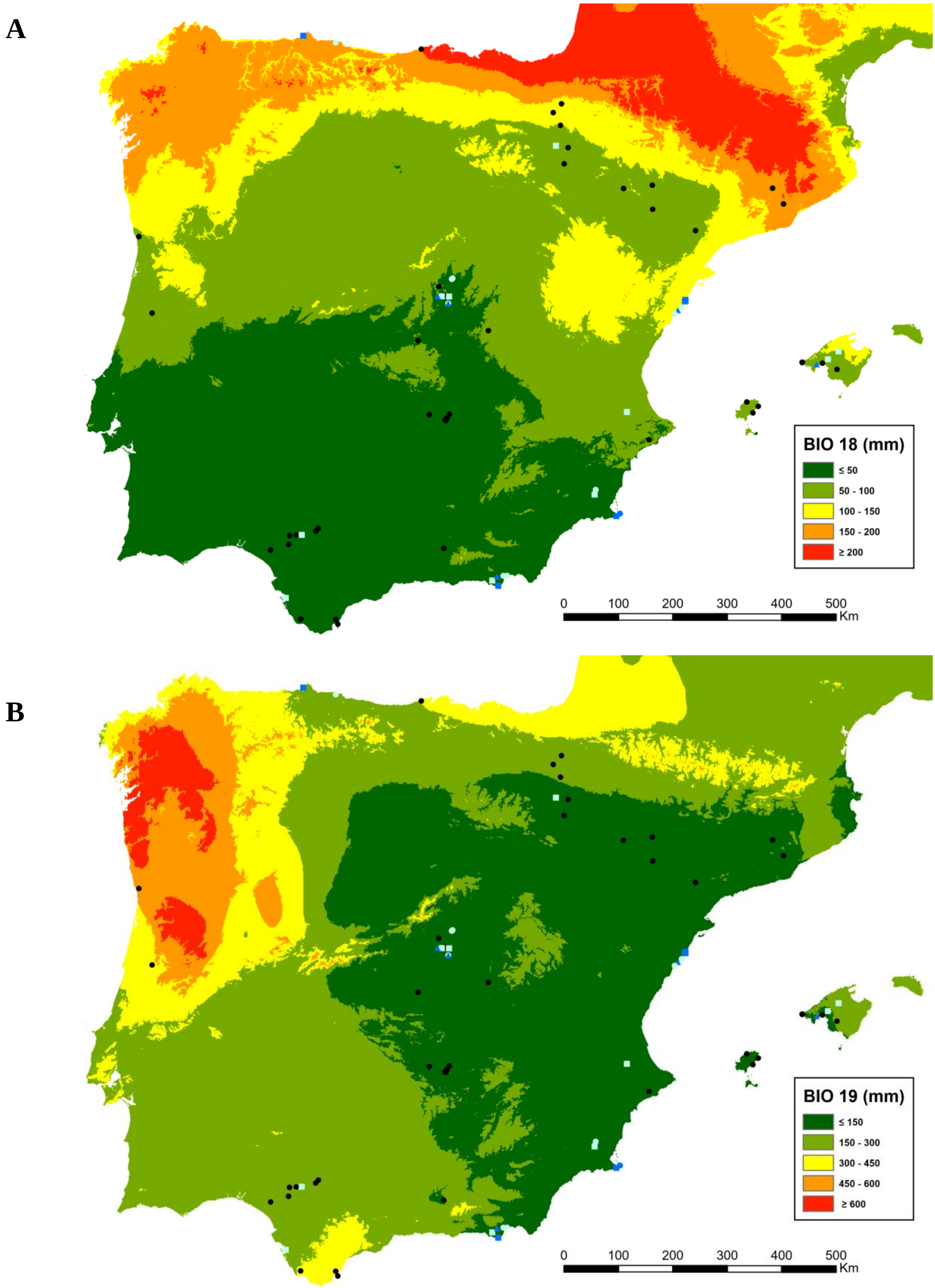
2.2: A) Mean temperature (º C) of wettest quarter (BIO8). B) Mean temperature (º C) of driest quarter (BIO9).



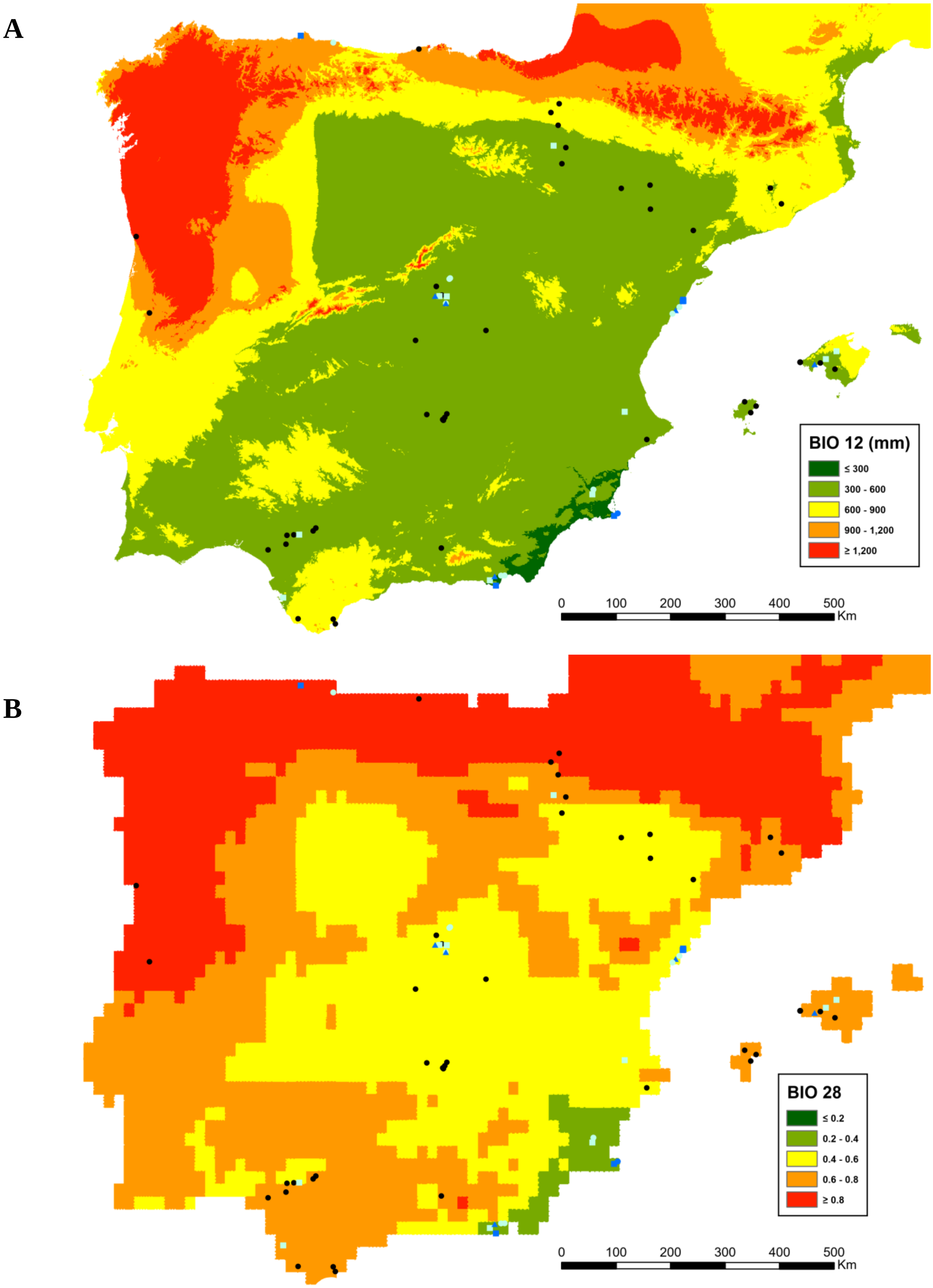
2.3: A) Mean temperature (º C) of warmest quarter (BIO10). B) Mean temperature (º C) of coldest quarter (BIO11).



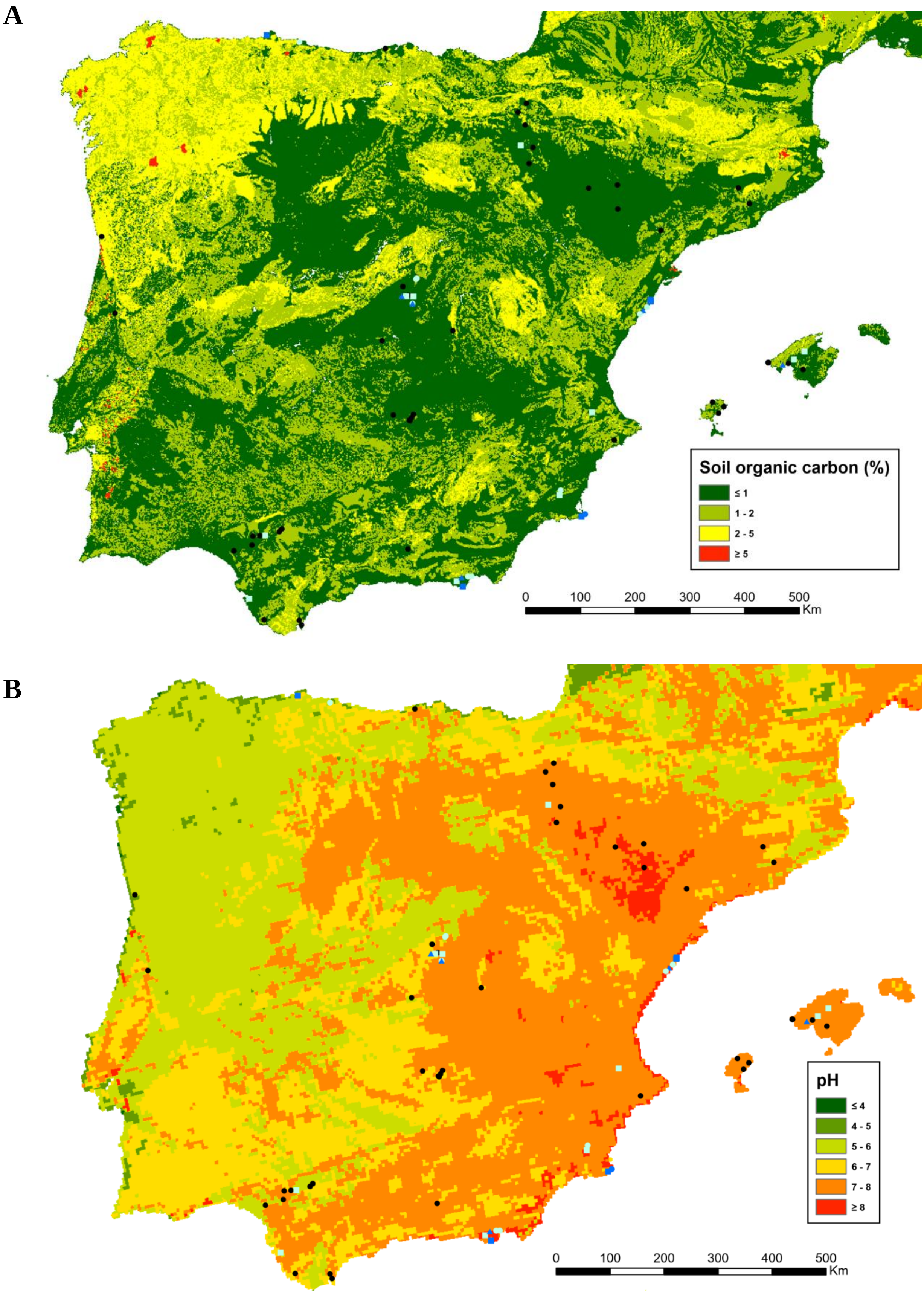
2.4: A) Precipitation (mm) of wettest quarter (BIO16). B) Precipitation (mm) of driest quarter (BIO17).



2.5: A) Precipitation (mm) of warmest quarter (BIO18). B) Precipitation (mm) of coldest quarter (BIO19).

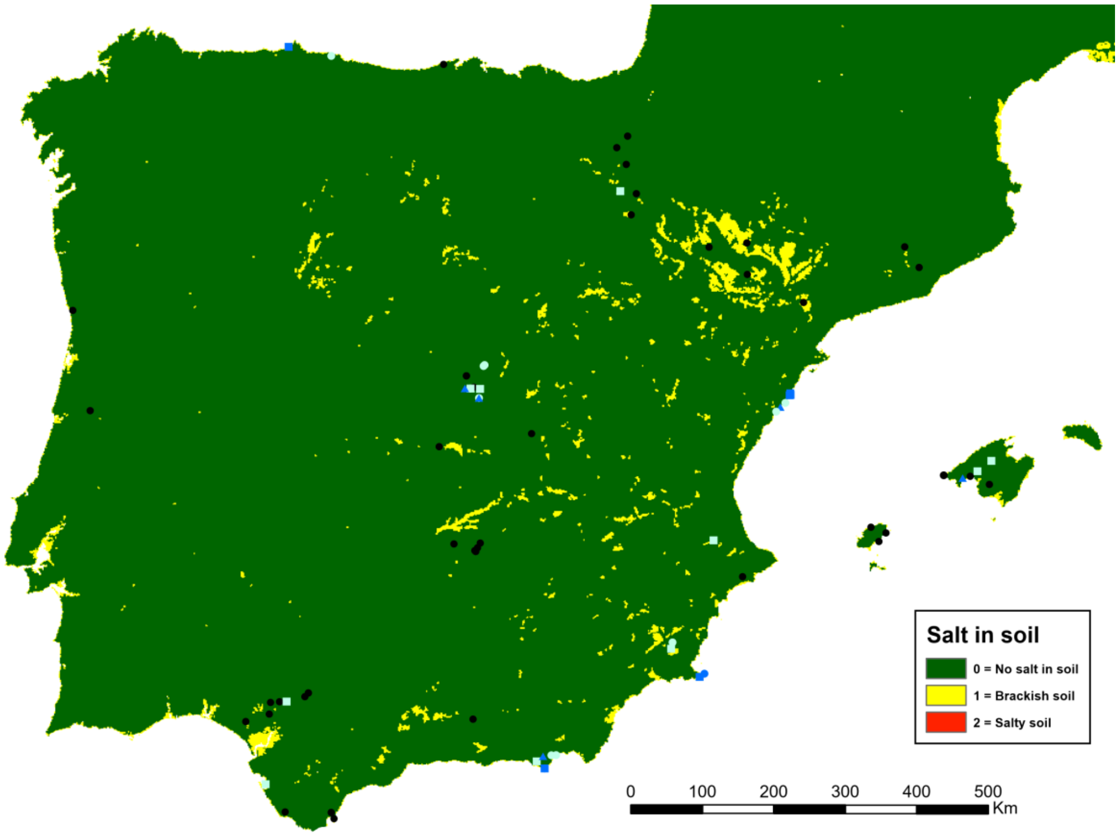


2.6: A) Annual precipitation (mm) (BIO12). B) Annual mean soil moisture index (SMI) (BIO28). Values close to 1 indicate wettest soils while values close to 0 indicate driest soils.

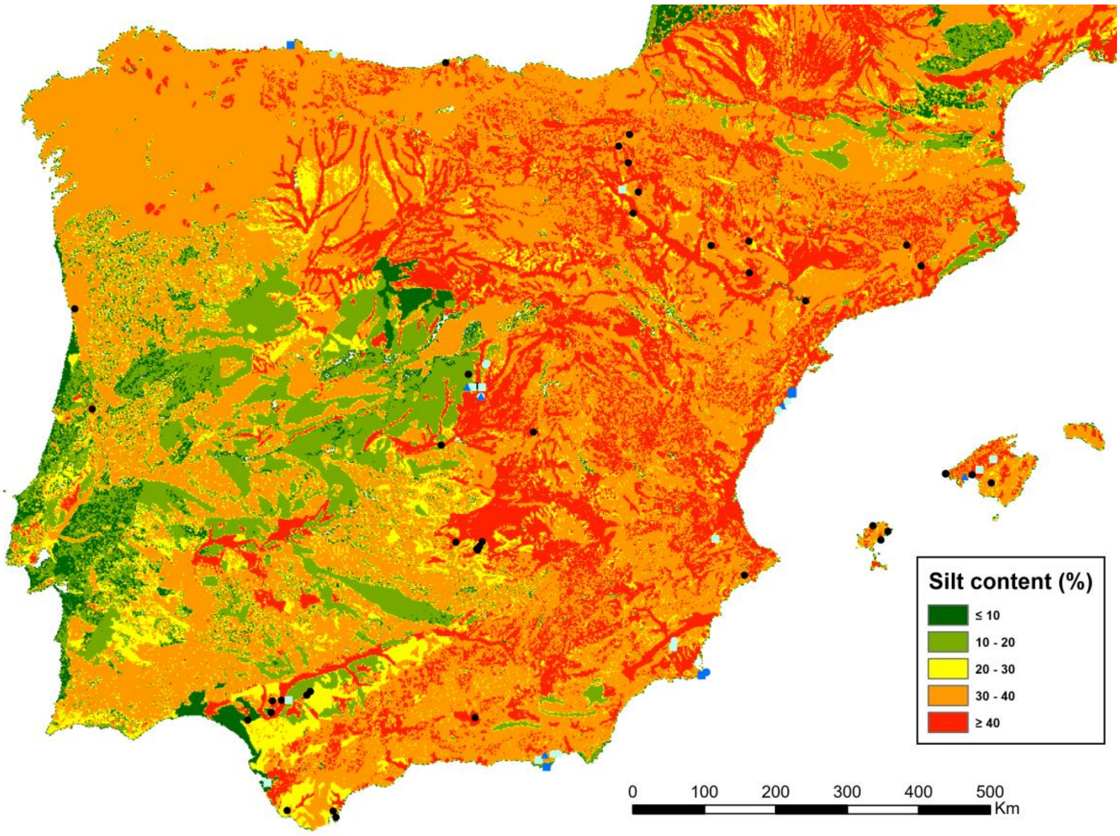


2.7: A) Soil organic carbon (%). B) Soil pH.

A



B



2.8: A) Salt in soil (0 = no salt, 1 = brackish soil, 2 = salty soil). B) Silt content (%).