Studies of the mesovoid shallow substratum can change the accepted autecology of species: the case of ground beetles (Coleoptera, Carabidae) in the Sierra de Guadarrama National Park (Spain)

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Abstract

Studies of the mesovoid shallow substratum can change the accepted autecology of species: the case of ground beetles (Coleoptera, Carabidae) in the Sierra de Guadarrama National Park (Spain). The family Carabidae is of particular interest not only due to its great specific diversity but also due to the geophilic nature of many of its members, which makes them good bioindicators of soil characteristics. The diversity of the epigean Carabidae is relatively well studied. However, there are no robust data on the presence of these beetles in hypogean habitats of non–karstic substrate and, therefore, without the development of caves. In the present study, we sampled the mesovoid shallow substratum (MSS) at various sites in the Sierra de Guadarrama National Park, with the aim of characterising the Carabidae hypogean fauna. Among many other organisms, we collected 12 species of Carabidae. Of these, despite being known from epigean/edaphic habitats, *Leistus (Leistus) constrictus* Schaufuss, 1862, *Nebria (Nebria) vuillefroyi* Chaudoir, 1866, *Trechus (Trechus) schaufussi pandellei* Putzeys, 1870, and *Laemostenus (Eucryptotrichus) pinicola* (Graells, 1851) are consistently reported from MSS habitats, albeit with certain differences as regards their occupation of subterranean spaces. The species from forest–dwelling (thermophilous) lineages, *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, presented a higher prevalence in subsoil cavities at lower altitudes, whereas those from orobiont (psychrophilic) lineages, *L. (L.) constrictus* and *N. (N.) vuillefroyi*, predominated in subsoils at higher altitudes. As regards the presence of these four species during their different life cycle stages, we found that *N. (N.) vuillefroyi* was present and abundant as both larval (in the three preimaginal stages) and imago stages, showing the most evident trend towards an hypogean lifestyle. In contrast, for the other three species, only one of the two stages showed a high presence on hypogean habitats. The facultative hypogean capabilities of *N. (N.) vuillefroyi* and *L. (L.) constrictus* calls into question the protected status conferred on both species when it was thought that they were exclusively epigean.

Key words: Mesovoid shallow substratum, Hypogean, Orobiome, Autoecology, Carabidae, Sierra de Guadarrama National Park, Iberian peninsula

Resumen

El estudio del medio subterráneo superficial puede cambiar la autecología aceptada de las especies: el caso de los carábidos (Coleoptera, Carabidae) en el Parque Nacional de la Sierra de Guadarrama (España). La familia Carabidae es de especial interés debido a la gran diversidad específica que atesora y al carácter geófilo de muchas de sus especies, lo que convierte a los integrantes de esta familia en buenos bioindicadores de las características del suelo. La diversidad de los carábidos de hábitos epigeos está relativamente bien estudiada; sin embargo, no hay datos sólidos sobre la presencia de estos coleópteros en el medio hipogeo de sustrato no kárstico y, por consiguiente, sin la formación de cuevas. En este estudio se realizaron capturas en el medio subterráneo superficial (MSS, en su sigla en inglés) de varios lugares del Parque Nacional de la Sierra de Guadarrama, con la finalidad de determinar las características de los carábidos hipogeos. Entre otros muchos organismos, se capturaron 12 especies de Carabidae, de las cuales *Leistus (Leistus) constrictus* Schaufuss, 1862; *Nebria (Nebria) vuillefroyi* Chaudoir, 1866; *Trechus (Trechus) schaufussi pandellei* Putzeys, 1870 y *Laemostenus*

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(Eucryptotrichus) pinicola (Graells, 1851) se capturaron frecuentemente en el medio subterráneo superficial pese a conocerse de medios epigeos y edáficos. No obstante, se observaron ciertas diferencias en la ocupación de los espacios subterráneos. Las especies provenientes de linajes de hábitos forestales (termófilos), como *T. (T.) schaufussi pandellei* y *L. (E.) pinicola*, se encontraron más frecuentemente en las oquedades del subsuelo de cotas más bajas, mientras que las especies procedentes de linajes con hábitos orobiontes (psicrófilos), como *L. (L.) constrictus* y *N. (N.) vuillefroyi*, predominaban en el subsuelo de cotas más elevadas. En cuanto a la presencia de estas cuatro especies durante sus diferentes fases del ciclo de vida, encontramos que *N. (N.) vuillefroyi* era abundante tanto en forma larvaria (en los tres estadios preimaginales) como en fase de imago, lo que muestra la clara tendencia hacia la adopción de un estilo de vida hipogeo. Por el contrario, en las otras tres especies solo una de las dos fases tiene una elevada presencia en el medio hipogeo. Dadas las capacidades hipogeas facultativas de *N. (N.) vuillefroyi* y *L. (L.) constrictus*, se cuestiona la figura de protección que se atribuyó a ambas especies cuando se asumía que eran de actividad totalmente epigea.

Palabras clave: Medio subterráneo superficial, Hipogeo, Orobioma, Autoecología, Carabidae, Parque Nacional de la Sierra de Guadarrama, Península ibérica

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Introduction

The mesovoid shallow substratum (MSS) was discovered as a hypogean habitat in the 1980s (Juberthie et al., 1980, 1981; Uéno, 1980, 1981), and is probably one of the most extensive but least researched subterranean habitats on the planet. The MSS consists of a network of cracks, fissures and interstices in the subsoil which occurs in very different lithologies and is formed by different processes (Juberthie et al., 1980, 1981; Oromí et al., 1986; Juberthie, 2000; Ortuño et al., 2013). In some respects, the environmental conditions of the MSS resemble those of caves (absence of light, high humidity and limited temperature variations) and the MSS can therefore host strictly hypogean species which have adapted to this habitat in accordance with the hygrophilous and stenoic nature of their lineages (Gers, 1992, 1998; Culver and Pipan, 2008; Nitzu et al., 2010, 2014; Pipan et al., 2011; Rendoš et al., 2012; Ortuño et al., 2013; Gilgado et al., 2015). However, as the MSS has a close association with the surface and soil horizons (Giachino and Vailati, 2010; Nitzu et al., 2014; Jiménez–Valverde et al., 2015), the ease with which organic matter enters the system is a substantial ecological difference from caves (Gers, 1998). This characteristic favours the presence of high densities of Arthropoda, many of them epigean or endogean, which encounter temporarily appropriate conditions in the MSS. The MSS acts as a climatic refuge, and it is therefore not surprising to find relict species sheltering in this habitat in response to major past climate changes (Christian, 1987; Hernando et al., 1999; Růžička, 1999; Ortuño et al., 2014a, 2014b). From an ecological, evolutionary and conservationist perspective, the MSS is a very important habitat that has remained unknown for a long time (Pipan et al., 2011; Ortuño et al., 2013; Jiménez–Valverde et al., 2015), partly due to the extreme difficulty in accessing and sampling its biocoenosis (Mammola et al., 2016).

Carabids are one of the most intensively studied groups of arthropods, constituting one of the megadiverse families of Coleoptera (Gaston, 1991). More than 30,000 species have been described (Niemelä, 1996; Lorenz, 2005), 1,450 of which appear in the Iberian context (Serrano, 2017). Carabidae form a taxonomic group that has been widely used as a valuable bioindicator species (Rainio and Niemelä, 2003) and as a key element in biogeographical studies (Noonan, 1979). The east to west line of many Iberian mountain ranges has fostered the isolation and speciation of hypsobiont forms (Ortuño, 2002). One of these ranges is the Central System, a mountainous region which hosts a remarkable diversity of Carabidae: close to 400 species/subspecies (Serrano et al., 2003). The Sierra de Guadarrama, located in the eastern half of the Central System, is perhaps one of the most outstanding mountain sectors, with almost 250 known species (Novoa, 1975; Serrano, 1989; Ortuño and Toribio, 1996, 2002). However, almost nothing is known of its hypogean habitats because the rocky substrate is mostly siliceous and therefore lacks caves, habitats that have traditionally provided information on hypogean life.

The objective of the present study was to increase our knowledge about the fauna of carabids of siliceous MSS, taking into consideration information on species distribution, prevalence and altitudinal range. To this end, underground spaces were sampled in the Sierra de Guadarrama, a mountainous sector that is ideal for this type of study due to the nature of its rocks and the glacial and periglacial landforms of its peaks and slopes that contain large colluvial and glacial deposits (Sanz, 1986; Pedraza and Carrasco, 2005; JCL and CAM, 2010) which host MSS. Study of MSS can contribute to the discovery of unknown preimaginal stages (instar) of many species and reveal the hypogean behavior of imagoes stages traditionally considered epigean. In sum, this would require reassessment of the currently accepted autecological knowledge of many species of Carabidae.

Material and methods

Study area

The study was conducted in the Sierra de Guadarrama, a mountainous sector which forms a large part of the Central System, the mountain range that divides the centre of the Iberian Peninsula into two sub–plateaus. Sampling was conducted within the geographical limits of the 33,960 hectare Sierra de Guadarrama National Park (BOE, 2013) and also in part of the Peripheral Protection Area covering 62,687.26 hectares (MAPAMA). There are three mountain belts within the protected area of this national park (fig. 1A): the Montes Carpetanos, the Siete Picos–La Mujer Muerta and the Cuerda Larga, the latter being the most complex of the three since it is associated with two other important belts, La Pedriza and the Sierra de los Porrones. The three mountain belts converge at two mountain passes, those of Navacerrada and Los Cotos, where there are two non–protected areas (fig. 1A) due to the presence of ski slopes (incompatible with the conservation policies of a national park). The lithology in these sectors of the Sierra de Guadarrama is dominated by the presence of orthogneiss (Vialette et al., 1987; PNSG a). Abundant scree slopes (colluvial or glacial deposits) have been generated by fragmentation of metamorphic rocks into smaller blocks due to glacial (Pedraza and Carrasco, 2005) and peri–glacial events (Sanz, 1986). Plutonic rocks such as granite are limited to a substantial part of Siete Picos and La Pedriza. These substrates were excluded from subterranean sampling because they are broken down during erosion processes and are thus not conducive to the formation of scree slopes (fig. 1A–1B).

The Sierra de Guadarrama has a Mediterranean climate, with marked continentality, characterized by dry, cool summers and cold winters. However, the diverse topography of the three mountain belts favours a considerable variety of microclimates (PNSG b; Salazar Rincón and Vía García, 2003; JCL and CAM, 2010; Palomo Segovia, 2012). The studied area is divided into three bioclimatic zones: supramediterranean, oromediterranean and crioromediterranean (Rivas–Martínez, 1984; Rivas–Martínez et al., 1987).

The supramediterranean zone extends from approximately 1,300 to 1,700 m a.s.l., dominated by the Pyrenean oak (*Quercus pyrenaica* Willd.), a species whose presence has been reduced by human activity in favour of the Scots pine (*Pinus sylvestris* L.). The oromediterranean zone extends from approximately 1,700 to 2,100 m a.s.l., although upper limits can reach higher altitudes depending on the orographic characteristics of the terrain in each place. This zone hosts the most extensive plant formations of the Sierra de Guadarrama National Park (JCL and CAM, 2010), divided into two belts: a lower belt (1,700 to 1,950 m a.s.l.) of forest dominated by *P. sylvestris* (fig. 1B) and an upper belt (1,950 to 2,100 m a.s.l.) characterized by scrub supra–forest (montane scrubland), composed primarily of two species (Novoa, 1977), *Cytisus oromediterraneus* Rivas Mart. et al. and *Juniperus communis alpina* (Suter) Celak., as well as *Adenocarpus hispanicus* (Lam.) DC. or *Erica arborea* L. to a lesser extent. The scrub alternates with pastureland, rocky outcrops and scree slopes, forming part of the high altitude landscapes of the Sierra de Guadarrama (fig. 1B). The crioromediterranean zone is comprised in the highest areas of the Sierra de Guadarrama (approx. 2,100 m a.s.l. up to the maximum altitude, 2,428 m a.s.l., at Peñalara peak). Typical vegetation consists of psychroxerophilic pastureland (with abundant presence of *Festuca curvifolia* Lag. ex Lange), sub–hygrophilous pastureland (dominated by *Nardus stricta* L. grasslands, typical of oligotrophic montane soils) (Rivas Martínez, 1963; Rivas Martínez et al., 1990) and peat bog (hosting species of the genus *Carex* L. 1753), although the presence of *P. sylvestris* has been documented in some south–facing areas (Muñoz Municio et al., 2004).

The scree slopes located in the crioromediterranean and oromediterranean zones present a variety of rupicolous plant species characteristic of rocky substrates (JCL and CAM, 2010). Precipitation in the highest bioclimatic zones generally occurs in the form of snow, which remains on the ground throughout the winter and much of the spring. In basins or areas protected from strong sun, snow deposits persist for longer and are known as snowfields.

Sampling

After evaluating the amount of sampling effort that could be realized, we selected 33 scree slopes across the Sierra de Guadarrama National Park with the intention of covering most of the geographic area and bioclimatic zones of the Park, while taking into account the structural quality of the MSS and its accessibility (fig. 1). We installed 33 subterranean sampling devices (SSD) which were slightly modified from the pilot model developed for the first Iberian sampling campaign of these characteristics (Barranco et al., 2013; Ortuño et al., 2013). These SSDs consisted of a pitfall trap and a PVC cylinder measuring 11 cm in diameter and 1 m long, and contained numerous perforations (8 mm in diameter) from the middle almost to the bottom of the cylinder (sampling depth: –0.5 m to –0.9 m) (see fig. 2 in Baquero et al., 2017). Another 4 SSDs measuring 0.5 m long and containing perforations in the lower 30 cm (sampling depth: –0.2 m to –0.4 m) were installed in sampling sites 1 to 4 (Siete Picos–La Mujer Muerta mountain belts) next to the 1 m long SSDs. Only four short SSDs were installed due to the enormous extra amount of work that additional traps implied. The pitfall trap, which fitted perfectly inside the cylinder, contained a liquid preservative (1.2–propanediol) and was baited with a vial containing very strong–smelling cheese, a standard procedure in this kind of studies (Gers, 1992; Giachino and Vailati, 2010; López and Oromí, 2010). The cylinder was buried vertically in the appropriate substrate, and when the top was level with the soil surface, the trap was lowered inside on a nylon thread to the bottom; then the cylinder was covered and isolated from the external environment using waterproof material covered by a layer of soil or stones (see figure 2 in Baquero et al., 2017).

The sites sampled fell within the National Park (31 locations) and, to a lesser extent, the Peripheral Protection Area (2 locations) (fig. 1B; see table 1 in Baquero et al., 2017). The SSDs were installed between 20/05/2015 and 09/07/2015, and collections were made at three different times between 20/05/2015 and 14/10/2016.

Samples were taken to the laboratory, and specimens were identified to the species level and stored in the entomological collection of the Department of Life Sciences, Faculty of Sciences, University of Alcalá, Alcalá de Henares, Madrid, Spain (Collection V. M. Ortuño). The relative percentage (prevalence) of each dominant species was calculated for each sector and for each bioclimatic zone.

Results

We collected a total of 12 Carabidae species in the MSS (with the 1 m SSDs).These samples were unevenly represented: *Carabus (Oreocarabus) guadarramus* Laferté, 1847 [larva: 1, imagoes: 3]; *Leistus (Leistus) constrictus* Schaufuss, 1862 [L: 237, I: 32]; *Nebria (Nebria) vuillefroyi* Chaudoir, 1866 [L: 148, I: 203]; *Nebria (Nebria) salina* Fairmaire and Laboulbène, 1854 [I: 16]; *Trechus (Trechus) quadristriatus* (Schrank, 1781) [I: 1]; *Trechus (Trechus) schaufussi pandellei* Putzeys, 1870 [L: 1, I: 234]; *Cryobius nemoralis nemoralis* (Graells, 1851) [I: 1]; *Steropus (Iberocorax) ghilianii* (Putzeys, 1846) [I: 1]; *Platyderus (Platyderus) varians* Schaufuss, 1862 [I: 6]; *Laemostenus (Eucryptotrichus) pinicola* (Graells, 1851) [L: 14, I: 572]; *Synuchus vivalis* (Illiger, 1798) [I: 1]; and *Cymindis (Cymindis) coadunata monticola* Chevrolat, 1866 [I: 1]. Only four species, *L. (L.) constrictus*, *N. (N.) vuillefroyi*, *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, were very abundant in different MSS in the National Park.

We collected a total of 269 specimens of *Leistus (Leistus) constrictus* with the 1 m SSDs, 237 (88 %) of which were preimaginal stages and 32 (12 %)

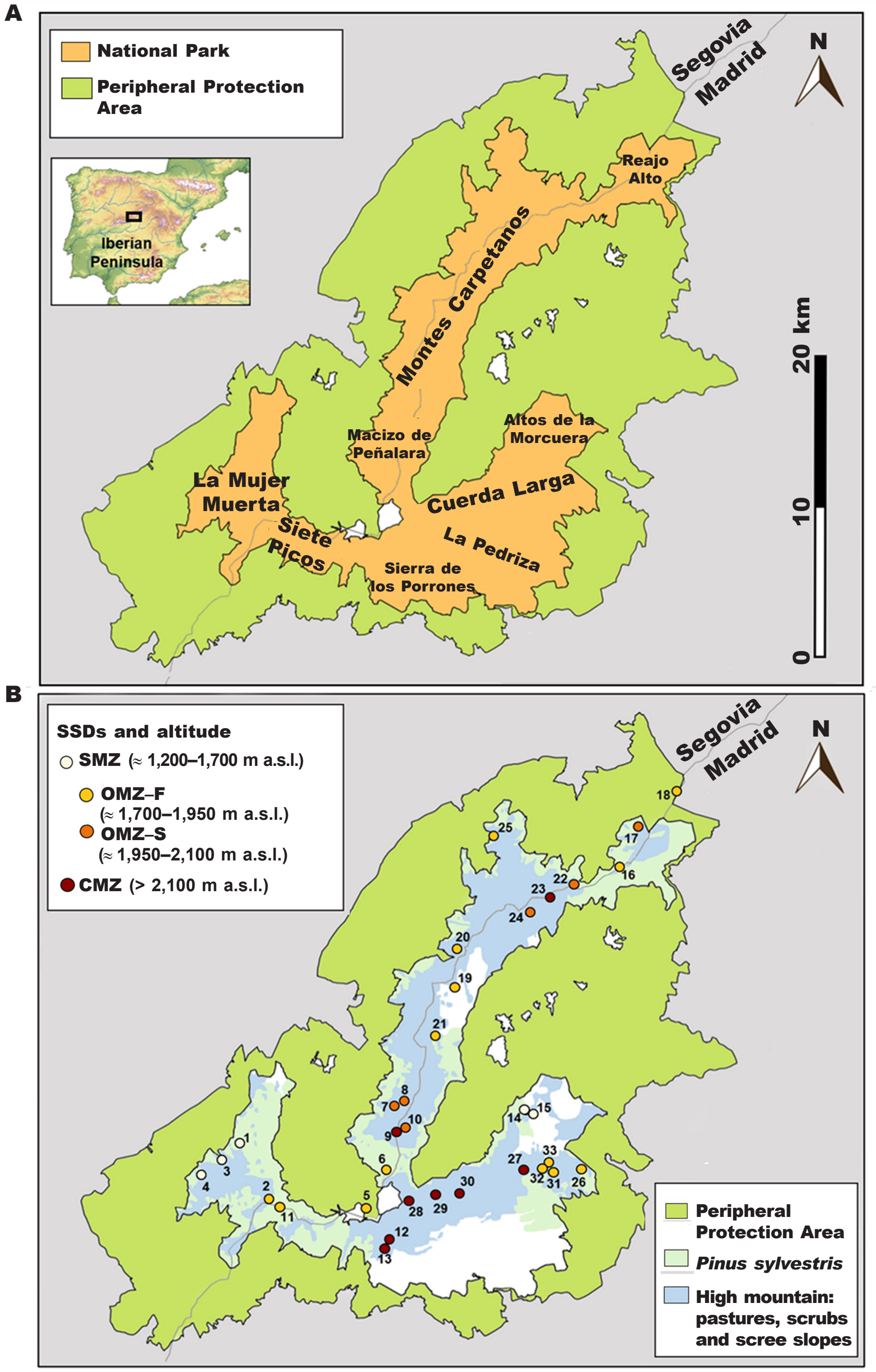

Fig. 1. A, basic orography of the Sierra de Guadarrama National Park; B, location of the subterranean sampling devices (SSD) in the Sierra de Guadarrama National Park, with the distribution of the two most extended ecosystems and indication of the bioclimatic zone for each device: SMZ, supra–mediterranean zone; OMZ–F, oro–mediterranean zone (forest); OMZ–S, oro–mediterranean zone (scrub); CMZ, crioro–mediterranean zone.

Fig. 1. A, orografía básica del Parque Nacional de la Sierra de Guadarrama; B, ubicación de los dispositivos de muestreo subterráneo (SSD por su sigla en inglés) en el Parque Nacional de la Sierra de Guadarrama, con la distribución de los dos ecosistemas más extensos e indicando el piso bioclimático para cada dispostivo: SMZ, zona supramediterránea; OMZ–F, zona oromediterránea (bosque); OMZ–S, zona oromediterránea (matorral); CMZ, zona crioromediterránea.

were imagoes. Similar percentages of the three preimaginal stages were collected (26 % instar–I; 41% instar–II; 33 % instar–III). The sex ratio (based always on imagoes) was highly skewed to males (87.5:12.5). This species was widely distributed throughout the MSS in the study area, but was particularly abundant in the Loma de Pandasco (SSD–30). Compared to the other three species, *L. (L.) constrictus* showed an uneven prevalence: 9 % being found in the Siete Picos–La Mujer Muerta, 17 % in the Montes Carpetanos, 24 % in the Cuerda Larga and associated mountainous complex, and 27 % in the area of convergence (the mountain passes of Los Cotos and Navacerrada). *Leistus (L.) constrictus* comprised 7 % of the carabid fauna present in MSS at levels below 1,700 m a.s.l., but increased significantly in the oromediterranean forest zone (16 %) and scrub supra–forest (21 %), reaching a maximum value of 26 % above 2,100 m a.s.l., in the crioromediterranean zone (fig. 2).

Nebria (Nebria) vuillefroyi was collected in large numbers in the 1 m SSDs, capturing 351 specimens: 148 (42 %) preimaginal stages and 203 (58 %) imagoes. Very dissimilar percentages of the three preimaginal stages were collected (55 % instar–I; 34% instar–II; 11 % instar–III). The sex ratio (imagoes) was slightly skewed to males (59:41). The 14 MSS sites where it was present considerably expand our chorological knowledge of this species, which was especially abundant in the Cerro de Navahonda (SSD–20) and Collado de Valdemartín scree slopes (SSD–28). This species accounted for 7 % of specimens collected in the area of convergence (mountain passes of Los Cotos and Navacerrada), 26 % in Montes Carpetanos and 36 % in Cuerda Larga and associated mountainous complex, whereas it was not found in Siete Picos–La Mujer Muerta. *Nebria (N.) vuillefroyi* was not present in the MSS below 1,700 m a.s.l. but showed a notable presence (15 %) in the oromediterranean forest zone, rising slightly to 20 % in the scrub supra–forest, and very significantly to 52 % at above 2,100 m a.s.l., in the crioromediterranean zone (fig. 2).

The 1 m SSDs also collected a high number of *Trechus (Trechus) schaufussi*: 235 specimens, all imagoes except for one larva. The sex ratio was skewed in favour of females (28:72). This species was collected in the MSS at 33 sampling sites, and was especially abundant in Cancho del Río Peces (SSD–1) (Siete Picos–La Mujer Muerta) and the scree slope at La Najarra–Cuatro Calles (SSD–26) (Cuerda Larga and associated mountainous complex). The geographical prevalence of this species in the MSS was uneven, accounting for 39 % of specimens in the Siete Picos–La Mujer Muerta, 6 % in Montes Carpetanos, 14 % in Cuerda Larga and associated mountainous complex, and 11% in the area de convergence (the mountain passes of Los Cotos and Navacerrada). The species was highly represented in the supramediterranean zone, with prevalence values of 50 %. As altitude increased, its prevalence in the MSS decreased, accounting for 13 % and 20 % in the oromediterranean forest and the scrub supra–forest, respectively, and only 6 % in the crioromediterranean zone (fig. 2).

Laemostenus (Eucryptotrichus) pinicola was very abundant, with 586 specimens being collected in the 1 m SSDs, mainly imagoes (572; 98 %), and only 14 (2 %) preimaginal stages. The sex ratio was slightly skewed to females (40:60). This species was widely distributed throughout the study area, and was especially abundant in the scree slopes near El Paredón (SSD–21) and Las Revueltas–Los Horcos (SSD–16) (Montes Carpetanos), and Majada Conejo (SSD–4) (Siete Picos–La Mujer Muerta). *Laemostenus (E.) pinicola* had a high prevalence in the MSS of all mountainous sectors, exceeding 50 % in all cases except for Cuerda Larga and its associated mountainous complex (with 26 %). In terms of altitudinal range, this species presented a high prevalence of 42 % in the MSS of the supramediterranean zone, 53 % in the oromediterranean forest, 39 % in the scrub supra–forest, and 16 % the crioromediterranean zone (fig. 2).

The high number of *T. (T.) schaufussi pandellei* and *L. (E.) pinicola* collected made it possible to try to compare the abundance of these species according to sampling depth. *Trechus (T.) schaufussi pandellei* was much less abundant – and even absent in the 0.5 m SSDs than in the 1 m SSDs (fig. 3A). However *L. (E.) pinicola* was more abundant in two of the 0.5 m SSDs (fig. 3B). Nevertheless, these results must be interpreted with caution due to the small number of short SDDs.

Discussion

Although the Iberian epigean carabid fauna can be considered relatively well known (Serrano, 2017), there is little information on their presence in the MSS (e.g., Ortuño and Toribio, 1994; Pons and Palmer, 1996; Ortuño, 1996, 2004; Fresneda et al., 1997; Toribio and Rodríguez, 1997; Carabajal, 1999; Hernando et al., 1999; Jeanne, 2000; Faille et al., 2012; Toribio, 2014; Ortuño et al., 2014a, 2017), and taxonomic publications predominate.

Novoa (1977) listed 50 species present in the Sierra de Guadarrama oak woods of the supramediterranean zone, highlighting 7 species as particularly frequent (fig. 2). None of these species was collected in the MSS sampled in this bioclimatic zone, but instead finding *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, and to a lesser extent, *L. (L.) constrictus* (fig. 2) in the subsoil. With regard to the oromediterranean zone, Novoa (1977) distinguished between the Carabidae fauna of *Pinus sylvestris* pine woods and the carabid fauna of scrub supra–forest. The pine woods hosted 45 species of Carabidae, 11 of which were especially representative of this forest environment (Novoa, 1977) (fig. 2). Of these species, only *T. (T.) schaufussi pandellei* and *L. (E.) pinicola* seem to be established in subterranean habitats at this altitude, constituting somewhat less than 75% of the Carabidae specimens found in the sampled MSS (fig. 2). *Laemostenus (E.) pinicola* was the dominant species (with more than 50 % of specimens, followed far behind by *L. (L.) constrictus* (16 %), although both species had an important presence in the samples

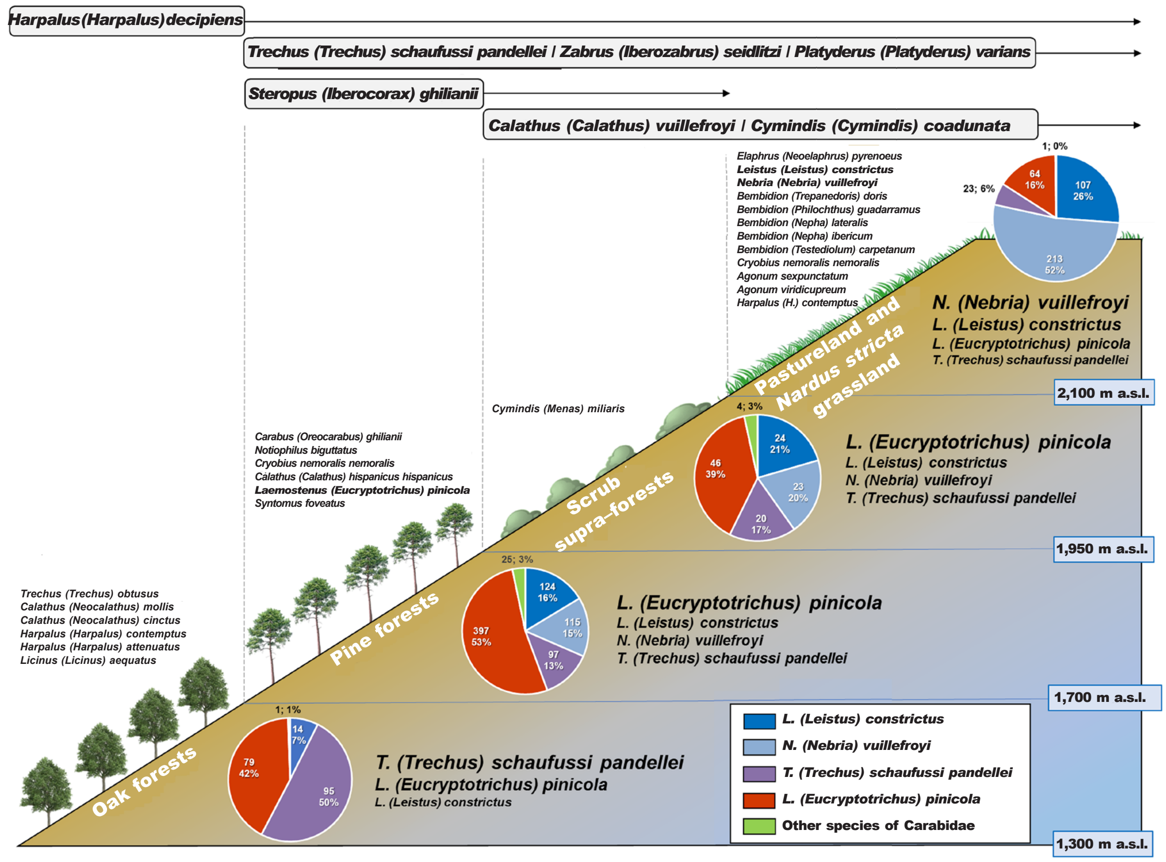

Fig. 2. Altitude distribution of the most conspicuous species of Carabidae in the epigeous environment (according to Novoa, 1977) of the Sierra de Guadarrama, and their correspondence in the mesovoid shallow substratum (according to results of this study).

Fig. 2. Distribución altitudinal de las especies más notables de Carabidae en el medio epigeo (según Novoa, 1977) de la Sierra de Guadarrama y su correspondencia en el medio subterráneo superficial (según los resultados de este estudio).

of supramediterranean subsoil. Notably, *N. (N.) vuillefroyi* showed a high presence (15 %) at altitudes well below its known optimal epigean habitat, while *T. (T.) schaufussi pandellei* had a reduced presence, turning from being the most abundant species in the sampled supramediterranean MSS to being the least abundant in the oromediterranean forest MSS (fig. 2). The carabid fauna of the sampled oromediterranean scrub supra–forest MSS did not correspond to that observed by Novoa (1977) in epigean habitats, with the exception of *T. (T.) schaufussi pandellei*. Novoa described the presence of 30 species, eight of which were particularly frequent and abundant, and five of which also occupied the pine wood belt (fig. 2). Of these, *T. (T.) schaufussi pandellei* was collected in some abundance in the MSS (17 % of specimens), close to the values for *N. (N.) vuillefroyi* and *L. (L.) constrictus* (20 % and 21 %, respectively). *Laemostenus (E.) pinicola* was the most abundant species, as in the subsoil of the pine wood belt (fig. 2). The crioromediterranean zone hosts a remarkable number of Carabidae species: Novoa (1977) described 42, 19 of which were particularly frequent at high altitudes in the Sierra de Guadarrama (fig. 2). However, given the different hygrophilous nature of these species, they were unevenly distributed in habitats such as psychroxerophilic pasturelands, *Nardus stricta* grasslands, peat bogs and snowfields. At this altitude, the sampled MSS hosted three species which also formed part of the most representative species of the typically orophilous epigean fauna in the Sierra de Guadarrama (fig. 2): *N. (N.) vuillefroyi*, *L. (L.) constrictus* and *T. (T.) schaufussi pandellei*. A fourth species, *L. (E.) pinicola*, which is dominant in the sampled subsoil of lower bioclimatic zones but not recognised as characteristic of crioromediterranean epigean habitats, also appeared in the sampled crioromediterranean MSS, although its presence was very low (fig. 2). At such high altitudes, the presence of Carabidae in the MSS changed dramatically from that observed at lower altitudes. *Nebria (N.) vuillefroyi* became the dominant species (with more than 50 %

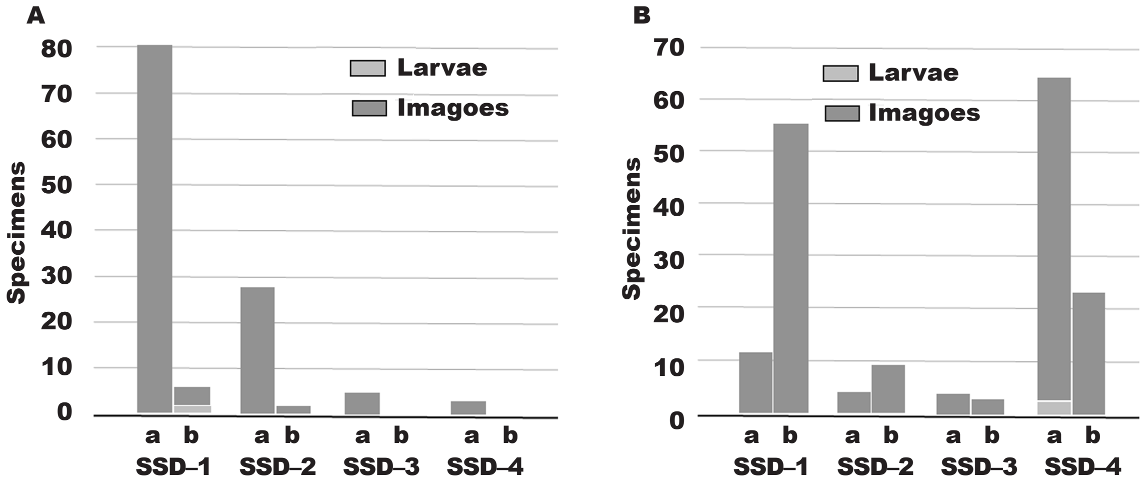

Fig. 3. Abundance of *Trechus (Trechus) schaufussi pandellei* (A) and *Laemostenus (Eucryptotrichus) pinicola* (B) in double installation in the 'Siete Picos– La Mujer Muerta' chain: a, SSD (1 m); b, SSD (0.5 m).

Fig. 3. Abundancia de Trechus (Trechus) schaufussi pandellei *(A) y* Laemostenus (Eucryptotrichus) pinicola *(B) en doble instalación en el cordal montañoso de Siete Picos–La Mujer Muerta: a, SSD (1 m); b, SSD (0.5 m).*

of the specimens), followed far behind by *L. (L.) constrictus* (26 %), *L. (E.) pinicola* (16%) and *T. (T.) schaufussi pandellei* (6 %) (fig. 2).

Some species which are very frequent in epigean habitats in the Sierra de Guadarrama appeared only very occasionally in the MSS samples, namely *Cryobius nemoralis nemoralis*, *Steropus (Iberocorax) ghilianii*, *Platyderus (Platyderus) varians* and *Cymindis (Cymindis) coadunata monticola*. Others, also very frequent, such as *Zabrus (Iberozabrus) seidlitzi* and *Calathus (Calathus) vuillefroyi*, were not observed at all in the MSS. This finding, coupled with the prevalence of the four dominant species in the hypogean habitat (fig. 2), suggests that occupation of this hypogean environment by Carabidae fauna in the Sierra de Guadarrama does not depend on the greater or lesser penetrability of colluvial and glacial deposits. The presence of *L. (L.) constrictus*, *N. (N.) vuillefroyi*, *T. (T.) schaufussi pandellei* and *L. (E.) pinicola* in the MSS, but not of other taxa inhabiting the epigean environment, must be sought in their autecological characteristics. The data obtained in the present study suggest that the MSS acts as a filter for epigean species in such a way that only a few manage to achieve an appreciable abundance in the subsoil. Preliminary data from a second year of survey suggest inter–annual consistency of these findings (Vicente M. Ortuño, unpublished).

Leistus (Leistus) constrictus is an endemic species restricted to the Guadarrama and Ayllón mountains (Perrault, 1979; Serrano, 2003, 2013), although known records indicate that it is not rare (Jeanne, 1966; Novoa, 1975; Perrault, 1979; Serrano, 1989; Ortuño and Toribio, 1996). It forms part of a group of orophilous species of *Leistus* Frölich, 1799, which inhabit a peri–plateau ring in the northern half of the Iberian Peninsula (Jeanne, 1976; Perrault, 1979). The data available to date indicate that it preferentially selects habitats at oromediterranean altitudes, leading a sublapidicolous life on damp soils in the pine wood belt (Novoa, 1975). Nevertheless, it is not one of the most frequent carabids in these woods (Novoa, 1977) (fig. 2). At higher altitudes, where soil xericity increases, it has been found in *Nardus stricta* grasslands and on the edges of snowfields (Novoa, 1977). Available evidence indicates that *L. (L.) constrictus* encounters difficulties inhabiting dry soil habitats. Nevertheless, it does not appear to seek alternatives to meet its hygrophilous needs, instead presenting ripicolous behaviour, as evidenced by Novoa (1980). When found on the banks of a water course, it is normally protected by woodland (see collection data in Serrano, 1989; Ortuño, personal observation). The data reported here represent the first record of *L. (L.) constrictus* as an inhabitant of the MSS. The hygrophilous nature of the species in this genus, coupled with their predation of Acari and Collembola (Lindroth, 1985) —both groups very abundant in the subsoil— would explain why *L. (L.) constrictus* is so abundant and widely distributed throughout the MSS in the Sierra de Guadarrama. Although some imagoes were collected in the MSS, most specimens (88 %) were preimaginal stages (previously unknown), a finding which suggests that this species is eminently hypogean during larval stages (fig. 4). This indicates that the known autecology for this species requires revision, and calls into question its vulnerability status due to habitat alteration (BOCM, 1992), to date based solely on knowledge of its epigean behaviour. This is not the first time that hypogean behaviour has been

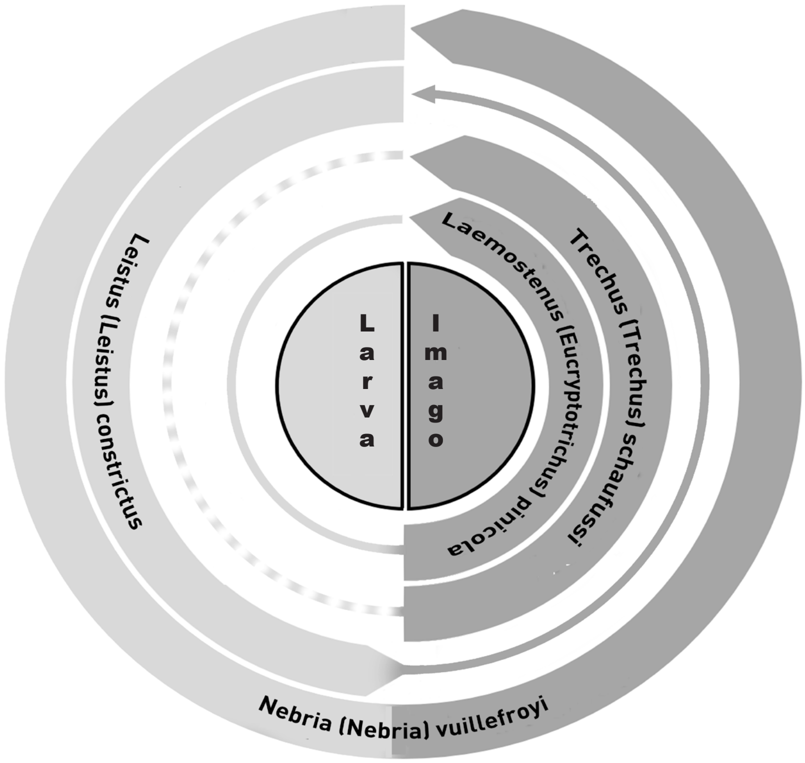

Fig. 4. Representation of the hypogean activity (larva and imago phases) of the four species of Carabidae predominant in the mesovoid shallow substratum samples from the Sierra de Guadarrama National Park.

Fig. 4. Representación de la actividad hipogea (fase larvaria y de imago) de las cuatro especies de Carabidae predominantes en las muestras del medio subterráneo superficial del Parque Nacional de la Sierra de Guadarrama.

reported in *Leistus*, previously noted by Assmann (1997) in relation to *Leistus (Leistus) starkei* Assmann, 1977, a species closely related to *L. (L.) constrictus*. The presence of *Leistus (Pogonophorus) puncticeps* Fairmaire and Laboulbene, 1854, in the MSS has also been observed in the eastern Iberian Peninsula (Jiménez–Valverde et al., 2015).

Nebria (Nebria) vuillefroyi is an orobiont species endemic to the Guadarrama (Bruneau de Miré, 1964) and Ayllón (Ortuño and Toribio, 1994) mountains. Although it has also been in the Sierra de Béjar (Ledoux and Roux, 1992), the Sierra de Gredos (Serrano, 2003, 2013) and, as a result of the proposed synonymy with *Nebria (Nebria) urbionensis* Arribas, 1991, also in the Sierra de Urbión (Ledoux and Roux, 1992). This widespread distribution requires corroboration and further more detailed evidence to support the synonymy proposed by Ledoux and Roux (1992), since *N. (N.) urbionensis* may be a cryptic species that resembles *N. (N.) vuillefroyi* (Arribas and Ortuño, in prep.). It has been known for more than a century that this species inhabits the highest altitudes in the Sierra de Guadarrama, although in a description of the species, Chaudoir (1866) did not specify its geographical origin. Its presence has been documented at several sites in this mountain range, based on imagoes observed on the edges of snowfields (Novoa, 1975; Ortuño and Toribio, 1996), and on instar–III (Vives, 1978). Snowfields are important habitats for the survival of some hygrophilous species of an orophilous nature such as *N. (N.) vuillefroyi*, since they provide soil moisture (due to the effect of melting) and are a good food source due to accumulated biomass from aerial plankton (Palanca and Castán, 1995). This species has been reported at altitudes below 2,000 m a.s.l., albeit sporadically, on stream banks in the Sierra de Guadarrama (between 1,700 and 1,769 m a.s.l.) and in the MSS of the Sierra de Ayllón at 1,650 m a.s.l. (Ortuño and Toribio, 1994). Here *N. (N.) vuillefroyi* is reported for the first time in the MSS of the Sierra de Guadarrama, revealing that larvae and imagoes maintain a constant presence in this habitat (fig. 4). The greater vulnerability of preimaginal stages coupled with the numerous specimens collected in the MSS suggest that this species mainly inhabits hypogean habitats. Imagoes seem to be facultative hypogean, although this lifestyle may become obligatory during much of the year when the snowfields disappear, and the summits become high altitude deserts. The MSS at high altitude provides high humidity, cool temperatures with fewer variations than outside, and a good supply of prey, facilitating occupation by this species. These environmental characteristics are also repeated in the MSS at lower altitudes, facilitating the presence of *N. (N.) vuillefroyi* at sites which do not normally host snowfields and therefore do not present optimal epigean characteristics (fig. 2). These observations indicate that the autecology assigned to date to this species is not complete, and that there is a need to reduce its vulnerability status due to habitat alteration (BOCM, 1992), since its optimum habitat is not restricted exclusively to nivicolous habitats or high altitude epigean environments.

Trechus (Trechus) schaufussi is a species endemic to the Iberian Peninsula, whose distribution is limited to various mountain sites (Jeanne, 1976). Although it may form part of the nivicolous insects (Novoa, 1975; Ortuño and Toribio, 1996), its hygrophilous needs also appear to be satisfied in forest habitats (Jeanne and Zaballos, 1986). It has also been observed in different subterranean habitats (Ortuño and Arribas, 2010). Nine subspecies are currently recognised (see Serrano, 2013), of which *T. (T.) schaufussi pandellei* represents the population in Guadarrama (Putzeys, 1870) and Ayllón mountains (Ortuño and Arribas, 2010). In the Sierra de Guadarrama, it is not confined exclusively to epigean habitats but also inhabits the subsoil (Ortuño and Arribas, 2010). The present study demonstrates that it is widespread throughout the sampled MSS in the National Park, in all the bioclimatic zones sampled (fig. 2). The near absence of preimaginal stages in the MSS compared to the remarkable abundance of imagoes was notable. This might be due to edaphobiont lifestyles as larvae, whereas the imagoes display hypogean activity (fig. 4). It is not surprising that without any apparent adaptation to hypogean habitats, species of the genus *Trechus* Clairville, 1806, seek shelter in the MSS driven by their geophilous and lucifugous habits and hygrophilous needs (Ortuño, 2004).

Laemostenus (Eucryptotrichus) pinicola is endemic to the Central System (Serrano, 2003), discovered in the Sierra de Guadarrama (Graells, 1851), and also found later in Gredos (Jeanne, 1968), Ayllón (Serrano, 1981), Béjar (Zaballos, 1986) and Estrella (Mateu, 1996) mountains. It has been observed in several montane habitats, although it has been considered a forest species (Jeanne, 1968) typical of rainforest (Vives and Vives, 1982), where it is sublapidicolous (Novoa, 1975) or lives under the bark and wood of dead pines (Graells, 1851). Its known altitudinal range is between 1,200 and 2,200 m a.s.l. (Zaballos, 1985), crossing the upper limit of the tree line, where it becomes less frequent (Novoa, 1975; Ortuño and Toribio, 1996). The lucifugous nature of this species (Ortuño and Toribio, 1996) is a widespread ecophysiological trait found to a varying degree in other Sphodrina species that have adopted subterranean habitats (Jeannel, 1937; Casale, 1988; Casale et al., 1998). This trait explains why it has been found not only under large sunken stones (Novoa, 1975; Zaballos, 1986) but also and especially in the MSS in all bioclimatic zones present in the study area (fig. 2). The specimens collected in the MSS suggest that imagoes but not larvae present intensive hypogean activity (fig. 4). This is the first time that this Sphodrini has been described in the MSS.

In the light of the above results, these four Carabidae species should be considered facultatively hypogean. However, the data suggest differences in subterranean occupation according to the altitude of the MSS studied and to the thermophilous or psycrophilic nature of the lineages of each species (fig. 2). The more thermophilous, *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, both from forest–dwelling lineages, were less prevalent in high altitude subterranean spaces, whereas the psychrophilic, *L. (L.) constrictus* and *N. (N.) vuillefroyi*, from orobiont (glacial/nivicolous) lineages, became more prevalent in the subsoil as altitude increased.

Regarding autecological and life cycle aspects, each of these four species shows a different interaction with the MSS (fig. 4). In *Nebria (Nebria) vuillefroyi,* the hypogean lifestyle seems to be an integral part of the life cycle (fig. 4) as evidenced by the numerous imagoes and larvae collected in the sampled MSS. This was very different to *L. (L.) constrictus*, also a Nebriini, in which the hypogean lifestyle was clearly attributable to the larvae, whereas imagoes were only sporadically present in the MSS (fig. 4). Some Nebriini have already been described in hypogean habitats in montane landscapes and areas subject to snow cover (Bruneau de Miré, 1985; Casale et al., 1998; Galán, 1993). These observations are consistent with the longstanding idea of a close interrelationship between some hypogean lineages and nivicolous fauna (Jeannel, 1943; Vandel, 1964; Bellés, 1987). *Laemostenus (E.) pinicola* showed yet another pattern: the hypogean activity was clearly evident in the case of imagoes but merely sporadic in that of larvae (fig. 4), which may have the soil preferences commonly found in many Carabidae. Lastly, *T. (T.) schaufussi pandellei* imagoes were present in the MSS, but not the larvae (fig. 4). Thus, clear and substantial differences between these four species were found with regards to subterranean occupation of imagoes and larvae. *Trechus (T.) schaufussi pandellei* and *L. (E.) pinicola* were more frequent at sampling sites in Siete Picos–La Mujer Muerta and in supramediterranean and oromediterranean forest bioclimatic zones (fig. 1B). This is probably because they are species from forest–dwelling lineages. The results of sampling at different depths suggested a preference of the imagoes of *T. (T.) schaufussi pandellei* for deeper subterranean spaces (fig. 3A). However, the data on *L. (E.) pinicola* indicate that this species was not as demanding (less stenoic) with respect to subterranean occupation depth (fig. 3B). This different response to hypogean habitats could correspond to the more stenoic nature of the Trechini lineage, favouring a more intensive and successful colonisation of subterranean environments than its Sphodrini counterparts (see Bellés, 1987; Casale et al., 1998).

Conclusions

Of the near 250 Carabidae species considered epigean and present in the Sierra de Guadarrama, only four, *L. (L.) constrictus*, *N. (N.) vuillefroyi*, *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, were systematically recovered in the sampled colluvial deposits. This suggests that penetrability and occupation of this habitat largely corresponds to the ecophysiological characteristics of the species, and that the MSS acts as a filter for the epigean Carabidae accessing hypogean environments.

The Carabidae species inhabiting the MSS in the Sierra de Guadarrama National Park differed in the subsoil occupation according to altitude. The species from forest–dwelling lineages (thermophilous species), *T. (T.) schaufussi pandellei* and *L. (E.) pinicola*, presented a higher prevalence at lower altitudes than those from orobiont (psychrophilic species) lineages, *L. (L.) constrictus* and *N. (N.) vuillefroyi*, which predominated in subsoils at higher altitudes.

Regarding the presence of the different life cycle stages of these four species in the MSS, we found that *Nebria (N.) vuillefroyi* is abundantly present in the subsoil at both larval and imago stages. In contrast, the other three species were only abundant in hypogean habitats in one of the two stages of the life cycle. We found that *L. (L.) constrictus* larvae were abundant in the MSS, thus forming part of the hypogean contingent, whereas the imago stage was rarely present. *L. (E.) pinicola* and *T. (T.) schaufussi pandellei* imagoes were abundant in the MSS, but the larval stages of both species were rare or absent, especially in the case of *T. (T.) schaufussi pandellei*.

Nebria (N.) vuillefroyi and *L. (L.) constrictus* are both protected species and have been classified as 'vulnerable to habitat alteration' (according to the Community of Madrid Regional Catalogue of Endangered Species). The present discovery of facultative hypogean behaviour in both species suggests that their protection status is worthy of revision.

We observed preliminary differences between the vertical occupations of subterranean spaces in the two more thermophilous Carabidae species collected. *L. (E.) pinicola* occupied both deeper and shallower spaces, whereas *T. (T.) schaufussi pandellei* predominated in deeper spaces. This finding suggests that *T. (T.) schaufussi pandellei* is more stenoic than *L. (E.) pinicola*.

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