



Global distribution of microwhip scorpions (Arachnida: Palpigradi)

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Abstract

Aim: Historically, research on global distribution patterns has mostly concentrated on conspicuous organisms and thus a large proportion of biodiversity on Earth remains unmapped. We examined the global distribution of palpigrades, a poorly studied group of low dispersive arachnids specialized to subterranean life. We asked what is their typical range size, the ecological factors driving their distributions, and to what extent sampling bias may influence the observed patterns.

Location: Global.

Taxon: Palpigrades (Arachnida: Palpigradi) in the genus *Eukoenia*.

Methods: We assembled a database of over 1000 localities and referring to 57 soil- and 69 cave-adapted palpigrades. We tested for differences in range sizes of soil- and cave-adapted species. We used variance partitioning analysis to explore the contribution of climate, nutrient availability and geology in driving observed distributions. Finally, we verified the potential correlation between the number of occurrence records and the number of palpigrades' researchers.

Results: Europe and Brazil emerged as centres of diversification of cave-adapted palpigrades. Conversely, the diversity of soil-adapted species was distributed over a broader geographical expanse, mainly in the Southern Hemisphere. Both cave and soil species had narrow distribution ranges, with a median value of 0.01 km²; only a few parthenogenetic species were distributed over multiple continents. The distribution of cave- and soil-adapted palpigrades was primarily explained by climatic conditions, and secondarily by nutrient and habitat availability. In the Alps, the distribution of cave-adapted species also bears the signature of historical events related to glaciation cycles. We observed, however, a pronounced people-species correlation, suggesting that the observed patterns are not generalizable to poorly explored areas.

Main conclusions: Our study highlights enormous gaps in current knowledge about the biogeography of palpigrades. Even if the information is largely incomplete and biased, we show how data can be harnessed to draw a preliminary picture of the global distribution patterns of palpigrades. Thus, we offer a jumping-off point for future studies on the macroecology and conservation of poorly known organisms.

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KEYWORDS

Arachnida, diversity pattern, edaphic, macroecology, species distribution modelling, subterranean biology, variance partitioning analysis

1 | INTRODUCTION

Since the pioneering work by the naturalist Alfred Russel Wallace (1876), understanding the geography of life has become the goal of disciplines such as macroecology, biogeography and conservation biology (Ficetola et al., 2017; Holt et al., 2013; Wüest et al., 2020). With the advent of geographical information system (Leitão & Santos, 2019), citizen-science (Hochachka et al., 2012) and internet-based ecology (Jarić et al. 2020), we are accumulating knowledge on species distributions at an unprecedented rate. Our understanding of biodiversity patterns is accelerating to such an extent that scientists have begun to believe that a “global map of life” may not be too far ahead in the future (Jetz et al., 2012). The feasibility of this utopian task resonates with the publication of a comprehensive atlas of vertebrate diversity (Jenkins et al., 2013), a high-resolution global map of forest coverage (Hansen et al., 2013) and the first global map of earthworms (Phillips et al., 2019). Despite these recent notable achievements, however, knowledge about the geography of life is still far from being evenly distributed across the tree of life.

Evidence suggests that we still have limited understanding on the geography of organisms that are not charismatic and/or that do not provide direct ecosystem services to humans. For example, our research interests are skewed towards animals rather than plants (Wandersee & Schussler, 1999); within tetrapods, the knowledge and conservation efforts devoted to mammals and birds is disproportionately greater than that of reptiles and amphibians (Bonnet et al., 2002; Clark & May, 2002; Fukushima et al., 2020); in insects, we have comprehensive monitoring schemes for colourful butterflies (van Swaay et al. 2008) and dragonflies (Galimberti et al. 2020), whereas limited information exists about other groups.

Parallel to this taxonomic bias in researchers' interests, there are objective obstacles to research related to the accessibility of species' habitats. This problem was recently formalized as the ‘Racovitza impediment’ (Ficetola et al., 2019), positing that we cannot understand and fully preserve the biodiversity of the environments that we are not able to map and explore. This bias is well-exemplified by ‘deepest habitats’ (Mammola, 2020), such as the bottom of the sea and the deep subsurface biosphere at depths of kilometers into the Earth's crust. *De facto*, organisms inhabiting these difficult-to-access habitats are likely to be less known compared to those living at the surface (Ficetola et al., 2019; Guerra et al., 2020; Mammola, Lunghi, et al., 2020; Pipan et al., 2020).

A case in point of poorly studied organisms that fulfil both the taxonomic and habitat-accessibility biases as described above is the arachnid order Palpigradi. While spiders and scorpions are typically at the forefront of one's mind when thinking about arachnid diversity, palpigrades belong to one of the minor arachnid orders (dubbed as the ‘neglected cousins’ of spiders; Harvey, 2002) that suffered from being

comparatively less studied. The order Palpigradi consists of more than 100 described species belonging to two families, Eukoeneriidae and Prokoeneriidae. They are small (0.65–2.8 mm), soft-bodied, eyeless and depigmented animals that bear a characteristic flagellum at the rear of their body. Palpigrades inhabit dark and moist habitats like soil, leaf litter and caves, where they are typically observed freely walking on the walls (Condé, 1996; Mayoral & Barranco, 2002b) or floating over the surface of drip pools (Christian et al., 2014).

Giribet et al. (2014) defined Palpigradi as “the most enigmatic arthropod order,” noting that it has been the latest arachnid Order to be discovered (Grassi & Calandrucchio, 1885), the latest for which digital photographs were acquired (Kováč et al., 2002), and the latest for which a phylogeny was assembled (Giribet et al., 2014). Their small body size and cryptic habits make their collection and study challenging. Although some soil-dwelling species can be relatively abundant when sampled with soil extractors (Adis et al., 1997; Christian et al., 2010), most species are known based on a single or few specimens and remain so after years from the description. Such rarity mostly reflects our inability to access their elective interstitial habitats (Howarth, 1983; Mammola, 2019). Palpigrades are also generally sensitive to disturbance, preventing researchers from keeping them alive in the laboratory (Mayoral & Barranco, 2002b) unless for short periods (Kováč et al., 2002). Accordingly, the few accounts on the life history of palpigrades are either casual and anecdotic observations in their natural habitats (Balestra et al. 2019; Ferreira & Souza, 2012; Ferreira et al. 2011) or studies based on indirect evidence (Smrž et al. 2013).

Here, we assembled the first global database on palpigrades aiming to shed some light on their global distribution patterns and ecology. We focused on the genus *Eukoeneria* because it accounts for 80% of the palpigrades species described so far, it has a worldwide distribution, and it includes both soil- and cave-dwelling species. We asked what is their typical range size and what are their general distribution patterns on a global scale. Given that *Eukoeneria* species are differentially adapted to two distinct subterranean habitats, soils and caves, we further tested the hypothesis whether habitat preferences leads to a differentiation in the life history of these species, which should be reflected in distinct ecological preferences and size of their distribution ranges.

2 | MATERIALS AND METHODS

2.1 | Occurrence database

A quick search in the Global Biodiversity Information Facility conducted as of June 2020 revealed that <200 georeferenced records for palpigrades were available. Cumulatively, this is less than the



number of occurrences for virtually any bird species listed in this database. Therefore, species records available in the literature and biological collections are the main source of distribution data for palpigrades.

We assembled a global database of georeferenced localities of *Eukoenenia* species, by systematically screening taxonomic, faunistic and ecological papers on palpigrades. When the coordinates of the localities were not present in the original papers, we obtained them from national speleological cadaster for natural caves or by georeferencing in Google Earth the localities of the collection. To maximize geographical coverage, we further incorporated records of species from Brazil and other countries not formally described yet, based on the specimens deposited in the following repositories: Collection of Subterranean Invertebrates of Lavras, Zoology Museum of the University of São Paulo and Zoobotanical Foundation of Rio Grande do Sul. These specimens were identified at the genus level following Rowland and Sissom (1980) and assigned to morphospecies for the analyses.

2.2 | Sampling bias

Occurrence databases of subterranean species tend to be spatially biased in that most research is concentrated in specific areas, usually accessible caves (Zagmajster et al., 2010). To avoid local overexpression of the numbers of occurrences (Mammola & Leroy, 2018), in all spatial analyses we aggregated occurrences at the resolution of the environmental predictors. We also removed from the database records of *Eukoenenia mirabilis* and *E. florenciae* from greenhouses in temperate zones, since we assumed that these soil species would not be able to survive in natural environments due to unsuitable climatic conditions observed at these latitudes.

To verify if there is a correlation between the degree of aggregation of known occurrences and the number of researchers studying palpigrades (species-people correlation; Barbosa et al., 2013), we used a linear regression to model the relationship between the number of occurrence in a country and the number of researchers operating in that country. We obtained the information on the number of researchers using the affiliations of the researchers as reported in the original papers included in the database.

2.3 | Ecological classification

To analyse biodiversity patterns, we classified palpigrades into two ecological guilds: 'soil-adapted', for species inhabiting soil and leaf litter habitats, and 'cave-adapted', for species found in caves and/or in the network of deep fissures. Although this is a simple classification, the assignment in these two categories was not always straightforward since some species have been sampled in both habitats. We, therefore, used morphological characters to corroborate the habitat-based classification, extracting traits from species' original descriptions.

Given that all palpigrades are eyeless and depigmented, the main anatomical traits to define subterranean specialization are the elongation of appendages and the optimization of sensory structures. In two technical contributions, Condé (1996, 1998) defined leg elongation as the ratios between the lengths of basitarsus and tibia of leg IV (IVbta/ti) and between the lengths of propeltidium (dorsal shield) and basitarsus of leg IV (B/IVbta). Specifically, we checked if the value of the ratios IVbta/ti and B/IVbta for each species are closer to that presented by soil- (average values equal to 0.81 and 3.26, respectively) or cave-adapted species (average values equal to 0.86 and 2.19, respectively), as reported in literature.

The optimization of sensory structures is expressed as the number of blades placed in the anterolateral region of the prosoma (Condé, 1996, 1998). According to Franz-Guess and Starck (2020), these blades are modified sensory setae acting as non-contact chemoreceptors and hygroreceptors. Soil-adapted species have from 1 to 3 blades (few species that have been found exclusively in the soil have 4–6), while cave-adapted ones have from 3 to 13 blades. Exceptions are *Eukoenenia madeirae*, *E. gadorensis*, *E. amatei* and *E. indalica*, considered to be cave-adapted despite having a single blade (Mayoral & Barranco, 2002a, 2017a, 2017b; Strinati & Condé, 1995).

2.4 | Range size

We estimated species range size for each species as:

- (i) the maximum linear extents of the range, namely the length of the line connecting the two occurrences farther apart (Esmaili-Rineh et al., 2020). We calculated distance according to the haversine method (Sinnott, 1984), which assumes a spherical earth. For species reported from one locality only, we assumed the maximum linear extents to be zero; and
- (ii) the area of the minimum convex polygon containing all occurrence points, calculated using the 'adehabitat' R package (Calenge, 2006). The computation of a minimum convex polygon requires a minimum of five localities; when the number of localities was <5, we arbitrarily assumed a minimum convex polygon' area equal to 100 m² multiplied by the number of localities.

We used a Wilcoxon signed-rank test to check whether the median range size of soil and cave species significantly differ.

2.5 | Ecological drivers of distributions

We selected a set of environmental predictors reflecting climatic conditions ('Climate'), habitat availability ('Habitat'), and nutrients availability ('Nutrient') that, in our expert opinion, are suitable broad-scale proxies for the factors that may limit the distribution of subterranean species (Table 1). We extracted climatic variables from WorldClim 2 (Fick & Hijmans, 2017), all at a spatial resolution

of 1 km² (30 arc-sec). We extracted soil and nutrients variables from SoilGrids (Hengl et al., 2017), at a depth of 2 m and at a spatial resolution of 250 m². We obtained a shapefile of carbonate extent from the 'World map of carbonate rock outcrops' (version 3.0) and calculated the availability of karst using the approach described in Mammola, Cardoso, et al. (2019). Pairwise Pearson *r* correlation values among this set of variables were all below ± 0.7 , implying a low degree of multicollinearity.

We used variance partitioning analysis (Borcard et al., 1992) to rule out the relative contribution of Climate, Habitat and Nutrient variables to the observed distribution patterns of soil- and cave-adapted palpigrades. The underlying idea of this analysis is to resolve the variance explained by each variable as well as the shared variation attributable to two or more variables to the same response matrix.

Due to the scarcity of palpigrades records, the number of spatially independent occurrences for most species was not sufficient to fit robust regression models. Using simulations, van Proosdij et al. (2016) estimated that the minimum sample size for modelling the distribution of a narrow-ranged species could theoretically be as low as three occurrences. However, when the sample size of a species is below 13 occurrences, model results are often flawed (van Proosdij et al., 2016). Accordingly, we initially selected all species with more than three spatially independent occurrences. Afterward, we checked model fit for species with less than 13 occurrences, and excluded species whose models overfitted the data or not converged.

As we lacked reliable absence data, we randomly sampled pseudo-absence points for each species (Barbet-Massin et al., 2012). For each species, we defined a 'calibration area' from where to sample pseudo-absence points. The calibration area is the geographic range that a species, theoretically, have been able to colonize through its evolutionary history (Barve et al., 2011). Given that there is no available information on the dispersal ability of palpigrades, we used the maximum linear extent (see previous section) and combined of the range as a proxy for potential dispersal over evolutionary time (Mammola & Leroy, 2018). We buffered each species occurrence by a radius equivalent to the maximum linear extent and combined all the obtained circles in a final shapefile that represented the calibration area. If the maximum linear extent of a species exceeded 2000 km, we used this value as a buffering radius; this choice avoided to inflate the calibration area for few palpigrades species whose distribution extended over different continents.

For each species' presences/pseudo-absences matrix, we extracted the values of environmental predictors and modelled the probability of presence using logistic regressions. To partition the relative contribution of climatic, habitat and nutrient variables in determining the observed distribution patterns, we fitted seven logistic regressions for each species: one for each individual set of variables (Climate, Habitat, Nutrient) and their combined effects (Climate + Habitat, Climate + Nutrient, Habitat + Nutrient, Climate + Habitat + Nutrient). In turn, we evaluated the contribution of each variable and combination of variables with pseudo-*R*² values, by

Variable	Type	Source	Rationale for inclusion
Annual mean temperature [°C]	Climatic [C]	WorldClim 2	Annual mean temperature approximate thermal conditions inside caves (Mammola & Leroy, 2018), but also in soils (Mammola et al., 2016)
Cumulative annual precipitations [mm]	Climatic [C]		Precipitations directly influence subterranean climatic regimes (Badino, 2010). Furthermore precipitations play a critical role in transferring nutrients in soil and caves (so-called hydrochory)
Coarse fragments volumetric [%]	Habitat [H]	SoilGrids	Provide an approximation of the three-dimensional spatial structure of soils (Schröder, 2008) and the availability of habitat pores (Pipan & Culver, 2017)
Carbonate rock [Area of the carbonate patch]	Habitat [H]	World Map of Carbonate Rock Outcrops	Proxy of the general availability of subterranean habitats in carbonate substrates (Christman & Culver, 2001)
Soil organic carbon content [g/kg]	Nutrients [N]	SoilGrids	Reflect the general availability of nutrients and the potential amount of energy inputs
Cation exchange capacity [cmolc/kg]	Nutrients [N]		reaching deep soil strata, as well as caves (Gers, 1998)

TABLE 1 Environmental predictors of palpigrades distribution. Climatic, soil and nutrient availability variables selected for species distribution modelling, and their relevance to represent subterranean conditions.

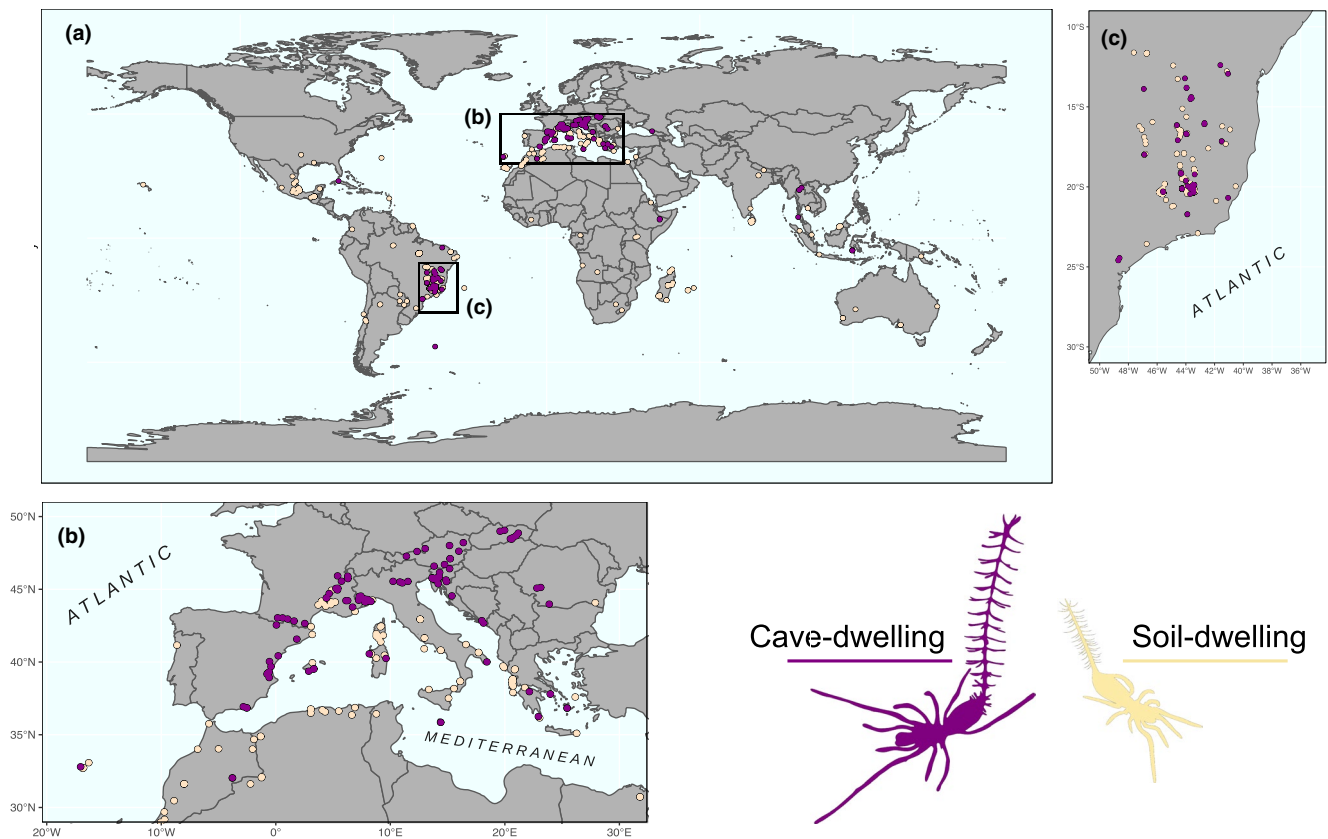


FIGURE 1 Distribution map of occurrences of paligrades species. (a) Global distribution; (b) Distribution in Europe and North Africa. (c) Distribution in Brazil.

partitioning their explanatory power using the 'modeva' R package (Barbosa et al., 2015).

We reported the contribution of variables in driving the distribution of soil and cave-dwelling species using Venn diagrams representing the consensus values among all modelled species. Specifically, the variable contribution' value for each intersection of sets was the average of contributions estimated for all modelled species.

3 | RESULTS

3.1 | Global distribution patterns

We gathered a total of 1081 unique paligrades localities (Figure 1a), belonging to 57 soil-adapted and 69 cave-adapted species. The distribution of records was left-skewed (Figure 2a), with most species occurring in one or very few sites (Appendix S1). The average (\pm SE) number of records per species was 2.90 ± 0.73 for cave-adapted and 15.38 ± 7.63 for soil-adapted species. Documented diversity of cave-adapted species mostly concentrated in Europe (Figure 1b) and Brazil (Figure 1c), whereas the diversity of soil-adapted species was distributed over a broader geographical expanse. The majority of records were in the Southern Hemisphere. With just a few exceptions, paligrades species were restricted to a single continent.

3.2 | Range size

The average (\pm SE) range size measured as a minimum convex polygon was $0.91 \pm 0.62 \text{ km}^2$ for cave species and $564.55 \pm 319.93 \text{ km}^2$ for soil species. This large difference between cave- and soil-adapted species was mostly due to a few outlying wide-ranging soil-adapted species, whereas the median value of the minimum convex polygon was 0.01 km^2 for both ecological groups and did not differ significantly (Figure 2b). A similar pattern was recovered when estimating the range as the maximum linear extents: the average was $169 \pm 87 \text{ km}$ for cave and $1517 \pm 590 \text{ km}$ for soil species, but the median was $<1 \text{ km}$ for both groups and did not differ significantly (Figure 2c).

3.3 | Ecological drivers of distributions

Since almost all paligrades species are known for less than three localities worldwide (Figure 2a), we were able to model the drivers of species distribution for 10 cave- and 14 soil-adapted species only (Appendix S1). The distribution of both groups was explained by similar environmental conditions (Figure 3). High influence of climate and habitat was detected for both groups, whereas the contribution of nutrient availability was on average more important for cave-adapted species (Figure 4c,e). For both groups, on average, 60% of

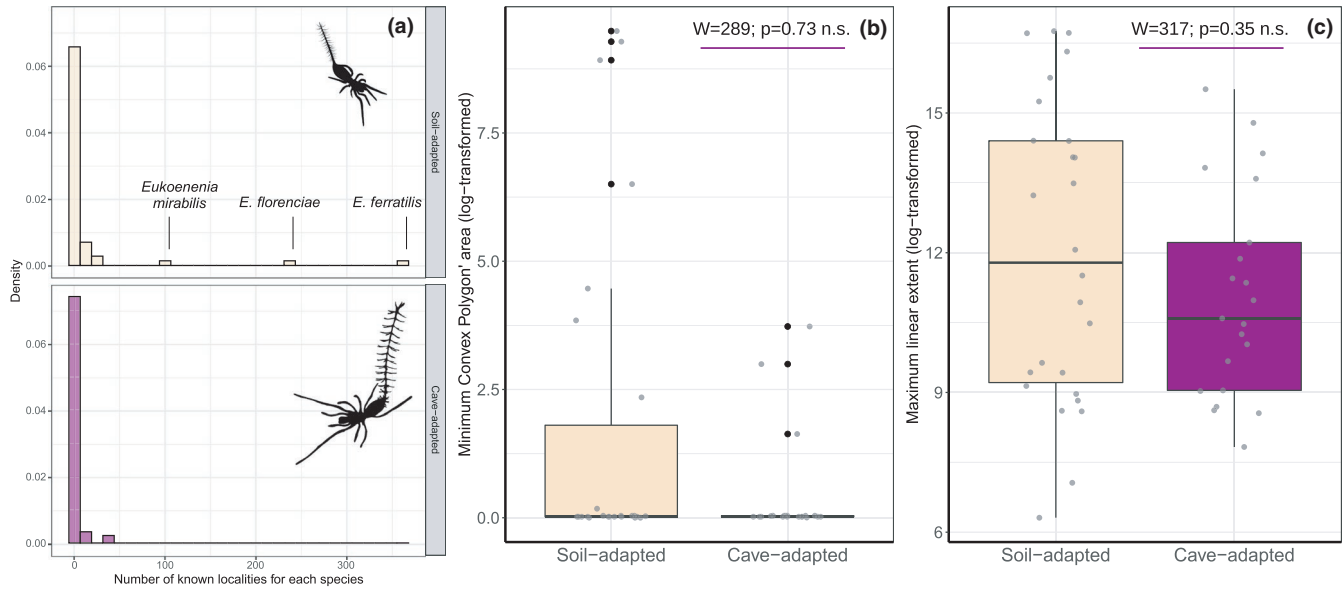


FIGURE 2 Descriptors of distribution range of paligrades. (a) Distribution of number of occurrence localities for soil- and cave-adapted paligrades. (b) Difference in minimum convex polygon' area size between soil- and cave-adapted paligrades. (c) Difference in maximum linear extent values between soil- and cave-adapted paligrades. In b and c values are log-transformed to aid visualization.

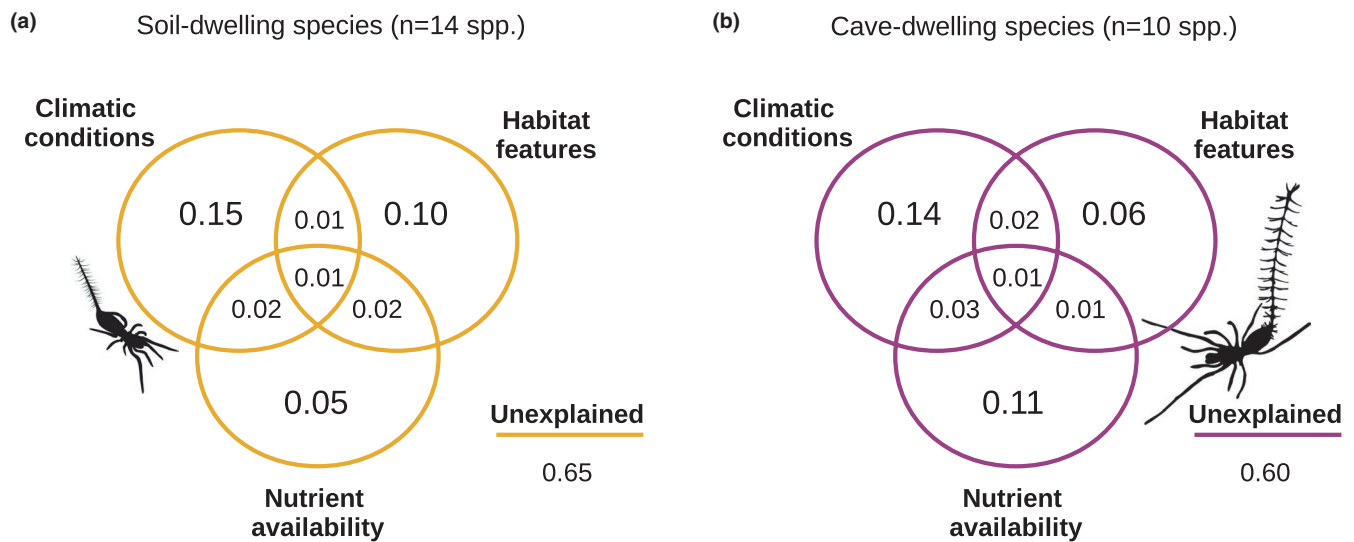


FIGURE 3 Variable contribution for soil- and cave-adapted paligrades according to the variance partitioning analysis. Variable contribution is expressed as pseudo- R^2 . Values at each intersection of sets is the average of contributions estimated for all modeled soil- (a) and cave-adapted species (b).

the model variance (up to 80–90% for few outlying species) remains unexplained (Figure 4h), suggesting that important drivers of distribution patterns are undetected.

3.4 | Species-people correlation

We found a positive, significant relationship between the number of occurrences in each country and the number of researchers studying paligrades (Figure 5), indicating the presence of a species-people correlation effect.

4 | DISCUSSION

4.1 | Distribution patterns and ecology

The picture about distribution patterns reported here is likely to be influenced by non-biological factors, such as sampling bias and species-people correlation. First, paligrades are severely understudied and most of their diversity remains to be disclosed, as emphasized by recent findings of clusters of new species even at rather local scales (Christian et al., 2014; Souza & Ferreira, 2018). Second, the concentration of known localities is likely to reflect the concentration of



researchers studying paligrades. This is a typical bias conditioning our understanding of biodiversity patterns (Fontaneto et al., 2012; Real et al., 2016). Most of the paligrades for which we were able to fit logistic regressions to understand the drivers of distribution were Brazilian and European species, namely those inhabiting areas where a sufficient sample size has been reached thanks to a historical legacy of studies or recent intense local sampling campaigns.

Yet, even if the database is biased and largely incomplete, being the first of its kind it allowed us to draw a preliminary picture of the global distribution patterns of paligrades. We showed that the distribution ranges of both soil and cave *Eukoeneria* species are very narrow even when compared to other subterranean species, and that range size does not significantly differ between the two guilds here considered. This suggests a limited dispersal potential for most species, as also empirically observed for other small-sized soil- and cave-dwelling specialists, such as proturans (Galli & Rellini, 2020) and diplurans (Sendra et al., 2020). An anecdotal example of this low dispersal ability can be found in the case of *Eukoeneria maquinensis* and *E. sagarana*, two cave-adapted paligrades from Brazil. Whereas these species inhabit two caves located at a distance <5 km in an interconnected karst system, a small creek that flows in-between the two caves is seemingly an effective barrier in preventing migration (Souza & Ferreira, 2012).

There were, however, a few outliers, namely species having a range size two orders of magnitude broader than the remaining species (Figure 2a). This is a recurrent ecological pattern in subterranean systems and elsewhere, where communities are generally formed by several rare species and a few common ones (Bregović et al., 2019). It is worth noting that continental-wide distribution has been observed in other soil-dwelling specialists; for example, these patterns can emerge as the result of continental drift paralleled by slow evolution, as in the amphi-Atlantic distributions of Protura (Galli & Rellini, 2020). In our case, the two most significant outliers are *E. floren- ciae* and *E. mirabilis*, two soil-adapted species with parthenogenetic

populations that have probably been moved beyond their historical ranges by humans (Harvey et al., 2006), for example through the soils used in greenhouses. The third outlier, *E. ferratilis*, also has a broad range in the central region of Minas Gerais, Brazil. This area is highly modified by mining activities, but it is unclear whether the species have been dispersed around by humans. Given that some populations show variability in morphological characters, a more detailed taxonomic account would be needed to detect potential overlooked diversity within the nominal species.

Ecological drivers of distribution were similar for both soil and cave species, with climatic conditions, habitat and nutrient availability all emerging as important to some extent. Climate was the most important driver of distribution for the majority of soil and cave species, a result that parallels the observation made in other macroecological accounts on subterranean diversity (Bregović & Zgmajster, 2016; Eme et al., 2015; Mammola, Cardoso, Angyal, et al., 2019). Nutrients emerged as a further important factor, especially for cave species, corroborating previous evidence on the influence of nutrient availability on species richness patterns in caves (Christman et al., 2016; Culver et al., 2006). Conversely, habitat availability was not preponderant in explaining the distribution of cave species. We interpret this as the possible result of our inability to capture micro-scale habitat conditions that likely govern the true spatial niche of paligrades (e.g., Potter et al. 2013).

4.2 | Historical drivers of distribution

4.2.1 | Europe

The large proportion of unexplained variance for both soil- and cave-adapted species suggests that important processes conditioning their distribution have been missed. Broad-scale distribution

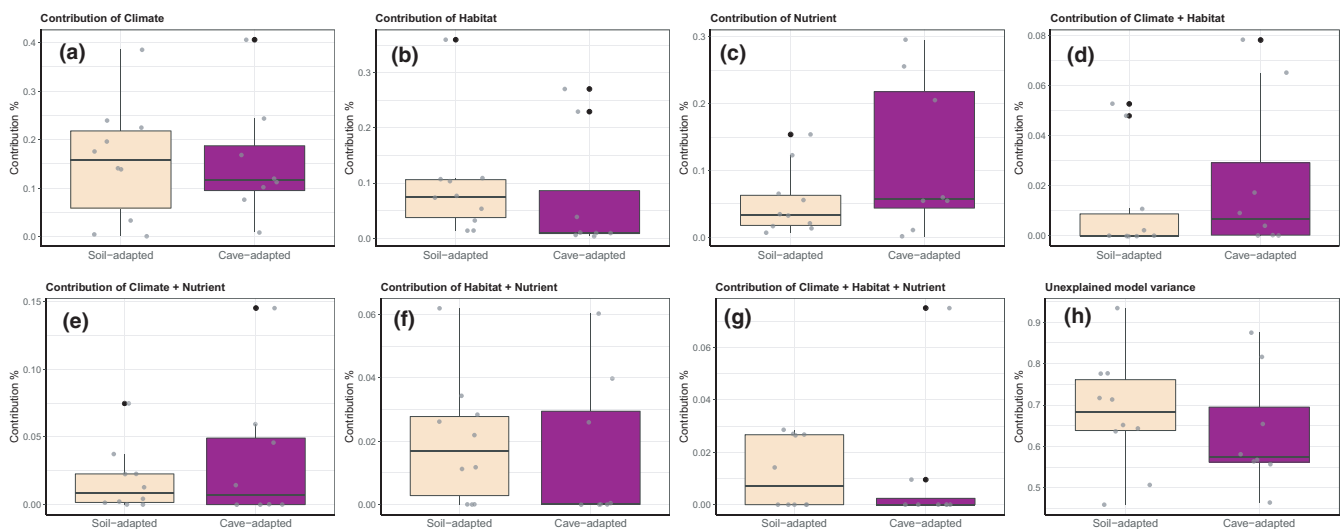


FIGURE 4 Difference in contributing variables between soil- and cave-adapted species according to the variance partitioning analysis. (a–c) Relative contribution of climatic, habitat and nutrient variables alone; (d–g) Contribution of different combinations of variables. (h) Unexplained model variance. Variable contribution is expressed as pseudo- R^2 .

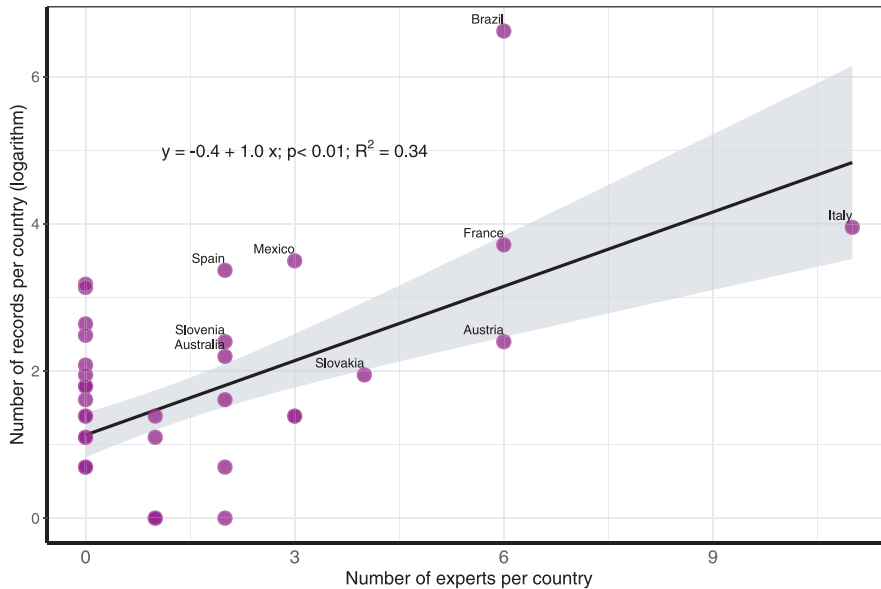


FIGURE 5 Species-people correlation in the distribution dataset. Predicted relationship and 95% confidence interval between the logarithm of the number of records for each country and the number of researchers operating in that country.

patterns are often not only determined by environmental conditions but are also the results of biogeographical and evolutionary processes (Warren et al., 2014). Even though we were not able to account for these effects due to the lack of suitable data, the influence of historical processes seems to be an important missed factor when looking at the distribution of records in the Alps (Figure 6). This is probably the best-documented region regarding palpigrades diversity, due to the relatively high number of studies in Italy (Pantini & Isaia, 2019), Slovenia (Zagmajster & Kováč, 2006) and Central Europe (Blick & Christian, 2004).

We could empirically observe how the current distribution of palpigrades in the Alps bears the signature of different past events related to Pleistocene glaciation cycles (Figure 6). Foremost, all

palpigrades records occur below the southernmost limit of the ice shield that covered northern and central Europe (Holdhaus, 1932). Moreover, by mapping the distribution of occurrences against the paleo-reconstruction of the Last Glacial Maximum ice shield on the Alps, we found that only three records of cave-adapted palpigrades overlapped with ice-covered areas. Most records fall in ice-free areas within the main shield or are located at its border. A similar distribution pattern of species 'tracking the ice' has been documented for other subterranean arachnids such as spiders (Mammola, Goodacre & Isaia, 2018) and harvestmen (Mammola, Goodacre & Isaia, 2019). Finally, we noted how most records of cave species in Europe were comprised within the mid-latitude subterranean biodiversity ridge (Culver et al., 2006), an area of high surface productivity where main

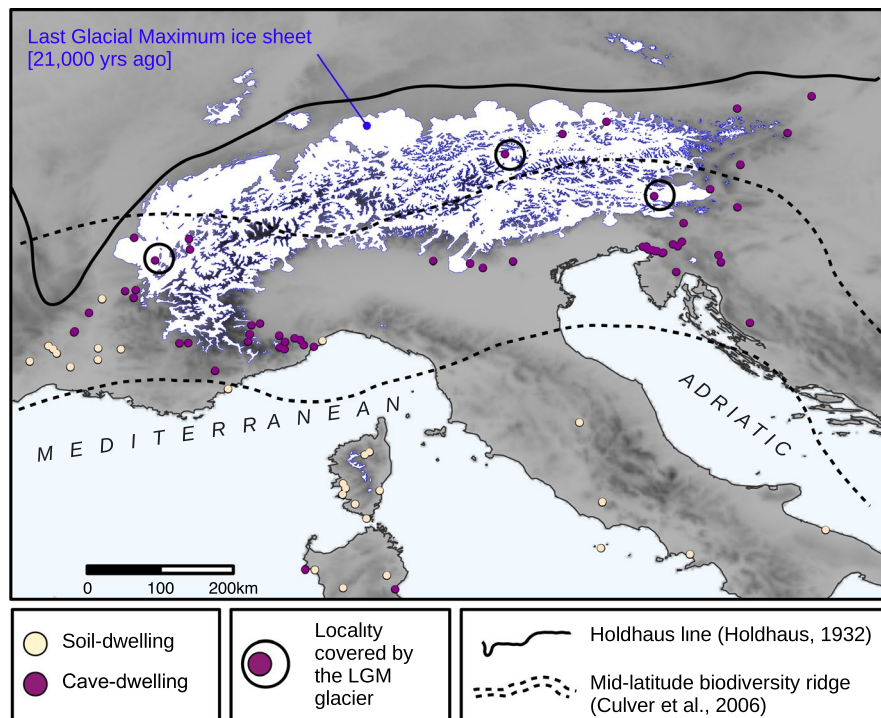


FIGURE 6 Palpigrades distribution in the Alps. Important biogeographic events that seemingly affected palpigrades distribution in this Alps are mapped. First, most occurrences are at the periphery or in ice-free areas within the Last Glacial Maximum ice shield (Ehlers et al., 2011). Second, most records of cave-adapted palpigrades are comprised between 42° and 46° latitude (mid-latitude biodiversity ridge; Culver et al., 2006). Third, all records are below the boundary of the main Pleistocene ice sheet.



hotspots of subterranean diversity are found in temperate regions. Indirectly, this finding may explain why nutrient availability emerged as an important factor in explaining the distribution of cave rather than soil species.

4.2.2 | Brazil

Brazil was the other occurrence-rich area in our database (Figure 1c). The number of species in Brazil has increased 10-fold in recent years (Souza & Ferreira, 2020). Most occurrences are concentrated in the Southeastern region and in a small area in Northern Brazil, a distribution pattern reflecting intense sampling efforts carried out in those caves by research institutions or consulting companies. Still, the actual distribution of the group in the Neotropics may be ampler due to the presence of other karst systems and native forests that have never been sampled.

Even if this picture is still rather crude, the great number of species already discovered emphasizes the importance of the Neotropics as a centre of subterranean diversification of palpigrades (Souza & Ferreira, 2018, 2020). Tropical South America has experienced climatic fluctuations since the beginning of the Pleistocene (Baker et al., 2001). The alternation of wetter and drier periods accompanied by variations in temperature determined significant changes in the distribution of forests (Baker et al., 2001; Carnaval & Moritz, 2008; Cheng et al., 2013). The retractions of forests in drier periods may have been responsible for the isolation of several lineages highly dependent on the humidity inside caves (Gnaspini, 1997). Deep subterranean habitats are characterized by pronounced environmental stability and thermal inertia – including tropical caves, although the climatic stability is seemingly less pronounced (Mejía-Ortiz et al., 2021). Subterranean habitats may thus have acted as ‘climatic refuges’ (Ledesma et al., 2020; Mammola, Piano, et al., 2019) for the survival and diversification of subterranean-adapted species. Likewise, the regions that remained permanently forested at the surface may have been important for the diversification of palpigrades in soils, as similarly observed in other arthropod groups (Hoffmeister & Ferrari, 2016; Peres et al., 2015). However, these explanations remain speculative: detailed studies on divergence time of the Brazilian lineages are needed if we want to understand the extent to which climatic fluctuations and consequent changes in rainfall regime and vegetation cover affected their speciation rates (Mammola, Amorim, et al., 2020).

4.3 | Implications for conservation

Most palpigrades included in this database have not been found beyond the specimens listed in the original description. In a lack of detailed data on the distribution, natural history, and long-term population trends, it is only possible to speculate about the conservation of these species. Yet, the small distribution and poor dispersal capacity of palpigrades can be regarded as intrinsic threats that

make these species vulnerable and susceptible to local extinctions (Mammola, Cardoso, Culver, et al., 2019). In general, habitat degradation and global climate change are among the most significant threats for narrow-ranging arthropods (Cardoso et al., 2020), given that are capable of leading to the local extirpation of populations that, for endemic species, will often correspond to global extinctions.

For example, in Brazil, most habitats of palpigrades are subjected to strong anthropic pressures due to intense mining activities, determining indiscriminate subterranean habitat loss (Souza & Ferreira, 2018). The risk of extinction of Brazilian palpigrades has been recently evaluated in the Red Book of Brazilian Threatened Fauna (ICMBio, 2018), and seven species were listed in a threatened category of extinction risk.

In other areas where human activities are degrading subterranean habitats, it is a priority to estimate the risk of extinction of palpigrades and use this assessment of extinction risk as an instrument to establish protection measures. Whenever reliable data about impacts or plausible near-future threats is available, using geographic and habitat information to assess these species under the current IUCN criteria would be straightforward (Cardoso et al., 2011).

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CONFLICTS OF INTEREST

None declared.

AUTHOR CONTRIBUTION

MFVRS assembled and curated data. SM and MI provided further data from Europe. SM planned the statistical approach, performed analyses and wrote the first draft of the manuscript. MFVRS and RF provided most literature on palpigrades. All authors contributed to the writing.

DATA AVAILABILITY STATEMENT

A curated distribution database of palpigrades will be published in an associated data paper (Souza et al., unpublished). Databases used in the analysis are available in Figshare (<https://doi.org/10.6084/m9.figshare.13265294.v1>). Environmental rasters used in the analyses are freely available in online repositories, namely: (a) climatic variables from WorldClim2 [raster files: “average temperature (°C)” and “precipitation (mm)”; 30 arc-sec resolution]; (b) soil variables from SoilGrid (<https://soilgrids.org/>) [raster files: “Coarse fragments,”

"Soil organic carbon," and "Cation exchange capacity (at pH 7)"; 2 m depth]; and (c) shapefile of carbonatic rocks from the "World map of carbonate rock outcrops" version 3.0 (<https://digital.lib.usf.edu/SFS0055342/00001>).

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**BIOSKETCH**

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Author contribution MFVRS assembled and curated data. SM and MI provided further data from Europe. SM planned the statistical approach, performed analyses and wrote the first draft of the manuscript. MFVRS and RF provided most literature and expertise on palpigrades. All authors contributed to the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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