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Ecology and Conservation of Italian spiders in a climate change scenario

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“In the end, we will conserve only what we love, we will love only what we understand,
and we will understand only what we are taught.”

Baba Dioum

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Abstract

Abstract

Despite their ecological importance and diversity, spiders (Arachnida: Araneae) are underrepresented in conservation research in comparison to other groups. The global response of spider species to the environmental variations has been investigated in detail only in the last few decades, but currently is proving to be a stimulating field of research. This thesis aimed at assessing the status of the conservation of different species of spiders occurring in Italy, focusing on their response to climate change. We firstly reviewed the status of spider conservation at the continental scale, and then we focused on several species mainly threatened by global warming. Our review revealed that existing international legislation considering spiders has limited coverage, as well as national and subnational conservation tools. Northern and Central European countries have the highest percentage of species assessed at the regional level, whereas in the Mediterranean basin, despite the highest spider diversity in Europe, conservation efforts are lacking both in terms of assessments and national or subnational legislation. Stemming from this general framework, we provided detailed insights into the conservation status of several emblematic spider species dwelling in habitats that are mostly affected by the impacts of climate change, namely *Argyroneta aquatica* and *Dolomedes plantarius* (wetlands), *Vesubia jugorum* (high-mountain habitats), species of the genus *Troglohyphantes* and *Histopona palaeolithica* (caves). We investigated present, past and future distribution ranges using species distribution models for different integrated emission scenarios. These, were combined with knowledge on species' dispersal limitation to account for the possibility that the species will not be able to move beyond the current range in the next decades. In one case, models were integrated with phylogeographic analyses to investigate the effects of past and future climate change on species distribution and genetic diversity. For all species, we assessed the extinction risk according to the global and regional guidelines of the International Union for Conservation of Nature (IUCN), and for one species we explored the relationship between habitat suitability and functional traits related to species performance. Overall, we found a common significant future shift towards higher latitudes and altitudes in the geographic range, and a global future reduction in habitat suitability. Ongoing climate change is predicted to cause relevant future impacts on these species and significant decline in their current distribution range and habitat quality. The application of the IUCN criteria qualifies most of them as threatened, raising concerns for the long-term persistence of these species and suggesting potential high risk of local extinction for the most restricted ones. Considering the current threats to the spider species investigated, the protection of large areas of suitable habitat should be considered as the most effective approach to their conservation. Understanding the conservation status and the level of extinction risk faced by poorly known species is one of the greatest challenges facing conservation biology. In the framework of a general lack of knowledge on the conservation status of spiders, the collection of these works aims at providing a significant contribution to the knowledge of the Italian spiders, from the ecological and especially conservation point of view.

1. Introduction

1.1. Climate change and biodiversity responses

Biodiversity is declining at an unprecedent rate.

Available data indicate that current species extinction rate is at least hundreds of times higher than average background extinction rate, suggesting that a sixth mass extinction is actually underway (Barnosky et al., 2011; Ceballos et al., 2015).

Five global threats are considered the main responsible of the biodiversity crisis: habitat loss and degradation, pollution, overexploitation, invasive species, and climate change (IPBES, 2019; see Bellard et al., 2022 for the ranking of the relative importance of these threats).

Global climate change is predicted to become an increasingly dominant problem in the biodiversity crisis over the next several decades (Bellard et al., 2012; Leadley et al. 2010), although a significant impact of climate change has been already detected in ecosystems (reviewed *e.g.* in Hughes, 2000; Hughes & Root, 2005; IPCC, 2001; Parmesan & Galbraith, 2004; Parmesan & Yohe, 2003; Peñuelas & Filella, 2001; Root et al., 2003; Sparks & Menzel, 2002; Walther et al., 2002; Wiens, 2016).

The global average surface temperature has increased by around 1°C over the last century, and is projected to rise by an additional 1°C to 4°C by 2100, depending on the future emission scenario considered (IPCC, 2021). Anthropogenic global warming has been identified as the main cause of many extreme weather and climate events, such as sea-level rise, altered precipitation, extreme temperatures, aridity and droughts, thawing permafrost, glaciers retreat, increase of storms and flooding. Moreover, additional threats emerge as climate change can exacerbate the detrimental effects on biological communities of other stressors such as, for instance, biological invasions, habitat fragmentation or human exploitations (McCarty, 2001; Root et al., 2003). This synergism of multiple pressures together is likely to represent an additional challenge to biodiversity and to its conservation.

The direct and indirect impacts of anthropogenic climate change have been documented to affect all levels of biodiversity, from organisms to biomes (Parmesan, 2006; Bellard et al., 2012). At the most basic levels, climate change likely causes the decrease of genetic diversity of populations, due to directional selection and rapid migration (Hoffmann & Sgrò, 2011). At the highest organizational levels, climate change is able to affect species interactions and therefore to modify community structures and ecosystem functions (Walther, 2010).

Species can potentially respond to the effects of climate change in several ways, from adaptation to extinction. In order to persist, organisms have the capacity to adapt to changing environmental conditions through (i) phenotypic plasticity, *i.e.* the expression of multiple phenotypic states by a single genotype under different environmental conditions (Houston & McNamara, 1992), (ii) microevolution, *i.e.* the genetic adaptation to new conditions through mutations or selection of a trait (Salamin et al., 2010), or (iii) through a combination of both. These mechanisms enable a rapid and effective response to environmental change (Charmantier et al., 2008).

Whatever the underlying mechanisms, species can respond adaptively to climate change by changing their phenology, their physiology, or their range (Bellard et al., 2012; Parmesan, 2006). These three potential responses are not mutually exclusive.

Phenology, *i.e.* the timing of periodic biological events, such as the lifetime pattern in organism growth, development and reproduction in relation to the seasons (Begon et al., 1996), is one of the most apparent responses of the species to the global climate change (Brown et al., 1999; Hughes, 2000; Parmesan, 2006; Parmesan & Yohe, 2003; Sparks & Menzel, 2002). Species respond to climate change by shifting towards earlier spring and delayed fall the timing of key phenological events (Both et al., 2006; Defila & Clot, 2001; Jonzén et al., 2006; Parmesan, 2006; Réale et al., 2003; Root et al., 2003; Roy and Sparks, 2000; Sparks & Menzel, 2002; Visser & Both, 2005; Walther et al., 2002). These phenological changes may help species keep synchrony with changing cyclical abiotic factors. However, a changing phenology may have severe negative consequential effects within the ecological communities, disrupting pre-existing synchrony between interacting species and increasing the mismatch in the seasonal timing between their life-history events and with other ecological factors (Both et al., 2006; Durant et al., 2003; Visser & Both, 2005; Winder & Schindler, 2004).

Although often less obvious than changes in species' phenology, physiological responses to climate change have been documented for many species, both endotherms and ectotherms, in both terrestrial and aquatic environments (Brakefield & de Jong, 2011; Fueller et al., 2010; Gardner et al., 2009; Johansen & Jones, 2011; Sheridan & Bickford, 2011; Somero, 2010). For these species, change in body size, shape, morphology, metabolism and other physical traits may provide better adaptation to changing local climate.

One of the best-documented responses to climate change is the spatial response, that is the shift in the geographical distribution of species tracking their suitable climatic conditions. Species may respond to climate change by moving their range towards different elevations or latitudes, to occupy areas within their metabolic temperature tolerances (Root et al., 2003). Poleward and upward shifts of species ranges have been observed across a wide array of taxonomic groups and geographical localities during the twentieth century (Easterling et al., 2000; Hughes, 2000; McCarty, 2001; Parmesan et al., 1999; Thomas & Lennon, 1999; Walther et al., 2002). These shifts may be composed of (i) range expansions at the cool edge of the species range (higher latitudes and elevations), (ii) range contractions at the warm edge (lower latitudes and elevations), (iii) or of both of them (Wiens, 2016). Rates of range shifts vary greatly among and within species, in relation to differential dispersal abilities, resulting in range expansions or in whole range displacements (Walther et al., 2002). On the other hand, latitudinal and altitudinal range shifts may entail a reduction in range size, particularly in species with limited dispersal, which are not able to track their suitable habitats, and in polar and mountaintop species, which are blocked by physical barriers from following their optimal isotherms (Bellard et al., 2022; Forero-Medina, 2010; Parmesan, 1996; Root et al., 2003).

Regardless of the adaptive response adopted by the species, a major concern is whether species will be able to achieve a sufficient response of any type or to achieve it fast enough to keep up with the rapid pace of change in ecological conditions (Chevin et al. 2010; Huntley et al., 2010; Salamin et al., 2010). The responses of plants and animals to a changing climate are indicative of their natural ability to adapt and evolve, yet future global warming is likely to exceed this ability in many species, resulting in increasing rates of local extinctions (Urban, 2015).

1.2. Climate change and distribution modelling

Given the ongoing extinctions from local to global scale (Parmesan, 2006), there is an increasing need to produce reliable projections of the effects of climate changes on biodiversity and its different levels of response (Visser, 2008). Although several approaches exist for studying the impacts of environmental change on species persistence, methods predicting the spatial response of the species have become the most commonly used tool. Correlative distribution models such as Ecological Niche Models (ENMs) and Species Distribution Models (SDMs) are effective tools to project potential species' distribution changes resulting from climatic change (Elith & Leathwick, 2009; Sillero, 2011; Thomas et al., 2004). These models correlate species occurrence data with environmental predictor variables to estimate the ecological requirements of species and to predict the relative suitability of habitat, and therefore the species' potential distribution (Guisan & Zimmermann, 2000). Occurrence data are mostly simple species presence, presence-absence or abundance observations (Guisan & Zimmermann, 2000). Despite the methodological caveats and limitations of these models (Guisan & Thuiller, 2005; Sinclair et al., 2010), the questioned reliability of their predictions (Davis et al., 1998), and the scepticism on their ability to reflect complex biotic interactions (Dormann, 2007), they have become one of the most popular modelling tools in ecology, biogeography and conservation biology over the past two decades (Leroy, 2022). Moreover, they have been proposed as valuable tools to fill the gaps in the knowledge of species distributions at all possible scales (the so called “Wallacean shortfall”; Cardoso et al., 2011b). This was mainly due to the simplicity and flexibility of their use, to the potentially unlimited number of applications across species and habitats, and to the increasing availability of biodiversity data and open-access analysis software (Zhang, 2017). Considering the difficulties to obtain exhaustive data on the distribution of species, these models offer many advantages for making predictions or inferences, even from incomplete information (Phillips et al., 2006). Because of the ability to predict species' distribution across space and time (Pearson & Dawson, 2003), identify suitable sites and core habitats for species (Guisan & Zimmermann, 2000), and evaluate the invasive potential of non-native species (Jiménez-Valverde et al., 2011), these models recently gained importance as a tool for conservation and management of species (Guisan et al., 2013). Accurate predictions of how species and ecosystems will respond to climate change, assist in implementing specific conservation strategies and in preparing effective conservation management programmes. In addition, since only very few species have been studied in detail in terms of their dynamic responses to climate change, correlative modelling often remains the only approach for studying the possible consequences of a changing environment on the distribution in poorly studied taxa, and are thus becoming increasingly important for predicting the distribution of understudied organisms, such as invertebrates (Mammola et al., 2021).

1.3. Bias in species conservation

Conservation and management of biodiversity in the face of ongoing global change requires the development of robust and reliable information on biodiversity status and trends. Ambitions to limit threats to species and ensure ecosystems integrity, rely on effective documentation on their status and monitoring of their changes over time (Oliver et al., 2021; Rounsevell et al., 2020). However, conservation studies are constrained by data that are taxonomically and geographically biased toward relatively well-studied taxa, such as vertebrates, and areas, such as temperate regions of Europe and North America and their associated ecosystems (Feeley et al., 2016; Troudet et al., 2017).

The majority of studies and reviews that explicitly aim to examine global patterns in the response of species' populations to climate variables focused on temperate regions, particularly in biodiversity hotspots and unpopulated areas, barely including information on the biotic response in tropical ecosystems (Feeley et al., 2016; Lawler et al., 2006). Tropical species are expected to have different responses to climate change than their temperate counterparts, and their exclusion from nearly all major global syntheses on climate change may have detrimental consequences on the conservation of tropical ecosystems, and may preclude a comprehensive understanding of the global effects of climate change (Feeley et al., 2016; Lenoir & Svenning, 2015). Similarly, a greater attention has been given to terrestrial ecosystems compared to aquatic ones (Lawler et al., 2006). Beyond geographic bias, most studies also suffer from a severe taxonomic bias. The scientific focus of the conservation research is oriented toward a small subset of species, while most of the biodiversity remains unknown or unstudied. Vertebrates, in particular, are overrepresented across a wide range of biological disciplines, although they represent only a small fraction of the Tree of Life (Donaldson et al., 2016; Troudet et al., 2017). Even within vertebrates, there is a strong bias towards charismatic endotherms such as mammals and birds, which receive more scientific attention per species than other groups (Lenoir & Svenning, 2015). This taxonomic bias, also referred to as "taxonomic chauvinism" (Bonnet et al., 2002), is pervasive in scientific literature in general, and even more in conservation research (Clark & May, 2002; Leather, 2009; Troudet et al., 2017).

Despite their global dominance in terms of richness, abundance and biomass, invertebrates are highly underrepresented in conservation studies (Cardoso et al., 2011b; Clark & May, 2002; Hochkirch, 2016; Stork, 2018; Titley et al., 2017; Troudet et al., 2017), resulting in them being underrepresented in conservation programmes, both at regional and international scales, such as in the International Union for Conservation of Nature (IUCN) Red List (Cardoso et al., 2011a). The global number of invertebrate species is unknown (the so-called “Linnaean shortfall”), as well as their distributions (“Wallacean shortfall”), abundances (“Prestonian shortfall”) and life histories (“Hutchinsonian shortfall”) (Cardoso et al., 2011b). This is in part due to taxon-specific limitations that make more difficult to work with invertebrates than with other groups, such as their extreme species richness, their ubiquity across space and time, and the difficulties related to study their diversity and their life history (Cardoso & Leather, 2019; Pawar, 2003; Troudet et al., 2017). Moreover, limited time and resources tend to polarize scientific attention and research efforts toward well-known, charismatic organisms, able to better attract societal preferences and public support, and therefore funds for conservation. Attractive “flagship” and “umbrella” species, for example, have been widely used to raise funds that support a variety of conservation initiatives (Caro, 2010), even if the effectiveness of this practice is now strongly questioned (Simberloff, 1998; Smith et al., 2012). In turn, funding allocation and public awareness influence the choice of research topics and how resources are allocated in scientific projects, in a complex feedback system in which scientific activities and research priorities act as the main drivers but are themselves influenced by both conservation policy and public perception of conservation needs (Martín-López et al., 2009).

Besides compromising the quality and reliability of the data available for biodiversity research, these scientific shortfalls lead to underestimate the effects of climate change and their intensity on the invertebrates, biasing the evaluations of their real rate of extinction and threat. Compared to vertebrates, invertebrates have similar or even higher extinction rates and proportions of threatened species (Cardoso et al., 2011a; McKinney, 1999; Moir et al., 2010), and are in urgent need of protection and monitoring (Cardoso et al., 2020; Samways et al., 2020).

As a consequence, the effects of such biases are also reflected in investment allocation and conservation projects, such as species action plans and species reintroductions, with the distribution of funds and projects to vertebrates being significantly highly overrepresented (Clark & May, 2002; Davies et al., 2018; Mammola et al., 2020b; Seddon et al., 2005; Titley et al., 2017). On average, each arthropod species received 1,000 times less funding for its conservation than each mammal species (Cardoso et al., 2011b). Focusing on large vertebrates only, does not guarantee the conservation of other species, resulting in less funding for other species' research (Ford et al., 2017).

Accordingly, there is the urgent need of data for conservation research, in order to have a more comprehensive picture of the elements that are now underrepresented, both at a taxonomic and geographic level (Cardoso et al., 2020; Wagner et al., 2021).

1.4. Spider conservation in Europe

Among terrestrial invertebrates, spiders (Arachnida: Araneae) are one of the most important groups in terms of abundance, diversity, biomass, evolutionary history and functional roles (Cardoso et al., 2008, 2011c; Coddington & Levi, 1991; Coddington et al., 1991, 2009; Dunlop et al., 2018; Foelix, 2011; Jocqué et al., 2013; Mammola et al., 2017; Nentwig, 2013; Turnbull, 1973). With more than 50,000 species currently described (World Spider Catalog, 2022), spiders are among the most common and ubiquitous animals in the majority of terrestrial habitats, from richly vegetated areas to deserts, from mountain summits to caves (Turnbull, 1973). A few species have even conquered the aquatic environment (McQueen & McLay, 1983; Seymour & Hetz, 2011).

Preserving spider diversity is essential as they play a fundamental ecological role both as preys and predators in most terrestrial ecosystems (Nyffeler & Birkhofer, 2017), thus provide vital ecosystem services to humans with respect to the control of arthropod pests in agroecosystems (King & Hardy, 2013; Michalko et al., 2019). Moreover, their silk, venom and hemolymph are a source of inspiration for biological engineering (Heim et al., 2009), pharmacology, and medicine (Corzo & Escoubas, 2003; Pineda et al., 2018). Due to their ecological requirements, their high sensitivity to small changes in habitat structure and their rapid responses to disturbance, spiders are considered reliable potential indicators of environmental change (Ghione et al., 2013; Maelfait & Hendrickx, 1998; Marc et al., 1999; Ossamy et al., 2016; Pearce & Venier 2006; Schwerdt et al., 2018; Scott et al., 2006).

Nevertheless, the global response of spider species to the potential effects of climate change has been investigated in detail only in the last few decades (Jiménez-Valverde & Lobo, 2007; Krehenwinkel & Tautz, 2013; Leroy et al., 2013, 2014; Mammola et al., 2018; Monsimet et al., 2020).

Compared to more popular groups of invertebrates, spiders are lagging in conservation studies and policies worldwide. Even in areas such as Europe where species are relatively well known, the support given to their conservation is markedly unfulfilling. For example, only one species among the nearly 5,500 spider species known from Europe (Nentwig et al., 2022), is listed in the EU Habitats Directive, whereas 50 butterflies out of 496 and 16 dragonflies out of 143 feature, demonstrating a remarkable taxonomic bias even within invertebrates (Cardoso et al., 2011a). Furthermore, extinction risk has been assessed for fewer than 100 European species in the Global Red List of the International Union for Conservation of Nature (IUCN), mostly from the Macaronesian archipelagos of Madeira and Selvagens (Cardoso et al., 2017). By comparison, the extinction risk of 97% of European butterflies (van Swaay et al., 2010) and dragonflies (Kalkman et al., 2010) has been assessed.

1.5. Case studies

In this work, we focused on some habitats that are expected to be particularly vulnerable to climate change. High-mountain habitats, wetlands and caves are examples of habitats where the effects of human-induced climate change on local communities are already noticeable, and are contributing to changes in species distribution and abundance (Finlayson et al., 2019; Mammola et al., 2018; Nogués-Bravo et al., 2007). Direct effects of climate change on spatial distribution, abundance and population dynamics are apparent in spiders, which, in common with other invertebrates, are heavily influenced by environmental conditions, and are thus reliable indicators of climate change effects on biodiversity.

1.5.1. Wetland spiders

In wetlands, climate change is causing large-scale degradation and loss of habitats through direct and indirect effects of changes in temperature, precipitation and humidity, and subsequently in patterns of evapotranspiration, alterations in hydrological regimes, and increases in the frequency of extreme climate events such as floods and droughts (Davidson, 2014; Erwin, 2009; Finlayson et al., 2019). Many species are intimately associated with wetlands, including spiders. *Argyroneta aquatica* (CLERCK) (Araneae: Dictynidae), and *Dolomedes plantarius* (CLERCK) (Araneae: Pisauridae), are two spider species closely associated to these habitats which appear to be particularly sensitive to global warming, either through direct effects on their physiology and their inability to adapt to warming temperatures, or through indirect effects as a result of wetland drying and degradation. Despite their wide Palearctic distribution, both spiders are locally rare and their distribution is fragmented, as wetlands are often few and far apart across their geographical range. This has implications on the species ability to move northwards or upwards as frequently observed for more mobile taxa. Accordingly, both species are the most commonly protected by national laws and included in Red Lists of European countries. In addition, *D. plantarius* has been classified as Vulnerable by the International Union for Conservation of Nature (IUCN) in 1996 (World Conservation Monitoring Centre, 1996), although this assessment pre-dates publication of the new IUCN standards (version 3.1, 2001) which precludes its comparison with current assessments. It is therefore, due for re-assessment.

1.5.2. High-mountain spider

High-mountain habitats are predicted to be particularly vulnerable to temperature variations. These habitats are suffering by warming temperatures that are approximately doubling the global average (Böhm et al., 2001), with a predicted greater risk of habitat loss and local extinction for alpine species. *Vesubia jugorum* (SIMON) (Araneae: Lycosidae) is an endemic alpine spider, restricted to the high-altitude rocky areas of the South-western Alps, at the border between France and Italy. Due to its restricted geographic range, its sensitivity to global warming and the continuing decline in its future bioclimatic range, this species has been assessed as Endangered in the IUCN Red List (Isaia & Mammola, 2018).

1.5.3. Cave spiders

Anthropogenic global warming is expected to significantly influence and modify the underground climate (Badino, 2004; Domínguez-Villar et al., 2014; Mammola et al., 2019c). Subterranean ecosystems and their conenoses are more sensitive to perturbation than other habitat types, because most subterranean species have lost the ability to withstand temperature variations over their evolutionary history (Mammola et al., 2018).

Spiders have undergone a relevant diversification in subterranean habitats (Mammola & Isaia, 2017; Mammola et al., 2018; Mammola et al., 2019c). In particular, species of the genus *Troglohyphantes* JOSEPH (Araneae: Linyphiidae) show a remarkable preference for subterranean habitats, mainly occurring in cold, wet and dark habitats such as caves, bunkers, mines, soil litter, rocky debris and other moist and shaded retreats (Mammola et al., 2018). These spiders are predominantly distributed in the main European mountain ranges, and are often restricted to very narrow areas, sometimes to just one or a few localities (Deeleman-Reinhold, 1978; Isaia et al., 2011, 2017; Mammola et al., 2018). *Troglohyphantes* spiders display different levels of subterranean habitat specialisation. Species found in both caves and surface habitats are often able to withstand ecological variations, while others are almost exclusively found in caves and are characterised by behavioural, physiological and morphological adaptations to the stringent conditions of the subterranean habitat (Deeleman-Reinhold, 1978; Isaia et al., 2017; Mammola et al., 2020a, 2022). These adaptive traits include reduction or loss of eyes and cuticular pigmentation, thinning of the integument, heavier spination, appendage elongation, reduction in the metabolic rate leading to higher resistance to starvation, alteration of the circadian rhythm, reduction in fecundity, slower development, delayed maturation and extended longevity when compared with their surface relatives (for a review, see Mammola & Isaia, 2017). As demonstrated by means of ecological niche modelling and physiological experiments (Mammola et al., 2018, 2019c), the increased specialisation to subterranean habitats seen in *Troglohyphantes* spiders, resulting from a long evolutionary history in a thermally stable environment, is accompanied by the concomitant narrowing of their thermal tolerance. While most species living close to the surface or in shallow subterranean environments have retained their ability to withstand temperature variations, specialised subterranean species of *Troglohyphantes* have lost such thermoregulatory mechanisms and are, therefore, particularly vulnerable to potential subterranean climatic variation induced by climate change (Mammola et al., 2019d). Despite being intensively studied from taxonomic, ecological and biogeographic standpoints, knowledge on the status of conservation and on the potential risk of extinction of these spiders is currently lagging.

Similarly to *Troglohyphantes,* the genus *Histopona* THORELL (Araneae: Agelenidae) also exemplify remarkable radiation in subterranean habitats. Within the genus, *H. palaeolithica* (BRIGNOLI) is renown in the Italian fauna for exhibiting a high level of subterranean adaptation, being the only *Histopona* species in Italy bearing six functional eyes rather than eight (Brignoli, 1971). This spider also remarkable lacks pigmentation. The species was described based on a female collected in 1967 in a cave on the Western Ligurian Prealps (Italy), but had never been collected after the original description and the male was as yet undescribed (Pantini & Isaia, 2019).

Fig. 1. Spider species considered in this thesis. *Argyroneta aquatica* (above left, Photo credit: Emanuele Biggi); *Dolomedes plantarius* (above right, Photo credit: Emanuele Biggi); *Histopona palaeolithica* (below left, Photo credit: Emanuele Biggi); *Vesubia jugorum* (below center, Photo credit: Nicolas Henon); *Troglohyphantes konradi* (below right, Photo credit: Francesco Tomasinelli).

2. Objectives

This work aims at assessing the status of the conservation of different spider species occurring in Italy, with a special focus on their response to climate change.

The topic of spider conservation has been developed following two different lines of inquiry. In the first one, the status of the spider conservation has been investigated at the continental scale, in order to depict the overall pattern of the current state of the art in Europe. Stemming from this general framework, the second line of inquiry focused more specifically on some emblematic threatened species occurring in Italy. In particular, the focus was on spider species occurring in habitats that are expected to be deeply impacted by climate change effects. In relation to their little flexibility to adjust to rapid environmental changes, high-mountain habitats, wetlands and caves were selected as insightful models for determining the effects of climate change on spiders. Accordingly, we aimed at shedding light on the impacts on the distribution and survival of climate-sensitive species, by integrating available information with specific field activities.

The results of the thesis are structured in eight papers, which are summarized in Table 1.

In **Paper I** (Milano et al., 2021), we provided an overview of the extant international and regional conservation tools focusing on spider conservation in Europe, and we reported all available information concerning the legal protection and conservation status of spiders in 42 European countries. We pointed out general patterns, limitations, gaps, and future directions of the field of the conservation of spiders, providing information on the most relevant current threats to survival and on the conservation needs of spider species in Europe.

In **Paper II** (Milano et al. 2018), we investigated the distribution of *Dolomedes plantarius* in Italy and the conservation status of the Italian populations, underlying the need for deepening the knowledge about their distribution and ecology, and the importance of their conservation in the framework of the overall conservation of the species.

In **Paper III** (Milano et al., 2022b), we extended the target to the global distribution of *Argyroneta aquatica* and *Dolomedes plantarius*, evaluating future trends in their geographic range *via* species distribution models. The modelling results provided the baseline for the first assessment of the extinction risk of the two species according to the current IUCN Red List Categories and Criteria, at both global and regional levels.

In **Paper IV** (Milano et al., 2023), we provided updated information on several aspects regarding the distribution, habitat characterisation, life history and conservation of *Vesubia jugorum*, in order to shed light on the species life cycle and phenology.

In **Paper V** (Mammola et al., 2019b), we investigated the relationship between habitat quality, predicted by species distribution models, and the individual performance of the natural populations of *Vesubia jugorum*, measured by means of morphological and reproductive traits.

Species distribution models, projected to past and future climatic scenarios, have been integrated with phylogeographic analyses in **Paper VI** (Milano et al., in preparation), in order to investigate the biogeographic events that shaped present day population structure of *Vesubia jugorum*, to evaluate the degree of genetic differentiation among its populations and their dispersal capacity, and to assess the sensitivity of the species to past and future global climate change.

In **Paper VII** (Milano et al., 2022a), we assessed the conservation status of the Alpine and the North-western Dinaric species belonging to the genus *Troglohyphantes*, according to the IUCN Red List Criteria.

In **Paper VIII** (Mammola et al., 2019a), we reported the discovery of a new population of *Histopona palaeolithica*, species never been collected after the original description, and we provided the first description of the male and the re-description of the female. In light of the rarity of this specialized stenoendemic species, we provided general information on its ecology and conservation status, as well as the information to assess its extinction risk based on the IUCN guidelines.

Table 1. Summary of the papers presented in this thesis with indication of their respective focal species, geographical setting, considered level of conservation, and full reference.

	Habitat	**Species**	**Geographic setting**	**Conservation level**	**Papers**
Paper I	Multiple	Multiple	Europe	Global and Regional	Milano et al. (2021). Spider Conservation in Europe: a review. *Biological Conservation*, **256,** 109020
Paper II	Wetlands	*Dolomedes plantarius*	Italy	Regional	Milano et al. (2018). Notes on the Italian distribution of *Dolomedes plantarius* (Clerck, 1757), species assessed for the IUCN Red List (Araneae: Pisauridae). *Fragmenta entomologica*, **50(1),** 69–74
Paper III	Wetlands	*Argyroneta aquatica*, *Dolomedes plantarius*	Europe	Global and Regional	Milano et al. (2022b). Trends in habitat suitability and conservation status of aquatic spiders in Europe. *Biological Conservation*, **257,** 109767
Paper IV	High-mountain habitats	*Vesubia jugorum*	Southwestern Alps	Global	Milano et al. (2023). Natural history and conservation of the wolf spider *Vesubia jugorum* (Araneae: Lycosidae), assessed as Endangered in the IUCN Red List. *Zoosystema*, **45(1),** 1–11
Paper V	High-mountain habitats	*Vesubia jugorum*	Southwestern Alps	Global	Mammola, Milano et al. (2019b). Associations between habitat quality, body size and reproductive fitness in the alpine endemic spider *Vesubia jugorum*. *Global Ecology and Biogeography*, **28(9),** 1325–1335
Paper VI	High-mountain habitats	*Vesubia jugorum*	Southwestern Alps	Global	Milano et al. (in preparation). Understanding past and future response to climate change of the IUCN endangered spider *Vesubia jugorum* (Araneae, Lycosidae).
Paper VII	Caves	*Troglohyphantes* spp.	Alps and Northwestern Dinarides	Global	Milano et al. (2022a). Species conservation profiles of the endemic spiders *Troglohyphantes* (Araneae, Linyphiidae) from the Alps and the north-western Dinarides. *Biodiversity Data Journal* **10,** e87261
Paper VIII	Caves	*Histopona palaeolithica*	Ligurian Alps	Global	Mammola, Milano et al. (2019a). Taxonomy, ecology and conservation of the cave-dwelling spider *Histopona palaeolithica*, with the description of *H. petrovi* sp. nov. (Araneae: Agelenidae). *Journal of Arachnology*, **47(3),** 317–325

3. Material and Methods

3.1. Data source

In **Paper I**, we collected all the data concerning the status of conservation in Europe by means of a comprehensive literature survey. We investigated all available conservation tools concerning spiders in Europe at international and regional levels. These included international conventions, regulations and EU Directives, national and subnational acts in force in the European countries considered, the IUCN Red List of Threatened Species, Regional Red Lists and Red Data Books. We examined 42 European countries that are included in the European spider network "Araneae – Spiders of Europe" (Nentwig et al., 2022). In order to have a standard reference for all countries considered, we derived national species checklists from the database "Araneae – Spiders of Europe" (Nentwig et al., 2022). For each country examined, we obtained all the published local Red Lists, Red Books and legal acts concerning spiders, by means of literature surveys and with the assistance of a wide network of local experts and contributors. Whenever a country was not covered, information was derived from bibliographic surveys. We considered only the most recent versions of the regional Red Lists and Red Data Books and the currently valid legislation, and we carried out separate analyses on the different geographic levels adopted in each.

Data on the model species investigated in the other papers, have been collected by means of literature surveys and field collections. For all the species, we compiled comprehensive georeferenced datasets of occurrences, issued from scientific literature, grey literature, online databases (mainly Araneae.it, Araneae – Spiders of Europe, and GBIF), private and Museum collections, and personal communications from European arachnologists.

In addition, for some species, namely *Dolomedes plantarius* (**Paper II**), *Vesubia jugorum* (**Papers IV**, **V** and **VI**), certain species of *Troglohyphantes* (**Paper VII**), and *Histopona palaeolithica* (**Paper VIII**), data from literature has been integrated with observations and original data collected during field surveys carried out across the species' known distribution range. For *D. plantarius*, the field activities focused specifically on northern Italy (**Paper II**). Some specimens of *V. jugorum*, were collected alive in the field for laboratory rearing, to analyse aspects of life cycle and natural history of the species (**Paper IV**).

3.2. Acquisition of trait measures

We considered a functional trait as a morphological feature, measured at the individual level, which reflects individual performance (Violle et al., 2007). We measured morphological and reproductive traits in the specimens of *Vesubia jugorum*, aiming to assess the fitness of the species (**Papers IV**, **V** and **VI**).

The body size of a predatory arthropod determines its ability to thrive and the proportion of resources that it can allocate to reproduction. A direct relationship between body size and reproductive success has been demonstrated in a number of spider species, including wolf spiders (Ameline et al., 2018; Anderson, 1990; Uetz et al., 2002). Egg-case (cocoon) size constitutes another indirect measure of fitness (Bowden et al., 2013; Marshall & Gittleman, 1994). These functional traits, measured at the individual level, constitute reliable proxies for the health of the populations (Jakob et al., 1996; Sokolovska et al., 2000).

For the morphological analysis we included only adult females, due to the variation in the size of juveniles and to the low number of males collected.

In **Paper V**, we measured five morphological traits related to the overall body size, namely femur, tibia and metatarsus length of the leg I, and carapace length and width. We used both leg and carapace measures because they are well correlated with the overall body size of spiders (Elgar et al., 1990; Hagstrum, 1971) and their sizes in adults are fixed. We also estimated cocoon size, as trait related to the reproductive success. In **Paper IV**, we measured the size of the femur of the fourth leg (femur IV) and the size of the cocoons. In **Paper VI**, we measured the length of the carapace and of the femur IV.

All the measurements of the morphological traits were carried out in laboratory, through Leica M80 stereoscopic microscope (up to 60 × magnification). To standardize data acquisition, we derived measurements from digital pictures taken with a Leica EC3 digital camera and calculated with Leica LAS EZ 3.0 software (Leica Microsystems, Switzerland) (Fig. 2a). All the measurements of the reproductive traits have been conducted in the field with a digital calliper (Fig. 2b).

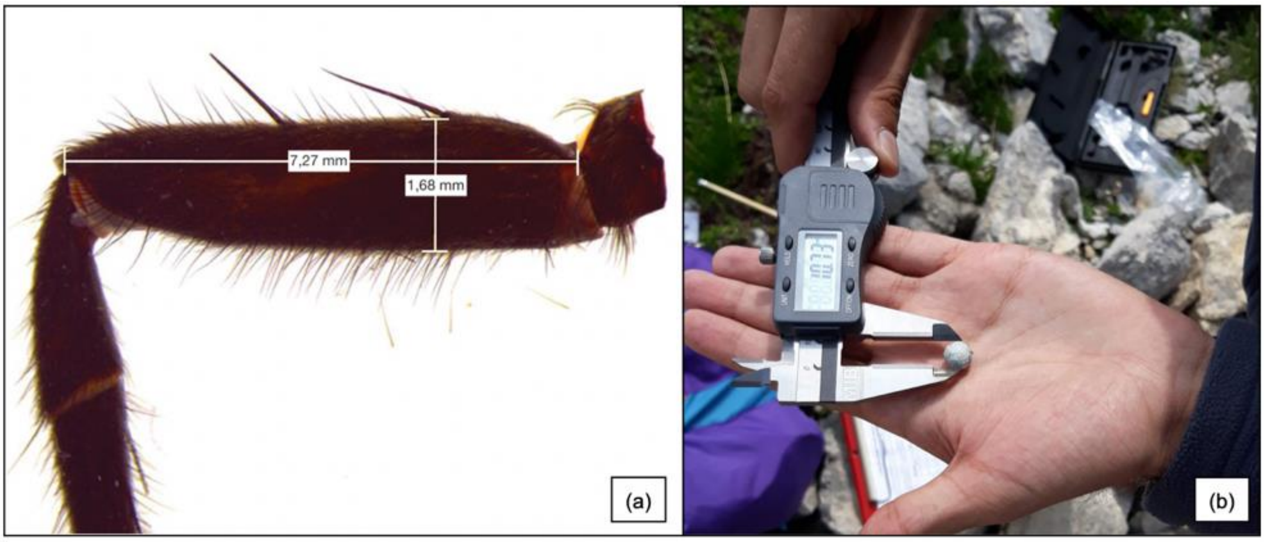


Fig. 2. Acquisition of the trait measures used in Papers IV, V and VI. (a) measurement of leg IV through Leica M80 stereoscopic microscope; (b) measurement of the cocoon diameter with a digital calliper.

3.3. Species distribution modelling

We modelled the potential distribution of some of the species considered in this work by using Species Distribution Models (SDMs). There exists a large suite of algorithms for modelling the distribution of species (Peterson et al., 2011), but it remains debated whether one algorithm is more suitable than another for modelling the distribution of terrestrial invertebrates (Mammola et al., 2021). Maximum Entropy (MaxEnt) is one of the most popular correlative modelling methods for analysing presence-only data (Elith et al., 2011; Phillips et al., 2006), and proved to be a robust species distribution modelling technique according to comparative studies (Elith et al., 2006; Valavi et al., 2021).

Given the overall lack of reliable absence data for our model species, in **Papers III**, **VI** and **VII** we constructed species distribution models using MaxEnt.

In **Paper V**, we combined MaxEnt with generalised boosted regression model (GBM) and generalised additive model (GAM), in order to generate a final model to represent the current distribution of the model species.

We modelled the current distribution range of the species using a combination of climatic and topographic variables, and, in **Paper V**, geomorphological variables. In general, we extracted the standard 19 bioclimatic variables for "present" conditions (1970–2000) and elevation data from WorldClim 2 (Fick & Hijmans, 2017), at different spatial resolutions according to the extent of the study areas. Principal Component Analyses were performed on the predictor variables to generate new axes that summarized variation in fewer, independent dimensions, thereby minimizing multicollinearity among variables.

In **Paper V**, for *V. jugorum* we selected the initial set of predictors on the basis of our knowledge of the species' biology. To represent the climate of the Maritime Alps in which the species occurs (Patsiou et al., 2014), we selected three climatic variables reflecting continentality: mean annual temperature, annual temperature range and cumulative annual precipitation. To represent non-climatic aspects of the species niche (Mammola et al., 2016; Tongiorgi, 1969), we generated variables representing the snow coverage, the distribution of rocky lands and of topographical variables such as roughness and slope exposure. Finally, to avoid collinearity among predictors, we calculated pairwise Pearson correlations and applied a standard $r > |0.70|$ threshold for removal of variables (Dormann et al., 2013).

In **Papers III** and **VII**, species dispersal ability has been taken into account in developing distribution models across the species' entire range, by filtering the aquatic habitats with a 2-km buffer around the wetlands (**Paper III**), and by buffering each occurrence records by a diameter of 60 km (100 km for a few species) (**Paper VII**).

We evaluated model performance with the Boyce index (Boyce et al., 2002). This is an appropriate metric when lacking absence data (Hirzel et al., 2006). Once the models had been validated, we generated final models using the full set of occurrence models and projected it into recent climate. For some species, we then projected the results into ancestral (**Paper VI**) and future (**Papers III** and **VI**) climatic conditions, in order to estimate variations in the distribution ranges relative to past and future climate changes.

To project the potential distribution of *Vesubia jugorum* into the past climatic conditions (**Paper VI**), we obtained downscaled and calibrated Paleoclimatic data for the Last Glacial Maximum (~21,000 years ago) from the Earth System Model based on Model for Interdisciplinary Research on Climate (MIROC-ESM; Watanabe et al., 2011).

To predict the future global distribution of the species considered in **Papers III** and **VI**, we used a new set of integrated emission scenarios, combining the Representative Concentration Pathways (RCPs) with specific socioeconomic and technological development, *i.e.* the Shared Socioeconomic Pathways (SSPs), as discussed in van Vuuren et al. (2014) and O'Neill et al. (2016). The SSPs are reference pathways describing plausible alternative trends in the evolution of society and ecosystems over a century timescale (O'Neill et al., 2014). We selected a sustainable (RCP2.6, SSP1) and a fossil-fuelled (RCP8.5, SSP5) development scenario and projected these in distinct 20-year-period outcomes, using different Coupled Model Intercomparison Project Phase 6 (CMIP6) climate models

3.4. IUCN assessment

We evaluated the extinction risk of the model species by assessing them against all five IUCN criteria (A–E), in accordance with version 3.1 of the IUCN Red List Categories and Criteria (IUCN, 2001).

We also evaluated the regional conservation status of *Argyroneta aquatica* and *Dolomedes plantarius* for each of the four European regions considered in **Paper III** (Northern, Western, Southern and Central-Eastern Europe), following the regional IUCN guidelines (IUCN, 2012a). If testing against different criteria resulted in different categories, the species was classified in the highest of the obtained categories of threat (IUCN, 2001).

We estimated the current and predicted Extent of Occurrence (EOO) and Area of Occupancy (AOO) using the respective functions in the R package 'red' (Cardoso, 2017).

For species with narrow distribution ranges or for which we had confidence about range limits, we used the minimum convex polygon encompassing all observations to calculate EOO and the 2 x 2 km cells known to be occupied to calculate AOO. When EOO was smaller than AOO, it was made equal as per the IUCN guidelines (IUCN Standards and Petitions Committee 2019).

For species for which we do not have full confidence about range limits, we modelled the range via species distribution modelling (see 3.3). In **Paper III**, to calculate EOO and AOO, we used a threshold value that maximises the sum of sensitivity and specificity (*sensu* Liu et al., 2013) to convert probability maps into binary maps of suitable *vs.* unsuitable areas. EOO and AOO were also calculated for each of the four European regions considered. Conversely, in **Paper VII**, we calculated EOO and AOO reporting their lower and upper confidence limits and the consensus values, calculated as all the cells predicted to be suitable for the species in at least 97.5%, 2.5% and 50% of the runs, respectively.

Moreover, general information on the ecology, life history, habitat and possible threats throughout the species range, as well as other information useful for assessing their extinction risk, has been provided for each species considered.

In **Paper III**, to quantify the impact of the future scenarios on predicted availability of suitable habitats for *A. aquatica* and *D. plantarius*, and therefore to estimate the future trends in their geographic range and population size at both global and regional levels, we measured the percent change in mean habitat suitability [(future – current) / current)*100] according to the worst of the two emission scenarios adopted (SSP5-RCP8.5), following a precautionary approach (*i.e.* the most prudent foresight for the conservation of the species, considering the range of different likely future outcomes predicted by the models). In addition, we also measured the change in mean habitat suitability considering a "no-dispersal" scenario, a condition based on the assumption that these species may not be able to track climate change, in relation to their limited dispersal abilities (Monsimet et al., 2020, 2022) and the general fragmentation of the landscape ('M area', according to Barve et al., 2011). For the assessment, the future trends have been calculated in accordance with the IUCN guidelines over a time period of 10 years, assuming a linear trend between the current and the first future timeframe (2021–2040). Long-term trends of habitat suitability have been estimated using the second future timeframe (2041–60).

3.5. Genetic analyses

In **Paper VI**, we conducted phylogeographic analyses to elucidate the evolutionary history and the present distribution pattern of *Vesubia jugorum*.

We removed one leg from each specimen of *Vesubia jugorum* collected for DNA extraction. After DNA amplification and sequencing, the final sequences were aligned after adding two outgroups.

Descriptive statistics (number of haplotypes, haplotype diversity, nucleotide diversity) of each sampling locality and haplogroup were calculated, and the geographic structure was visualized by building a median-joining haplotype network.

Pairwise genetic distances within and between sampling localities were calculated as % uncorrected *p*-distances with 1000 non-parametric bootstrap replicates. Similarly, genetic distances were calculated also within and between haplogroups. Genetic distances were also plotted against geographic distances, the latter calculated from sampling coordinates. A Mantel test (Mantel, 1967) was then performed to evaluate a correlation between genetic and geographic distance matrices.

Phylogenetic inference was performed using both maximum likelihood (ML) and Bayesian inference (BI). The substitution rate was obtained from literature, since no reliable fossil records or well-dated biogeographic events were available for calibrating the tree, and was set to 0.01679 substitutions per million years, as obtained by Piacentini & Ramirez (2019) for the COI gene in the family Lycosidae.

In order to assess the presence of cryptic species, a DNA-based species delimitation technique was applied.

4. General Discussion

4.1. Spider Conservation in Europe (Paper I)

Despite their ecological importance and diversity, spiders are underrepresented in conservation policies in comparison to other groups. In **Paper I** we reviewed all extant conservation tools focusing on spiders in Europe. Only nine spider species occurring in Europe are considered in international conservation tools. One is included in the Bern Convention and in the Habitats Directive, whilst the remaining eight are listed in the Global IUCN Red List of threatened species.

At the national and subnational levels 178 species are mentioned in the legislation of 19 European countries (Fig. 3). Central-Eastern European countries have the highest number of protected species. Conversely, Northern European countries have a very low percentage of species protected, but the lowest percentage of threatened species, possibly in relation to the low degree of environmental pressures therein. In Mediterranean countries, few species are mentioned in national or subnational legislation, despite their higher values of spider diversity and the high level of pressure on local biodiversity.

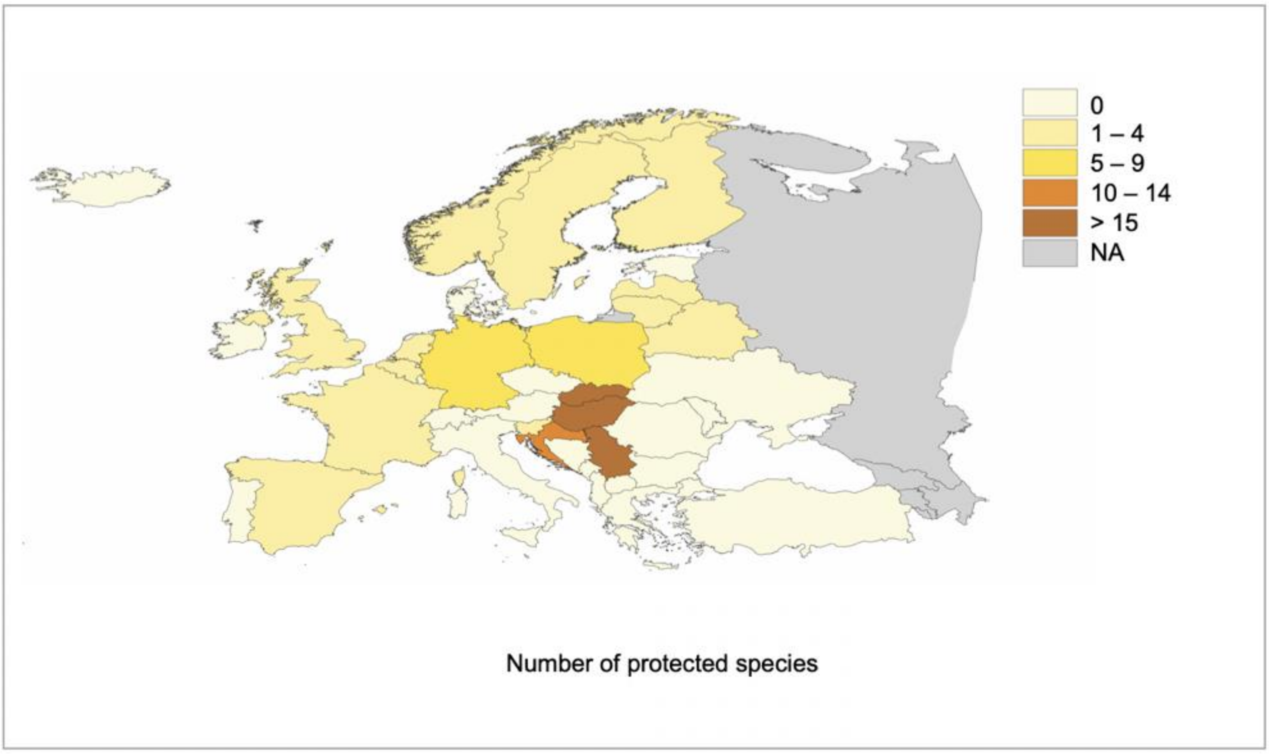
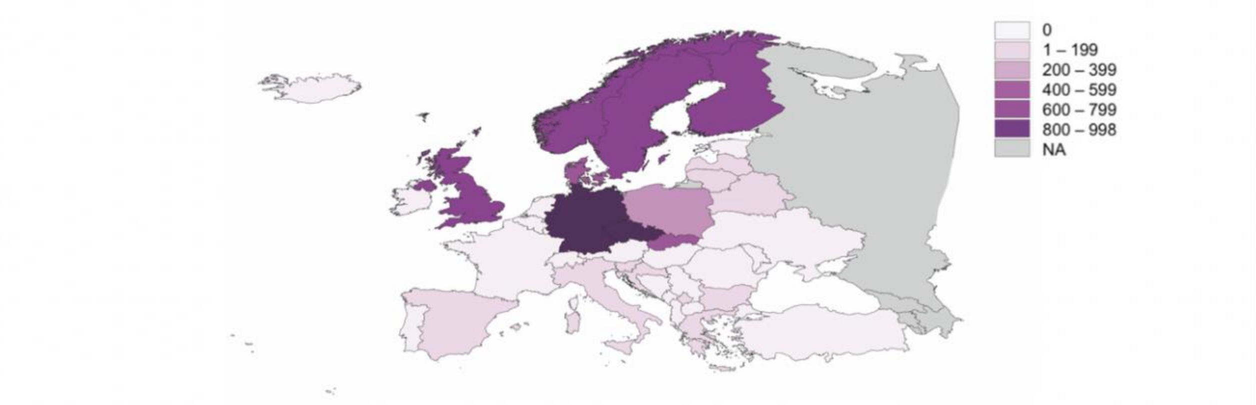
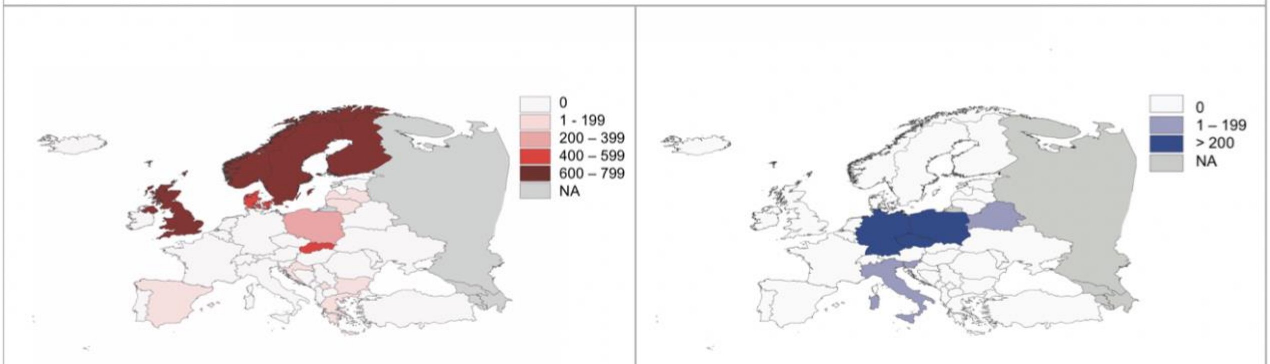


Fig. 3. Number of spider species protected by legislation in European countries. Central-Eastern European countries have the highest number of protected species. Note that an additional 38 species are listed as species of “principal importance” for conservation, receiving a lower level of protection under UK laws (see text). NA = Not Available.

In addition, 1,552 spiders are mentioned in Regional Red Lists and Red Books in 28 European countries (Fig. 4). Northern and Central European countries have the highest percentage of spider species assessed at the regional level. This can be attributed to these countries having a greater number of arachnologists and local experts, resulting in a broader understanding of the spider fauna occurring within their national borders and, consequently, in higher numbers of spiders being assessed in national inventories. Conversely, in Eastern European and Mediterranean countries, only iconic species have been comprehensively assessed. This low coverage in the assessment of the status of native spider species is likely due to the scant number of local arachnologists and to the related lack of taxonomic (many less-known or recently described species) and geographical (only generic or partial data on species distribution range) information. Even if in some countries most of the species are recognized to be present, little is known regarding their distribution, and the overall knowledge of spiders is far from complete (Cardoso, 2008).



(a) Number of species in national Red Lists



(b) Number of species in national IUCN Red Lists

(c) Number of species in national non-IUCN Red Lists

Fig. 4. Number of spider species considered by inventories of threatened species in Europe. (a) Number of species listed in national Red Lists in Europe (Malta, not displayed in map, is in the range 1-199; (b) Number of species listed in national IUCN Red Lists in Europe; (c) Number of species listed in national non-IUCN Red Lists in Europe (Malta, not displayed in map, is in the range 1-199). Northern and Central European countries stand for having the highest number of species mentioned in Red Lists. NA = Not Available.

Different criteria were used for assessing the conservation status of species. Several threatened species datasets in Europe follow IUCN criteria, but some countries utilise alternative categories and criteria. Many countries based their national Red Lists or Red Data Books on the most recent version of IUCN criteria (IUCN, 2001, 2012a, 2012b), or adopted the 1994 IUCN criteria for its national lists (IUCN, 1994), whilst others adopted a pre-1994 version. The remaining countries with national inventories used national guidelines, or based them on expert opinion, or utilised national criteria or regional IUCN guidelines which were integrated with different systems of evaluation.

This lack of standardisation in the categories and criteria used is problematic. If it were the case that every country applied its own approach, the criteria adopted would be subject to high levels of subjectivity which would reduce the comparability among regional Red Lists. Such variation in national listings makes it difficult to synthesize information from different countries which is vital in order to create a general overview; this, in turn, can hamper efforts to consolidate information and provide recommendations. To reduce bias and limit these inconsistencies, in **Paper I** we recommended that standardised categories and criteria, as well as a unified categorisation system, should be implemented and utilised. Currently, the only widely adopted system worldwide is the one by IUCN, which theoretically allows comparison of results from different countries and taxa under a common framework. This could be adopted across countries to guarantee such comparability and hence contributing to analyses beyond national borders.

Overall, the highest number of regionally extinct and threatened spider species has been assessed in Central-Eastern Europe (Fig. 5). These results show similar geographic patterns to those seen in other terrestrial invertebrate groups, for which there is more comprehensive information available (Nieto & Alexander, 2010; Nieto et al., 2014; van Swaay et al., 2010). It has been shown that Central and Eastern European countries are hotspots for threatened species within Europe, and it is likely that spiders follow a similar trend. This trend can be attributed to several factors acting in this area: high anthropogenic pressure in these countries; agricultural improvements; changes of grassland and woodland management; infrastructure development; the degradation and drainage of wetlands, as well as isolation and loss of habitat connectivity. These threats are mostly in line with those identified as the more relevant to spider species worldwide (Branco & Cardoso, 2020). In addition, it could be argued that intensive environmental changes associated with industrialization and agricultural intensification are more recent in Eastern countries, making the related effects on species more visible than elsewhere in Europe.

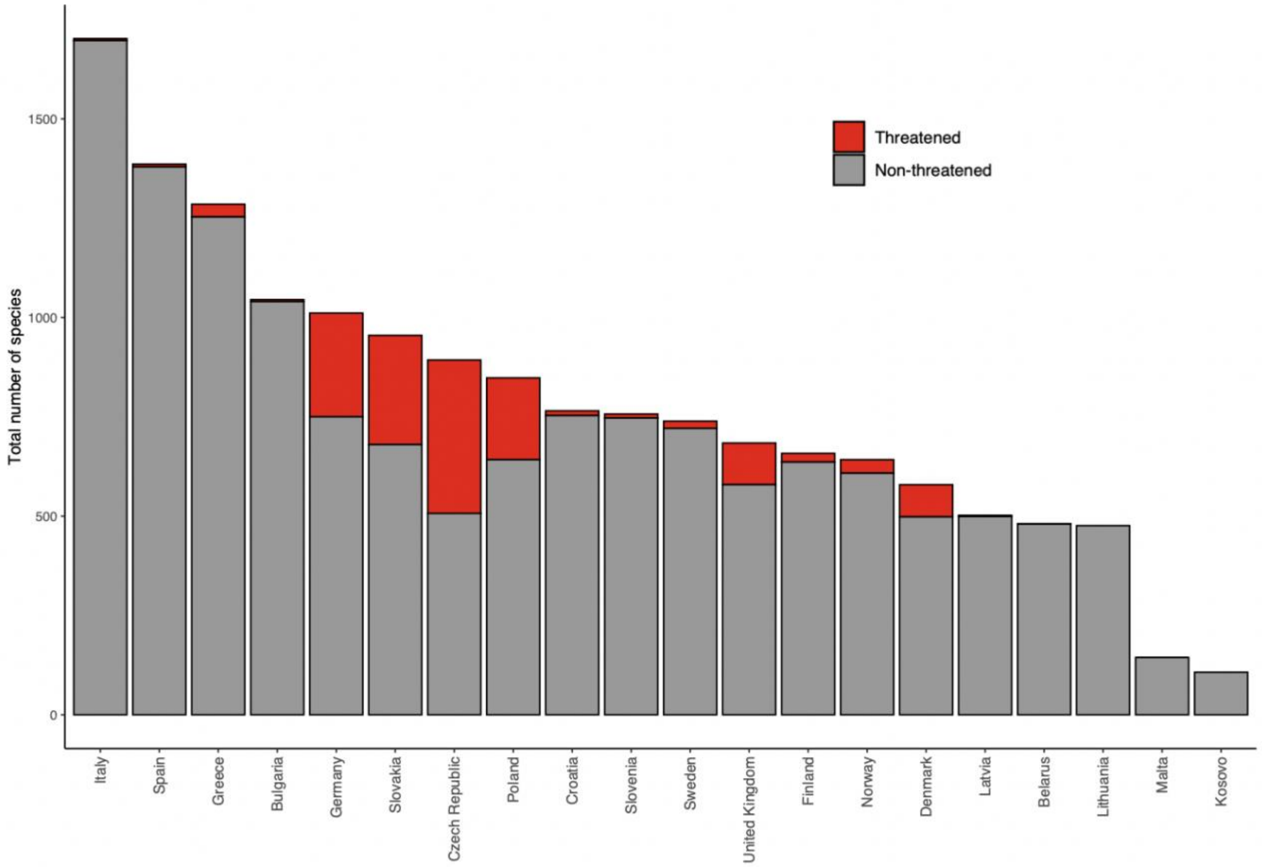


Fig. 5. Number of spider species considered as threatened in national Red Lists and Red Data Books in relation to the total number of spider species per country as reported in Nentwig et al. (2020). There is no correlation between the number of species occurring in a country and the number of threatened species in Red Lists and Red Data Books.

In Mediterranean Europe, the large-scale transformation in land use over the last few decades, the prevalence of wildfires, tourist development, and unbridled urbanisation has resulted in large-scale alterations of the natural environment (Cuttelod et al., 2008). This has very likely impacted a high number of spider species and many with restricted ranges are possibly threatened or locally extinct. However, without accurate knowledge concerning their actual status, the real proportion of threatened species is hard to quantify.

In contrast, Northern European countries have the lowest percentage of threatened species. In these countries the majority of threatened species live primarily in forests, and thus changes of the forest environment, *e.g.* forestry, reduction of old forests, reforestation, and forest management, represent the major threats (SLU Artdatabanken, 2020; Bruun & Lissner, 2019; Henriksen & Hilmo, 2015; Hyvärinen et al., 2019). Furthermore, a large proportion of threatened species occur in semi-natural habitats, mainly traditional meadows and pastures, which have declined greatly over the past hundred years (SLU Artdatabanken, 2020; Bruun & Lissner, 2019; Henriksen & Hilmo, 2015; Hyvärinen et al., 2019). Climate change inevitably poses a large threat to species found in northern alpine areas, as well as to species occurring in wetlands and mires (SLU Artdatabanken, 2020; Hyvärinen et al., 2019).

Among European species, *Dolomedes plantarius*, *Argyroneta aquatica* and *Eresus kollari* ROSSI are the most frequently mentioned in European conservation measures. The extent of consideration given to these species is related in part to their wide distribution, and especially to their ecological traits and their strict association with declining habitats.

4.2. Wetland spiders (Papers II and III)

To the best of our knowledge, no study has attempted to quantify the current and potential future global distribution of the aquatic spiders *Argyroneta aquatica* and *Dolomedes plantarius* and their future trends in habitat suitability, taking account of their dispersal abilities. Moreover, despite these being the spider species that feature most frequently in regional Red Lists and protection programmes across Europe (see **Paper I**), they are still lacking risk assessments at a global level in accordance with the last version of the IUCN Red List Categories and Criteria (IUCN, 2001).

Paper III builds on and goes beyond previously available works on the conservation of aquatic spiders (Leroy et al., 2013, 2014; Monsimet et al., 2020) by investigating their current habitat suitability and by assessing the potential impacts of future climate change on their global and regional distributions, taking account their dispersal abilities and using the most up-to-date knowledge.

The estimated core range of the present-day suitable areas was quite similar in both species (Fig. 6) and mainly centred in Northern and Central Europe, where wetlands, although strongly reduced in size compared to their original extent, are in a near pristine state and still cover large and continuous areas (Verhoeven, 2014). The most suitable and unfragmented areas were found in the northern regions of Continental Europe facing the North and Baltic Seas and in the southern Fennoscandia. Numerous small, isolated patches of highly suitable habitat are located from south-western to eastern Europe, namely in Italy, Spain, southern France and the Balkans, mainly along the most important river basins or lakes, or in protected nature reserves.

Trends in the overall extent of the future suitable area of both species, obtained by comparing the current and future predicted habitat suitability under sustainability (SSP1-RCP2.6) and fossil-fuelled development (SSP5-RCP8.5) scenarios, predicted a general decrease in the current suitability for both species (Fig. 7). The range contraction was particularly pronounced in Central-Eastern and Western Europe, where vast areas of wetlands occur in highly modified landscapes or have completely disappeared (Verhoeven, 2014), and where some important river basins (*e.g.*, the Rhine and the Danube) are losing ecological connectivity with the surrounding riparian buffer zones. In Southern Europe, the overall geographic range seems to be less affected by future climate change. By contrast, a future global increase in suitability in Northern Europe was projected, attesting a progressive northward shift of the species bioclimatic range within a relatively short time-scale.

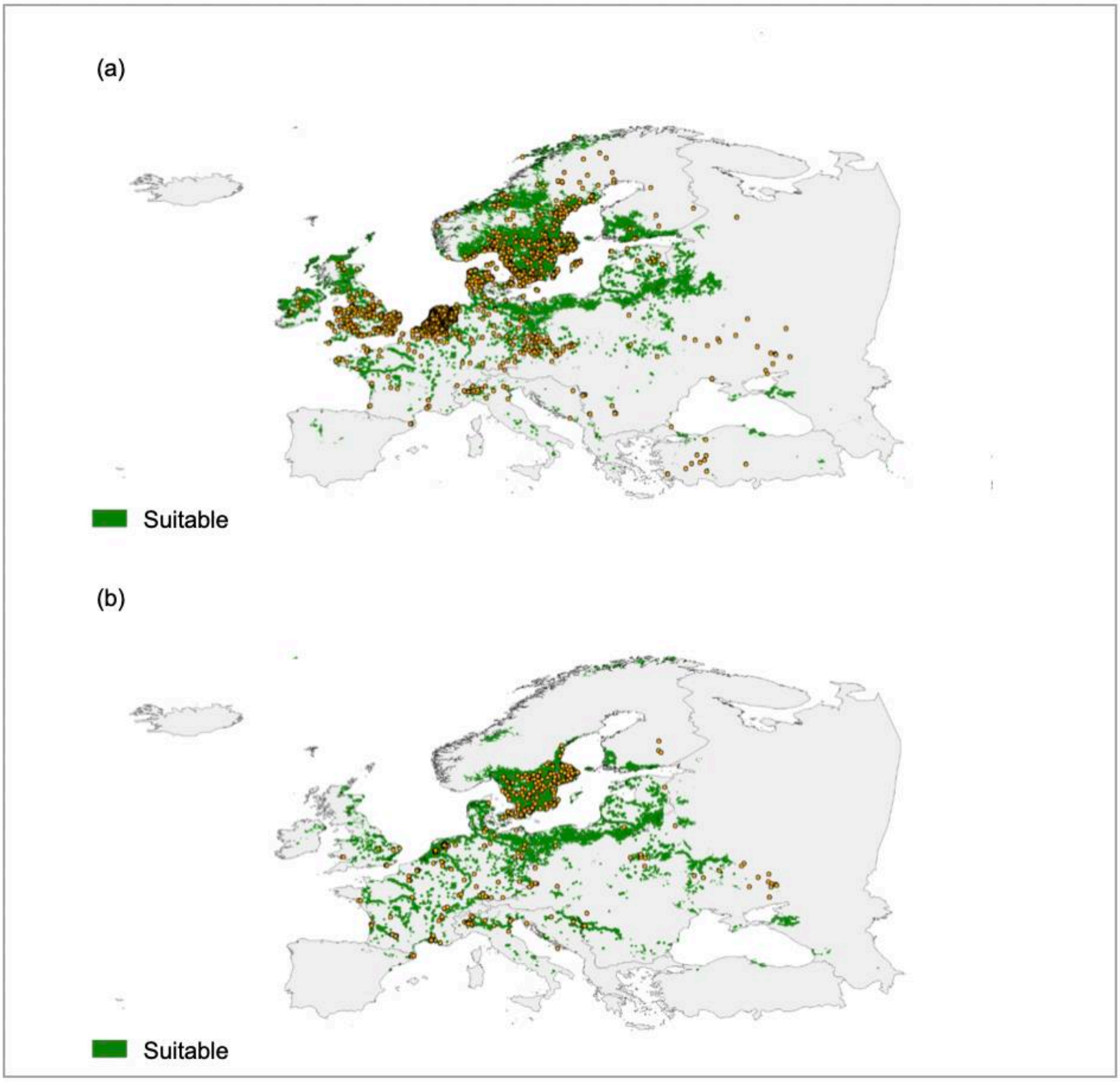


Fig. 6. Occurrences and potential distribution maps of *Argyroneta aquatica* (a) and *Dolomedes plantarius* (b) under current climatic conditions. The predicted species' area of occupancy (*i.e.*, areas with habitat suitability > model threshold value) is shown in green.

These areas, and in particular Fennoscandia and the Baltic regions, are expected to become climatic refugia for *Argyroneta aquatica* and *Dolomedes plantarius* (see also Monsimet et al., 2020). The magnitude of the decrease in projected future range of both species was predicted to be even more significant as a result of their limited dispersal abilities (Duffey, 2012; Leroy et al., 2014; Monsimet et al., 2020, 2022), their habitat specialisation (Dickel et al., 2022; Duffey, 1995; Seymour & Hetz, 2011; Smith, 2000; van Helsdingen, 1993) and the fragmentation of the landscape (Leadley et al., 2014). In view of this, any substantial expansion of these species in Northern Europe seems unlikely. The possibility that these species will not be able to respond to rapid shifts in suitable conditions and to move beyond the current range in the next decades, justifies predicting an increase in local extinction rates in the near future.

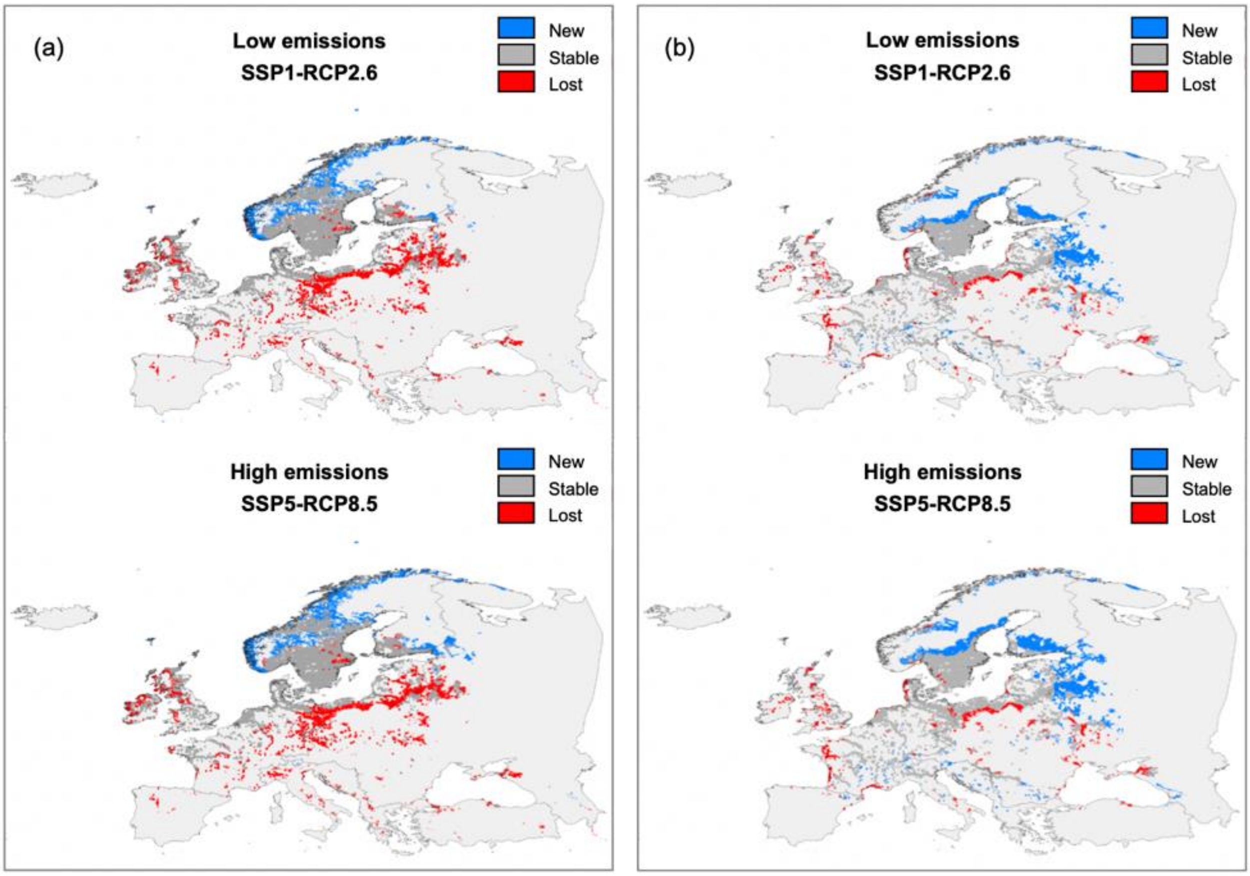


Fig. 7. Changes in the predicted distribution range of *Argyroneta aquatica* (a) and *Dolomedes plantarius* (b) in 2021–2040 according to a sustainable (SSP1-RCP2.6) and a fossil-fuelled (SSP5-RCP8.5) development scenario. Areas that are currently suitable and will still be suitable in the future are shown in dark grey; areas currently suitable that will lose their suitability in the future are shown in red; areas that are currently not suitable but will become suitable in the future are shown in blue.

The available information on these species has been used in **Paper III** to provide a baseline for the first assessment of their global conservation status according to the current IUCN guidelines (IUCN, 2001, 2012b). We confirmed the inclusion of *Dolomedes plantarius* in the Vulnerable category under criterion A3, on the basis of the projected decline in the area of occupancy over the next 10 years due to climate change. The relationship between population reduction and habitat loss may not be linear, but, in the absence of more specific information, it is a reasonable assumption (IUCN Standards and Petitions Committee, 2019). Using equivalent assumptions, our results suggested the inclusion of *Argyroneta aquatica* in the Near Threatened category under criterion A3c. This was justified by the rate of decline in area of occupancy being very close to qualifying for the Vulnerable category over the next decade, and exceeding the threshold for the inclusion in this category in the following 20 years. Thus, despite being widespread species, with large population sizes and ranges, *A. aquatica* and *D. plantarius* may qualify as being threatened with extinction on the Red List as they are undergoing rapid and continuing decline in population size.

The IUCN criteria applied at the regional level (IUCN, 2012a) showed a difference between European regions. In Central-Eastern Europe both species will experience a dramatic decline in the near future, and the populations occurring in the region are considered to be Critically Endangered. This trend is accentuated by the continuing decline and fragmentation of wetland habitats related to intensive environmental changes occurring in this region, as highlighted in **Paper I**. Conversely, no significant decline was projected in Northern Europe, where the local risk of extinction is very low and the regional populations are considered Least Concern.

In Southern Europe, the vulnerability of some populations to altered climatic patterns has been highlighted in view of their isolation and fragmentation within wetland areas. However, despite the overall predicted decrease in regional suitability, southern populations are expected to persist due to the occurrence of extensive and continuous water basins in this region (*e.g.* the Po valley, the Danube basin, the Ebro Delta).

In **Paper II** we provided a special focus on the known distribution of *Dolomedes plantarius* in Italy, where it preferably occurs in the lowland wetlands of the northern districts. In Italy, this species is considered Vulnerable by the List of the Threatened Invertebrates of the Italian Fauna (Groppali & Priano, 1992) and it is mentioned in the regional legislation of Lombardia, where it is listed among invertebrates of regional interest (see Milano et al., 2018). The current status of the Italian populations appears particularly critical, due to the geographical isolation of the populations at the periphery of the species range, and in view of the predicted north shift of the bioclimatic suitability caused by the ongoing climatic changes. The Alps constitute an important geographical barrier that preclude the populations of Northern Italy from reaching more suitable areas in northern Europe, as seen in **Paper III** for other isolated populations in Europe (*e.g.* in North-eastern Spain and Balkans). Moreover, in the Italian northern districts, the progressive loss of wetlands resulting from agricultural exploitation, associated with changes in the hydrological regime and water pollution due to agricultural products, have fragmented and jeopardized the natural populations, which are facing a remarkable decline. Accordingly, it seems likely that most of the populations are currently restricted to natural protected areas.

4.3. High-mountain spider (Papers IV, V and VI)

In **Paper IV** we provided new information on the ecology, distribution, habitat characterisation, life history and conservation of *Vesubia jugorum*. This alpine endemic spider occurs almost exclusively in rocky areas at high elevations, such as rocky debris, boulder fields and scree. The new findings reported in **Paper IV** validate the potential current geographic distribution of this species predicted by species distribution models in **Papers V** and **VI**, attesting the importance of these tools to overcome gaps in spatial data in threatened species. *Vesubia jugorum* likely has a multi-annual life cycle, with a growing season of 5-6 months per year, corresponding to the snow-free period, and 10-12 instars to complete the development, reaching the adult stage at least after four seasons. It seems plausible that the spider overwinters for 6-7 months under stones in the upper layers of the rocky debris, which are insulated by a deep blanket of snow, where the temperature remains stable around 0°C and the metabolic rate of the spider possibly decreases (Danks, 2006; Zhang, 2005). Overwintering individuals are generally adult females or immatures at different stages in their development. Adult males are found for a short period, and presumably die after mating. Females with egg-cases (cocoons) build circular and silk-lined retreat under stones, with a small opening in the silken walls. The cocoons are globular, white and contain on average 200 eggs. As seen in **Paper V**, average cocoon size is positively correlated with the average female size. Females produce more than one cocoon within the same season, and exhibit maternal cares of both cocoons and spiderlings. *V. jugorum* is a cursorial hunter which preys actively pouncing on the prey from a close distance, using the strong, spiny legs for grabbing and surrounding it. This “full leg basket” technique, is common in lycosoid spiders, which hunt without web (see Eggs et al., 2015). Laboratory observations showed a generalist predatory habit for *V. jugorum*, which is coherent with the general opportunistic habit found in most high alpine spiders, dwelling in habitat with limited resources.

Ecological Niche Modelling presented in **Paper V** revealed a positive relationship between the probability of presence of *Vesubia jugorum* and percentage of rock and cumulative precipitation. In particular, timing, duration and thickness of seasonal snow coverage seems to play a major role in determining the distribution of the species by possibly influencing the duration of its growing season. Habitat quality for *V. jugorum* declines in areas where the mean annual number of days of snow cover during the year is < 40, which is typical for lower elevations, and where the mean annual number of days of snow coverage is > 100, a condition occurring either above 2800-3000 m within the core of the species distribution or at northern latitudes within the species range.

Moreover, in **Paper V** we demonstrated a positive, significant relationship between habitat quality, predicted by species distribution models, and the individual performance of *Vesubia jugorum*, measured by means of functional traits (femur I length and egg-case size). In *V. jugorum*, the length of femur I and the size of cocoon were found to be positively related with habitat suitability. The largest individuals (*i.e.*, the individuals with longer femurs) and females with larger cocoons occurred in the core of the species distribution, where the amount of predicted high-quality habitat was greatest and the related habitat suitability value was higher (> 0.7 in a range between 0 and 1). Conversely, in areas with lower habitat suitability (< 0.25), individuals had smaller femurs and smaller cocoons (Fig. 8).

In predatory arthropods, specimens with greater body size have greater predatory efficiency and a higher benefit in terms of reproductive success and performance, compared to smaller ones. Therefore, populations having smaller specimens can be considered of higher concern in a conservative perspective. In light of this relation, a long-term monitoring programme was designed in the context of the species conservation, for evaluating the ongoing impact of climate change on the species survival and for detecting changes in populations.

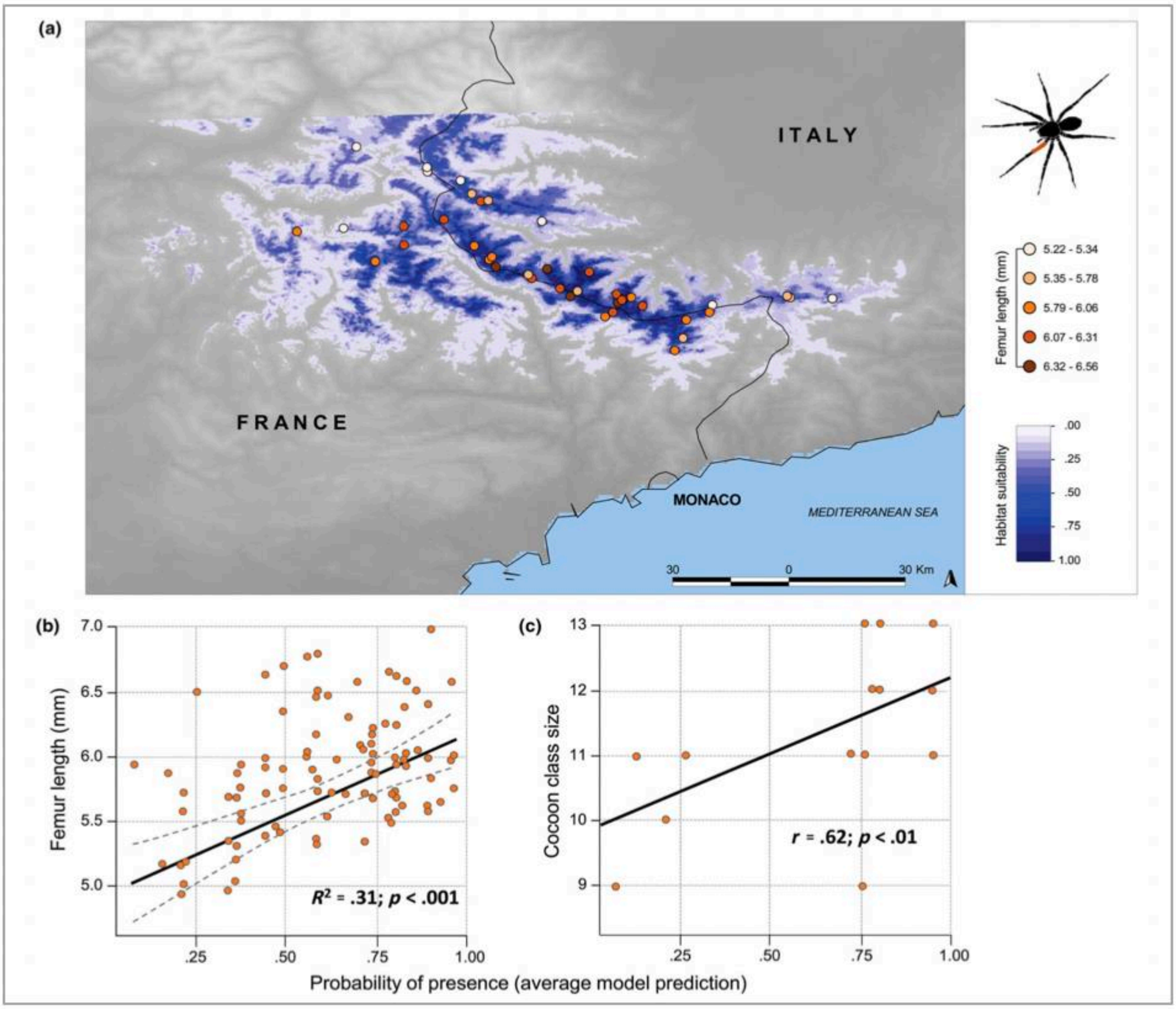


Fig. 8. Species distribution and relationship between projected habitat quality and functional traits. (a) Projected habitat quality for *Vesubia jugorum*. (b) Predicted linear relationship (solid line) and 95% confidence interval (dotted lines) between habitat quality and femur length, derived from the linear mixed model. (c) Relationship between cocoon size and projected habitat quality. The black line represents the positive linear trend according to the Pearson correlation. Due to the proximity of values, some points are superimposed.

In **Paper IV** we provided the results of the baseline phase of the monitoring programme, that confirm the positive relationship between functional traits and habitat suitability suggested in **Paper V**, and corroborate this method as a practical, non-invasive approach to the assessment of population health through time. Specimens with largest femur occurred in localities where the predicted habitat quality was highest, confirming the use of this trait for monitoring purposes. The use of the femur IV in **Paper IV** rather than the femur I (as done in **Paper V**) does not seem to bias the significance of the relation. The results obtained during this first step of the monitoring, provided baseline information on the status of the populations, and will be compared with the results of the future monitoring campaign, planned for 2024, to detect potential population decline over time and to inform suitable response measures and coordinate conservation policies.

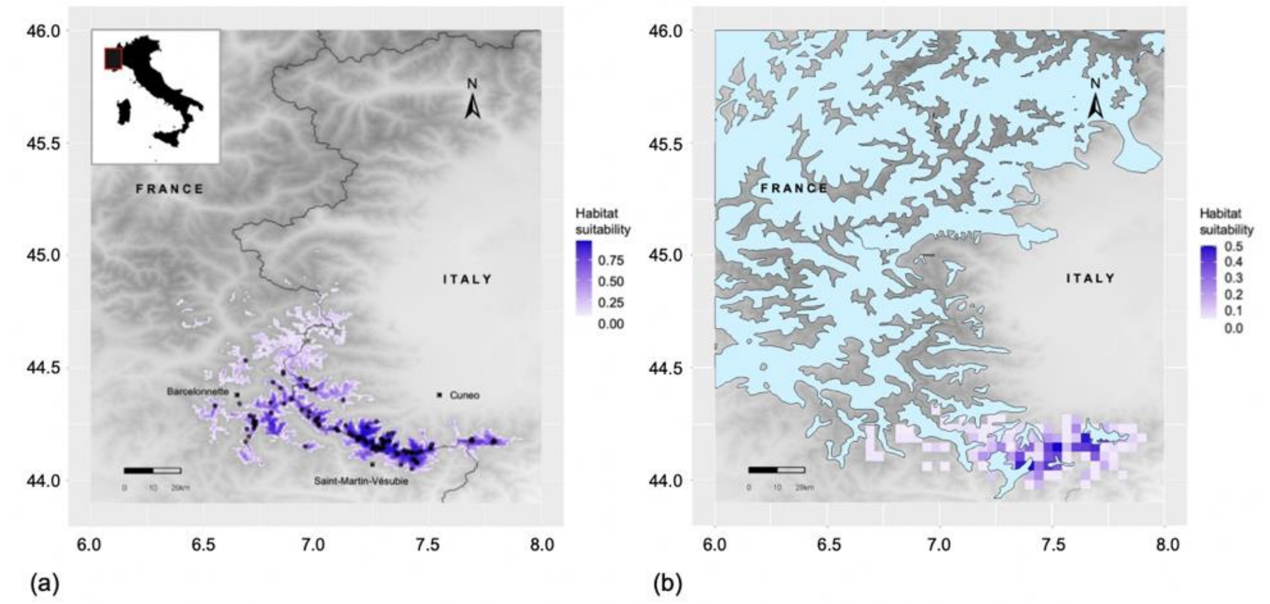


Fig. 9. Maps of the bioclimatic suitability of *Vesubia jugorum* projected at the present climate (a) and during the Last Glacial Maximum (b). The predicted species distribution is shown in blue. Limits of the ice cover in the Last Glacial Maximum (Ehlers et al., 2011) are reported for the Pleistocene projection (light-blue shapes in the lower map).

According to the results obtained in **Paper VI** by integrating species distribution modelling with phylogeographic analyses, Pleistocene climatic oscillations played an important role in shaping the current distributional pattern and the observed genetic diversity of *Vesubia jugorum*.

The present-day suitable area of *Vesubia jugorum* estimated by the model in **Paper VI** was consistent with the known distribution provided in **Paper IV**, with the highest-quality areas corresponding to the Argentera-Mercantour massif, in the central portion of the Maritime Alps. Additional areas of suitable habitat were projected at the eastern and north-western corners of the species' known range (Ligurian and Cottian Alps, respectively), and in the south-western limits of the known distribution, across the Provence Alps (Fig. 9a).

The projection of the potential distribution of *Vesubia jugorum* into the past climatic conditions (Fig. 9b), showed a distribution range smaller compared to the present one, and mostly centred in the south-eastern part of the current distribution, which was devoid from glaciers (Ehlers et al., 2011). In particular, the Marguareis-Mongioie and the Argentera-Mercantour massifs provided areas of high suitability, namely the two areas where the current suitability is higher nowadays. Conversely, the northern portion of the current range was likely unsuitable during the Last Glacial Maximum (LGM).

Such scenario is congruent with the phylogenetic reconstruction that we obtained for the species lineages. The cooler conditions and the ice shields would have caused an overall contraction of the wide ancestral distribution, prompting the species to find refuge in the southern latitudes, at the periphery of the Pleistocene glaciers, and in isolated refugia scattered across the species' distribution. Tentatively, populations inhabiting the northern valleys of the Southwestern Alps most likely disappeared due to ice shield advance or persisted in peripheral refugial areas and unglaciated mountain peaks ('nunataks') in the interior of the Pleistocene ice shields. During warmer interglacial periods, when the glaciers retreated and new areas became available, these geographically isolated lineages likely re-colonized areas previously unsuitable or covered by glacial masses (post-glacial colonization hypothesis, *sensu* Guerrina et al., 2021). The colonization of the northern portions of the range and the plausible re-establishment of connections among populations sheltered in isolated mountain refugia, would have enabled gene flow dynamics, thus preventing the accumulation of among-populations genetic differentiation. At the same time, it is likely that the southernmost populations occurring in the central portion of the Maritime Alps survived *in situ* via short altitudinal shifts, following their climatic optimum (long-term stability hypothesis, *sensu* Guerrina et al., 2021), and remained isolated from the rest of the range, evolving higher level of genetic differentiation. Indeed, the high levels of haplotype diversity observed in some cases, would provide evidence that this area of the Southwestern Alps could be the centre of origin for the extant lineages of *Vesubia jugorum*, and could have acted as a refugium for the species during Pleistocene glacial-interglacial phases.

Future forecasts obtained in **Paper VI** by projecting the habitat suitability under sustainability (SSP1-RCP2.6) and fossil-fuelled development (SSP5-RCP8.5) scenarios, showed significant shifts in the bioclimatic range towards higher altitude and latitudes (Fig. 10). In both future scenarios, a general decrease in the current suitability was observed, particularly remarkable in the central and south-eastern parts of the distribution range. The reduction of the availability of future suitable areas will be more significant in the Ligurian and in the Provence Alps, where isolation of the remaining patches will increase. We regard such peripheral populations as the most threatened by the ongoing climatic change. In the Maritime and southern Cottian Alps, despite fewer changes in suitability are expected, a general thinning of the suitable areas was observed, suggesting a general shift towards higher altitude. By contrast, an increase in suitable habitat in the north of the range, with the appearance of new suitable areas in the northern Cottian and in the Graian Alps, was predicted. Many areas of currently available suitable habitat in the Maritime Alps are not predicted to retain their high suitability, and an increasing isolation of the central current range from the newly northern suitable areas was expected.

The most relevant factors potentially influencing the future colonization of newly appeared suitable areas are represented by the species' dispersal ability and by habitat connectivity. As pointed out in **Paper IV**, *Vesubia jugorum* is strongly linked to high-altitude rocky lands. The phylogenetic history of this species, in association with the presence of biogeographical barriers delimiting the current species range and the putative limited dispersal ability of the species, let us to conclude that the possibility of the species to disperse and colonise new suitable areas within the next years is highly improbable, corroborating our hypothesis about the vulnerability of this species.

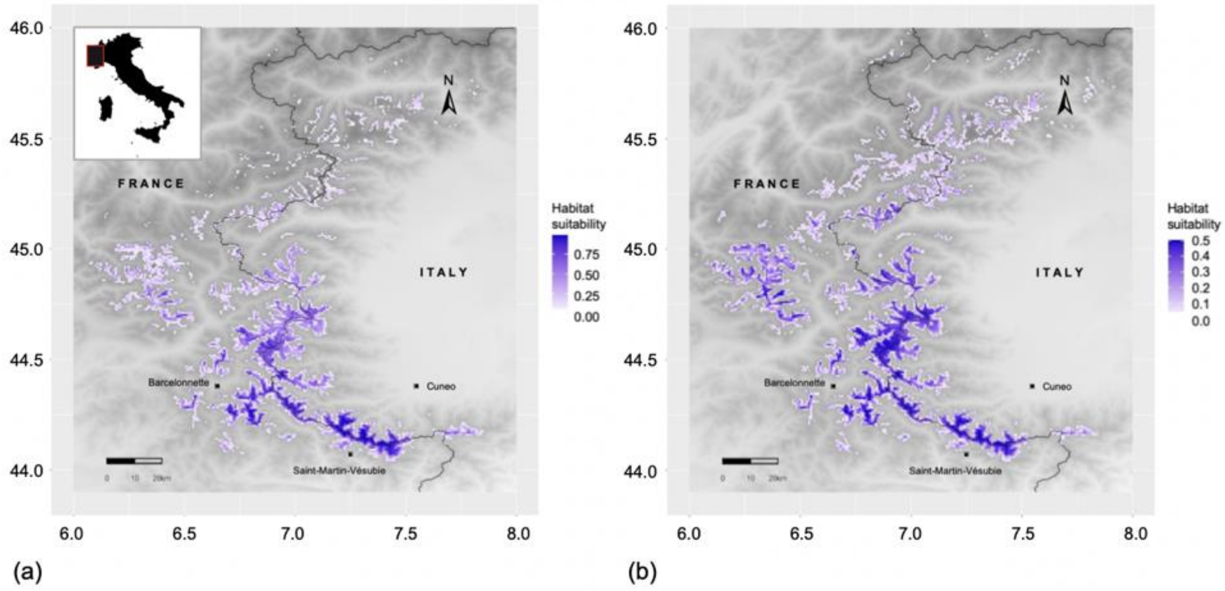


Fig. 10. Maps of the predicted distribution range of *Vesubia jugorum* in 2021–2040 according to (a) a sustainable and (b) a fossil-fuelled development scenario.

4.3. Cave spiders (Papers VII and VIII)

In **Paper VII** available distribution data allowed to calculate the Extent Of Occurrence (EOO) and Area Of Occupancy (AOO) of 62 out of the 66 species of the cave-dwelling genus *Troglohyphantes* occurring in the Alps and in north-western Dinarides. Most of the species considered have a narrow distribution range, generally restricted to one single country, with an estimated EOO < 20,000 km^2 and AOO < 2,000 km^2, meeting the thresholds for the inclusion in the threatened categories. Only five species have a more widespread distribution (EOO > 20,000 km^2), extending across multiple countries. The quality of the data on distribution of four species was not sufficient to provide a reliable estimation of the distribution range.

Trends in EOO, AOO and habitat quality were considered to be stable for 30 species, mainly exhibiting low levels of subterranean specialisation mostly found in the vicinity of the cave entrance or in shallow subterranean habitats and for which no current major threats are known. It seems likely that these species are more tolerant to ecological variations and higher temperature increases compared to the species showing high level of subterranean adaptation (Mammola et al., 2019c). Conversely, a continuing decline in EOO, AOO and habitat quality was inferred for 30 species. The majority of them were subterranean specialised species with fine-tuned thermal tolerance to the constant and narrow temperature ranges of the subterranean habitat, for which anthropogenic global warming was expected to reduce the habitat quality and the extent of the distribution (Mammola et al., 2018; Mammola et al., 2019d). Accordingly, changes in subterranean microclimatic conditions due to climate change represent a major threat for these species.

Land-use change and habitat alteration were identified as additional relevant threats for several species. In particular, forestry and silvicultural practices, intensive agricultural activities, urbanisation and infrastructure development, are considered to be important drivers of increased extinction risk of these species. For several subterranean species, a secondary impact has been recognised to be driven by tourism in caves, which possibly has impacts on the cave ecosystem and the biocoenosis dwelling therein. Quarrying activities represented the major threat to one highly adapted subterranean species of *Troglohyphantes* occurring in a single cave, for which the nearby quarries are expected to cause critical damage to cave habitat, altering microclimate and decreasing overall habitat quality.

The same threat has been reported in **Paper VIII** for *Histopona palaeolithica*, which is restricted to a single cave in the Caprazoppa promontory, in the Western Ligurian Prealps (Italy). The estimated EOO and AOO are both extremely small, less than 1 km^2. Accordingly, this species is potentially exposed due to its extremely narrow geographic distribution range. The whole area of the Caprazoppa promontory is currently subject to quarrying activities, which are likely to represent a major threat to the species' survival. As a result of changes in local microclimatic conditions due to quarrying activities, we inferred a decline in EOO, AOO and habitat quality. In addition, given the low tolerance to habitat changes of this subterranean organism, a drastic decline in the habitat suitability of this species as a consequence of climate change is expected. Dispersal ability for this species is not known, but since this is a highly specialized cave-dwelling species with restricted range, it is assumed that it has a very low dispersal capacity. Secondary impacts could derive from tourism, due to the high number of climbers and hikers in the area. The cave opening is easily accessible and located at the base of the climbing site. Even if climbing activities do not present a direct threat to the species' survival, the possible accumulation of litter thrown by tourists into the cave could cause changes in the cave environment and decrease habitat quality.

5. Conclusion and Perspectives

Spiders are largely neglected in conservation research, and one of the main problems facing their conservation is the general lack of information. The majority of species are poorly known and information usually pertains their geographic distributions. Comprehensive and reliable data on population size, trends and threats affecting them are not available for most spider species, making the determination of their true conservation status rather difficult.

The main goal of my PhD thesis was to provide a significant contribution to the knowledge of the ecology and the conservation status of different spider species occurring in Italy, with a special focus on their response to climate change.

Climate change is expected to have pronounced future negative effects on the ecosystems, providing great challenges to the survival of wild species. However, the effects of climate change have rarely been studied for spiders, and the responses of spider species to such impacts are still relatively unknown (Branco & Cardoso, 2020). The assessment of the climate change impacts on the species considered in this thesis is a step towards this direction. We observed a general pattern of decrease in the current suitable range of the species, and an increasing population vulnerability. Climate change is expected to lead to a substantial loss of suitability in the future, particularly in wetlands, caves and high-montane areas. In most of the species considered in this work, we predicted a significant shift towards higher altitudes and latitudes of the species' bioclimatic suitability within a relatively short time-scale. The magnitude of the predicted shift is expected to be more significant under scenarios of higher levels of greenhouse gas emissions. However, the abilities of these species to track their habitat suitability might be limited in relation to their limited dispersal abilities and the general fragmentation of the landscape. Most of the species considered in this thesis are habitat specialists, with relatively narrow ecological requirements and limited dispersal propensity. In particular, some cave spiders displayed high levels of adaptation to the subterranean habitat, resulting in a narrow thermal tolerance and therefore in a particular vulnerability to potential subterranean climatic variation induced by climate change (Mammola et al., 2019b). Accordingly, our model species might be unable to respond to rapid shifts and to track climate change as rapidly as required under any future scenario, becoming trapped within their current, declining geographical ranges. The application of the latest version of IUCN criteria to these species resulted mostly in their inclusion in threatened categories, on the basis of their projected decline and their population vulnerability, suggesting their increasing risk of local and global extinction due to climate change.

The evaluation of the extinction risk of these species, can be used as a baseline to inform conservation planning and influence management decisions concerning the conservation of the species and their habitats (Miller et al., 2007).

Considering the current scarcity of data, predicting the impacts of climate change on species and ecosystems and their influence on species extinction rates is vital in motivating and informing strategic conservation actions at global and local scales. Despite their inherent uncertainties and limitations, Species Distribution Models currently represent one of the main tools for forecasting the impacts of global climate change on species distribution (Guisan & Thuiller, 2005), and are useful to identify conservation opportunities in newly available habitats under changing climate (Guisan et al., 2013).

The understanding of the long-term dynamics of the populations is fundamental to evaluate how they can change through time and their possible decline in response to environmental disturbance. In this context, the monitoring of spider populations, as we have seen for *Vesubia jugorum*, helps to provide baseline data against which changes can be evaluated, providing key information for assessing the conservation status of a species.

Considering the fundamental ecological role of spiders in most terrestrial ecosystems (Nyffeler & Birkhofer, 2017), and their sensitivity to anthropogenic changes, our model species are useful indicators of the general quality of the habitats and of the response of biodiversity to climate change. Understanding how species respond to climate change and predicting the impacts of such effects on their habitats is therefore vital in alerting scientists and informing decision-makers, and in developing proactive strategic actions at global and local scales aimed at mitigating these risks.

Climate change is expected to act in either additive or synergistic ways with other drivers, particularly habitat loss and land-use change (McCarty, 2001; Root et al., 2003). The impacts of multiple pressures are likely to exacerbate the detrimental effects of climate change on biological communities, representing an additional challenge to species and to their conservation. Accordingly, in addition to the fundamental policies at global scale to reduce emissions, a sound strategy to preserve threatened habitats and biota would consist of proactive management to reduce non-climate stressors (Erwin, 2009). According to the results obtained in the case studies here presented, a pragmatic approach to the conservation of spider species could be the implementation of large-scale management plans and restoration programmes for their habitats and ecological networks, ensuring better structural and functional connectivity among suitable patches. The protection of large areas of suitable habitat has been addressed as the most effective approach to spider conservation (Branco & Cardoso, 2020). The current major threats to spiders indicate the need to increase the coverage of existing protected areas and to designate new ones, in order to include more spider species that need protection.

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Paper I

Spider conservation in Europe: a review

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Abstract

Despite their ecological importance and diversity, spiders (Arachnida: Araneae) are underrepresented in conservation policies in comparison to other groups. We review all extant conservation tools focusing on spiders in Europe, highlighting general patterns, limitations, gaps, and future directions. We assembled a comprehensive online database reporting all available information concerning the legal protection and conservation status of 4,154 spider species. Existing international legislation has limited coverage, with only one species listed in the Bern Convention and EU Habitats Directive. At the national and subnational levels, 178 species are formally mentioned in the legislation of 19 European countries. Moreover, the International Union for Conservation of Nature (IUCN) includes assessments for 301 species worldwide, 167 of these threatened and eight native to Europe. In addition, spiders are mentioned in Regional Red Lists and Red Books in 28 out of 42 European countries considered in this review. Northern and Central European countries have the highest percentage of species assessed at the regional level in Red Lists and Red Books. The Mediterranean basin has the highest spider diversities in Europe but conservation efforts are lacking, both in terms of assessments and national or subnational legislation. Among European species, *Dolomedes plantarius*, *Argyroneta aquatica* and *Eresus kollari* are the most frequently mentioned in European conservation measures, possibly due to their ecological traits and their strict association with declining habitats. Considering the current threats to spiders in Europe, the protection of large areas of suitable habitat should be considered as the most effective approach to spider conservation.

Keywords: IUCN, invertebrate conservation, Araneae, Red List, environmental legislation, threatened species

1. Introduction

Compared to other animal groups, especially vertebrates, invertebrates have similar or even higher extinction rates and proportions of threatened species (Cardoso et al., 2011), and are in urgent need of protection and monitoring (Cardoso et al., 2020; Samways et al., 2020). Yet, in conservation programmes invertebrates are largely neglected, both at regional and international scales. In addition, despite the global dominance of invertebrates in terms of richness, abundance, biomass and importance in ecosystem functioning (Stork, 2018; Wilson, 1987), the majority of biodiversity conservation research and effort is currently focussed on a few, well-known vertebrate taxa (Clark and May, 2002; Cardoso et al., 2011; Davies et al., 2018; Fukushima et al., 2020; Leather, 2013; Mammola et al., 2020b; Titley et al., 2017).

Among terrestrial invertebrates, spiders (Arachnida: Araneae) are one of the most important groups in terms of abundance, diversity, biomass, evolutionary history, and functional roles (Cardoso et al., 2008; Coddington and Levi, 1991; Coddington et al., 1991, 2009; Dunlop et al., 2018; Foelix, 2011; Jocqué et al., 2013; Mammola et al., 2017b; Nentwig, 2013; Turnbull, 1973). With more than 48,000 species currently described (World Spider Catalog, 2020), spiders are among the most common and ubiquitous animals in the majority of terrestrial habitats, where they play an important role as generalistic predators (Turnbull, 1973). A few species have even conquered the aquatic environment (McQueen and McLay, 1983; Seymour and Hetz, 2011). Spider assemblages are particularly diverse in richly vegetated areas, but they can also be found in habitats with stringent environmental constraints such as deserts, caves, and alpine habitats.

Preserving spider diversity, apart from being ethical in the framework of establishing a sustainable relationship with wildlife in general, is essential in recognition of the fact that they play a fundamental ecological role. They are an important food source for higher trophic levels (*e.g.* reptiles, birds, mammals) and are predators in most terrestrial ecosystems (Nyffeler and Birkhofer, 2017), thus providing vital ecosystem services to humans with respect to the control of arthropod pests in agroecosystems (King and Hardy, 2013; Michalko et al., 2019). Moreover, their silk, venom and hemolymph are a source of inspiration for biological engineering (Heim et al., 2009; Ko and Wan, 2018), pharmacology, and medicine (Corzo and Escoubas, 2003; Pineda et al., 2018; Riciluca et al., 2012). Yet, compared to more popular groups of invertebrates, spiders are lagging in conservation studies and policies worldwide. For example, only one species among the nearly 4,500 spider species known from Europe, is listed in the EU Habitats Directive, whereas 50 butterflies out of 496 and 16 dragonflies out of 143 feature, demonstrating a remarkable taxonomic bias even within invertebrates (Cardoso, 2011). Furthermore, extinction risk has been assessed for fewer than 100 European species in the Global Red List of the International Union for Conservation of Nature (IUCN), mostly from the Macaronesian archipelagos of Madeira and Selvagens (Cardoso et al., 2017). By comparison, the extinction risk of 97% of European butterflies (van Swaay et al., 2010) and dragonflies (Kalkman et al., 2010) has been assessed.

We reviewed all international and regional conservation tools focusing on spider conservation in Europe, with the goal of highlighting general patterns, limitations, gaps, and future directions in the field of spider conservation. As a result, we compiled a thorough database reporting all available information about the conservation of spiders in European countries, noting Red Lists, Red Books, and any supranational, national and subnational legal acts referring to spiders (see Table A1 in Appendix A and Milano et al., 2021a, 2021b). We also intend to add this information to the joint European network "Araneae – Spiders of Europe" (Nentwig et al., 2020).

2. Data sources

Conservation tools concerning spiders in Europe were investigated at international and regional levels. These included international conventions, regulations and EU Directives, national and subnational acts in force in the European countries considered, the IUCN Red List of Threatened Species, Regional Red Lists and Red Data Books. An overview of the conservation tools currently dealing with spiders in Europe is presented in Table 1.

We examined 42 European countries that are included in the European spider network "Araneae – Spiders of Europe" (Nentwig et al., 2020). Enclave and semi-enclave countries (Monaco, San Marino, and Vatican City), non-independent countries (Andorra), North African and South Caucasian countries, as well as the Outermost Regions and Overseas Countries and Territories of European countries were excluded. Russia is not considered in this review, due to the lack of a national Red List for spiders and the difficulty of comparing the numerous (at least 140) regional non-IUCN Red Data Books (Popov et al., 2017).

In order to have a standard reference for all countries considered, we derived national species checklists from the most recent version of "Araneae – Spiders of Europe" (Nentwig et al., 2020). Updates or changes to national checklists not implemented in this source were not considered.

For each country examined, we obtained all the published local Red Lists, Red Books and legal acts concerning spiders, by means of literature surveys and with the assistance of a wide network of local experts and contributors (see acknowledgements). Whenever a country was not covered, information was derived from bibliographic surveys. We considered only the most recent versions of the regional Red Lists and Red Data Books and the currently valid legislation, and we carried out separate analyses on the different geographic levels adopted in each.

To ensure comparability, we assumed the categories of threat from different category systems as equivalent. Species listed as "Critically Endangered (Possibly Extinct)" were considered as Critically Endangered (CR). Species not evaluated or listed in the category "Not Applicable" (NA), were not considered in this review, as they are ineligible for assessment (IUCN, 2012b).

2.1. Disclaimer on taxonomy and terminology used in this work

The nomenclature used in this work refers to the latest version of the World Spider Catalog (2020). Species assessed by Red Lists or Red Books currently regarded as *nomina dubia* were not considered. For species split subsequently into multiple species, we applied the original assessments to the new species and note the taxonomic changes. In the case of a species lumped with another assessed within a different IUCN category, we adopted a precautionary approach and retained the higher risk category. Synonymies, misidentifications, and nomenclatural changes all followed current taxonomy as represented in the World Spider Catalog (2020). As a consequence, the final number of species reported in this review may differ from the number assessed in the original Red Lists and Red Data Books.

According to the definition of the IUCN (IUCN, 2012a), we used the term “Regional” in reference to any sub-global geographical level of assessment. However, here we used the terms “national”, “subnational” and “supranational” Red Lists in order to discriminate the level at which the regional assessment was performed. The term “Global” is used when referring to the IUCN Red List of Threatened Species. We use the term “international” to define tools involving more than one country, irrespective of whether they have a European (Bern Convention and Habitats Directive) or global origin (IUCN).

3. International conservation tools

Among the extant international tools focusing on the preservation of nature in Europe, very few mention European spiders. They are limited to the Bern Convention, the Habitats Directive and the Red List of Threatened Species of the IUCN. The Convention on International Trade in Endangered Species of wild fauna and flora (CITES) also considers spiders, but none of the spider species mentioned therein occur naturally in Europe, and therefore it is not considered in this work (for details, see Table 1 and Appendix B).

3.1. Bern Convention

The Bern Convention (Council of Europe, 1979), is the first formal international convention providing specific attention to the conservation of species in Europe, including spiders. A provisional list of candidate invertebrate species was initially proposed for inclusion in the Convention by the IUCN Conservation Monitoring Centre (Collins and Wells, 1987). The list was subsequently adopted by the Standing Committee as the basis for additions to the appendices of the Convention.

Two spider species were included in the provisional list: *Dolomedes plantarius* (Clerck 1757) (Pisauridae) and *Macrothele calpeiana* (Walckenaer 1805) (Macrothelidae), but only the latter was retained in the Bern Convention. *Macrothele calpeiana* is currently listed in the “strictly protected fauna” of Appendix II, granting it special protection against all forms of disturbance, capture, keeping, deliberate killing, and damage or destruction of breeding or resting sites. The restricted distribution of *M. calpeiana* (back then regarded as endemic to the Southern Iberian Peninsula), and the fragmentation and destruction of its putative preferred habitat in cork oak forests (*Quercus suber* L.), represented the main reasons for its inclusion in the Convention (Snazell, 1986; Snazell and Allison, 1989).

3.2. Habitats Directive

Following on from the Bern Convention, the Habitats Directive (92/ 43/EEC) was the first international law to regulate European conservation policy concerning spiders.

Once again, the only spider species mentioned in the Habitats Directive is *M. calpeiana*, listed in Annex IV among the species of European interest in need of strict protection. Unlike the Bern Convention, the Directive is mandatory, and the Member States are obliged to protect and monitor the conservation status of *M. calpeiana* and its habitat (Article 12), particularly through the establishment of a network of protected sites. Its main range of distribution is included in, or close to, Natura 2000 network sites and protected areas in the South-Western Iberian Peninsula. The inclusion of this species in the Habitats Directive was a consequence of its appearance in the Bern Convention, which deeply influenced the Directive in both conception and drafting, and constituted the basis for the composition of the lists in the Directive's Annexes (Epstein, 2013; van Helsdingen and Decae, 1992).

3.3. IUCN Red Lists and Red Data Books

The IUCN was established in 1948, and was the first international network to consider spiders in conservation issues. One of the most important tools promoted by the IUCN is the Red List of Threatened Species (or, the "Global" Red List), established in 1964 and widely accepted as the most comprehensive and objective source of information on the conservation status of species and their extinction threats (Lamoreux et al., 2003; Rodrigues et al., 2006; but see Cardoso et al., 2011, 2012). The Global Red List is based on a number of objective criteria, which are relatively easy to apply, repeatable and scientifically recognized as adequate indicators of the health of global biodiversity (IUCN, 2001).

The first IUCN Red List of Threatened Animals was published in 1986 (IUCN Conservation Monitoring Centre, 1986) and it included 18 spider species, amongst which were the spiders mentioned in the first IUCN Invertebrate Red Data Book published three years before (Wells et al., 1983). This provided information on the threats to survival and conservation needs of six spider species: the theraphosid *Brachypelma smithi*, three subterranean linyphiids (*Troglohyphantes gracilis* Fage 1919, *T. similis* Fage 1919, and *T. spinipes* Fage 1919), and two lycosids (*Adelocosa anops* Gertsch 1973 and *Pardosa diuturna* Fox 1937).

Table 1. Conservation tools currently in force in Europe mentioning spiders, with focus on their objectives, signatory parties, legal value and species mentioned, with relative conferred status. The year (in brackets) refers to the date the conservation tool came into force.

Level	Conservation tool	Objectives	Signatory parties	Legal value	Spider species mentioned	European species included	Conferred status	Notes
International	Bern Convention (1982)	● to conserve wild flora and fauna and their natural habitats ● to promote cooperation between States ● to give particular attention to endangered and vulnerable species including endangered and vulnerable migratory species	51 EU countries, other European countries, some African and Middle Eastern countries	No	1	1	Strictly protected	● opened for signature in 1979 by European environment ministers, and came into force in 1982 with the approval of the Council of the European Union ● the first international act addressing the conservation of wild species in Europe ● a voluntary agreement, constituting no law or obligation, aiming to protect wild flora, fauna, and their natural habitats (listed in the appendices).
	CITES (1975 worldwide, 1996 in EU)	● to ensure that international trade in specimens of wild animals and plants does not threaten their survival	183 countries from all continents	Yes	36	0	Species not necessarily threatened with extinction but that may become so unless trade is closely controlled (Appendix II)	● the conservation agreement with the largest membership ● an international agreement between governments aiming to regulate and monitor the international trade in wild species ● drafted as a result of a resolution adopted in 1963 at a IUCN meeting ● although legally binding on the Parties, CITES does not take the place of national laws ● none of the spiders listed occur naturally in Europe

	Habitats Directive (92/43/EEC) (1992)	● to protect habitats and species listed in the directive’s Annexes	27 EU countries	Yes	1	1	Strictly protected	● the EU response to the Bern Convention ● the main legal document regulating Europe’s nature conservation policy, together with the Birds Directive (2009/147/EC), ● a European law, mandatorily transposed to national laws of EU countries.
	IUCN Red List of Threatened Species (1964)	● to evaluate and classify the global conservation status of the species, classifying them in categories of risk	No signatory parties, only partner Member Organisations (States, government agencies, NGOs, Scientific Societies)	No	293	8	Critically Endangered (2 species), Endangered (1 species), Vulnerable (4 species), Data Deficient (1 species)	● the first international organization to focus on the protection and sustainable use of natural resources ● one of the main authorities on environmental management and nature conservation ● commonly used in decision-making process and as a guide to revise international or local agreements such as CITES
Regional	National IUCN Red Lists and Red Data Books	● to evaluate and classify the conservation status of species at national level, classifying them in categories of risk following the IUCN standards	No signatory parties. 13 Countries providing Red Lists	No	1098	1098	Species listed in the IUCN categories	● commonly used in decision-making process
	National non-IUCN Red Lists and Red Data Books	● to evaluate and classify the conservation status of species at national level, classifying them in categories of risk according to modified IUCN criteria, national guidelines or expert opinions	No signatory parties. 7 Countries providing Red Lists	No	1178	1178	Varying categories of extinction risk	● commonly used in decision-making process

	Sub- or supranational IUCN Red Lists and Red Data Books	● to evaluate and classify the conservation status of species at the subnational level, classifying them in categories of extinction risk following the IUCN standards	No signatory parties. 12 regions providing Red Lists	No	1041	1041	Species listed in the IUCN categories	● commonly used in decision-making process
	Sub- or supranational non-IUCN Red Lists and Red Data Books	● to evaluate and classify the conservation status of species at the subnational level, classifying them in categories of extinction risk according to modified IUCN criteria, national guidelines or expert opinions	No signatory parties. 19 regions providing Red Lists	No	1099	1099	Varying categories of extinction risk	● commonly used in decision-making process
	National laws	● to protect the species within the national territory	19 Countries	Yes	178	178	Legally protected at the national level	● The preeminent instruments to protect species

Currently, 301 spider species are listed in the Global IUCN Red List (IUCN, 2021). Three are Extinct, 164 are assigned to one of the three categories of risk (Critically Endangered, Endangered, Vulnerable), and 97 are in Near Threatened or Least Concern categories; further 37 species are in the Data Deficient category. Almost half of the species listed in the IUCN Red List are endemic to the Seychelles Islands (IUCN, 2021). This disproportion is due to the work of Gerlach (2014), who provided the first comprehensive assessment based on formal IUCN criteria of spiders within a geographically restricted region.

More recently, Red Lists and Red Books have been drawn up for geographic areas at different spatial scales (i.e. at the regional level) and for different purposes. Regarding the spatial scales, species evaluated as threatened in the Global Red List are considered endangered worldwide, but this assessment may not coincide with their conservation status at a national or subnational level. While the Global Red List addresses the current and future conservation status of species, i.e. their relative risk of extinction, Regional Red Lists may contribute to the effective conservation of threatened species on a smaller scale, influencing their protection and recovery. Regarding the purposes, whilst Red Books generally contain in-depth analyses of species' status, distribution, factors of decline and conservation measures, Red Lists are usually shorter and more specific, presenting concise references to distribution and status. Table 2 details those European countries which have used IUCN and Red List approaches to spider conservation.

3.4. Spider species occurring in Europe mentioned in international conservation tools

International conservation tools offer significant opportunities for the conservation and protection of biodiversity due to their cross-border approaches, long-term commitments, and consideration of the biology of the species (Trouwborst et al., 2017). Species distributions are seldom confined within national boundaries and conservation is an international concern that requires active collaboration among countries through trans-national actions.

At present, only nine spider species out of >4,000 occurring in Europe (Nentwig et al., 2020) are considered in international conservation tools. One is included in the Bern Convention and in the Habitats Directive, whilst the remaining eight are listed in the Global IUCN Red List of threatened species (IUCN, 2021).

The only spider mentioned in the Bern Convention and the Habitats Directive is *Macrothele calpeiana*. However, doubts have been raised regarding the needs of protection of this species and the ecological consequences of its ongoing spread in Europe probably due to commercial export of olive trees (Jiménez-Valverde et al., 2011; further details in the section "Spider species of conservation concern in Europe").

Importantly, the conservation status of *M. calpeiana* has been recently assessed according to the IUCN criteria (Branco et al., 2019), proving this species to be eligible for the Least Concern category.

Eight native European spiders are listed in the global IUCN Red List of threatened species (IUCN, 2021):

- *Anapistula ataecina* Cardoso & Scharff 2009 (Symphytognathidae): a cave-dwelling spider endemic to a geographically restricted karst system in southern Portugal (Cardoso and Scharff, 2009), regarded as Critically Endangered (Cardoso, 2010).

- *Dolomedes plantarius* (Pisauridae): a semi-aquatic spider species with a Euro-siberian distribution. As a result of habitat loss and degradation, in 1996 the species was classified as Vulnerable by IUCN (World Conservation Monitoring Centre, 1996a). Because it was assessed before the publication of the new IUCN standards (version 3.1, 2001), the evaluation of *D. plantarius* is outdated and hard to compare with more recent ones.

- *Macrothele cretica* Kulczyński 1903 (Macrothelidae): a species endemic to Crete. Until recently, information was inadequate for evaluation of the global risk of extinction, and it was therefore listed as Data Deficient (World Conservation Monitoring Centre, 1996b). This species is listed as Vulnerable in the Red Book for Greece (Chatzaki, 2009).

- *Nothophantes horridus* Merrett & Stevens 1995 (Linyphiidae): Critically Endangered in the global IUCN Red List (Cardoso and Hilton-Taylor, 2015). Thought to be a subterranean-specialist living in limestone fissures, this species is endemic to the UK, where it is known from only three locations in the Plymouth area. It is considered Endangered on the British Red List (Harvey et al., 2017), and is listed in Section 41 of the Natural Environment and Rural Communities Act (2006) as a Species of Principal Importance in England.

- *Vesubia jugorum* (Simon 1881) (Lycosidae): a spider endemic to high altitude rocky areas in the South-Western Alps, straddling the border between France and Italy (Mammola et al., 2016). This species was listed as Endangered in the Global IUCN Red List of Threatened species on the basis of its limited geographic range and the predicted reduction of its natural habitat in the near future due to climate change (Isaia and Mammola, 2018).

- *Troglohyphantes gracilis*, *T. similis* and *T. spinipes* (Linyphiidae): three subterranean species restricted to Slovenia (Mammola et al., 2018a), where they figure in the national Red List due to their rarity (category R) (Uradni list Republike Slovenije, 2002). These species were listed in the first IUCN Red List (IUCN Conservation Monitoring Service, 1986) due to their restricted geographical distribution, and were assessed as Vulnerable in the 1996 IUCN Red List (World Conservation Monitoring Centre, 1996c, 1996d, 1996e), but their status has not been updated since.

4. Regional conservation tools

Of the European countries which have enacted legislation to safeguard and manage species within their territory, 19 have legislated in some way for spiders. Spider conservation is also promoted by regional Red Lists in 28 countries: we refer to those based on IUCN Criteria as “IUCN Red Lists” and those which do not strictly follow IUCN standards as “non-IUCN Red Lists”.

4.1. Spider conservation in European countries

Essential up-to-date information on current spider conservation from each country is presented in Tables 2 and 3. Due to space limitations, a detailed overview referring to (1) Regional IUCN Red Lists implemented at the national or subnational level, (2) Regional non-IUCN Red Lists, and (3) any legislation mentioning spiders promoted by the countries involved, is reported in Appendix B.

4.2. Red Lists and Red Data Books of spiders in Europe

A first review on spiders in European Red Lists reporting data from seven countries was published in 2000 (Franc, 2000). Since then, 20 countries have adopted national or subnational red lists considering spiders as an appropriate basis for prioritising and developing national conservation policies. Among the 42 European countries considered in this review, 28 (67%) currently have a list of threatened spider species, 20 of which operate at national level. Eight countries have Red Lists only at the subnational level, whilst seven countries have both national and subnational lists. Fig. 1 provides the geographic distribution of national Red Lists and Red Books in the European countries.

Different criteria were used for assessing the conservation status of species. Several threatened species datasets in Europe follow IUCN criteria, but some countries utilise alternative categories and criteria. The IUCN assessment process has received wide acceptance and is being used consistently at national and other regional scales (Gärdenfors, 2001). Ten countries based their national Red Lists or Red Data Books on the most recent version of IUCN criteria (IUCN, 2001, 2012b), namely Bulgaria, Croatia, Denmark, Finland, Greece, Kosovo, Norway, Spain, Sweden and Great Britain. Slovakia adopted the 1994 IUCN criteria for their national lists (IUCN, 1994), whilst Latvia and Lithuania adopted a pre-1994 version.

The remaining countries with national inventories used national guidelines (see Blick et al., 2016), or based them on expert opinion (see, e.g., Groppali and Priano, 1992), or utilised modified IUCN Categories and Criteria (see for example Głowaciński and Nowak, 2004, Řezáč et al., 2015 and Staręga et al., 2002). Many such Red Lists were developed before the regional IUCN guidelines were published, as is the case with Germany where a standardised assessment scheme was developed and has been maintained since the 1970s by the Federal Agency of Nature Conservation (DS/IRV, 1971; Sukopp, 1974). As previously noted, other national lists were drawn up using alternative and highly individual categorization systems, for example, Italy (Groppali and

Priano, 1992) and Slovenia (Uradni list Republike Slovenije, 2002). In these inventories categories of risk differ widely and criteria and category definitions are often neither explicit nor transparent.

In addition to national Red Lists, the Czech Republic, Denmark, Germany, Italy, Poland, Slovakia, and Spain also have subnational ones, which assess the conservation status of spiders in one or more specific regions or districts of the country. Germany has the highest number of inventories of threatened spiders (13), including the national list and the supranational list (Wadden Sea).

Eight countries have supra- or subnational Red Lists but no national one. In France, spiders occurring in Nord-Pas-de-Calais and Picardie were assessed following the regional IUCN guidelines (Groupe ornithologique et naturaliste du Nord-Pas-de-Calais, 2018; Picardie Nature, 2016). As a result of the IUCN assessment carried out for selected taxonomic groups occurring in the whole Carpathian Region (Kadlečík, 2014; Mateleshko and Potish, 2011) a certain proportion of spiders in the Carpathian areas of Hungary, Romania, Serbia and Ukraine have been assessed according to IUCN guidelines. Furthermore, in Ukraine, there are also two other regional Red Lists (Tokarsky, 2013; Zalevskiy and Bronskov, 2017), drafted according to the national criteria adopted by the Red Book of Ukraine (Akimov, 2009).

The remaining countries (Austria, Belgium, Netherlands) used national criteria (e.g., Komposch and Steinberger, 1999) or regional IUCN guidelines which were integrated with different systems of evaluation (e.g., Maelfait et al., 1998; Vangsgård et al., 1996). In Belgium (Maelfait et al., 1998), where the conservation of nature is responsibility of the regional governments, the Flemish red list of spiders is based on the 1994 IUCN criteria (IUCN, 1994) and on the criteria used in Germany (Schnittler et al., 1994). In the Red Book of the Wadden Sea area (Von Nordheim et al., 1996), the approach to assessment is based on a combination of the IUCN criteria and the German (Blab et al., 1984) and the Danish (Asbirk and Søgaard, 1991) systems. The geographic distribution of the subnational Red Lists in the European countries is displayed in Fig. C3 Appendix C.

Although many European countries and regions now have Red Books and Lists of their threatened spiders, the lack of standardisation in the categories and criteria used is problematic. The alteration or misinterpretation of IUCN guidelines may lead to confusion if modifications of the criteria are not explicitly stated (Miller et al., 2007). If it were the case that every country applied its own approach, the criteria adopted would be subject to high levels of subjectivity which would reduce the comparability among regional Red Lists. For example, terms such as “vulnerable” or “endangered” have different meanings according to different evaluation systems. In addition, the category “rare” is used by several authors (Blick et al., 2016; Groppali and Priano, 1992; Komposch and Steinberger, 1999; Maelfait et al., 1998) even though it pertains to the ecological characteristics of a species rather than its category of risk (de Grammont and Cuarón, 2006).

Table 2. Regional Red Lists (RLs) and Red Data Books (RDBs) at national and subnational level in the European countries, showing the number of spider species known for each country, relative number of species assessed and number of species considered as extinct and/or threatened, compliance with IUCN standards, references to the species list, and number of native European spider species on the Global Red List. For detailed information on spider conservation in each European country, see Appendix B.

	Spider species	RLs and RDBs	N species assessed	N species extinct and/or threatened	System adopted	References	N species in global IUCN RL
Albania	491	No	0	0	NA	NA	0
Austria	1035	Subnational (Carinthia)	325	57	non-IUCN	Komposch and Steinberger, 1999	1
Belarus	481	National	1	1	IUCN modif	Red Book of the Republic of Belarus, 2015	1
Belgium	743	Subnational (Flanders)	604	213	IUCN modif	Maelfait et al., 1998	1
Bosnia-Herzegovina	171	No	0	0	NA	NA	0
Bulgaria	1045	National	5	5	IUCN	Golemansky et al., 2015	1

Croatia	765	National	12	12	IUCN	Ozimec et al., 2009	1
Cyprus	431	No	0	0	NA	NA	0
Czech Republic	893	National	875	386	IUCN modif	Řezáč et al., 2015	1
		Subnational (Upper Silesia)	316	5	IUCN 1994	Staręga et al., 2001	
		Subnational (Carpathians)	285	170	IUCN	Gajdoš et al., 2014	
		Subnational (Carpathians)	14	13	IUCN	Witkowski et al., 2003	
Denmark	579	National	538	81	IUCN	Bruun and Lissner, 2019	1
		Subnational (Wadden Sea)	14	5	IUCN modif	Vangsgård et al., 1996	
Estonia	528	No	0	0	NA	NA	1
Finland	658	IUCN	604	22	IUCN	Hyvärinen et al., 2019	1

France (Metropolitan)	1712	Subnational (Picardie)	51	5	IUCN	Picardie Nature, 2016	2
		Subnational (Nord-Pas-de-Calais)	469	70	IUCN	Groupe ornithologique et naturaliste du Nord-Pas-de-Calais, 2018	
Germany	1011	National	968	261	non-IUCN	Blick et al., 2016	1
		Subnational (Baden-Württemberg)	357	150	non-IUCN	Nährig et al., 2003	
		Subnational (Bavaria)	838	321	non-IUCN	Blick and Scheidler, 2004	
		Subnational (Berlin)	544	162	non-IUCN	Kielhorn, 2017	
		Subnational (Brandenburg)	548	123	non-IUCN	Platen et al., 1999	
		Subnational (Lower Saxony and Bremen)	673	234	non-IUCN	Finch, 2004	
		Subnational (Mecklenburg-West Pomerania)	569	94	non-IUCN	Martin, 2012	
		Subnational (North-Rhine Westfalia)	662	92	non-IUCN	Buchholz et al., 2011	

		Subnational (Saxony)	612	176	non-IUCN	Hiebsch and Tolke, 1996	
		Subnational (Saxony-Anhalt)	643	195	non-IUCN	Sacher and Platen, 2001, 2004	
		Subnational (Schleswig-Holstein)	565	43	non-IUCN	Lemke et al., 2013	
		Subnational (Thuringia)	622	209	non-IUCN	Sander et al., 2001	
		Subnational (Wadden Sea)	55	38	IUCN modif	Vangsgård et al., 1996	
Greece	1285	National	32	32	IUCN	Chatzaki, 2009	2
Hungary	815	Subnational (Carpathians)	181	0	IUCN	Gajdoš et al., 2014	1
Iceland	85	No	0	0	NA	NA	0
Ireland	415	No	0	0	NA	NA	0
Italy	1702	National	25	2	non-IUCN	Groppali and Priano, 1992	2

		National	123	3	IUCN modif	Ruffo and Stoch, 2006	
		Subnational (Bolzano-Alto Adige)	273	82	non-IUCN	Noflatscher, 1994	
Kosovo	107	National	8	0	IUCN	Ibrahimi et al., 2019	0
Latvia	502	National	4	3	IUCN pre-1994	Spuris, 1998	1
Liechtenstein	532	No	0	0	NA	NA	0
Lithuania	476	National	1	0	IUCN pre-1994	Ministry of Environment, Order D1-814 of 10th September 2018	1
Luxembourg	117	No	0	0	NA	NA	0
Malta	144	National	5	0	IUCN modif	Schembri and Sultana, 1989	0
Moldova	293	No	0	0	NA	NA	0
Montenegro	673	No	0	0	NA	NA	1

Netherlands	646	Subnational (Wadden Sea)	26	11	IUCN modif	Vangsgård et al., 1996	1
North Macedonia	820	No	0	0	NA	NA	0
Norway	642	National	605	34	IUCN	Henriksen and Hilmo, 2015	1
Poland	848	National	263	206	IUCN modif	Staręga et al., 2002	1
		National	3	3	IUCN modif	Głowaciński and Nowak, 2004	
		Subnational (Carpathians)	120	87	IUCN	Gajdoš et al., 2014	
		Subnational (Upper Silesia)	477	41	IUCN 1994	Staręga et al., 2001	
		Subnational (Bielsko-Biała)	288	18	IUCN 1994	Staręga et al., 2001	
		Subnational (Częstochowa)	247	1	IUCN 1994	Staręga et al., 2001	
		Subnational (Katowice)	270	2	IUCN 1994	Staręga et al., 2001	

		Subnational (Opole)	325	22	IUCN 1994	Staręga et al., 2001	
Portugal (excluding Macaronesia)	831	No	0	0	NA	NA	1
Romania	1009	Subnational (Carpathians)	360	25	IUCN	Gajdoš et al., 2014	1
Serbia	734	Subnational (Carpathians)	44	15	IUCN	Gajdoš et al., 2014	1
Slovakia	955	National	415	275	IUCN 1994	Gajdoš and Svatoň, 2001	1
		Subnational (Carpathians)	355	203	IUCN	Gajdoš et al., 2014	
		Subnational (Carpathians)	15	15	IUCN	Witkowski et al., 2003	
Slovenia	759	National	53	10	non-IUCN	Uradni list Republike Slovenije, 2002	4
Spain (excluding Macaronesia)	1386	National	10	7	IUCN	Verdú et al., 2011	1
		Subnational (Andalusia)	22	6	IUCN	Barea-Azcón et al., 2008	

Sweden	739	National	726	21	IUCN	SLU Artdatabanken, 2020	1
Switzerland	1003	No	0	0	NA	NA	1
Turkey	1081	No	0	0	NA	NA	0
Ukraine	1073	Subnational (Carpathians) Subnational (Ukrainian Carpathians) Subnational (Kharkiv) Subnational (Donetsk)	80 1 6 12	14 0 0 0	IUCN IUCN non-IUCN non-IUCN	Gajdoš et al., 2014 Mateleshko and Potish, 2011 Tokarsky, 2013 Zalevskiy and Bronskov, 2017	1
United Kingdom	684	National	639	105	IUCN	Harvey et al., 2017	2

Such variation in national listings makes it difficult to synthesize information from different countries which is vital in order to create a general overview; this, in turn, can hamper efforts to consolidate information and provide recommendations.

To reduce bias and limit these inconsistencies, we recommend that standardised categories and criteria, as well as a unified categorisation system, are implemented and utilised. Currently, the only widely adopted system worldwide is the one by IUCN, which theoretically allows comparison of results from different countries and taxa under a common framework. This could be adopted across countries to guarantee such comparability and hence contributing to analyses beyond national borders. An effort must be made to guarantee similar interpretation of criteria, which is often hard and rarely accomplished, but essential for future protection of species whose ranges span different countries.

4.3. Threatened species in Red Lists and Red Data Books across Europe

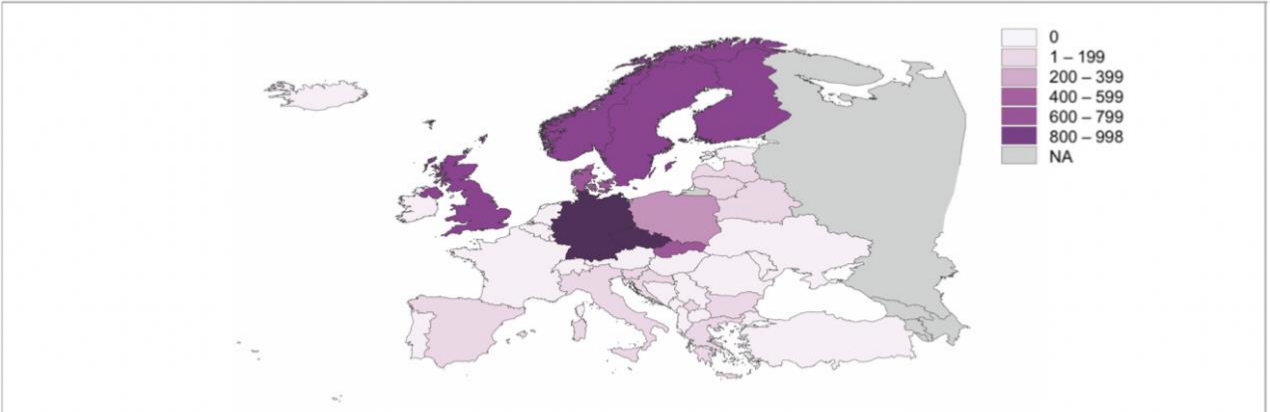
One of the main problems facing spider conservation in Europe is the general lack of information on their true conservation status. Data are incomplete in the vast majority of the spider species, and are usually limited to the knowledge of their national occurrence. Detailed information on national distributions of species, ecological requirements, and threats affecting them at the regional level, are available only for certain countries. Efforts have been made primarily in Central and North-Western European countries, where national inventories of threatened species cover the highest percentage of resident spider species.

Overall, 1,552 (37%) of the 4,154 spider species currently known in the European countries considered (Nentwig et al., 2020) are assessed by regional inventories focusing on their conservation status. Czech Republic, Denmark, Finland, Germany, Norway, Sweden and the UK, list the majority of their native spider fauna, all with coverage >90% (Fig. 3). This can be attributed to these countries having a greater number of arachnologists and local experts, resulting in a broader understanding of the spider fauna occurring within their national borders and, consequently, in higher numbers of spiders being assessed in national inventories (see Table C3 in Appendix C). Conversely, in many other countries, only iconic species have been comprehensively assessed. The countries with the lowest species assessed-known ratio are Belarus and Lithuania (both 0.2%; 1 species out of 481 and 476, respectively), followed by Bulgaria (0.5%; 5 species out of 1,045) and Latvia (0.8%; 4 species out of 502). This low coverage in the assessment of native spider species is likely due to the scant number of local arachnologists and to the related deficit of adequate information with regard to the national distribution of species and their population size and dynamics.

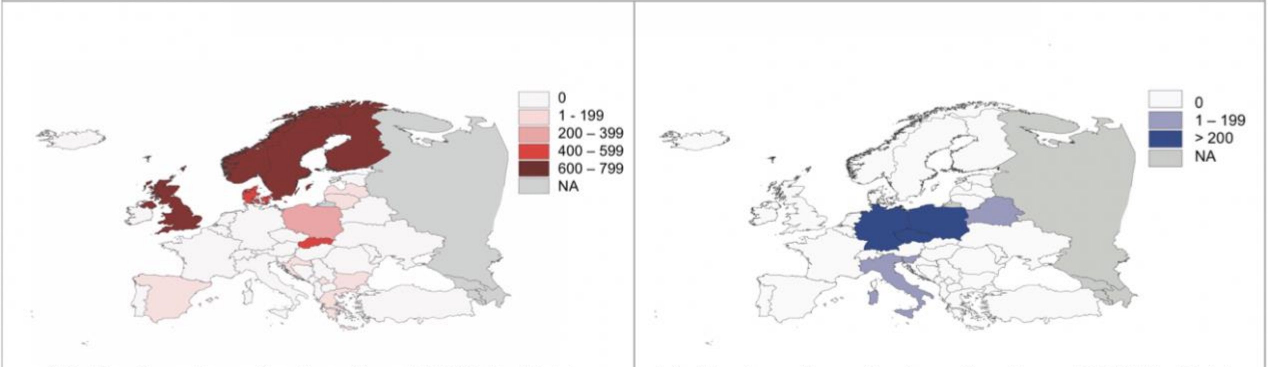
The Mediterranean countries also have a low proportion of spiders assessed. Italy is one of the most species-rich countries in Europe (1,702 spider species), but has only assessed 148 species (8.7%). In Spain the ratio is even lower, with 10 out of 1,386 species (0.7%) listed in the national

Red Book, whilst Greece has 1,285 species recorded but only 32 (2.5%) have been assessed (see Fig. 3 for an overall comparison).

This significant lack of information on the status of spider species in the Mediterranean region is mainly the result of taxonomic (many less-known or recently described species) and geographical (only generic or partial data on species distribution range) uncertainty. Even if in some countries most of the species are recognized to be present, little is known regarding their distribution, and the overall knowledge of spiders is far from complete (Cardoso, 2008). Furthermore, the high frequency of endemic species in the Mediterranean countries, which are generally not well known or studied, contributes to the general difficulty in assessing species conservation status.



(a) Number of species in national Red Lists



(b) Number of species in national IUCN Red Lists

(c) Number of species in national non-IUCN Red Lists

Fig. 1. Number of spider species considered by inventories of threatened species in Europe. (a) Number of species listed in national Red Lists in Europe (Malta, not displayed in map, is in the range 1-199; (b) Number of species listed in national IUCN Red Lists in Europe; (c) Number of species listed in national non-IUCN Red Lists in Europe (Malta, not displayed in map, is in the range 1-199). Northern and Central European countries stand for having the highest number of species mentioned in Red Lists. NA = Not Available.

Regarding supranational Red Lists, the most species-rich list is the Carpathians Red List (Kadlečík, 2014), which considers 1,067 spider species (1,040 according to the current taxonomy) that occur across Czech Republic, Hungary, Poland, Ukraine, Romania, Serbia and Slovakia. This list complements the former version of the IUCN Carpathian List (Witkowski et al., 2003), which listed only 15 species of spiders for the Czech Republic and Slovakia. Other supranational lists available in Europe are the Red List of Upper Silesia (Staręga et al., 2001), assessing 508 spiders (506 following the current taxonomy) from the Polish and Czech Silesia, and the Red List of the Wadden Sea (Vangsgård et al., 1996), with 55 species assessed, occurring across the coastal region along Denmark, Germany and the Netherlands.

All the current Red Lists and Red Books on spiders in Europe were published after 1989, which is the year of publication of the oldest still valid national list on threatened spiders (the Red Data Book for the Maltese Islands by Schembri and Sultana, 1989). Conversely, Denmark, Finland, Norway, Sweden and the UK have the most recent Red Lists, all published after 2015. Among Central European countries, Germany and Czech Republic have very recent assessments as well (2016 and 2015, respectively).

Due to both the difficulty in comparing the different evaluation systems used to produce national red lists, and to the lack of information on the conservation status of species, any depiction of Europe’s threatened spider fauna cannot be complete or balanced. However, the inclusion of certain species in red lists across Europe does provide useful insights into species of conservation concern in Europe in general.

Overall, the highest number of regionally extinct and threatened spider species has been assessed from Central-Eastern Europe (Fig. 4). Czech Republic has the highest number of species assessed as regionally extinct, 26 out of 893 species occurring nationwide (3%), followed by Slovakia with 15 species (1.6%), and Germany with 7 species (0.7%) considered extinct or lost. Czech Republic also has the highest number of species considered as threatened (360 species, corresponding to more than 40% of the national spider fauna), followed by Slovakia with 260 species (27%), Germany with 254 (25%) and Poland with 206 spider species (24%).

These results would suggest a geographical pattern with a greater concentration of threatened species in Central and Eastern European countries. However, this picture remains crude. First, different assessment methods have been adopted in drafting national Red Lists so the definition of “threatened” may be inconsistently applied. Second, in some countries, assessments are limited to species supposed to be threatened *a priori*, i.e. those selected on the basis of expert judgment, without taking into consideration the entire national fauna. Third, some countries consider a limited number of species which are often regionally or ecologically clustered. Fourth, some countries do not even have a national Red List on spiders. Accordingly, these results are preliminary and are limited to those countries which both have a Red List and assess their spiders at national level.

Table 3. Acts of law concerning spiders in European countries, with number of species and number of protected species.

	Spider species	Legal Acts	N species
Albania	491	None	0
Austria	1035	LGBl. Nr. 70/2007 32. Stück (Carinthia) LGBl. Nr. 59/2015 (Carinthia) Vienna Nature Conservation Regulation (Wr. NschVO)	22 109 2
Belarus	481	Law on Protection of The Environment 1992 no. 1982-XII, Ministry of Natural Resources and Environmental Protection Decree 2014 no. 26	1
Belgium	743	Species Decree (Flemish Government Decree 2009)	4
Bosnia-Herzegovina	171	None	0
Bulgaria	1045	None	0
Croatia	765	Nature Protection Act (Official Gazette 70/05, NN 139/2008)	12
Cyprus	431	None	0
Czech Republic	893	None	0
Denmark	579	None	0
Estonia	528	None	0
Finland	658	Nature Conservation Act 1096/1996, Nature Conservation Decree 160/1997 Appendix 4 471/2013	2
France (Metropolitan)	1712	None	0
Germany	1011	Bundesartenschutzverordnung (BartSchV) 2005	6
Greece	1285	None	0
Hungary	815	Government Decree no. 348/2006 (XII.23.), Appendix 2 of the Ministerial Decree no. 13/2001 (V.9) Köm	16
Iceland	85	None	0
Ireland	415	None	0
Italy	1702	L.R. 10/2008, D.g.r. n. 8/7736	2
Kosovo	107	None	0
Latvia	502	Regulation nr. 396 of Minister of Cabinet	1
Liechtenstein	532	None	0

Lithuania	476	Law on the Protected Fauna, Flora and Fungi Species and Communities (No. VIII-499), Order D1-814 of Ministry of Environment	1
Luxembourg	117	None	0
Malta	144	None	0
Moldova	293	None	0
Montenegro	673	None	0
Netherlands	646	None	0
North Macedonia	820	None	0
Norway	642	None	0
Poland	848	Decree of the Ministry of Environment 2016, concerning the Bill of Nature Protection No. 92/2004	9
Portugal (excluding Macaronesia)	831	Decree Law no. 140/99 Annex B-IV	1
Romania	1009	None	0
Serbia	734	Official Gazette of the RS no. 5/2010, 47/2011, 32/2016 and 98/2016	17
Slovakia	955	Ministry of Environment Decree SR nr. 158/2014	17
Slovenia	759	Regulation on the Protection of Endangered Species Ur. l. RS 57/93	3
Spain (excluding Macaronesia)	1386	Royal Decree 139/2011 DOE nr. 30 decreto 37/2001:2349-2364 Orden 6/2013 (Valencian Community) Decreto Foral 254/2019 (Community of Navarre)	1 1 1 1
Sweden	739	Species Protection Ordinance SFS 2007:845 Section 6	1
Switzerland	1003	None	0
Ukraine	1073	Order z0847-18 no. 237 Order z1202-17 no. 333	6 12
United Kingdom	684	Wildlife and Countryside Act 1981 Schedule 5	2*
Turkey	1081	None	0

*Note that an additional 38 species are listed as species of “principal importance” for conservation, receiving a lower level of protection under UK laws (see text).

Nevertheless, our results show similar geographic patterns to those seen in other terrestrial invertebrate groups, for which there is more comprehensive information available (Nieto and Alexander, 2010; Nieto et al., 2014; van Swaay et al., 2010). It has been shown that Central and Eastern European countries are hotspots for threatened species within Europe, and it is likely that our results on spiders follow a similar trend.

It is likely that this trend can be attributed to several factors: high anthropogenic pressure in these countries; agricultural improvements; changes to grassland and woodland management; infrastructure development; the degradation and drainage of wetlands, as well as isolation and loss of habitat connectivity. These threats are mostly in line with those identified as the more relevant to spider species worldwide (Branco and Cardoso, 2020). In addition, it could be argued that intensive environmental changes are more recent in Eastern countries, making the related effects on species more visible than elsewhere in Europe. These factors have led to a considerable decline in terrestrial invertebrates, particularly in Central and Eastern Europe (Birkhofer et al., 2017; Cálix et al., 2018; Farkač et al., 2005; Hallmann et al., 2017; Maes et al., 2019; Nieto and Alexander, 2010; Nieto et al., 2014; Seibold et al., 2019; van Swaay et al., 2010, 2012).

These geographical patterns have also been confirmed at a smaller scale. In the Carpathians Red List, the highest number of threatened species was recorded in the Slovak, Czech and Polish Carpathians (Kadlečík, 2014). In the Slovak part of the Carpathian Mountains, 1% of the spider species considered are regionally extinct (n=13) and more than 20% are threatened. Three spider species are known to occur in this region that are considered extinct in the Czech Carpathians, 25% of spiders have been assessed as threatened, whilst 15% are threatened in the Polish Carpathians (Kadlečík, 2014). For these regions the main threats are associated with industrialization and agricultural intensification around the mid-20th century, leading to a gradual anthropisation of the territory, and subsequent habitat loss and degradation (Kadlečík, 2014).

In Mediterranean Europe, the large-scale transformation in land use over the last few decades, the prevalence of wildfires, tourist developments, and unbridled urbanisation has resulted in large-scale alterations of the natural environment (Cuttelod et al., 2008). This has very likely impacted a high number of spider species and many with restricted ranges are possibly threatened or extinct. However, without accurate knowledge concerning their actual status, the real proportion of threatened species is hard to quantify.

In contrast, Northern European countries have the lowest percentage of threatened species. In Finland, only 21 spiders (3% of the national spider fauna), are considered threatened, and one species is described as regionally extinct (Hyvärinen et al., 2019). In Sweden, 20 species (3%) are assessed as threatened, and one as regionally extinct (SLU Artdatabanken, 2020). Norway considers 34 spiders endangered or 5% of the national spider fauna (Henriksen and Hilmo, 2015), whilst Denmark has assessed 79 species as threatened (14%) and two species extinct (Bruun and

Lissner, 2019). In these countries the majority of threatened species live primarily in forests, and thus changes to the forest environment, e.g. forestry, reduction of old forests, reforestation, and forest management, represent the major threats (SLU Artdatabanken, 2020; Bruun and Lissner, 2019; Henriksen and Hilmo, 2015; Hyvärinen et al., 2019). Furthermore, a large proportion of threatened species occur in semi-natural habitats, mainly traditional meadows and pastures, which have declined greatly over the past hundred years (SLU Artdatabanken, 2020; Bruun and Lissner, 2019; Henriksen and Hilmo, 2015; Hyvärinen et al., 2019). Climate change inevitably poses a large threat to species found in northern alpine areas, as well as to species occurring in wetlands and mires (SLU Artdatabanken, 2020; Hyvärinen et al., 2019).

4.4. Spiders in legislation in European countries

Generally, the institutions which most directly influence conservation actions and legislation are national or subnational governments. Conservation policies are mainly implemented at national and subnational levels. But, in Mediterranean countries the current national legislation on the protection of fauna and flora mainly derives from the transposition of EU legislation. National governments apply the provisions set forth under binding international conventions on nature conservation.

Among the 28 European countries that provided a threatened species list, 19 included spiders in national or subnational legislation (Figs. 2 and 5, Table 3). These consider the threat status of a species when designating conservation priorities, planning conservation efforts or allocating conservation funds.

Most acts of law which incorporate spiders among nationally protected fauna are issued in Central-Eastern European countries. Austria has the highest number of spiders under legal protection, with 111 species, followed by Slovakia, Serbia and Ukraine, all of them listing 17 spider species, and then by Hungary with 16 species, Croatia with 12, and Poland with nine.

On one hand, Northern European countries have a very low percentage of species protected, but the lowest percentage of threatened species, possibly in relation to the low degree of environmental pressures therein. On the other hand, in Mediterranean countries, few species are mentioned in national or subnational legislation, despite their higher values of spider diversity and the high level of pressure on local biodiversity.

The reasons behind this geographic pattern are not trivial. This could be related to the role of arachnologists in influencing local conservation policies. However, we failed to find a significant relation between the number of spider species listed in legal acts and the number of species assessed as threatened in regional Red Lists and Red Data Books. The same non-significant result was found when correlating the number of spider species listed in legal acts to the number of local arachnologists and experts on country basis (see Table C3 in Appendix C).

Socio-cultural aspects provide a more reliable explanation, in particular when considering local cultural values and the associated perception of wildlife. It is likely that different cultural backgrounds create variable levels of information on the subject of the environment and generate different perceptions about nature conservation. The availability of information on environmental issues may have strong implications for how individuals relate to the environment and perceive environmental policies, resulting in a greater influence in these areas and in related conservation actions. As illustrated in the European Commission report on the attitude of European citizens towards the environment (Eurobarometer, 2008), the best informed citizens are likely to live in the northern and western part of the EU, while those who tend to feel they lack information are likely to come from Southern Europe and the new Member States. The media representation of spiders in Southern Europe does not help either (data from Italy; Mammola et al., 2020a). Accordingly, it seems likely that an enhanced awareness of wildlife promotes wildlife conservation even in a neglected group such as spiders.

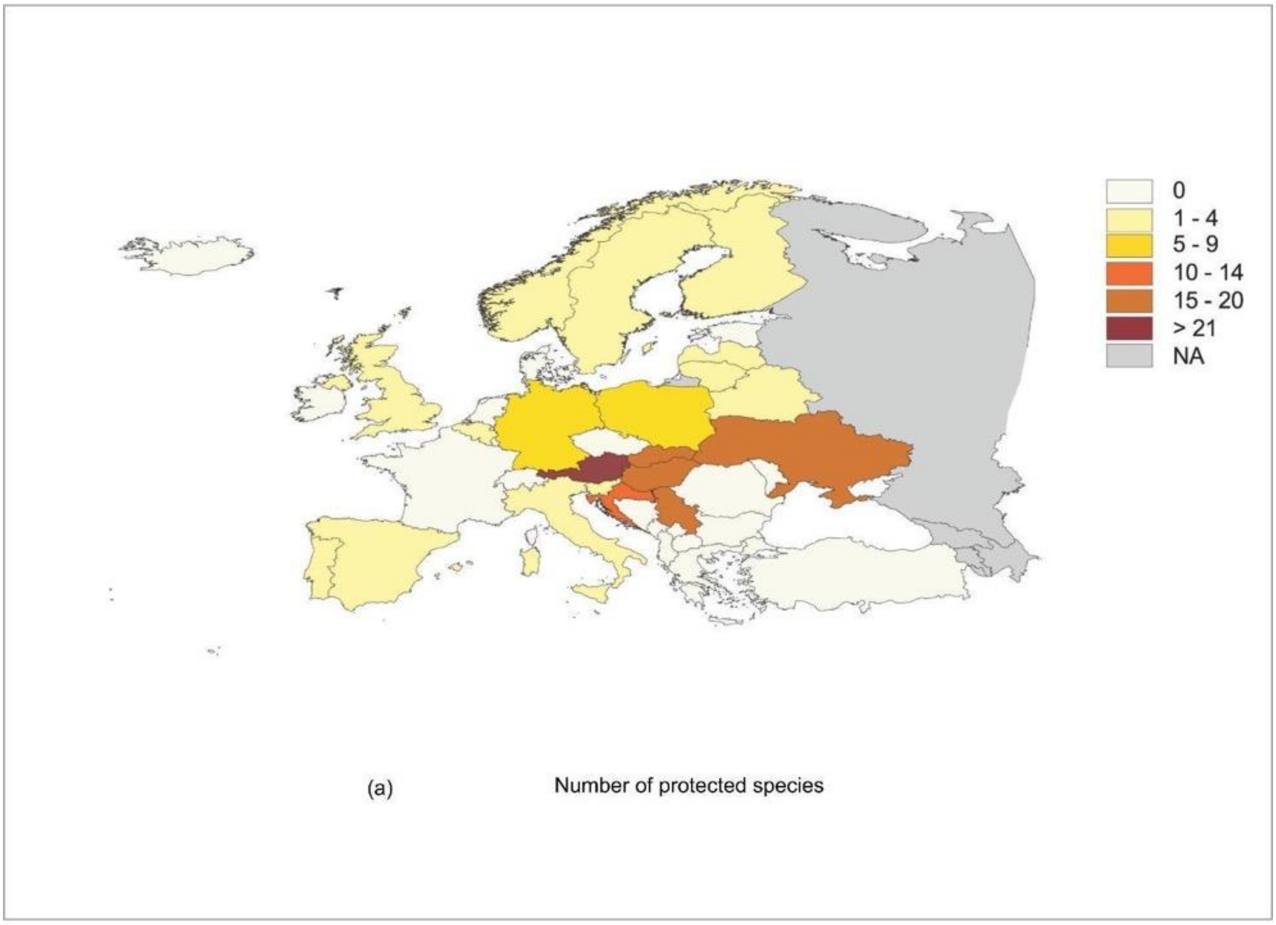


Fig. 2. Number of spider species protected by legislation in European countries (a). Central-Eastern European countries have the highest number of protected species. Note that an additional 38 species are listed as species of “principal importance” for conservation, receiving a lower level of protection under UK laws (see text). NA = Not Available.

In some countries a nature conservation economic value per specimen is also provided. In Hungary, this amounts to a monetary value from 5,000 forints to 10,000 forints (ca. 15–30 €) depending on the species. Protected species in Slovakia are valued at 230 €. These economic values refer to all listed species, whether alive or dead, or any part or derivative thereof. According to these economic values, whoever kills a specimen of the protected species may be subjected to the payment of the relative amount.

5. Spider species of conservation concern in Europe

5.1. Macrothele calpeiana

Macrothele calpeiana (Fig. 6) is the only spider protected at the European level, being listed both in the Bern Convention and in the EU Habitats Directive.

The appropriateness of legal protection for this species, as for many other invertebrates, has been called into question (Bellvert and Arnedo, 2016; Jiménez-Valverde et al., 2011; van Helsdingen, 1993; van Helsdingen and Decae, 1992), showing that the selection of species to be protected by environmental legislation at the European scale can be subject to bias (Cardoso, 2011; Leandro et al., 2017).

The rationale underlying the protection of *M. calpeiana* derived fundamentally from knowledge available at the time (Snazell, 1986; Snazell and Allison, 1989), which described both the species and its habitat as threatened. This knowledge has since developed considerably as a result of new and extensive research, which was very likely catalysed by its protected status, and thus consequently revealed a different conservation status.

In addition, *M. calpeiana* is, among spiders, one of those species which better complies with the aesthetic standards that seem to be preferred for a species to be eligible for protection (Collins and Wells, 1987), as the species is highly recognisable and easily identified and detected by the general public. In general, protected invertebrates are significantly bigger than the average invertebrate size (see Leandro et al., 2017), and the fact that *M. calpeiana* is the largest spider in Europe is a relevant factor.

As for many other invertebrates listed in Habitats Directive, the inclusion of *M. calpeiana* does not accurately reflect whether its protection is actually necessary.

5.2. IUCN red listed spiders

In the IUCN Global Red List of threatened species, only eight native European spiders currently appear (IUCN, 2021). This scant number explains to some extent the existing under-representation of spiders in the international conservation tools, and indicates a substantial disparity between groups. The number of species in the global IUCN Red List is highly biased in favour of the best-known and more charismatic animals, notably vertebrates, and, amongst invertebrates, Odonata, Lepidoptera and Orthoptera (see Fig. C1). Taxonomic bias in biodiversity conservation has been widely recognized (Cardoso et al., 2011; Donaldson et al., 2016; Leandro et al., 2017; Leather, 2013; Mammides, 2019; Titley et al., 2017), and is mainly due to data deficiencies and technical limitations. However, this unbalanced consideration has deep implications for scientific research and conservation priorities towards spiders, suggesting a compelling need for more evaluations of the conservation status of such species.

Overall, at the national level, 55 spiders in Europe were assessed as Regionally Extinct (or comparable categories) from eight different countries. Among them, only one species, the linyphiid *Agyneta decora* (O. Pickard-Cambridge 1871) is considered extinct in two countries, the Czech Republic and Slovakia.

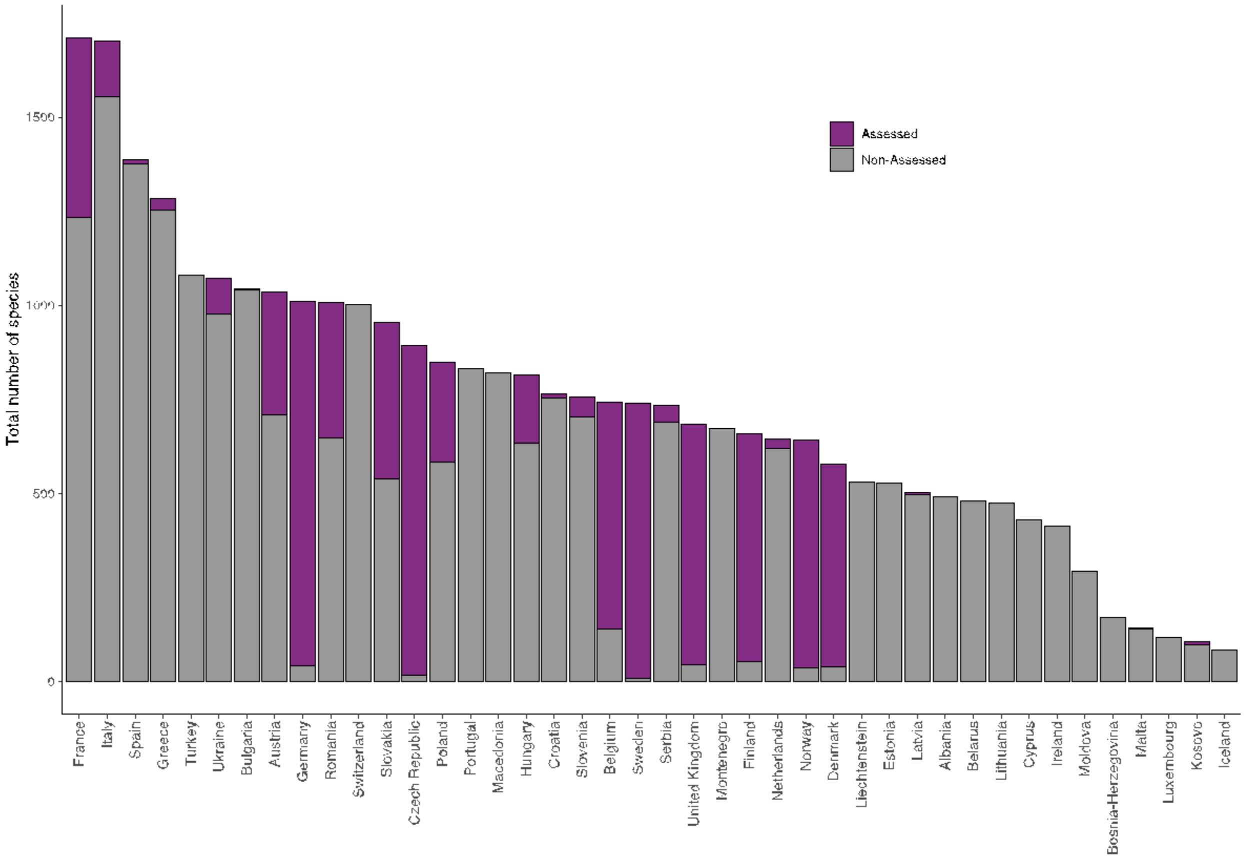


Fig. 3. Number of spider species assessed in Red Lists and Red Data Books in Europe in relation to the total number of spider species per country as reported in Nentwig et al. (2020). There is no correlation between the number of species occurring in a country and the number of species assessed in Red Lists and Red Data Books.

In the European countries considered, 714 spider species (17%) have been identified as threatened with extinction in national Red Lists, and listed in the IUCN categories Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) or other comparable categories used by other classification systems. In addition, 30 species appear in the threatened categories of national Red Lists or Red Data Books from five or more European countries (Table 4). Many of the 714 species are habitat specialists or have highly restricted ranges (324 species occur in only one country, and 202 species at most in two countries) (Nentwig et al., 2020).

Despite this, only 178 European spiders have full legal protection across the European countries (Fig. 5) and only 17 species feature in conservation acts of two or more countries (Table 5). Here we present information on the most frequently mentioned spider species in the European conservation tools.

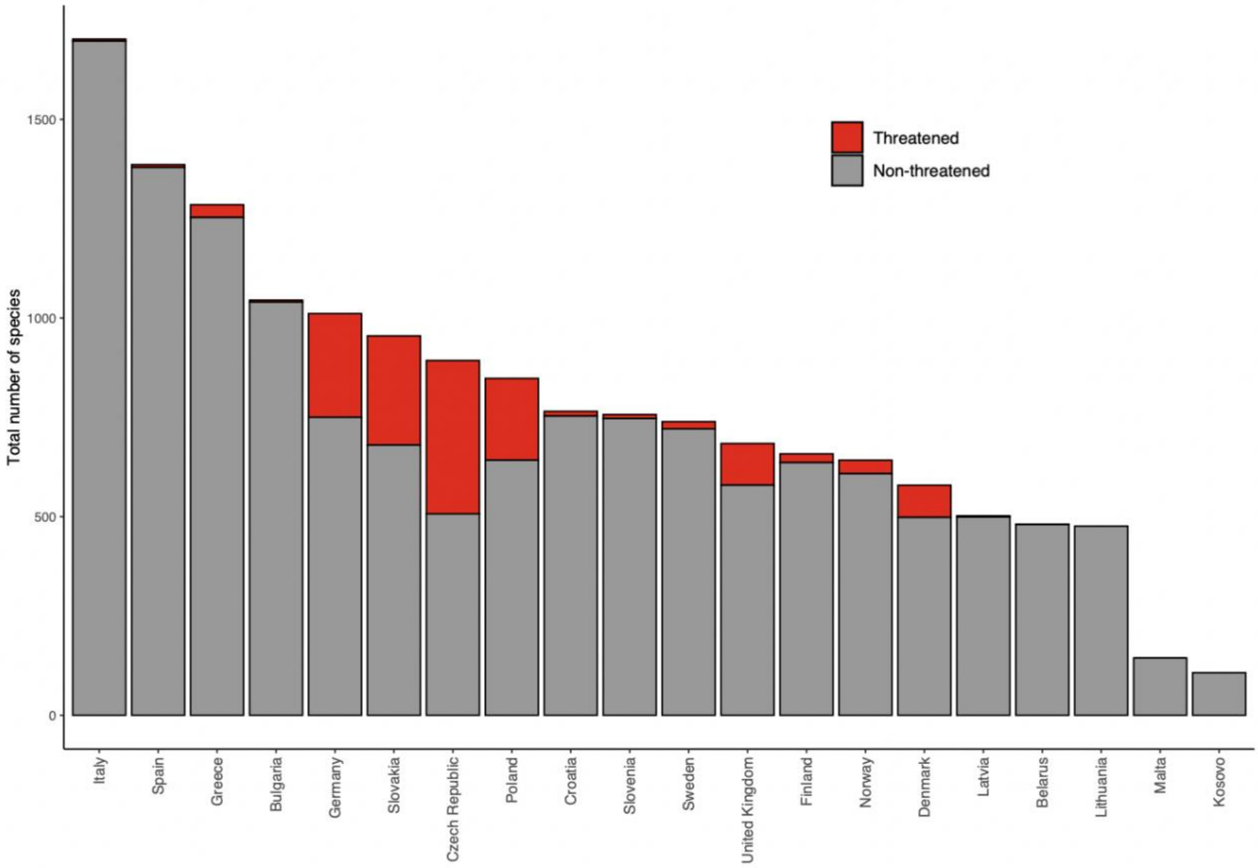


Fig. 4. Number of spider species considered as threatened in national Red Lists and Red Data Books in relation to the total number of spider species per country as reported in Nentwig et al. (2020). There is no correlation between the number of species occurring in a country and the number of threatened species in Red Lists and Red Data Books.

5.3. Dolomedes plantarius

Dolomedes plantarius (Fig. 6) is the spider species featuring the most in Red Lists and protection programmes across Europe. It has been assessed by 13 out of 20 European countries in national Red Lists and Red Data Books and features as threatened in seven of them (Table 4). Nine European countries consider *D. plantarius* in acts of law, protecting the species and its habitat (Table 5). The extent of consideration given to this species is related in part to its wide distribution, and especially to the large-scale degradation and loss of its wetland habitat (Duffey, 1995; Leroy et al., 2013, 2014; van Helsdingen, 1993). This habitat has been increasingly subjected to alteration due to land-use intensification, changes in hydrology, physical modification, eutrophication, and pollution (Junk et al., 2013; Smith, 2000). Wetlands are recognized as being of paramount importance for biodiversity and as a preferential target of conservation efforts, mainly due to the number of threatened and charismatic taxa (Finlayson et al., 2019; Geijzendorffer et al., 2018).

5.4. Argyroneta aquatica

Argyroneta aquatica (Fig. 6) also inhabits wetlands and has benefited both from this conservation interest and from interest in its unique biology, since it is the only almost wholly aquatic spider species (Seymour and Hetz, 2011). It has been assessed by the national Red Lists of 11 countries, six of which consider it to be threatened (Table 4), and is included in the conservation legislation of seven countries (Table 5).

5.5. Marpissa radiata

Marpissa radiata (Grube 1859) (Fig. 6) is another species strictly associated with wetlands. It figures in national Red Lists and Red Data Books of nine countries, seven of which consider it vulnerable (Table 4). However, this species is protected only in Austria, in the 59th Regulation of 2015 of Carinthia (LGBl. Nr. 59/2015). Even if widespread in Europe, this species is rather rare, being confined to wet habitats, and is considered threatened in most of its distribution range as a consequence of wetland decline.

5.6. Eresus spiders

Spiders of the genus *Eresus* (Fig. 6) often feature in European conservation tools. Currently, 12 species are known to occur in Europe (Nentwig et al., 2020) but only three of them, *E. kollari*, *E. sandaliatus*, and *E. moravicus* Řezáč 2008, feature in inventories on threatened species or in conservation acts. These species were formerly lumped into one morphospecies and have been treated as such in most conservation tools, but recent taxonomic revisions have shown three species are involved (Řezáč et al., 2008; Miller et al., 2012). *Eresus kollari* is one of the most considered spider species in conservation acts of law, figuring as legally protected in seven European countries (Table 5). In addition, it occurs in the national Red Lists of seven countries, and is considered threatened in five of them (Table 4). *Eresus sandaliatus* is considered in five countries, and is protected in four (Tables 4, 5). *Eresus* spiders are mainly threatened by habitat loss and degradation due to anthropogenic pressure, and by large-scale fragmentation of their habitats. Recently, they have become flagship species for the conservation of relic rocky steppes in several Central European countries (Řezáč et al., 2008), and their habitat requirements have been studied in detail (Řezáč et al., 2007, 2018; Řezáč and Heneberg, 2014, 2019). The fact that these species are amongst the most beautiful spiders in Europe (Miller et al., 2012) — which also makes them the most collectable European spiders, also present in the pet trade — may have strongly influenced their inclusion in conservation tools and their consideration as species of conservation concern.

5.7. Atypus spiders

The European species of the genus *Atypus* (Atypidae) (Fig. 6) are well covered by conservation measures (Tables 4, 5). *Atypus affinis* Eichwald 1830 has been assessed by six national Red Lists, is considered threatened by three of them and figures in the conservation legislation of four European countries. *Atypus muralis* Bertkau 1890 is both listed as threatened, and protected, in five countries. *Atypus piceus* (Sulzer 1776) is listed as threatened in three countries and is protected by law in four countries. These spiders mainly occur in open xerothermic grasslands and are threatened by changes in the management of their habitats, including intensive grazing or the overgrowth of grass and woody plants (Řezáč et al., 2007; Řezáč and Heneberg, 2014).

6. Perspectives and conclusions

6.1. Ongoing conservation actions in Europe

At an international level, the increased adoption of tools compliant with the IUCN Red List has added to the number of assessments of spider species. These tools aim to increase the number of evaluations in order to obtain an indicator that reliably represents the overall conservation status of this group (Shirey et al., 2019). However, changes in the overall conservation status of European spiders are still hard to define, due to a lack of both comprehensive knowledge and monitoring data for individual species. To reliably determine trends, it would be necessary to obtain solid baseline knowledge of the current conservation status of species and to perform regular and timely assessments of these species over time, as recently recommended by Harvey et al. (2020) in the roadmap for insect conservation and recovery.

In this regard, the conservation profiles of a sample of 200 species — including several European species — randomly selected from the spider Tree of Life, has been evaluated (Seppälä et al., 2018a, 2018b, 2018c, 2018d). These contributions aim to create a baseline for comparison with a future spider Sampled Red List Index which will ideally operate as a randomized indicator of the changing state of a taxonomic group based on the IUCN Red List criteria (Baillie et al., 2008).

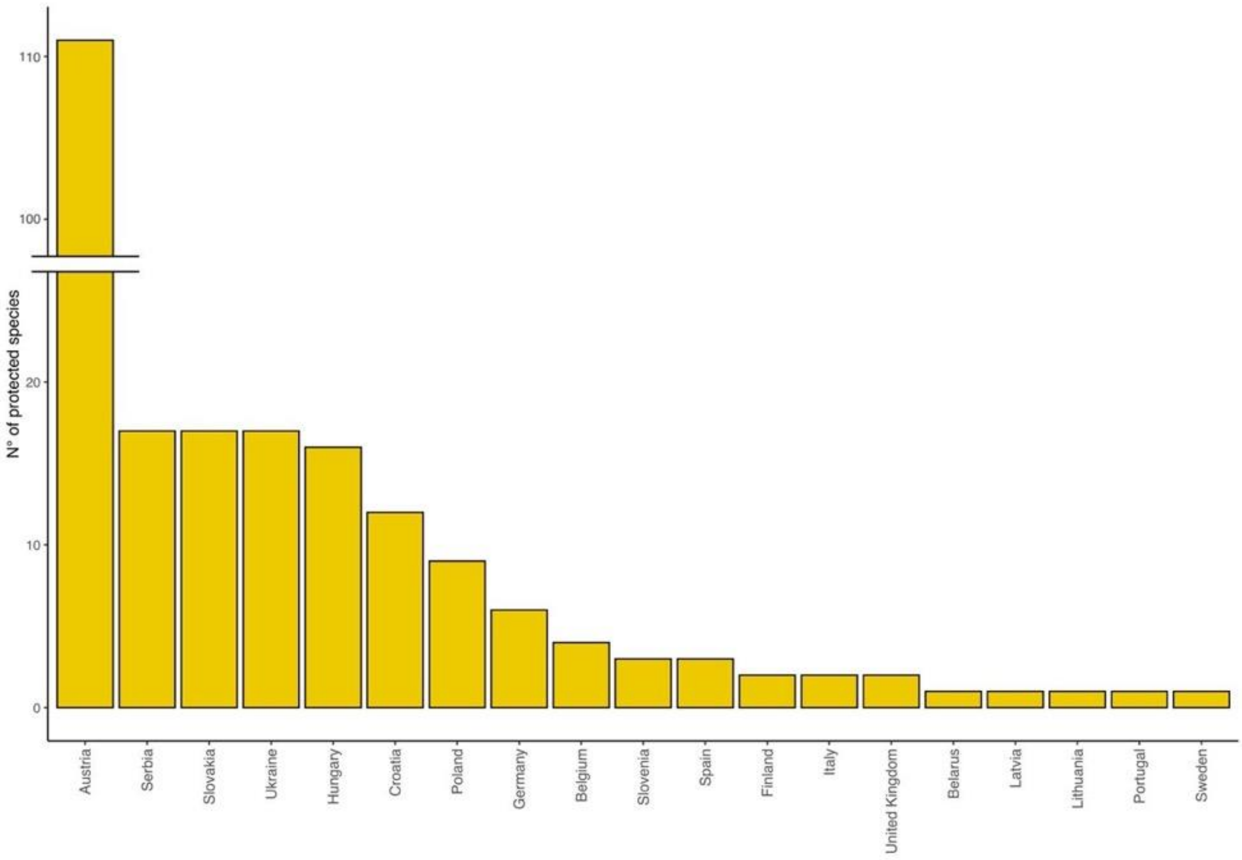


Fig. 5. Number of legally protected spider species in European countries. Note that an additional 38 species are listed as species of “principal importance” for conservation, receiving a lower level of protection under UK laws (see text).

In addition, new standardized sampling protocols for megadiverse taxa have been developed (Borges et al., 2018; Cardoso, 2008, 2009). These aim to facilitate biodiversity assessment and monitoring, and have clear and direct applications in spider conservation. Other approaches suitable for terrestrial invertebrates may be difficult to apply for spiders. For instance, involving citizen scientists in spider surveys may be very useful by way of improving a general lack of knowledge of the group (see Hart et al., 2018 and Wang et al., 2018 for successful examples), and ultimately developing effective conservation strategies (Devictor et al., 2010). However, given that for many species, an expert-based examination of sexual characters is required, this approach may be of limited use.

Our understanding is that several species are currently under regional assessment in different parts of Europe. For example, a recent study confirmed the status of *Macrothele cretica* as Vulnerable since its distribution is restricted to western Crete and its habitat is threatened, putting it at risk of extinction (Chatzaki and Komnenov, 2019).

Similar studies focusing on *Dolomedes plantarius* in Italy (Milano et al., 2018), on the cave-dwelling stenoendemic *Histopona palaeolithica* Brignoli 1971 (Agelenidae) (Mammola et al., 2019a), on the endemic alpine *Pimoa delphinica* Mammola, Hormiga & Isaia 2016 (Pimoidae) (Mammola et al., 2017a), and on cave-dwelling species of *Troglohyphantes* in the Western Alps (Mammola et al., 2018b) underline the need for more detailed knowledge of their status in order to provide new assessments of extinction risk. Concerning *Vesubia jugorum,* a five-year monitoring program led by the University of Turin and the Natural Parks of Mercantour (France) and Alpi Marittime (Italy) began in 2019, aiming to monitor the health of local populations through a trait-based approach (see Mammola et al., 2019b).

In Great Britain, all spiders listed as Species of Principal Importance under the NERC Act (2006) in England, and equivalents acts in Wales, Scotland and Northern Ireland, have action plans prepared for their conservation at national and often also at regional levels. For many of these rare species, the primary action is still to improve understanding of their status and ecology to inform future conservation action. For some species the plans and conservation actions are well-developed. *Eresus sandaliatus* and *Dolomedes plantarius* are both subjects of long-term monitoring and translocation programmes. Translocations of *E. sandaliatus* began in 2003 and have increased the number of locations from one to around 17. Translocations of *D. plantarius,* begun in 2010 (Smith et al., 2013), have increased the number of sustainable populations from three to seven. Both translocation programmes followed IUCN guidelines (IUCN/SSC, 2013). They have substantially reduced the threat of extinction of these species in Britain and have been used to test the development of the IUCN Green List (Akçakaya et al., 2018) for assessing conservation recovery.

In Sweden, two spiders are included in national action plans, namely *Eresus sandaliatus* and *Cheiracanthium pennyi* O. Pickard-Cambridge 1873*;* the latter is considered in actions aiming to restore sand dune habitats.

Several projects aiming to create inventories of threatened spiders or to update the existing ones, are currently in progress in European countries (See Table C2 in Appendix C).

6.2. Concluding remarks

Regional Red Lists and Red Data Books are the most reliable source of information on the current conservation status of spiders in Europe. Accurate evaluations of the conservation status of species represent a tool of paramount importance in conservation efforts focussing on threatened spiders. These tools provide quantitative data for informing national conservation priorities and for developing species-based management strategies. The IUCN developed a system of criteria aiming to enhance the objectivity and comparability of these Red Lists. Even though these lists do not confer any legal protection to the species assessed, they inform and influence conservation policies and legislation.

Fig. 6. Highlights in spider conservation in Europe. *Dolomedes plantarius* (above left, Photo credit Emanuele Biggi), *Marpissa radiata* (above right, Photo credit Janusz Kupryjanowicz), *Argyroneta aquatica* (below left, Photo credit Emanuele Biggi) and *Eresus* spp. (below right, Photo credit Emanuele Biggi) benefit from full legal protection in several countries across Europe and have been assessed as threatened in most European countries. *Macrothele calpeiana* (below center, Photo credit Tiziano D'Elia) is the only native European spider species that features in the Habitats Directive and the Bern Convention.

Unfortunately, the availability of Red Lists on spiders is far from homogeneous across European countries, many of which lack regional inventories or have outdated ones. This means that there are large knowledge gaps in the conservation status of the European spider fauna. For many species, data is incomplete or out-of-date, resulting in assessments based on poor quality information, and thus excluding potential candidate species from threatened species lists. To gain a better indication of the current status of a national fauna, data needs to be analysed and digitised, so that research priorities for species conservation may be more efficient and timely.

A major shortfall is the lack of monitoring of spider populations, which is essential to assess the long-term dynamics of species and their possible decline. Documenting changes in populations provides key information for assessing the conservation status of a species. Monitoring helps to provide baselines against which changes can be evaluated, and to understand the population dynamics of species and how they can change in response to environmental disturbance. Comprehensive and reliable population trends are not available for most European spider species. As a consequence, spider species are very rarely assessed based on population size (Criteria A, C and D) and most of the available assessments are based on species' geographic range (Criterion B). In turn, species with restricted distributions (endemic) are most frequently assessed, whilst information on declines in more common species is lacking. An exception is the Amber List (Harvey et al., 2017), recently adopted in Great Britain to highlight common species appeared to have undergone substantial decline, and which therefore need more frequent and detailed assessment (for details, see Appendix B). It is one possible approach to identifying and initiating actions for rapidly declining species that do not yet qualify for threatened status. Better monitoring of spider populations in Europe is urgently needed in order to understand and assess their potential risk of extinction.

This patchy understanding of the conservation status of spiders in Europe, together with the generally scant consideration given to this group, represents a considerable obstacle to the inclusion of spiders in conservation legislation and conservation planning.

Some studies (e.g. Chichorro et al., 2020) suggest using, in the absence of reliable data on species distribution and population trends, species traits as predictors of extinction risk. Using traits could help to reduce the knowledge gap, allowing prioritization of future research, monitoring and conservation efforts even for largely unknown and neglected taxonomic groups (Lowe et al., 2020). The recent development of the World Arachnid Trait database is a major step towards achieving this goal (Pekár et al., 2021).

In spite of the recognised ecological role of this group, and the scientific efforts to assess the conservation status of spider species and highlight the extent to which they are threatened, spiders are rarely included in legislation and funding programs devoted to conservation. For example, given that virtually no spider species are included in the Habitats Directive, the conservation of spiders as a group receives no EU financial investment through the LIFE program (Mammola et al., 2020b).

To date, almost one third of the European spiders have been assessed in at least one European country (1,552 out of 4,154 total species occurring). Among these, almost half are considered as threatened (714), and only very few species benefit from legal protection (178) in at least one country. The existing knowledge of the risk of extinction of many European spiders is not properly reflected in effective conservation measures. Although the main aim of the Red Lists should be assessing the risk of extinction of the species rather than determining conservation priorities (Mace et al., 2008), they are widely used to identify those species for which it is urgent to implement effective conservation actions. However, for spiders, assessments of conservation status have been seldom conflated in calls for species protection. This suggests that these lists are not effective in influencing national species conservation policies, and exposes the lack of a direct link between lists of threatened spider species and legislation.

Conversely, some of the spiders listed in legislation are far from being threatened. This is the case for *Macrothele calpeiana* (Fig. 6), for which there is a substantial debate questioning the need for its protection.

Table 4. Spider species in Europe ranked according to their number of occurrences in extinct and/or threatened categories across European National Red Lists and Red Data Books (NRL & NRDB) (only >5 occurrences are shown).

Genus	**Species**	**Author**	**Family**	**Occurrences in NRL & NRDB**
Dolomedes	*plantarius*	(Clerck, 1757)	Pisauridae	7
Marpissa	*radiata*	(Grube, 1859)	Salticidae	7
Argyroneta	*aquatica*	(Clerck, 1757)	Dictynidae	6
Brommella	*falcigera*	(Balogh, 1935)	Dictynidae	6
Gnaphosa	*nigerrima*	L. Koch, 1877	Gnaphosidae	6
Lasiargus	*hirsutus*	(Menge, 1869)	Linyphiidae	6
Midia	*midas*	(Simon, 1884)	Linyphiidae	6
Hygrolycosa	*rubrofasciata*	(Ohlert, 1865)	Lycosidae	6
Attulus	*distinguendus*	(Simon, 1868)	Salticidae	6
Marpissa	*pomatia*	(Walckenaer, 1802)	Salticidae	6
Enoplognatha	*oelandica*	(Thorell, 1875)	Theridiidae	6
Lasaeola	*prona*	(Menge, 1868)	Theridiidae	6
Psammitis	*sabulosus*	(Hahn, 1832)	Thomisidae	6
Xysticus	*luctator*	L. Koch, 1870	Thomisidae	6
Atypus	*muralis*	Bertkau, 1890	Atypidae	5
Cheiracanthium	*pennyi*	O.P.-Cambridge, 1873	Cheiracanthiidae	5
Clubiona	*juvenis*	Simon, 1878	Clubionidae	5
Eresus	*kollari*	Rossi, 1846	Eresidae	5
Berlandina	*cinerea*	(Menge, 1872)	Gnaphosidae	5
Echemus	*angustifrons*	(Westring, 1861)	Gnaphosidae	5
Haplodrassus	*minor*	(O.P.-Cambridge, 1879)	Gnaphosidae	5
Carorita	*limnaea*	(Crosby & Bishop, 1927)	Linyphiidae	5
Centromerus	*levitarsis*	(Simon, 1884)	Linyphiidae	5
Centromerus	*semiater*	(L. Koch, 1879)	Linyphiidae	5
Trichoncus	*hackmani*	Millidge, 1955	Linyphiidae	5
Agroeca	*lusatica*	(L. Koch, 1875)	Liocranidae	5
Zora	*armillata*	Simon, 1878	Miturgidae	5
Heliophanus	*dampfi*	Schenkel, 1923	Salticidae	5
Neon	*valentulus*	Falconer, 1912	Salticidae	5
Robertus	*ungulatus*	Vogelsanger, 1944	Theridiidae	5

Table 5. Spider species in conservation acts in Europe ranked according to the number of countries protecting them (only >2 countries are shown).

Genus	**Species**	**Author**	**Family**	**Number of Countries**
Dolomedes	*plantarius*	(Clerck, 1757)	Pisauridae	9
Argyroneta	*aquatica*	(Clerck, 1757)	Dictynidae	7
Eresus	*kollari*	Rossi, 1846	Eresidae	7
Atypus	*muralis*	Bertkau, 1890	Atypidae	5
Atypus	*affinis*	Eichwald, 1830	Atypidae	4
Atypus	*piceus*	(Sulzer, 1776)	Atypidae	4
Eresus	*sandaliatus*	(Martini & Goeze, 1778)	Eresidae	4
Dolomedes	*fimbriatus*	(Clerck, 1757)	Pisauridae	4
Argiope	*lobata*	(Pallas, 1772)	Araneidae	3
Arctosa	*cinerea*	(Fabricius, 1777)	Lycosidae	3
Macrothele	*calpeiana*	(Walckenaer, 1805)	Macrothelidae	3
Araneus	*grossus*	(C. L. Koch, 1844)	Araneidae	2
Argiope	*bruennichi*	(Scopoli, 1772)	Araneidae	2
Gnaphosa	*nigerrima*	L. Koch, 1877	Gnaphosidae	2
Arctosa	*stigmosa*	(Thorell, 1875)	Lycosidae	2
Geolycosa	*vultuosa*	(C. L. Koch, 1838)	Lycosidae	2
Philaeus	*chrysops*	(Poda, 1761)	Salticidae	2

This lack of connection between Red Lists and legal protection diminishes the usefulness and appropriateness of both tools in spider conservation.

The number of spider species, and especially the quality of data underlying the choice of species to protect, should be improved in legislation, both at the regional and international level. Accordingly, the appropriateness of the implementation of some European spiders in CITES should be evaluated. Because no native European spider is currently included in CITES, and as there is no quantitative data on the existing trade in spiders from Europe, more studies should verify which species might be harmed by trade, and its potential impact should be assessed.

To date, the protection of large areas of suitable habitat has been addressed as the most effective approach to spider conservation (Branco and Cardoso, 2020). Indeed, the protection of sites hosting key habitats plays a crucial role in effective conservation strategies (Coetzee et al., 2014; Geldmann et al., 2013; Gray et al., 2016; Harvey et al., 2020). The Natura 2000 network of protected areas accounts for 18% of the EU’s land territory (European Environmental Agency, 2012). Even considering ecological corridors connecting these areas, which may mitigate large-scale future threats (see for example Leroy et al., 2014), the percentage of protected areas is far from adequate to conserve spider diversity. Spider species within these habitats will presumably benefit but a large proportion of threatened species are poorly covered by the Natura 2000 network, and no priority areas specifically for conserving spiders exist. The new 2030 Biodiversity Strategy intends to transform at least 30% of the European territory into managed protected areas. This plan is ambitious, but absolutely necessary to halt the loss of spider diversity. The current threats to spiders in Europe indicate the need to expand existing protected areas and to designate new ones in order to include more spider species that need protection (Mammola et al., 2020b). With the limited resources available for the protection of biodiversity, areas hosting high concentrations of endemic and threatened spider species should be considered clear priorities for conservation.

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Declaration of competing interest

We declare that there are no conflicts of interest regarding this research and manuscript.
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CRediT authorship contribution statement

FM and MI conceived the study. FM and MI contributed equally to the work. AG, MN and HS proofread English and provided substantial ameliorations to the original text. FM retrieved data on legal acts and Red Lists across Europe, built the species database, and wrote the first draft. MI suggested the general line of enquiry, coordinated the group of contributors, created maps, and provided amendments to the first draft and to the final revised version. TB provided information on Austria, Germany and Switzerland. PC provided information on Finland, Portugal and Macaronesia and contributed substantially to the organization of the text. MC provided information on Greece. CSF provided information on CITES and spider trading. PG provided information on Slovakia and other Eastern European countries. AG provided information on Great Britain. SH provided valuable contribution to different sections of the manuscript during the first round of revision. NMH provided information on Spain. SM revised different sections of the manuscript, improved the revised version and prepared barcharts. WN provided information on spider distribution in Europe and ensured the collaboration with Araneae – Spider of Europe network. MN provided information on Great Britain and Ireland. JP provided information on France. NP provided information on Ukraine. MR provided information on the Czech Republic. JS provided information on Sweden. HS provided information on Great Britain and contributed significantly to the final version of the text. KW provided information on Poland and other Eastern European countries. All authors contributed significantly to the writing of the manuscript by means of comments and additions to the text.

Data repository statement

Our data are stored within World Arachnid Trait database (Milano et al., 2021a, 2021b) at https://spidertraits.sci.muni.cz/datasets/160 and https://spidertraits.sci.muni.cz/datasets/162.

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Paper II

Notes on the Italian distribution of *Dolomedes plantarius* (Clerck, 1757), species assessed for the IUCN Red List (Araneae: Pisauridae)

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Notes on the Italian distribution of *Dolomedes plantarius* (Clerck, 1757), species assessed for the IUCN Red List (Araneae: Pisauridae)

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Abstract

The great raft spider, *Dolomedes plantarius*, is a semi-aquatic spider species with an Eurosiberian distribution. As a result of habitat loss and degradation, in 1996 the species was classified as *Vulnerable* in the IUCN Red List of Threatened Species, but since then the status has never been updated. We present the frame of the existing knowledge on the distribution of this rare spider species in Italy, based on literature data and on original records gathered in recent years. Finally, we discuss the conservation value of the Italian populations, in light of their peripheral position within the species range and in light of the future reduction of the bioclimatic range of the species due to climate and land cover changes associated with anthropic disturbance.

Key words: Great raft spider, wetlands, habitat loss, conservation.

Introduction

From the perspective of biological conservation, spiders (Araneae, Arachnida) are among the less explored taxa, although they are one of most important groups in terms of adaptive radiation and its ecological role as top-predators. Among the 1,632 known species in Italy (Pantini & Isaia 2017) - one of the most species-rich countries in Europe - only few species are considered by international and national conservation policies (Milano et al. 2018).

Among them, the great raft spider, *Dolomedes plantarius* (Clerck, 1757) (Araneae, Pisauridae) is a large-sized spider (male body-length: 10-16 mm; female body-length: 13-20 mm; Nentwig et al. 2018) closely associated with lowland wet habitats. Together with the congeneric *D. fimbriatus* (Clerck, 1757), it is the only representative of the genus in Europe. Despite the two species share similar ecological requirements and may be found in syntopy, *D. plantarius* is considered rarer and more stenoecious than *D. fimbriatus*, the former being strictly associated with standing waters such as rushlands, sedgelands and fens, and the latter associated with a variety of swampy areas, including flowing waters, alluvial forests and bog forests.

Due to the high variability of the body coloration and size, the correct identification of the two European species is possible only by means of the examination of sexual characters under the stereomicroscope (van Helsdingen 1993).

As the vernacular name suggests, the great raft spider is closely associated with standing meso-oligotrophic waters, from which many aspects of its life-history depend, from feeding to courtship and reproduction (Duffey 1995; van Helsdingen 1993). Individuals can be found along the edges of marshlands, bogs, canals, turf ponds and swamps, hunting on the water surface or among emergent and marginal vegetation, where females build their typical nursery webs.

Although Bonnet (1930) considered *D. plantarius* widespread all over the Palearctic region, the species is locally rare, suggesting a high vulnerability and a declining trend over much of the range (Duffey 1995; van Helsdingen 1993). In particular, the decline is related to the loss and the degradation of wetland habitats, namely of lowland fens, to the fragmentation of the populations, that are genetically isolated, and to the progressive eutrophication of the water throughout much of its range (Smith 2000).

As the result of its extreme vulnerability, the species is listed in the Regional Red Lists of several European countries (see Milano et al. 2018). In the United Kingdom, the species is classified as *Vulnerable* (Harvey et al. 2017), is fully protected under Schedule 5 of the Wildlife and Countryside Act 1981 and is the subject of a Species Action Plan (UK Biodiversity Steering Group 1999). In the light of this, a translocation program was initiated in 2010, with the establishment of three new populations at new sites in the Norfolk and Suffolk Broads (Harvey et al. 2017; Smith & Baillie 2011).

The species entered the IUCN Red List of Threatened Species in 1996, being included in the *Vulnerable* category (World Conservation Monitoring Centre 1996). Since then, the assessment has never been updated. New information on the species distribution available at the European level and recent studies demonstrating the dramatic consequences of climate and land cover changes on the range of the species, firmly underline the need of a revision of its conservation status.

In this paper, we present the frame of the existing knowledge on *Dolomedes plantarius* in Italy, based on literature data and on original records gathered in recent years. In light of our results and considering the role of Italian populations in the conservation of the species, we underline the need for long term monitoring programs, aiming to assess the status of the Italian populations and the need of further studies, aiming at deepening the knowledge about the distribution and the ecology of the Italian populations.

Material and Methods

We examined all available literature data referring to the presence of *Dolomedes* spiders in Italy. For the bibliographic survey, we referred to the reference list of the updated version of the Italian checklist of the Italian spiders (Pantini & Isaia 2017).

Moreover, we checked for the presence of *Dolomedes* spiders in private and Museum collections in Italy, and we conducted a number of field activities in northern Italy (2014-2018) with the help of different contributors (see acknowledgments), with a special focus on the region of Piemonte. The individuals collected were examined and identified using a Leica M80 stereoscopic microscope (up to 60x magnification). Specimens are preserved in 75° ethanol and are stored in Marco Isaia’s collection at the Department of Life Sciences and Systems Biology of the University of Torino.

Results

The distribution of *Dolomedes plantarius* in Italy is presented in Fig. 1 and detailed in Tab. 1. The bibliographic survey led us to record the occurrence of this species in Piemonte, Lombardia, Veneto, Emilia-Romagna, Toscana and Sardegna. A number of outdated references documenting the occurrence of this species in Lombardia (Pavesi 1873, 1879), Veneto (Contarini 1843) and Campania (Trani 1902) were considered doubtful due to the high degree of uncertainty of the identifications [the same criteria was adopted by Brignoli (1977) in a first outline of the Italian distribution of this species].

Our field activities led to the discovery of several new records in the rice-growing area of Piemonte (16 localities) and in the wetland of Punta Alberete (Emilia-Romagna). Most of the records fall within natural protected areas.

Material

Piemonte: *Province of Torino*: Candia, shores of Lago di Candia (Reed bed), Parco Naturale del Lago di Candia, 21.VII.2010, Paschetta leg. 1 ♂. *Province of Alessandria*: Valenza, Lanca di San Bernardo (oxbow lake), “Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba”, 10.VIII.2011, Paschetta leg. 1 ♀; Camino, Lanca di Brusaschetto (oxbow lake), “Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba”, 07.V.2018, Cavalcante leg. 1 ♀; Frassineto Po, Lanca Terranova, “Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba”, 24.V.2018, Cavalcante, Isaia & Milano leg. 1 ♀; Lanca Sesia Morto, “Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba”, 24.V.2018, Cavalcante leg. 1 ♂. *Province of Vercelli*: Livorno Ferraris, Fontana Leira, 10.VII.2014, Cavalcante & Evangelista leg. 1 ♂; Castell’apertole, Centro *Emys* Piemonte, 27.V.2018, Cavalcante & Fiore leg. 1 ♂; Tricerro, Fontana Gigante, “Riserva Naturale Speciale di Fontana Gigante”, 27.VIII.2015, Cavalcante leg. 1 ♀; VII.2015, Cavalcante leg. 1 ♀; Crescentino, “Palude di San Genuario, Riserva Naturale Speciale e Zona di Salvaguardia della Palude di San Genuario”, 10.VI.2015, Cavalcante leg. 1 ♂; 23.V.2018, Cavalcante leg. 1 ♂; Albano Vercellese, “Parco fluviale delle lame del Sesia” (oxbow lake), 25.V.2017, Cavalcante & Fiore leg. 1 ♂; Trino, Madonna delle Vigne (fen), 06.VI.2017, Cavalcante leg. 1 ♂; Ronsecco, Lachelle, Prato Lungo (fen), 21.VII.2017, Fasano leg. 1 ♀; Palazzolo Vercellese, in an irrigation canal, 14.IV.2018, Cavalcante & Fiore leg. 1 ♂; wetland in the nearby of the village, “Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba”, 05.V.2018, Cavalcante leg. 1 ♂. ***Emilia-Romagna***: *Province of Ravenna*, Punta Alberete, “Parco del Delta del Po”, VII.2015, Cavalcante leg. 1 ♀.

Discussion

Dolomedes plantarius is closely associated with lowland wetlands, a delicate habitat increasingly subjected to alteration mostly due to changes in the water regime, physical modification, eutrophication and pollution. Just like other wetland species, as a result of habitat degradation and loss (Davidson 2014), populations of *D. plantarius* are facing a remarkable decline. This has prompted a number of conservation authorities and several European countries to consider *D. plantarius* threatened with extinction (see Milano et al. 2018).

In relation to the progressive loss of its natural habitat, in 1983, *D. plantarius* was firstly reported in the IUCN Invertebrate Red Data Book as a species in need of conservation (Wells et al. 1983). Some years later, based on similar arguments, Collins & Wells (1987) reported *D. plantarius* among the threatened invertebrates in Europe, and proposed the species as a suitable candidate for inclusion in the Appendix II of the Bern Convention. The first official assessment of the conservation status of the species dates back to 1986, with the inclusion of *D. plantarius* in the *Vulnerable* category (IUCN Conservation Monitoring Center 1986). This status was maintained in the following updates of the Red List (Groombridge 1993; IUCN 1990; Wilcox 1988). After the publication of the 1994 IUCN Red List Categories and Criteria (version 2.3), *D. plantarius* was re-assessed and again placed in the *Vulnerable* category against criterion A (i.e. population size reduction; World Conservation Monitoring Centre 1996). However, being assessed before the publication of the new IUCN standards (version 3.1, 2001), the evaluation of *D. plantarius* remains outdated and hardly comparable with the recent ones.

Regardless of the outdated IUCN assessment, many European countries recognized the importance of the conservation of this spider and listed it on their Regional Red Lists. Currently, *D. plantarius* is cited in the Red List of the following European countries: Finland (Rassi et al. 2010), Norway (Henriksen & Hilmo 2015), Great Britain (Harvey et al. 2017), Flanders (Belgium, Maelfait et al. 1998), Germany (Blick et al. 2016), Austria (Carinthia; Komposch & Steinberger 1999), Czech Republic (Řezáč et al. 2015), Slovenia (Gajdoš & Svatoň 2001), and the region of the Carpathian Mountains (Gajdoš et al. 2014).

Concerning Italy, *D. plantarius* is mentioned as *Vulnerable* on the List of the Threatened Invertebrates of the Italian Fauna (Groppali & Priano 1992) and in the regional legislation of Lombardia, where it is listed in the D.g.r. 8/773 24.07.2008 among invertebrates of regional interest (see Milano et al. 2018).

In Italy, *D. plantarius* seems mostly distributed in the Northern district (Fig. 1), namely in Piemonte (Leroy et al. 2013; this work), Lombardia (Vugdelić, 2006 in Leroy et al. 2013), Veneto (Hansen 2002, 2007) and Emilia-Romagna (this work). However, the species has been formerly reported in central and southern Italy (see Tab. 1 and Fig. 1). Data from Toscana (di Caporiacco 1936) and Sardegna (Kraus 1955) refer to plausible records dating back to the first half of XX century. These isolated localities represent the southernmost records for the species in Italy and figure among the southernmost in Europe.

In accordance with Brignoli (1977) and van Helsdingen (1993), old citations dating back to XIX century are in need of verification, due to the confusion of *D. plantarius* with *D. fimbriatus*. Accordingly, before Bonnet (1930), *D. plantarius* was called *D. fimbriatus*, while *D. fimbriatus* was referred to as *D. limbatus* (Hahn, 1831), making many published records not reliable (van Helsdingen 1993). More specifically, the presence of *D. plantarius* in the province of Naples (Campania) reported by Trani (1902), is uncertain, being more likely based on specimens of *D. fimbriatus*. Similarly, records from the provinces of Pavia (Pavesi 1873) and Varese (Pavesi 1879) in Lombardia also need verification. However, the presence of the species in this region is validated by the records of Bonnet (1930) for Brianza and Vugdelić (2006) for the province of Varese. Similarly, data on the occurrence of *D. plantarius* in Veneto by Contarini (1843), were confirmed by the recent records of Hansen (2002, 2007).

The Italian situation is particularly critical, due to the geographical isolation of the populations at the periphery of the range. Peripheral populations are often genetically and morphologically divergent from central populations, and are particularly important for the evolutionary future of the species (Lesica & Allendorf 1995). In the case of *D. plantarius,* this frame is particularly dramatic in view of the predicted north shift of the species caused by climatic changes (Leroy et al. 2013). Accordingly, species distribution models predict a sharp decrease of the current suitable range, with a remarkable loss in the South and the appearance of newly-suitable areas in the North. In consequence of that, the condition of the Italian populations appears particularly critical: the Alpine barriers blocking the species dispersion northward, will preclude the species from reaching future more suitable areas located North of the Alps. Therefore, the only available option for these peripheral populations will be the unlikely local adaptation to the new environmental conditions.

Moreover, it seems likely that in the Italian northern districts, the progressive loss of wetlands resulting from agricultural exploitation have fragmented and jeopardized natural populations, which are now restricted to natural protected areas. This seems particularly remarkable in the provinces of Vercelli and Alessandria (Piemonte), where natural lowland wetlands are widely replaced by rice fields. Intensive agricultural use in these renowned rice-growing areas, associated with changes in the hydrological regime and water pollution due to agricultural products, resulted in a severe alteration of the natural ecosystems, with dramatic consequences on the survival of populations of *D. plantarius*. Accordingly, it seems likely that most of the populations currently survive in unexploited protected wetlands, i.e. "Parco fluviale del Po tratto vercellese/alessandrino e Riserva Naturale del torrente Orba", S.I.C. Fontana Gigante and S.I.C. Palude di San Genuario. Despite additional studies which may further support this hypothesis, we argue that the preservation of the wetland habitat is crucial for the conservation of the species. It seems clear that, in lack of specific conservation measures and

Table 1 – List of the Italian records of *Dolomedes plantarius* (Clerck, 1757).

Region	Municipality	Locality	Reserve	Author	Year of collection
Emilia-Romagna	Ravenna (RA)	Punta Alberete	Parco del Delta del Po	This work	2018
Lombardia	Pavia (PV)	Unspecified locality	–	Pavesi, 1873	1873
Lombardia	Varese (VA)	Isolino di Varese	Riserva Naturale Palude Brabbia	Pavesi 1879	1878
Lombardia	–	Unspecified locality in Brianza (MB)	–	Bonnet 1930	1930
Lombardia	Corgeno (VA)	Lago di Comabbio	–	Vugdelić 2006 in Leroy et al. 2013	2002
Piemonte	Verbania (VB)	Lake margin near Camping Isolino (Reed bed)	Riserva Naturale Speciale del Fondo Toce	Leroy et al. 2013	2009
Piemonte	Verbania (VB)	Lake margin near Camping Isolino (Reed bed)	Riserva Naturale Speciale del Fondo Toce	Leroy et al. 2013	2009
Piemonte	Candia (TO)	Shores of Lago di Candia (Reed bed)	Parco Naturale del Lago di Candia	Leroy et al. 2013	2010
Piemonte	Candia (TO)	Shores of Lago di Candia (Reed bed)	Parco Naturale del Lago di Candia	Leroy et al. 2013	2010
Piemonte	Candia (TO)	Shores of Lago di Candia (Reed bed)	Parco Naturale del Lago di Candia	Leroy et al. 2013	2010
Piemonte	Candia (TO)	Shores of Lago di Candia (Reed bed)	Parco Naturale del Lago di Candia	Leroy et al. 2013	2010
Piemonte	Candia (TO)	Shores of Lago di Candia (Reed bed)	Parco Naturale del Lago di Candia	This work	2010
Piemonte	Valenza (AL)	Lanca di San Bernardo (oxbow lake)	Parco fluviale del Po tratto vercellese/ alessandrino e Riserva Naturale del torrente Orba	This work	2011
Piemonte	Livorno Ferraris (VC)	Fontana Leira	–	This work	2014
Piemonte	Tricerro (VC)	Fontana Gigante	Riserva Naturale Speciale di Fontana Gigante	This work	2015
Piemonte	Crescentino (VC)	Palude San Genuario	Riserva Naturale Speciale e Zona di Salvaguardia della Palude di San Genuario	This work	2015
Piemonte	Palazzolo Vercellese (VC)	Nearby of Palazzolo Vercellese (irrigation canal)	–	This work	2018
Piemonte	Trino (VC)	Madonna delle Vigne (fen)	–	This work	2017
Piemonte	Albano Vercellese (VC)	Parco fluviale delle lame del Sesia (oxbow lake)	Parco fluviale delle lame del Sesia	This work	2017
Piemonte	Crescentino (VC)	Palude San Genuario	Riserva Naturale Speciale e Zona di Salvaguardia della Palude di San Genuario	This work	2018
Piemonte	Camino (AL)	Lanca di Brusaschetto (oxbow lake)	Parco fluviale del Po tratto vercellese/ alessandrino e Riserva Naturale del torrente Orba	This work	2018
Piemonte	Frassineto Po (AL)	Lanca Terranova	Parco fluviale del Po tratto vercellese/ alessandrino e Riserva Naturale del torrente Orba	This work	2018
Piemonte	Palazzolo Vercellese (VC)	Wetland in the nearby of the village	Parco fluviale del Po tratto vercellese/ alessandrino e Riserva Naturale del torrente Orba	This work	2018
Piemonte	Frassineto Po (AL)	Lanca Sesia Morto	Parco fluviale del Po tratto vercellese/ alessandrino e Riserva Naturale del torrente Orba	This work	2018
Piemonte	Livorno Ferraris (VC)	Castell'apertole. Centro Emys Piemonte	–	This work	2018
Piemonte	Tricerro (VC)	Fontana Gigante	Riserva Naturale Speciale di Fontana Gigante	This work	2015
Piemonte	Ronsecco (VC)	Lachelle, Prato Lungo	–	This work	2017
Sardegna	Sassari (SS)	Unspecified locality	–	Kraus 1955	1952
Toscana	Monterchi (AR)	Unspecified locality	–	Di Caporiacco 1936	1925
Toscana	Arezzo (AR)	Alluvial deposits of Tevere	–	Di Caporiacco 1936	1926
Veneto	Padova (PD) and Venezia (VE)	Padova and Venezia (unspecified locality)	–	Contarini 1843	1843
Veneto	Quarto d'Altino (VE)	San Michele Vecchio (oxbow lake of Sile)	–	Hansen 2002	1992
Veneto	Venezia (VE)	Laguna di Venezia, Valle Averto	–	Hansen 2007	1992

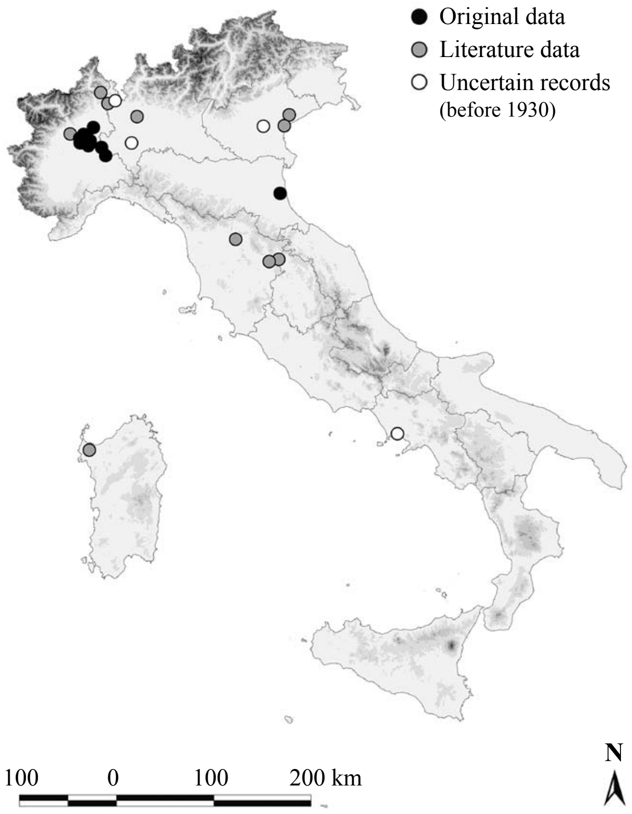

Fig. 1 – Distribution map of *Dolomedes plantarius* (Clerck, 1757) in Italy. Black dots refer to original data published in this work. Grey dots refer to literature data. Records before Bonnet (1930) are considered doubtful (white dots).

national legislation, the preservation of natural population of *D. plantarius* highly depends from the protection of other wetland species targets of conservation (i.e. amphibians and birds), with similar ecological requirements.

Therefore, if from one side we emphasize the importance of umbrella species in the preservation of *D. plantarius* in Italy, from the other we underline the need of a detailed understanding of the ecological requirements of this species in order to optimize conservation efforts. Moreover, we advocate specific monitoring of the Italian populations, aiming to assess their conservation status and to deepen the knowledge on the distribution in Italy of this species of elevated conservation concern.

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Paper III

Trends in habitat suitability and conservation status of aquatic spiders in Europe

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Photo credit: Emanuele Biggi

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Abstract

Wetlands, one of the most biodiverse ecosystems in the world, are increasingly subjected to area loss and degradation due to land-use and climate changes. These factors impact their unique biodiversity, including numerous invertebrates that depend on them. Here we investigated the current and future habitat suitability of the aquatic spiders *Argyroneta aquatica* and *Dolomedes plantarius*. We evaluated future trends in their geographic range, aiming at assessing their extinction risk according to the International Union for Conservation of Nature (IUCN) Red List criteria, at both global and regional levels. We investigated present and future distribution ranges using species distribution models for two integrated emission scenarios (SSP1-2.6 and SSP5-8.5) and combining three general circulation models. These were combined with knowledge on species' dispersal limitation to account for the possibility that these species will not be able to move beyond the current range in the next decades. We found a significant future northern shift in the geographic range and a global reduction in habitat suitability for both species, corresponding to a loss of 28.9 % for *A. aquatica* and 38.1 % for *D. plantarius* in the next 10 years. The application of the IUCN criteria qualifies *A. aquatica* as Near Threatened and *D. plantarius* as Vulnerable. Regional assessments provided similar patterns of range reductions and population vulnerability across all European regions, particularly for Central-Eastern and Western Europe. Conversely, Northern Europe is expected to become a climatic refugium for both species. This work goes beyond the available studies on the conservation of these species by taking account their dispersal abilities in quantifying future trends in their habitat suitability using the most up to date knowledge. Conservation strategies should be directed towards limiting the impact of climatic and non-climatic stressors on wetlands, and towards implementing management plans and restoration programmes to increase habitat suitability and connectivity among wetland patches.

Keywords: IUCN, Wetlands, Invertebrate conservation, Extinction risk, Climate change, Shared Socioeconomic Pathways (SSPs)

1. Introduction

Wetlands harbour high biodiversity and are of immense value for the livelihoods of local communities, providing a wide spectrum of benefits (Mitsch and Gosselink, 2015; Finlayson et al., 2019). Recognition of the great value of wetlands led in 1971 to the establishment of the Ramsar Convention on Wetlands, aimed at halting habitat loss and degradation through the designation and management of Wetlands of International Importance ('Ramsar Sites') (Carp, 1972). The protection and restoration of wetlands is also central to the EU Habitats Directive (92/43/ EEC), the EU Birds Directive (2009/147/CE), the Convention on Migratory Species ('Bonn Convention') and the Bern Convention (Council of Europe, 1979), not to mention much legislation at national level.

In spite of widespread conservation attention, wetlands have been increasingly subjected to alteration and degradation (Finlayson et al., 2019). It is estimated that 64 % of the world's wetlands have been lost since 1900 (Leadley et al., 2014), but losses may have exceeded 70 % in inland wetlands, which are disappearing at a faster rate than coastal ones (Davidson, 2014). This loss is continuing in many regions, with the greatest overall losses observed in Europe and Asia (Verhoeven, 2014). Estimates suggest that Europe has lost up to 80 % of its wetland area in the last 75 years (EU, 2007). Wetlands are affected by a wide range of threats, including land-use intensification, changes in water use and availability, physical modification, increasing urbanisation, eutrophication and pollution (Finlayson et al., 2019). In addition, recent studies have highlighted that human-induced climate change is having an unprecedented impact. It is causing large-scale degradation and loss of wetlands through direct and indirect effects of changes in temperature, precipitation and humidity, and subsequently in patterns of evapotranspiration, alterations in hydrological regimes, and increases in the frequency of extreme climate events such as floods and droughts (Erwin, 2009; Davidson, 2014). Sea level rise and the increasing frequency of tidal surges, with associated salinization of soil and freshwater resources, pose additional, more proximate but less predictable threats to coastal wetlands (Herbert et al., 2015; Grieger et al., 2020).

Many species are intimately associated with wetlands, from fungi to vertebrates, including many insects, such as the Odonata and the EPT group – Ephemeroptera, Plecoptera and Trichoptera. These insect groups are commonly used to infer on the health of wetland ecosystems through several measures such as biotic integrity indices (Weigel et al., 2002; Lunde and Resh, 2011). Many other taxa are less commonly found in wetlands, but still include species that are dependent on them for part or the entire life cycle, and yet are often less studied. Spiders are among these taxa, with few but important and charismatic species living exclusively on wetlands.

Due to their close association with these habitats, the diving bell spider, *Argyroneta aquatica* (Clerck, 1757) (Araneae: Dictynidae), and the fen raft spider, *Dolomedes plantarius* (Clerck, 1757) (Araneae: Pisauridae), appear to be negatively impacted by wetland decline. These two Palearctic spiders are closely associated with standing, base-rich, oligo-mesotrophic water, on which many aspects of their life-history depend, from feeding to courtship and reproduction (van Helsdingen, 1993; Duffey, 1995; Perevozkin et al., 2004). *Argyroneta aquatica*, in particular, conducts a wholly aquatic life, being able to hunt, consume prey, moult, deposit eggs, and copulate underwater (Crome, 1951; Schütz et al., 2007; Seymour and Hetz, 2011; Mammola et al., 2016). This species seems particularly influenced by the structure of the aquatic vegetation and by its trophic interactions with other species (Mammola et al., 2016; see also Aakra and Dolmen, 2003 and Özkütük et al., 2013 on the relatively high ecological plasticity observed in some populations). *Dolomedes plantarius* can be found along the edges of marshlands, bogs, canals, turf ponds and swamps, hunting on the water surface or among emergent and marginal vegetation, where females build their typical nursery webs (van Helsdingen, 1993; Smith, 2000; Duffey, 2012). Apparently, this species has narrower habitat requirements compared to *A. aquatica*, being significantly influenced by water pH and marginal emergent vegetation structure (Dickel et al., 2022).

Despite their wide Palearctic distribution, both spiders are locally rare. The loss and degradation of wetland habitats is expected to have serious impacts on their survival, suggesting a high vulnerability and a declining trend throughout much of their range (Leroy et al., 2013, 2014). Accordingly, both species are the most commonly protected by national laws and included in Red Lists of European countries (Milano et al., 2021). In addition, *D. plantarius* has been classified as Vulnerable by the International Union for Conservation of Nature (IUCN) in 1996 (World Conservation Monitoring Centre, 1996), although this assessment pre-dates publication of the new IUCN standards (version 3.1, 2001) which precludes its comparison with current assessments. It is therefore, due for reassessment.

One of the main threats to aquatic spiders is climate change. Either through direct effects on the physiology of the species and their inability to adapt to warming temperatures, or through indirect effects as a result of wetland drying and degradation, they are considered to be particularly sensitive to global warming. In addition, their distribution is fragmented by nature, as wetlands are often few and far apart across their geographical range. This has implications on the species ability to move northwards or upwards as frequently observed for more mobile taxa. Any threat assessment must take into account this dispersal limitation to avoid underestimating the extinction risk for both species.

Here, we modelled current and future global distributions of *A. aquatica* and *D. plantarius via* species distribution models. Compared to previous spatial modelling studies on these species (Leroy et al., 2013, 2014; Monsimet et al., 2020), this is the first time that dispersal ability has been taken into account in developing distribution models across the species' entire range. Moreover, based on the most up to date knowledge of the species occurrences and integrated emission scenarios, our modelling results provided the baseline for the first assessment of the extinction risk of the two species according to the current IUCN Categories and Criteria (IUCN, 2001). Specifically, we address the following questions: i) What are the trends in the species' geographic range and population size across different emission scenarios?; ii) Can we harness this information to infer the extinction risk of these species?

In light of the accelerating degradation of wetland habitats globally (Finlayson et al., 2019), we hypothesize a future declining trend in the geographic range and population size for both species, and an increase in their extinction risk according to the IUCN criteria. Furthermore, given that anthropogenic pressure on wetlands varies across Europe, and different regions will be differently affected by climate change (Brander et al., 2012; Čížková et al., 2013), we predict that degree of extinction risk will vary across regions.

2. Material and methods

2.1. Response variables

We compiled a georeferenced dataset of occurrences for both species, issued from the Global Biodiversity Information Facility online database (GBIF, 2020; accessed on 20 July 2020), scientific literature, grey literature and personal communications from European arachnologists (see acknowledgements). The initial database included 7301 occurrences for *Argyroneta aquatica* and 1305 for *Dolomedes plantarius.*

To avoid overrepresentation of certain regions as a result of sampling heterogeneity, we performed spatial thinning using the function *thin* in the ‘red’ R package (Cardoso, 2017). We thinned occurrences through 100 iterations, eliminating records closer than 0.5% of the maximum distance between any two records.

2.2. Model calibration

We calibrated and projected models within the spatial extent hypothesized to be suitable to each species, in relation to their bioclimatic preferences. Considering the distribution range of the two species, we first approximated the extent of the study area by masking the bioclimatic layers to 35 to 75° latitude and -13 to 65° longitude. The distributions of both species were approximated, excluding outlying occurrences from Eastern Asia (*e.g.* China, Korea and Japan for *A. aquatica*) to avoid overestimations and disjunctions within the overall distribution of the species. Since both species are dependent on aquatic habitats (van Helsdingen, 1993; Duffey, 1995; Perevozkin et al., 2004; Seymour and Hetz, 2011), we further refined the calibration area by filtering to aquatic environments. We defined aquatic habitats using the Global Lakes and Wetlands Database Level 3 (GLWD-3) (Lehner and Döll, 2004) and used a 2-km buffer around wetlands to crop environmental predictors.

2.3. Predictor variables

We modelled the distribution of the two species using a combination of climatic and topographic variables. We extracted the standard 19 bioclimatic variables for “present” conditions (historical climate data) and elevation data from WorldClim 2 (Fick and Hijmans, 2017), all at a spatial resolution of 2.5 arc-minutes (*ca.* 1 km). A Principal Component Analysis was performed on the predictor variables to generate new axes that summarized variation in fewer dimensions, thereby minimizing multicollinearity.

To predict the future global distribution of both species, we used a new set of integrated emission scenarios, combining the Representative Concentration Pathways (RCPs) with specific socioeconomic and technological development, *i.e.* the Shared Socioeconomic Pathways (SSPs), as discussed in van Vuuren et al. (2014) and O'Neill et al. (2016). The SSPs are reference pathways describing plausible alternative trends in the evolution of society and ecosystems over a century timescale (O’Neill et al., 2014). We selected a sustainable (RCP2.6, SSP1) and a fossil-fuelled (RCP8.5, SSP5) development scenario and projected these in two distinct 20-year-period outcomes (2021–2040 and 2041–2060), with a spatial resolution of 2.5 arc-minutes.

Among available Coupled Model Intercomparison Project Phase 6 (CMIP6) climate models, we selected three based on their value in the range of estimates of climate sensitivity (Knutti et al., 2017): the fifth version of the Canadian Earth System Model (CanESM5) in the high end of the range, with an equilibrium climate sensitivity of 5.6 °C (Swart et al., 2019); the IPSL-CM6A-LR climate model in the medium part of the range, with a sensitivity of 4.6 °C (Boucher et al., 2020); and the sixth version of the Model for Interdisciplinary Research on Climate (MIROC6) in the low part of the range, with a climate sensitivity of 2.6 °C (Tatebe et al., 2019).

2.4. Modelling procedure

Given the lack of reliable absence data for our model species, we constructed species distribution models using a presence-background algorithm (MaxEnt), with the function *maxent* in the ‘dismo’ R package (Hijmans et al., 2014). Considering the sample size of our occurrence datasets, we fitted both MaxEnt models with default settings (Morales et al., 2017).

We computed the models on the recent climate (historical climate data) and on the occurrence points of *Argyroneta aquatica* and *Dolomedes plantarius*. We evaluated model performance with the Boyce index (Boyce et al., 2002) using the *ecospat.boyce* function in the ‘ecospat’ R package (Broennimann et al., 2018). This is an appropriate metric when lacking absence data (Hirzel et al., 2006). We ran 50 bootstrap replicates, retaining a random partition of 20 % of the points from each run to assess predictive performance. Once the model had been validated, we generated a final model using the full set of occurrence models and projected it into recent climate. We then projected the MaxEnt models in two future timeframes (2021–2040 and 2041–2060), and calculated the mean value across all projections for each combination of global climate models adopted.

We constructed and reported species distribution models following the ODMAP (Overview, Data, Model, Assessment and Prediction) protocol (Zurell et al., 2020), a tool designed to maximise reproducibility and transparency of distribution modelling exercises (Appendix B).

After modelling species distributions at the global level, we divided the extent of the study area in four regions, namely Northern Europe (encompassing Fennoscandia and Baltic Countries), Western Europe (France, Switzerland, Germany, Benelux and British Isles), Southern Europe (Iberian and Italian peninsulas, Balkan countries bordered by Mediterranean and Turkey) and Central-Eastern Europe (from Austria, Czech Republic and Poland up to the Ural Mountains).

2.5. IUCN assessment

We evaluated the extinction risk of *A. aquatica* and *D. plantarius* by assessing the two species against all five IUCN criteria (A–E), in accordance with version 3.1 of the IUCN Red List Categories and Criteria (IUCN, 2001). We also evaluated the regional conservation status of both species for each of the four European regions, following the regional IUCN guidelines (IUCN, 2012). If testing against different criteria resulted in different categories, the species was classified in the highest of the obtained categories of threat (IUCN, 2001).

We estimated the current and predicted Extent of Occurrence (EOO) and Area of Occupancy (AOO) using the respective functions in the R package ‘red’. To calculate EOO and AOO, we used a threshold value that maximises the sum of sensitivity and specificity (*sensu* Liu et al., 2013) to convert probability maps into binary maps of suitable *vs.* unsuitable areas. EOO and AOO were also calculated for each of the four regions.

To quantify the impact of the future scenarios on predicted availability of suitable habitats for both species, and therefore to estimate the future trends in their geographic range and population size at both global and regional levels, we measured the percent change in mean habitat suitability [(future – current) / current)*100] according to the worst of the two emission scenarios adopted (SSP5-RCP8.5), following a precautionary approach (*i.e.* the most prudent foresight for the conservation of the species, considering the range of different likely future outcomes predicted by the models). In addition, we also measured the change in mean habitat suitability considering a “no-dispersal” scenario, a condition based on the assumption that these species may not be able to track climate change, in relation to their limited dispersal abilities (Monsimet et al., 2020, 2022) and the general fragmentation of the landscape (‘M area’, according to Barve et al., 2011). For the assessment, the future trends have been calculated in accordance with the IUCN guidelines over a time period of 10 years, assuming a linear trend between the current and the first future timeframe (2021–2040). Long-term trends of habitat suitability have been estimated using the second future timeframe (2041–60). Further details are reported in Appendix A.

3. Results

3.1. Species distribution models and model performance

After spatial thinning, we kept 172 occurrences for *D. plantarius* and 449 for *A. aquatica* to generate the species distribution models. For both species, we retained the first six principal components from climatic variables, which cumulatively explained 99 % of the overall variance in the dataset. The Boyce index indicated that the distribution models had high explanatory ability (Boyce index >0.80; median of the 50 bootstraps).

3.2. Current potential distribution

The present-day suitable areas estimated by the model for the two species differed slightly in extent (Fig. 1). The estimated core range was quite similar, mainly centred in Northern and Central Europe, ranging from northern France to the Baltic states. The most suitable and unfragmented areas were found in the northern regions of Continental Europe facing the North and Baltic Seas and in the southern Fennoscandia. *Argyroneta aquatica* was spread further to the north, including most of the British Isles and central and southern Fennoscandia. Conversely, *D. plantarius* showed a more easterly potential distribution, reaching Belarus and Ukraine. Numerous highly suitable, small, isolated patches were also estimated for both species in Southern and South-Eastern Europe, namely in Italy, Spain, southern France and the Balkans.

3.3. Future projected distribution at a global scale

Trends in the overall extent of the future suitable area, obtained by comparing the current and future predicted habitat suitability under sustainability (SSP1-RCP2.6) and fossil-fuelled development (SSP5-RCP8.5) scenarios, are reported in Table 1. Future forecasts (Figs. 2 and 3) showed a general decrease in the projected suitability for both species. This trend was particularly pronounced in the central-eastern and, to a lesser degree, the southern and western ranges. By contrast, we highlighted a general increase in suitable habitat in the northern regions of the range, with the availability of suitable new areas in Fennoscandia and, for *D. plantarius*, also in North-Eastern Europe.

Future predictions for *A. aquatica* indicated a general decrease in suitable habitat (Table 1). The SSP1-RCP2.6 scenario predicted a decrease of 18.2 % in the overall extent expected for the first 20-year-period (2021–2040), while the SSP5-RCP8.5 scenario resulted in a higher average decrease, reaching 20.5 % for the same period. For the years 2041–2060, a larger decrease was expected for the SSP1-RCP2.6 scenario (24.1 %) and an even greater one for the SSP5-RCP8.5 scenario (32.8 %). Similarly, *D. plantarius* is expected to experience a significant negative net change in future habitat suitability (Table 1). Between 2021 and 2040, a decrease is expected of 13.6 % under the SSP1-RCP2.6 scenario and 15.5 % under the SSP5-RCP8.5 scenario. Between

2041 and 2060, suitable area was expected to shrink again, with a net change of − 15.3 % for SSP1-RCP2.6 and − 29.9 % for SSP5-RCP8.5.

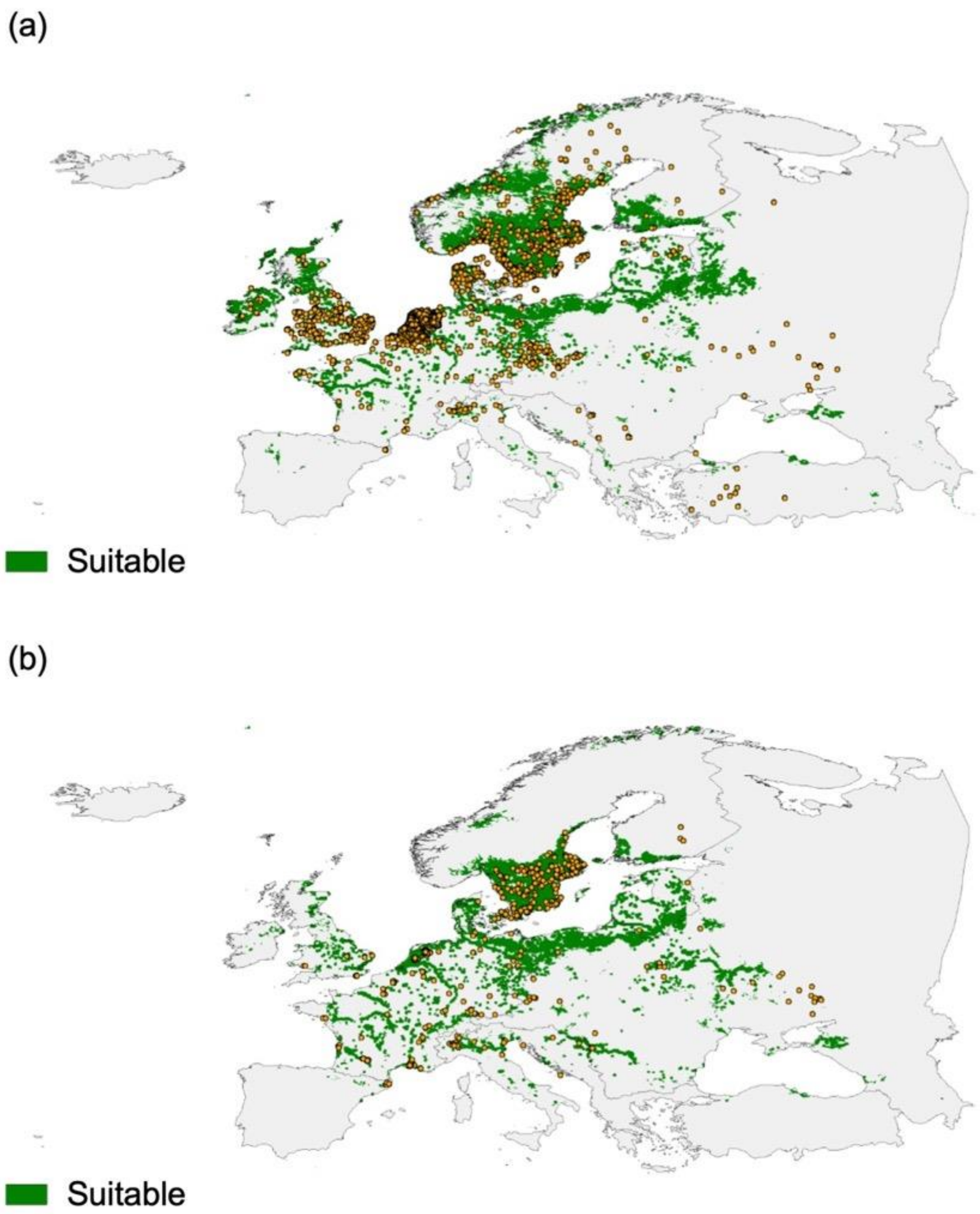

Fig. 1. Occurrences and potential distribution maps of *Argyroneta aquatica* (a) and *Dolomedes plantarius* (b) under current climatic conditions. The predicted species' area of occupancy (*i.e.*, areas with habitat suitability > model threshold value) is shown in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1. Trends in the future extent of bioclimatic suitable range and effective reachable range in *Argyroneta aquatica* and *Dolomedes plantarius* according to different scenarios and in two different ranges of 20-year-period.

		Argyroneta aquatica				*Dolomedes plantarius*			
		2021–2040		2041–2060		2021–2040		2041–2060	
		SSP1-RCP2.6	SSP5-RCP8.5	SSP1-RCP2.6	SSP5-RCP8.5	SSP1-RCP2.6	SSP5-RCP8.5	SSP1-RCP2.6	SSP5-RCP8.5
Europe	Bioclimatic suitable range	–18.23	–20.51	–24.15	–32.85	–13.65	–15.47	–15.27	–29.94
	Effective reachable range	–25.97	–28.91	–32.26	–43.46	–32.59	–38.13	–38.78	–56.77
Northern Europe	Bioclimatic suitable range	1.74	0.80	–4.65	–13.23	12.86	16.36	10.39	–13.99
	Effective reachable range	–11.49	–13.47	–17.83	–30.52	–13.55	–18.18	–20.85	–49.18
Central-Eastern Europe	Bioclimatic suitable range	–82.00	–82.57	–83.40	–86.33	–82.61	–85.62	–83.86	–88.58
	Effective reachable range	–83.71	–85.35	–87.93	–92.55	–84.90	–88.50	–86.90	–93.29
Southern Europe	Bioclimatic suitable range	–49.59	–53.43	–58.10	–71.34	–14.18	–21.25	–14.83	–28.25
	Effective reachable range	–53.61	–57.09	–62.65	–76.36	–22.31	–27.78	–25.25	–42.32
Western Europe	Bioclimatic suitable range	–25.64	–31.41	–32.77	–44.04	–4.98	–14.68	–12.51	–20.31
	Effective reachable range	–26.00	–31.77	–33.14	–44.54	–25.56	–34.30	–33.93	–42.75

When the limited dispersal abilities and the general fragmentation of the landscape for both species are considered, the decrease in the projected future range was predicted to be considerably higher. In *A. aquatica,* the extent of the area decreased by 26 and 28.9 % in the first 20-year-period, and by 32.3 and 43.5 % in the following period (2041–2060), according to the SSP1-RCP2.6 and SSP5-RCP8.5 scenarios, respectively. In *D. plantarius* the contraction will be even more considerable, with values of 32.6 % and 38.1 % according to the two scenarios in 2021–2040, and with a further contraction in the following period reaching 38.8 % in the SSP1-RCP2.6, and 56.8 % in the SSP5-RCP8.5 scenario.

3.4. Future projected distribution at a regional scale

Trends in the future potential distribution of the two species differed between regions (Table 1). *Argyroneta aquatica* was predicted to have the most significant contraction in Central-Eastern Europe. This becomes even more critical when the species' poor dispersal ability is considered. In Northern Europe this species experienced fewer changes in suitability, with an almost stable future trend in both scenarios and timeframes. However, when the effective reachable range is considered, the decrease would be more relevant in all cases. In contrast to other regions, dispersal ability did not seem to affect the decrease predicted by the models for Western and Southern Europe. In Southern Europe the decrease in the bioclimatic suitable range was greater than in Western Europe, particularly in the first timeframe, followed by a further decrease in the following period.

Dolomedes plantarius was expected to have a significant expansion in its future suitable bioclimatic range in Northern Europe, coupled with an important contraction in range in Central-Eastern, Southern and Western Europe. However, when dispersal ability is taken into consideration, the extent of its effective reachable range was projected to decrease in all the regions. As with *A. aquatica*, the future suitable range of *D. plantarius* was expected to undergo the most critical decrease in Central-Eastern Europe, according to different scenarios. In Southern and Western Europe, a contraction in the future distribution range was also expected, but less remarkable.

3.5. IUCN global assessment

Available information on the projected decline in the area of occupancy of both species has been used according to criterion A3c to suspect overall reduction in population size in the future, assuming a constant population density throughout both the species range and with time. In *Argyroneta aquatica*, according to the worst emission scenario (SSP5- RCP8.5), the rate of decline in the current area of occupancy is expected to reach 29 % in the next 10 years, very close to qualifying for the Vulnerable category under criterion A3 (a future reduction in population size ≥30 %). As a result of the continuing loss of wetland habitats and limited dispersal ability of this species, this decline is expected to exceed this threshold in the following timeframe (43 %). Accordingly, *A.*

aquatica qualifies for the Near Threatened category under criterion A3c, as the species comes close to, but does not fully meet, the conditions required for the inclusion in a threatened category.

In *Dolomedes plantarius* the projected rate of future decline in the extent of suitable habitat based on the more pessimistic scenario is 38 % in the next 10 years. This meets the ≥30 % threshold for population size reduction required for the inclusion in a threatened category, and qualifies the species as Vulnerable under criterion A3c.

The assessments are detailed in Appendix A and summarized in Table 2.

4. Discussion

To the best of our knowledge, no study has attempted to quantify the current and potential future global distribution of these species and their future trends in habitat suitability, taking account of their dispersal abilities. This study builds on and goes beyond previously available works on the conservation of aquatic spiders by assessing the impacts of future climate change on the global and regional distributions of these spiders, using the most up to date knowledge on their occurrences and a new set of integrated emission scenarios driven by innovative socio-economic assumptions.

4.1. Current and future projected distribution

The estimated current core range of the two species was mainly located in north-central Europe, where wetlands, although strongly reduced in size compared to their original extent, are in a near pristine state and still cover large and continuous areas (Verhoeven, 2014). Numerous small, isolated patches of highly suitable habitat are located from south-western to eastern Europe, mainly along the most important river basins or lakes, or in protected nature reserves. All scenarios dealing with future habitat suitability of both species predicted a global decrease in the current distribution range. The range contraction is particularly critical in Central-Eastern and Western Europe, where some important river basins (*e.g.*, the Rhine and the Danube) are losing ecological connectivity with the surrounding riparian buffer zones. In Southern Europe, the overall geographic range seems to be less affected by future climate change. By contrast, a future global increase in suitability in Northern Europe was projected, attesting a progressive northward shift of the species' bioclimatic range within a relatively short time-scale, matching results of previous studies (Leroy et al., 2013, 2014; Monsimet et al., 2020).

Patterns of poleward shifts are documented for an increasing number of taxonomic groups (Chen et al., 2011), including spiders (Hickling et al., 2006; Kumschick et al., 2011; Krehenwinkel and Tautz, 2013; Leroy et al., 2013, 2014; Krehenwinkel et al., 2016; Mammola and Isaia, 2017; Monsimet et al., 2020).

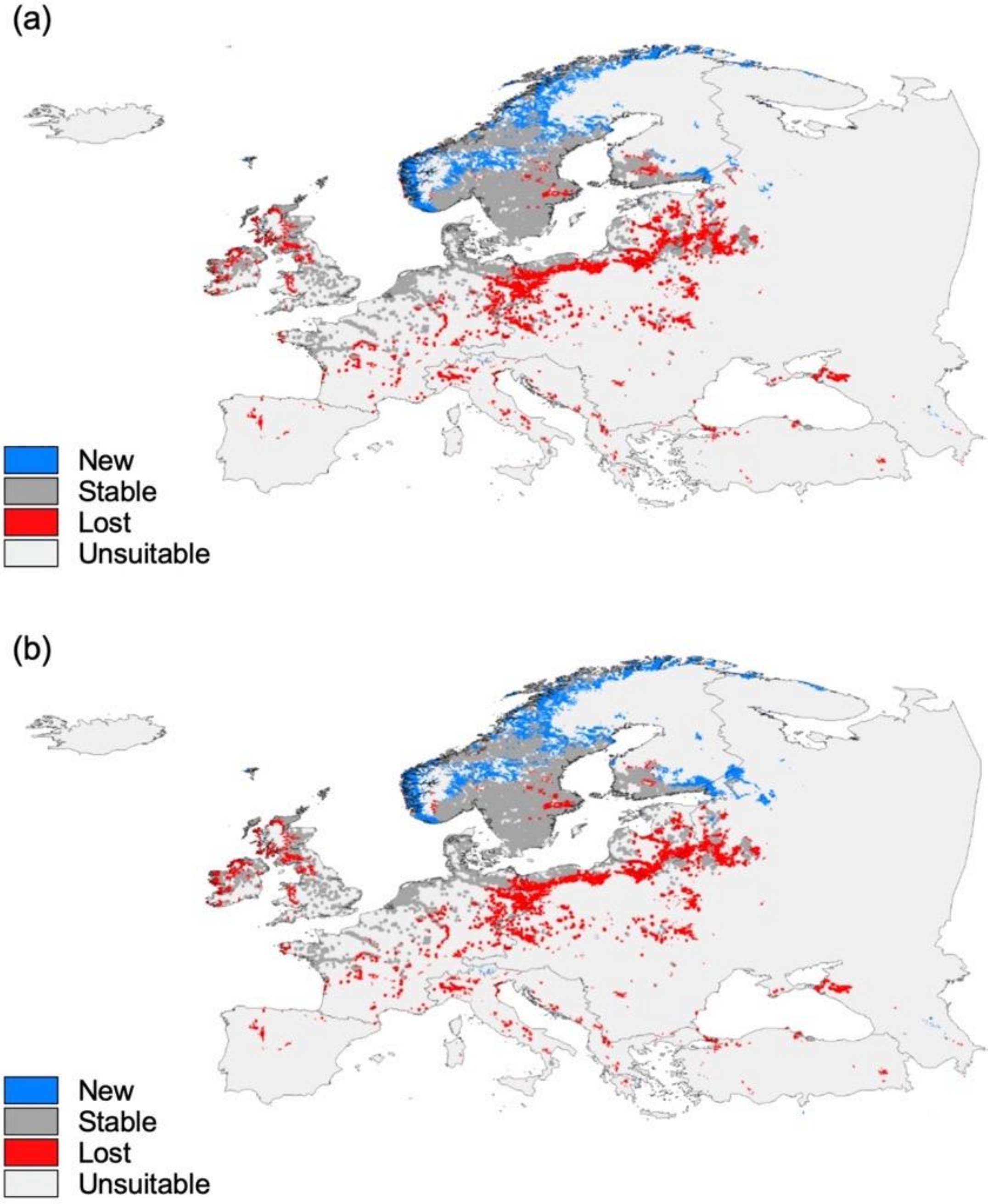

Fig. 2. Changes in the predicted distribution range of *Argyroneta aquatica* in 2021–2040 according to (a) a sustainable and (b) a fossil-fuelled development scenario. Areas that are currently suitable and will still be suitable in the future are shown in dark grey; areas currently suitable that will lose their suitability in the future are shown in red; areas that are currently not suitable but will become suitable in the future are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Northern Europe, and in particular Fennoscandia and the Baltic regions, are expected to become climatic refugia for *A. aquatica* and *D. plantarius*, providing suitable bioclimatic conditions for species persistence through time (see also Monsimet et al., 2020). By contrast, in the central-eastern and western parts of the range, where vast areas of wetlands occur in highly modified landscapes or have completely disappeared (Verhoeven, 2014), future scenarios projected a dramatic loss in habitat suitability for both species. In other words, the current suitability was predicted to decrease progressively, in particular in the central-eastern and western portions of the range, in spite of a slight increase in the suitability of areas north and north-east of the current range. The magnitude of the decrease in projected future range of both species was predicted to be even more significant as a result of their limited dispersal abilities and the fragmentation of the landscape.

The potential northern expansion in habitat suitability for *A. aquatica* and *D. plantarius* has already been widely described but the ability of these species to exploit this opportunity is open to question for three reasons. First, their propensity to disperse is thought to be limited (Leroy et al., 2014). In *D. plantarius*, a low propensity to long-distance dispersal has been reported (Duffey, 2012; Monsimet et al., 2020, 2022) whereas no information on the dispersal ability of *A. aquatica* is available (but see Bonte et al., 2003). Because of their limited dispersal propensity, these species may be unable to respond to rapid shifts in suitable conditions and become trapped within their current geographical ranges. As seen for other groups (Devictor et al., 2012; Schloss et al., 2012; Corlett and Westcott, 2013; Chivers et al., 2017), dispersal rates may be insufficient to track climate change as rapidly as required under any future scenario.

Secondly, both species are habitat specialists (van Helsdingen, 1993; Duffey, 1995; Smith, 2000; Seymour and Hetz, 2011; Dickel et al., 2022), a condition likely to restrict their dispersal through non-aquatic habitats. In addition, rapid dispersal is only possible between adjacent and interconnected suitable habitats; landscape connectivity is the key factor controlling dispersal and can remove the potential for colonisation of new areas of climatically suitable habitat. Degradation and fragmentation of freshwater ecosystems is expected to continue to reduce habitat connectivity in European wetlands (Leadley et al., 2014). There are also important geographical barriers, such as the Baltic Sea that blocks the dispersal of the Western and Central-Eastern populations northward, and the southern European mountain ranges that preclude the isolated populations of North-eastern Spain, Northern Italy and Balkans from reaching more suitable areas in northern Europe (Milano et al., 2018).

Thirdly, the cold tolerance of these species could affect their future survival in potential northern refuges. Studies on *D. plantarius* (Monsimet et al., 2021) revealed a low cold tolerance, influencing this species' ability to expand and survive in the coldest areas of Northern Europe. Colder overwintering conditions, resulting from a decline in snow cover and consequent reduction in insulation of the subniveal habitat, are expected to threaten the species' survival.

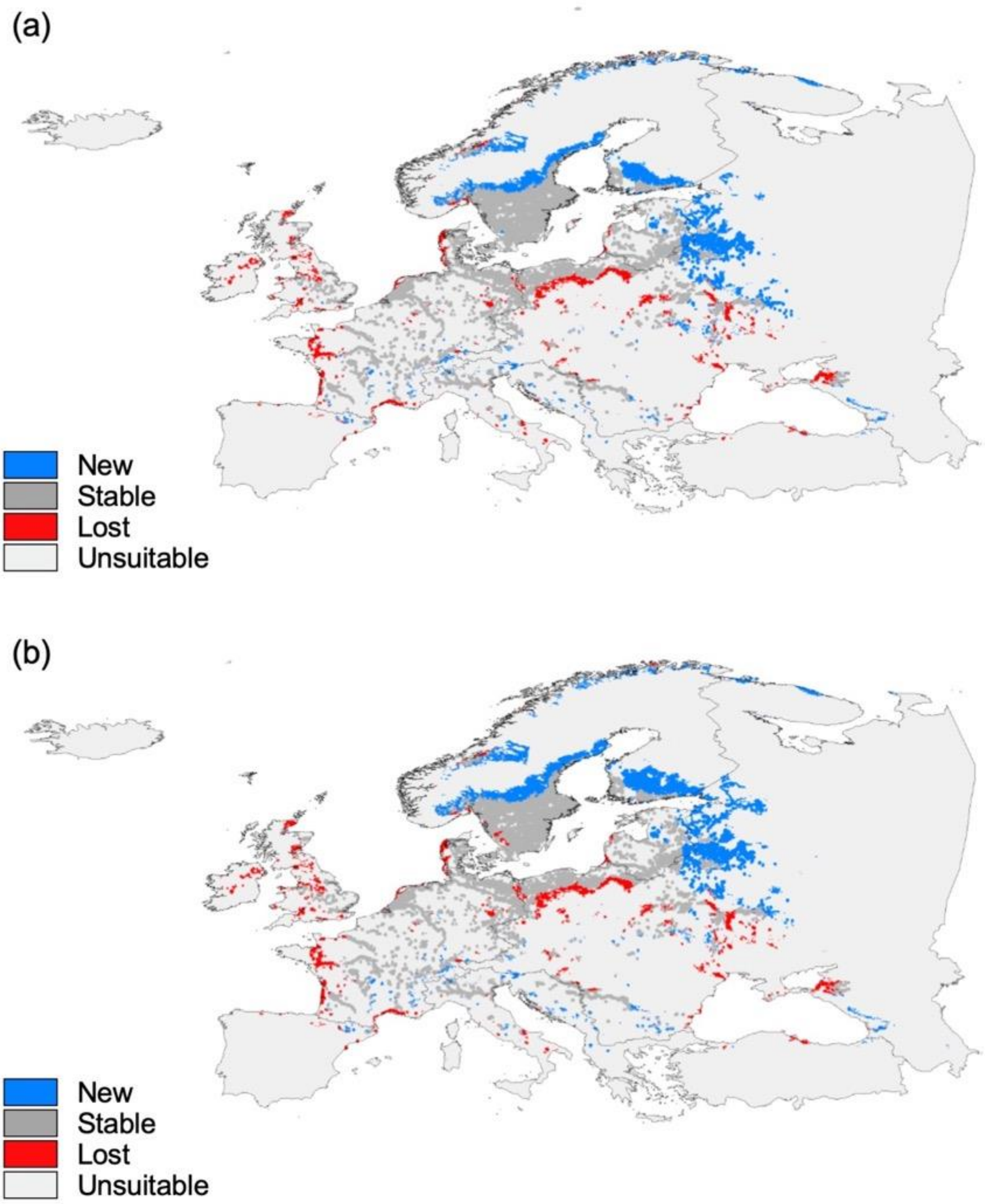

Fig. 3. Changes in the predicted distribution range of *Dolomedes plantarius* in 2021–2040 according to (a) a sustainable and (b) a fossil-fuelled development scenario. Areas that are currently suitable and will still be suitable in the future are shown in dark grey; areas currently suitable that will lose their suitability in the future are shown in red; areas that are currently not suitable but will become suitable in the future are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In view of this, any substantial expansion of these species in Northern Europe seems unlikely. The predicted trend of decline in suitable range is expected to be more significant than that obtained by considering only the potential bioclimatic suitability (as shown in Table 1), and justifies predicting an increase in local extinction rates in the near future.

It must be stressed that species distribution models are prone to several limitations, mainly related to the spatial and detection biases inherent in presence-only datasets and to the environmental variables adopted, which could limit the accuracy of the models and may entail uncertainties in future predictions. Despite the recent methodological advances in the development of species distribution models, MaxEnt remains one of the most robust species distribution modelling techniques, and the most commonly used algorithm for arthropods (Mammola et al., 2021). It overcomes some of the difficulties associated with sparse and irregularly sampled data and with the lack of reliable absence data, and is able to generate accurate predictions with different variables (Phillips et al., 2009; Zeng et al., 2016). To minimize bias, we calibrated our models within aquatic environments, excluding *a priori* habitats thought to be unsuitable for our model species. Nevertheless, there are several impacts of climate change affecting the short- and medium-term suitability of wetland environments that our models are not able to detect. Sea level rise and the altered frequency of tidal surges could increase the risk of permanent saltwater intrusions into coastal freshwater wetlands, shifting the vegetation towards salt-tolerant associations and altering the structure and processes of coastal wetland ecosystems (Barlow and Reichard, 2010; Herbert et al., 2015; Grieger et al., 2020), with significant negative implications for our model species. Beyond climate change, these species could be impacted by the destruction and modification of natural habitats resulting from habitat loss and land-use change, but we have not evaluated these factors. The exclusion of land-use and other biotic variables in our models was due to the paucity of high-quality data concerning the species' habitat requirements (see Duffey, 2012 for *D. plantarius*), which are available at the microhabitat scale for some regions only (*e.g.* Dickel et al., 2022 for Scandinavian wetlands).

4.2. IUCN global assessment

Our modelling results provided a baseline for the first assessment of the global conservation status of the two species according to the current IUCN guidelines (IUCN, 2001, 2012). Despite these being the spider species that feature most frequently in regional Red Lists and protection programmes across Europe (Milano et al., 2021), they are still lacking threat assessments at a global level to which this work expects to contribute. To date, no global IUCN assessment has been provided for *A. aquatica*. *Dolomedes plantarius* was first reported in the 1983 IUCN

Invertebrate Red Data Book as a species in need of conservation in relation to the progressive loss of its natural habitat (Wells et al., 1983). Some years later, Collins and Wells (1987) reported *D. plantarius* among the threatened invertebrates in Europe, proposing its inclusion in Appendix II of the Bern Convention. The first official IUCN assessment of the conservation status of *D. plantarius* dates back to 1986, and listed the species as Vulnerable (IUCN Conservation Monitoring Centre, 1986). This status was maintained in subsequent updates of the Red List (Wilcox, 1988; IUCN, 1990; Groombridge, 1993). After the publication of the 1994 IUCN Red List Categories and Criteria (version 2.3), *D. plantarius* was re-assessed and again placed in the Vulnerable category against criterion A (World Conservation Monitoring Centre, 1996). However, it has not been reassessed since the revision of the IUCN standards in 2001, and so the evaluation is now outdated and not comparable with the new criteria.

Using the latest version of IUCN criteria, we confirm the inclusion of *D. plantarius* in the Vulnerable category under criterion A3, on the basis of the projected decline in the area of occupancy over the next 10 years due to climate change. The IUCN criteria allow cautious use of various kinds of indirect evidence to estimate the decline rate, such as decline in geographic range or habitat (Mace et al., 2008). The relationship between population reduction and habitat loss may not be linear, but, in the absence of more specific information, it is a reasonable assumption (IUCN Standards and Petitions Committee, 2019).

Using equivalent assumptions, our results suggest the inclusion of *A. aquatica* in the Near Threatened category under criterion A3c. This is justified by the rate of decline in area of occupancy being very close to qualifying for the Vulnerable category over the next decade, and exceeding the threshold for the inclusion in this category in the following 20 years.

Thus, despite being widespread species, with large population sizes and ranges, which prevents their inclusion in threatened categories under criteria B (small geographic range size), C (small population size) and D (very small population size and range), *A. aquatica* and *D. plantarius* may qualify as being threatened with extinction on the Red List as they are undergoing rapid and continuing decline in population size. Even large populations would be driven to extinction by continuing decline or by extreme fluctuations from which they cannot recover (Mace et al., 2008).

4.3. Regional assessments

Our models predicted different trends for European regions, allowing us to provide regional assessment for the two species. We projected no significant decline in Northern Europe, where the local risk of extinction is very low and the regional populations are considered Least Concern. Conversely, in Central-Eastern Europe both species will experience a dramatic decline in the near future, and several populations in the region are predicted to quickly disappear. This trend is accentuated by the continuing decline and fragmentation of wetland habitats related to intensive environmental changes occurring in this region. Central and Eastern European countries are considered hotspots for threatened species, due to several factors affecting the local biodiversity. These include high anthropogenic pressure, agricultural improvements, changes to grassland and woodland management, infrastructure development, degradation and drainage of wetlands, as well as isolation and loss of habitat connectivity (Milano et al., 2021). For both *A. aquatica* and *D. plantarius,* our assessments considered the populations occurring in the region to be Critically Endangered. Climate change is also likely impacting the distribution of these species in their Western European range. Although the rate of decrease is thought to be lower in this region, future decline is still likely. In addition, the severe habitat fragmentation and isolation due to human activity may cause local extinctions especially in isolated populations inhabiting the smallest habitat fragments. Because of projected decreases in range, the populations of both species in this region have been considered Vulnerable. In Southern Europe, the vulnerability of some populations to altered climatic patterns has been highlighted by their isolation and fragmentation within wetland areas, where they act as biogeographic islands. However, despite the overall predicted decrease in regional suitability, southern populations are expected to persist due to the occurrence of extensive water basins in this region (*e.g.* the Po valley, the Danube basin, the Ebro Delta).

The interdependency among adjacent regions is a potentially important parameter. According to the IUCN regional guidelines (IUCN, 2012), where the existence and status of populations outside a region may affect the risk of extinction within it, the preliminary category should be changed to level that more appropriately reflects the regional extinction risk. In other words, the estimation of Extent of Occurrence and Area of Occupancy and their relative trends should consider neighbouring populations.

If the immigration from neighbouring regions is deemed possible, the risk of extinction is probably lower than if the regional population was isolated. However, for species with poor dispersal abilities, like *D. plantarius* and *A. aquatica*, recolonisation from 'reservoir' populations outside the region is very unlikely to compensate for local extinctions, and there is no need to consider adjusting the category for the regional assessment.

5. Concluding remarks

Climate change is expected to have pronounced future negative effects on wetlands, providing great challenges to the survival of wetland species (Erwin, 2009; Davidson, 2014). Predicting the impacts of such effects on wetland species is therefore vital in motivating and informing strategic actions at global and local scales. Aquatic spiders could be successfully used as sensitive indicators of the health of wetland ecosystems and to forecast the response of wetland biodiversity to climate change. Considering their strategic role in the wetland food web, and their sensitivity to anthropogenic changes, they represent useful indicators of the general status of these ecosystems (Maelfait and Hendrickx, 1998; Scott et al., 2006). The evaluation of their extinction risk can be used as a baseline to inform conservation planning and influence management decisions concerning the conservation of these species and their habitats (Miller et al., 2007). In addition, information on the threatened status of wetland species and habitats is expected to significantly enhance interest in their conservation, raising public awareness and promoting conservation action (Milano et al., 2021).

Conservation strategies should be therefore directed towards the current anthropogenic threats that continue to drive wetland biodiversity loss. Global policies devoted to the containment of anthropogenic climate change will be very important to limit the negative impact that predicted warming will have on wetland species. However, climate change can be expected to act in concert with other pressures (Bowler et al., 2020), many of which, although not considered in our work, may influence the extinction risk of our model species in the short to medium term. Accordingly, a sound strategy to preserve wetland habitats and biota would consist of proactive management to reduce non-climate stressors (Erwin, 2009).

Concerning our model species, a pragmatic approach to their conservation could be the implementation of large-scale management plans and restoration programmes for wetland habitats and ecological networks, ensuring better structural and functional connectivity among wetland patches.

In light of the physiological and behavioural peculiarities of *A. aquatica* and *D. plantarius*, which contribute to the biological richness and diversity of the wetlands, an increase in the number of protected areas with management plans dedicated to the conservation of both habitat and species should be considered. This approach is recommended by Branco and Cardoso (2020) as one of the most effective approaches to spider conservation.

Considering the future decline in extent and number of the existing wetlands, and the highly fragmented distribution of suitable habitats occurring in some eco-regions, the adoption of captive-rearing and translocation programmes, as successfully performed in Britain for *D. plantarius* (https://www.dolomedes.org.uk/conservation; Smith, 2020), coupled with long-term monitoring, should also be considered.

If matched with the correct policies at global scale to reduce emissions, conservation efforts at a local scale might successfully reduce the adverse impacts of climate change and provide safety nets for these species.

Table 2. Assessment of the extinction risk of *Argyroneta aquatica* and *Dolomedes plantarius* at the global level and for each region, with relative IUCN criteria.

	Argyroneta aquatica					*Dolomedes plantarius*				
IUCN Criterion	Northern Europe	Central-Eastern Europe	Western Europe	Southern Europe	Global Extent	Northern Europe	Central-Eastern Europe	Western Europe	Southern Europe	Global Extent
Criterion A (Population size reduction)	LC	CR	VU	EN	NT	LC	CR	VU	NT	VU
Criterion B (Geographic range)	LC	LC	LC	LC	LC	LC	LC	LC	LC	LC
Criterion C (Small population size and decline)	DD	DD	DD	DD	DD	DD	DD	DD	DD	DD
Criterion D (Very small or restricted population)	DD	DD	DD	DD	DD	DD	DD	DD	DD	DD
Criterion E (Quantitative Analysis)	DD	DD	DD	DD	DD	DD	DD	DD	DD	DD
Final Assessment	LC	CR	VU	EN	NT	LC	CR	VU	NT	VU

Declaration of competing interest

All authors declare that they have no conflicts of interest.

Data availability

Data will be made available on request.

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Appendices. Supplementary data

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Paper IV

Natural history and conservation of the wolf spider *Vesubia jugorum* (Araneae: Lycosidae), assessed as Endangered in the IUCN Red List

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Photo credit: Nicolas Henon

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Natural history and conservation of the wolf spider *Vesubia jugorum* (Simon, 1881) (Araneae, Lycosidae), assessed as Endangered in the IUCN Red List

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ABSTRACT

Vesubia jugorum (Simon, 1881) (Lycosidae Sundevall, 1833) is a wolf spider inhabiting high altitude rocky areas of the Southwestern Alps. Due to its restricted geographic range, its sensitivity to global warming and its continuing decline, this species has been recently assessed as Endangered (EN) by the IUCN Red List. On the basis of the research carried out in the recent years, we here provide updated information about its distribution, habitat characterisation, life history and conservation. Field observations and laboratory rearing suggest a multi-annual life cycle for this species, with a growing season of five-six months and 10-12 instars to reach the adult stage. Adult males are found for a short period, and die after mating. During winter, adult females and immatures at different stages likely survive in the upper layers of the rocky debris under the snow, where the temperature remains stable around 0-2°C. Recent studies based on species distribution modelling have demonstrated a significant relationship between habitat suitability and functional traits related to species performance, which we briefly recall here. In light of this relation, a long-term monitoring programme was designed in collaboration with Parc national du Mercantour (France) and Parco Alpi Marittime (Italy), aiming at providing the conservation status of the species and possible future trends. Here, we present the results of the baseline phase of the monitoring programme, based on 17 sites across the French-Italian border, that confirm the positive relationship between functional traits and habitat suitability, and corroborate it as a practical, non-invasive approach to the assessment of species health.

KEY WORDS
Endemic species,
monitoring,
phenology,
life cycle,
climate change,
habitat suitability,
biodiversity
conservation.

RÉSUMÉ
Histoire naturelle et conservation de l'araignée-loup Vesubia jugorum *(Araneae, Lycosidae), une espèce "En danger" sur la Liste rouge de l'UICN.*
Vesubia jugorum (Simon, 1881) (Lycosidae Sundevall, 1833) est une espèce d'araignée-loup habitant les zones rocheuses de haute altitude des Alpes du Sud-Ouest. En raison de son aire de répartition géographique restreinte, de sa sensibilité au réchauffement climatique et de son déclin continu, cette espèce a récemment été classée comme «espèce en danger d'extinction (EN)» sur la Liste rouge de l'UICN. Sur la base des recherches menées ces dernières années, nous fournissons ici des informations actualisées sur sa distribution, la caractérisation de son habitat, son cycle biologique et sa conservation. Les observations sur le terrain et l'élevage en laboratoire suggèrent un cycle de vie pluriannuel pour cette espèce, avec une saison de croissance de cinq à six mois et 10 à 12 stades pour atteindre le stade adulte. Les mâles adultes sont trouvés pendant une courte période et meurent après l'accouplement. Pendant l'hiver, les femelles adultes et les immatures à différents stades survivent probablement dans les couches supérieures des débris rocheux sous la neige, où la température reste stable autour de 0-2°C. Des études récentes ont démontré une relation significative entre la qualité de l'habitat et les traits fonctionnels liés à la performance de l'espèce, que nous rappelons ici brièvement. En fonction de cette relation, un programme de monitoring sur le long terme a été conçu en collaboration avec le Parc national du Mercantour (France) et le Parco Alpi Marittime (Italie), visant à décrire l'état de conservation de l'espèce et les tendances futures possibles. Nous présentons ici les résultats de la phase de référence du monitoring, qui confirme la relation positive entre traits fonctionnels et qualité de l'habitat, et qui s'est avérée être une approche pratique et non invasive pour évaluer la santé de l'espèce.

MOTS CLÉS
Espèce endémique,
surveillance,
phénologie,
cycle biologique,
changement climatique,
qualité de l'habitat,
conservation
de la biodiversité.

INTRODUCTION

Vesubia jugorum (Simon, 1881) is an alpine endemic species of wolf spider inhabiting high altitude rocky areas at high elevations in the Southwestern Alps (Tongiorgi 1969; Mammola *et al.* 2016). The species was originally described by Simon (1881) based on a specimen collected in unspecified locality nearby Saint-Martin-Vésubie, in the département des Alpes-Maritimes, south-eastern France. The distribution was later investigated by Tongiorgi (1968; 1969), Maurer & Thaler (1988) and more recently by Isaia *et al.* (2007; 2015), Mammola *et al.* (2016; 2019), and Milano *et al.* (2019). The current number of verified occurrences for this species published in scientific literature is 101 (detailed in Mammola *et al.* 2019), mostly encompassing the Province of Cuneo in north-western Italy (65 localities), the Département des Alpes-Maritimes (19 localities) and the Département des Alpes-de-Haute-Provence (17 localities), in south-eastern France. The known distribution range covers an area of approximately 2500 km². Most of the species occurrences fall within protected areas and sites of the Natura 2000 network, namely the Special Area of Conservation and Special Protection Area of the Maritime Alps (SAC/SPA IT1160056 Alpi Marittime), the Natural Park of Marguareis (EUAP0214 and SAC/SPA IT1160057 Alte Valli Pesio e Tanaro) and the Special Protection Area Alte Valli Stura e Maira (SPA IT1160062) in Italy, and the Special Area of Conservation and Special Protection Area of the Mercantour National Park (SAC FR9301559 and SPA FR9310035 Le Mercantour) in France.

Recent studies based on species distribution modelling focusing on the sensitivity of the species to global warming, showed a significant reduction in its future bioclimatic range (Isaia *et al.* 2016; a forthcoming paper by Milano *et al.*), raising concerns to the long-term survival of this species. In view of this, *Vesubia jugorum* was assessed by the International Union for Conservation of Nature (IUCN), and classified as Endangered (EN) in the IUCN Red List of Threatened species, on the basis of its limited geographic range and the projected continuing decline of its natural habitat in the near future due to climate change (Isaia & Mammola 2018).

Mammola *et al.* (2019) demonstrated a significant relationship between habitat quality, predicted by species distribution models, and the individual performance of *Vesubia jugorum*, measured by means of functional traits (femur I length and egg-case size). This is a well-known and widely adopted ecological principle in the monitoring of many plants and vertebrates (Thuiller *et al.* 2004; Michel *et al.* 2017; Lunghi *et al.* 2018; Benito Garzón *et al.* 2019), but was rarely investigated among arthropods (Mammola *et al.* 2019). In *V. jugorum*, the length of femur I and egg-case (cocoon) size were found to be positively related with habitat suitability. The largest individuals (i.e., the individuals with longer femurs) and females with larger cocoons, occurred in the core of the species distribution, where the amount of predicted high-quality habitat was greatest and the related habitat suitability value was higher (> 0.7 in a range between 0 and 1). Conversely, in areas with lower habitat suitability (< 0.25), individuals had smaller femurs and smaller cocoons. On these bases, measuring variation in morphological traits of *V. jugorum* has been suggested as a practical, non-invasive means of assessing population health through time (Mammola *et al.* 2019).

In the context of the species conservation, a long-term monitoring programme has been designed for evaluating the ongoing impact of climate change on the species survival and for detecting changes in populations, aiming at setting conservation actions and at informing stakeholders about the future management of the species. According to the IUCN, monitoring is one of the main sources of information on the population status, and a significant tool in the conservation strategy of the species. In 2019, a transnational monitoring programme involving Italy and France, coordinated by the University of Turin in collaboration with Parc national du Mercantour and Parco Naturale Alpi Marittime, has started.

Thanks to the work conducted during these years by our research team, we gathered new data on the ecology, the distribution and the life history of this species, that we sum up in this work along with the description of the monitoring programme and the presentation of the results obtained during the baseline phase of 2019.

TABLE 1. — Overview of the sites designed by the monitoring programme, with relative country, elevations (**Elev.**) in meters and coordinates in decimal degrees (Datum: WGS84).

Site	Country	Locality	Elev.	Latitude	Longitude
1	France	Col de la Bonette	2564	44.347	6.797
2	France	Col de la Cayolle	2420	44.265	6.736
3	France	Col de Mallemort	2570	44.474	6.854
4	France	Col de Vars	2289	44.534	6.692
5	France	Col du Trem	2472	44.050	7.430
6	France	Grande Séolane	2536	44.333	6.551
7	France	Lac de l'Agnel	2356	44.120	7.460
8	France	Rocca dell'Abisso	2611	44.140	7.510
9	France	Serriére de la Lombarde	2359	44.200	7.161
10	Italy	Colle del Chiapous	2540	44.181	7.319
11	Italy	Colle dell'Arcana	2260	44.461	6.941
12	Italy	Colle della Ciriegia	2534	44.140	7.280
13	Italy	Corborant	2764	44.265	7.000
14	Italy	Marguareis – Canale dei Genovesi	2000	44.180	7.687
15	Italy	Mongioie – Bocchin dell'Aseo	2298	44.175	7.793
16	Italy	Passo della Gardetta	2599	44.404	6.996
17	Italy	Passo Sant'Anna	2390	44.220	7.090

MATERIAL AND METHODS

SAMPLINGS AND LABORATORY REARING

Field observations and collection of living specimens were conducted across the known species distribution range from mid-June to late September, in the years from 2016 to 2019. Additional samplings, aiming at extending the known distribution range of the species, have been performed in different localities of France and Italy in 2019 (see Acknowledgements), and during the "Explor'Nature Colmars-les-Alpes 2021" and "Explor'Nature Valdeblore 2022" events organised by Parc national du Mercantour (1-4 July 2021 and 30 June-3 July 2022, respectively), within the territory of the municipalities of Colmars-les-Alpes (département des Alpes-de-Haute-Provence) and Valdeblore (département des Alpes-Maritimes). Both areas were predicted as suitable by species distribution models (see Mammola *et al.* 2019), but never investigated before. The specimens are preserved in EtOH95% and the material is stored in the Marco Isaia collection (coll. MI) at the Department of Life Sciences and Systems Biology of the University of Torino and in the collection of the Muséum national d'Histoire naturelle, Paris (MNHN).

During our surveys in summer 2016 and summer 2018, 50 spiders were collected alive in the field for laboratory rearing. Spiders were collected by hand and placed in individual Falcon® Tubes of 50 mL. In laboratory, we housed the collected specimens individually in plastic terraria (18 cm × 12 cm × 7.5 cm), supplied with wet sponge or cotton wool as a source of water. The specimens were kept at room temperature during the day (19-26°C), and in an IPP 30 Peltier Memmert climatic chamber at night where the temperature was kept stable for approximately 12 hours at 4-6°C. The spiders were fed *ad libitum* with insects collected during the sampling and with laboratory-reared house crickets, *Acheta domesticus* (Linnaeus, 1758). Spiderlings that emerged from egg sacs, were reared in the laboratory, and fed with fruit flies, *Drosophila melanogaster* Meigen, 1830. The numbering of ontogenetic stadia was counted after the emergence from egg (not considering the first molt inside egg sac, see Dolejš *et al.* 2014).

Natural microclimatic conditions experienced by *Vesubia jugorum* throughout the year, were derived from data-loggers positioned for one year at the ground level under stones, in a suitable area at 2589 m in the nearby of the meteorological station of Rocca dell'Abisso (2753 m a.s.l., Valdieri, Province of Cuneo). Meteorological data from the station of Rocca dell'Abisso were provided by Arpa Piemonte (https://www.arpa.piemonte.it/rischinaturali/accesso-ai-dati/annali_meteoidrologici/annali-meteo-idro/banca-dati-meteorologica.html).

THE MONITORING PROGRAMME

The monitoring programme was designed on the basis of the currently known distribution range of *Vesubia jugorum*, and on the basis of the significant relationship between habitat quality and the performance of individuals recovered in Mammola *et al.* (2019). Accordingly, the programme focussed on morphological and reproductive traits that might constitute reliable proxies for the health of the populations of *V. jugorum*: the size of the femur of the fourth leg (femur IV), as a representative measure of the overall body size, and the size of the cocoons, as trait related to the reproductive success. The monitoring programme was designed to be regularly repeated at five-year intervals, considering the life cycle of the species.

The surveys of the baseline phase were carried out from 11 July to 20 September 2019 (72 days), during the peak of the growing season of the species, in 17 sites selected by

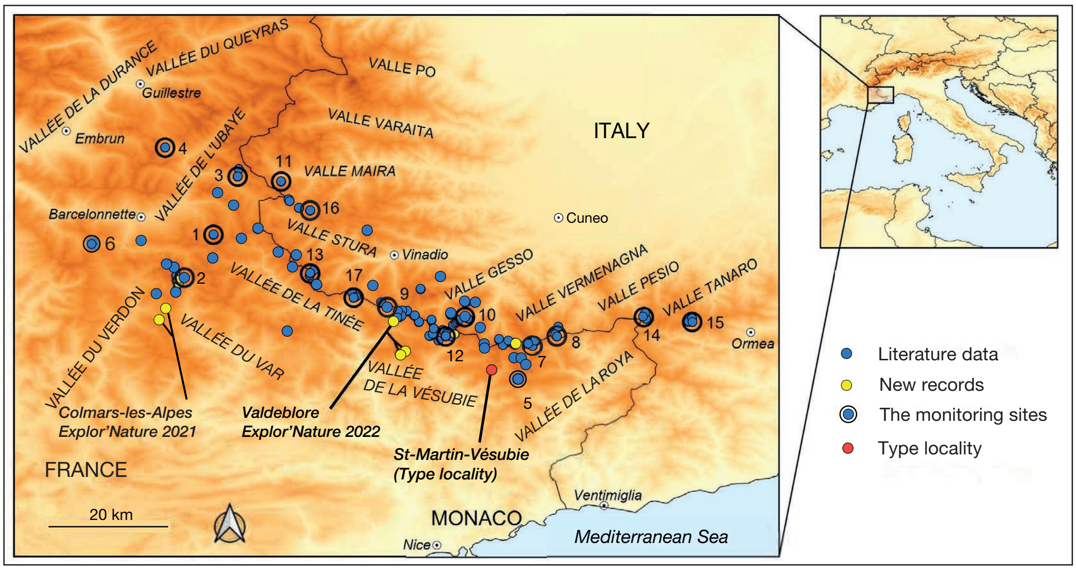

Fig. 1. — The updated distribution of *Vesubia jugorum* (Simon, 1881). Symbols: ●, type locality; ●, literature data; ○, new records published in this work; ◉, the 17 sites chosen for the long-term monitoring programme.

Table 2. — New occurrences of *Vesubia jugorum* (Simon, 1881) collected in 2019, 2021 and 2022. For each locality, coordinates are in decimal degrees (Datum: WGS84), municipality, elevation in meters, numbers of specimens collected (**n**) and date of discovery are specified.

Country	Locality	Municipality	n	Date	Elevation (m)	Lat.	Long.
Italy	Lago Bianco dell'Agnello	Entracque	1	8.VIII.2019	2200	44.124	7.424
France	Col du Mercantour	Saint-Martin-Vésubie	1	18.VIII.2019	2532	44.145	7.299
France	Lac des Garrets	Entraunes	1	22.VIII.2019	2299	44.248	6.728
France	Col de la Petite Cayolle	Uvernet-Fours	1	5.IX.2019	2460	44.256	6.726
France	Tête de l'Encombrette	Colmars-les-Alpes	2	3.VII.2021	2200	44.198	6.701
France	Dent de Lièvre	Colmars-les-Alpes	5	3.VII.2021	2138	44.174	6.686
France	Vallon des Millefonts	Valdeblore	1	30.VI.2022	2150	44.103	7.185
France	Mont Pepoiri	Valdeblore	5	1.VII.2022	2360	44.110	7.196
France	Tête de la Roubine	Valdeblore	1	3.VII.2022	2274	44.171	7.173

our own expert opinion as representatives of the overall distribution range of the species (Table 1 and Figs 1; 2). For each sampling site, we set the collection of a minimum of five adult females with cocoons over a limit of searching time of three hours.

After the sampling, the leg IV of each specimen collected was removed and stored in EtOH95%. As demonstrated in literature (Wrinn & Uetz 2008), the removal of a leg IV in a spider does not represent harm to the individual. The measurement of the femur IV was carried out in laboratory, through Leica M80 stereoscopic microscope (up to 60 × magnification). To standardize data acquisition, we derived measurements from digital pictures taken with a Leica EC3 digital camera, and we calculated them with Leica LAS EZ 3.0 software (Leica Microsystems, Switzerland). After the removal of the leg IV in the field, the specimens were released in their natural habitat. Whenever present, the cocoon diameter was measured with a digital calliper (Fig. 2). After the measurement, the cocoon was returned to the individuals.

Regression analyses

We conducted all analyses using R software (R Core Team 2021). We tested the relationship between the length of femur IV collected in the monitoring and the habitat suitability index of the sampling sites as in Mammola *et al.* (2019) by means of linear mixed models (LMMs) with the 'lmer' *R* package (Bates *et al.* 2015). Mixed models allowed us to address the violation of models assumption of spatial independence, caused by multiple measurements of the same population.

In R notation, the structure of the linear mixed models was:

$$Y \sim H + 1|S$$

where S are the sampling sites (excluding Col de Vars, where no specimens were collected) used as random factors, Y represents one of morphological variables (i.e. femur IV length and cocoon size), and H represents values of habitat suitability, expressed in a range between 0 and 1. Values of habitat suitability were calculated by averaging the values of each pixel of the species distribution model from Mammola *et al.* (2019) with a 500-m buffer around each sampling site, using QGIS software (version 3.14) (QGIS Development Team 2022).

FIG. 2. — Long-term monitoring programme of *Vesubia jugorum* (Simon, 1881): **A**, a typical high-altitude rocky area colonized by *Vesubia jugorum*; **B**, a female with its cocoon; **C**, measurement of the cocoon diameter with a digital calliper; **D**, removal of leg IV from a female; **E**, measurement of leg IV through Leica M80 stereoscopic microscope; **F**, a female with cocoon found in its retreat.

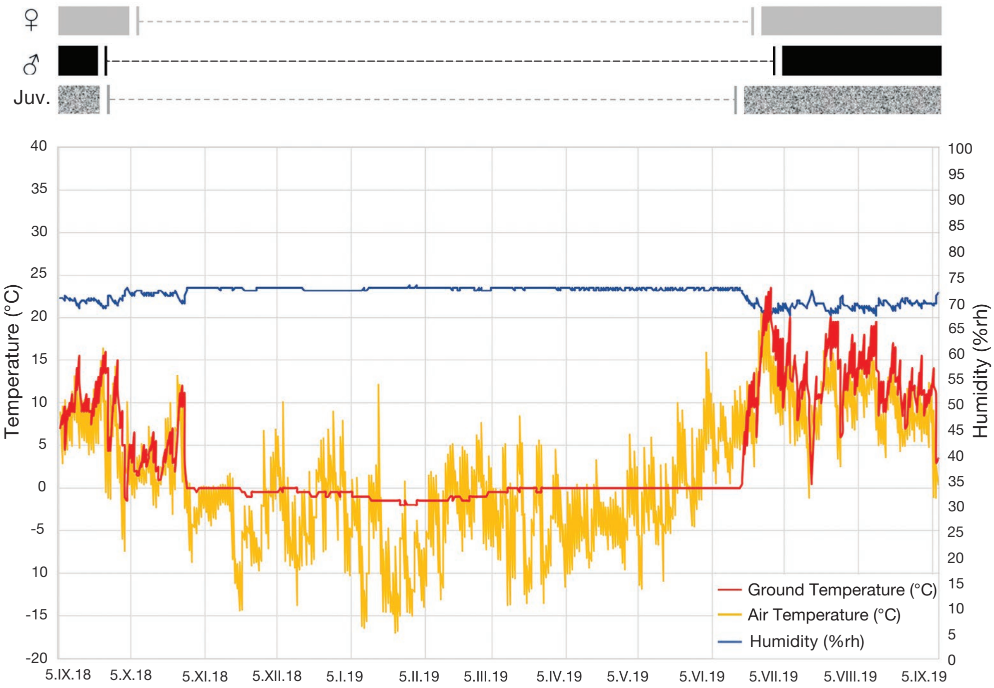

Fig. 3. — Life cycle of *Vesubia jugorum* (Simon, 1881) derived from field observations conducted across the species distribution range during the 2016-2019 sampling seasons. Daily fluctuations in temperature (**red line**) and humidity (**blue line**) derived from data-logger positioned across 2018 and 2019 at the ground level under stones, in the nearby of Rocca dell'Abisso (Valdieri, 2589 m a.s.l.). Daily fluctuations in air temperature (**orange line**) derived from the meteorological station of Rocca dell'Abisso (2753 m a.s.l.). Growing season is indicated by **light grey** (females), black (males) and **dotted dark grey** (juveniles) bars. **Dash line** refers to the overwintering. See text for further details.

RESULTS

Order ARANEAE Clerck, 1757
Family Lycosidae Sundevall, 1833

Vesubia jugorum (Simon, 1881)

Trabea jugorum Simon, 1881: 83.

Vesubia jugorum – Simon 1909: 402.

Material. — **France** • 2 ♀; département des Alpes-Maritimes, Valdeblore, Mont Pepoiri, western slope, in rocky debris; 2360 m a.s.l.; 1.VII.2022; Isaia and Tolve leg., coll. MI • 1 ♀; same data as for preceding; MNHN • 2 ♀; Colmars-les-Alpes, Téte de l'Encombrette, southern slope; steep alpine scree; 2200 m a.s.l.; 3.VII.2021; Isaia and Tolve leg., coll. MI • 5 ♀; Colmars-les-Alpes, Dent de Lièvre, northern slope; flat rocky debris area; 2138 m a.s.l.; 3.VII.2021; Isaia and Tolve leg., coll. MI.

Observations. — **Italy** • 1 specimen; Province of Cuneo, Entracque, Lago Bianco dell'Agnello; 2200 m a.s.l.; 8.VIII.2019: Giordana vid. **France** • 1 ♀; département des Alpes-Maritimes, Entraunes, Lac des Garrets; 2299 m a.s.l.; 22.VIII.2019; Lucas vid. • 1 ♀; Saint-Martin-Vésubie, Col du Mercantour; 2532 m a.s.l.; 18.VIII.2019; Assmann vid. • 1 ♀; Valdeblore, Vallon des Millefonts, western slope, in rocky debris; 2150 m a.s.l.; 30.VI.2022; Breton vid. • 2 ♀; Mont Pepoiri, western slope, in rocky debris; 2360 m a.s.l.; 1.VII.2022; Isaia and Tolve vid. • 1 ♀; Valdeblore Tête de la Roubine, southern slope, in rocky debris; 2274 m a.s.l.; 3.VII.2022; Isaia and Tolve vid. • 1 ♀; département des Alpes-de-Haute-Provence, Uvernet-Fours, Col de la Petite Cayolle; 2460 m a.s.l.; 5.IX.2019; Lucas vid.

Remark

These new findings extend the current known distribution range of the species from the previous 2456 km² to the current 2628 km². To date, the known occurrences of *Vesubia jugorum* are 110, i.e., 66 in Italy (Province of Cuneo) and 44 in France (24 in département des Alpes-Maritimes and 20 in département des Alpes-de-Haute-Provence). The new updated distribution of *V. jugorum* is presented in Fig. 1, and the new records are detailed in Table 2.

Microclimatic data

Temperature data derived from data-loggers positioned under stones showed daily fluctuations in temperature and relative humidity during the warm season until late October, when the temperature quickly drops to 0°C and remains almost constant until the following mid-June. Data from the meteorological station of Rocca dell'Abisso showed strong fluctuations of the air temperatures during the year, ranging from –17° in winter to 22 °C in summer (Fig. 3).

Observational data on life cycle, phenology and diet

Observational data likely confirm for *Vesubia jugorum* a stenochronus life cycle. Females and juveniles were generally found throughout the summer season, from mid-June to late September (only one record from Mongioie at the beginning of October), whereas adult males were found for a shorter period, from July to mid-September (Fig. 3). No observations were ever carried out in winter due to the high snow coverage in suitable areas. During the summer season, different cohorts were found simultaneously. The highest abundance of adult specimens occurred in July and August, likely corresponding with the mating period. Males were encountered less frequently and their density was generally low, an observation that may be possibly biased by the higher mobility of males and the greatest difficulty in catching them.

Females with cocoons have been found – always in their retreats – from the end of June to the early days of September. Females build circular and silk-lined retreat under stones, with a small opening in the silken walls, occasionally digging an additional small recess into the soil. Females with cocoons did not seem to be territorial, as up to three females have been found in adjoining retreats under the same stone. The cocoons are globular, white and contain on average 200 eggs (89-343, n = 10). According to our observations, females produce more egg sacs in the same season. The production of a second egg sac has been observed in laboratory-reared specimens.

Females of *Vesubia jugorum* exhibit maternal cares of both cocoons and spiderlings. They carry their cocoon underneath their abdomens attached to the spinnerets. If they lose their egg sac, or if the egg sac is removed, they look for it in the surrounded area until they found it or a surrogate (e.g. a rounded piece of cotton). Under laboratory conditions, females fed while carrying egg sacs or pulli. Female looks after the cocoon for around one month after the laying, until the offspring hatch. The first moult occurs inside the egg sac while the second-instar juveniles emerge from the cocoon through a cleft in the seam, and climb onto their mother opisthosoma, and, occasionally, carapace. Maternal care for spiderlings lasts one week to ten days, after which the spiderlings disperse by falling off from the female body. Shortly after, they moult to the third instar. On average, the duration of the instars is 40 days, with earlier stages moulting every two weeks and later stages being longer up to two months. Given the remarkable size reached by adult specimens, and considering the duration of the growing season, it seems likely that the specimens require an average of 10-12 instars to complete the development, reaching the adult stage over multiple years.

As proved by the specimen collected in earliest time of the growing season, overwintering individuals are generally adult females or immatures at different stages in their development. Unfortunately, we have no data on overwintering behaviour. However, we observed a tendency of the individuals to aggregate during the growing season in areas of high suitability (see, e.g., the high population density observed in July 2019 at Colle della Ciriegia, a highly suitable site where many specimens have been found in a few minutes), and to disaggregate when the temperature drops (no specimens found in samplings carried out in the same locality in mid-October). It seems likely that specimens are very mobile within the rocky areas, showing a higher tendency to aggregate in the snow-free period and to disaggregate as the cold season approaches.

Vesubia jugorum is a cursorial hunter which preys actively. The spider approaches the prey and pounces on it from a close distance, grabbing and surrounding it using the strong, spiny legs. After grabbing it, the prey is bitten with the chelicerae and released with the legs. *Vesubia jugorum* was observed masticating the prey organisms with the chelicerae, maximizing food assimilation and thus increasing the total energy extracted from each prey item. Laboratory observations showed a generalist predatory habit for *V. jugorum*. Accepted preys included Orthoptera, Diptera, Lepidoptera, Coleoptera, Isopoda Oniscidea and Araneae. Cannibalism was common, often involving juveniles or smaller individuals, and in general occurring between pairs of specimens with great differences in both mass and size.

TABLE 3. — Measurements of the functional traits for each monitoring site, with relative values of habitat suitability. For each locality, the mean length of femur IV (in mm), mean cocoon size (in mm), and sample size (**n**) measured for each site was reported. Habitat suitability is derived from Mammola *et al.* (2019), setting an average value calculated on a 500-m circle buffer around each site.

Locality	**Femur length mean (n)**	**Cocoon size mean (n)**	**Habitat suitability**
Colle del Chiapous	7.206 (5)	NA	0.784
Corborant	6.794 (5)	NA	0.784
Serriére de la Lombarde	7.288 (5)	10.828 (4)	0.737
Colle della Ciriegia	7.074 (5)	11.262 (5)	0.716
Passo della Gardetta	6.218 (5)	8.407 (4)	0.638
Col de la Bonette	6.494 (5)	NA	0.470
Passo Sant'Anna	6.938 (5)	9.535 (5)	0.452
Marguarais – Canale dei Genovesi	6.165 (2)	NA	0.436
Colle dell'Arcana	6.526 (5)	9.776 (4)	0.388
Col de la Cayolle	6.202 (5)	NA	0.341
Col du Trem	6.996 (5)	11.468 (2)	0.315
Rocca dell'Abisso	6.820 (2)	NA	0.300
Lac de l'Agnel	7.053 (4)	NA	0.294
Grande Séolane	7.050 (3)	NA	0.211
Mongioie – Bocchin dell'Aseo	5.778 (5)	9.093(4)	0.170
Col de Mallemort	5.882 (5)	NA	0.109

Vesubia jugorum shares its habitat with other Alpine spider species such as *Alopecosa alpicola* (Simon, 1876), *Drassodes thaleri* Hervé, 2009, *Drassodex simoni* Hervé, Roberts & Murphy, 2009, *Attulus longipes* (Canestrini, 1873), *Xysticus desidiosus* Simon, 1875 and *Pardosa nigra* (C. L. Koch, 1834) (see Isaia *et al.* 2015). Tentatively, areas where *V. jugorum* is locally abundant are generally avoided by *Pardosa nigra*, which is slightly smaller in comparison, but possibly shares similar ecological requirements.

RESULTS OF THE MONITORING BASELINE PHASE

During the monitoring surveys, 71 females and 29 cocoons were collected. In 12 out of 17 sampling sites, the target of five adult females was achieved, whereas in the remaining five sites the sampling stopped after three searching hours, without reaching the target of five adult females collected. Col de Vars was the only site where no individual was captured. According to the models performed in Mammola *et al.* (2019), this site has a very low value of habitat suitability. For this reason, Col de Vars was excluded from the monitoring programme.

The results of the measurements of the functional traits collected in each locality with their relative values of habitat suitability (extracted from Mammola *et al.* 2019) are reported

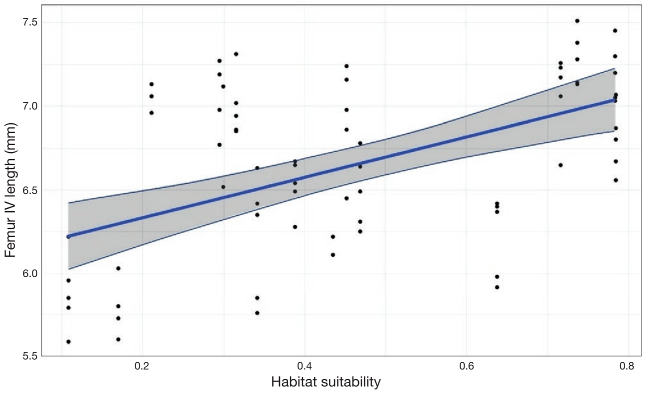

FIG. 4. — Predicted relationship (**blue line**) and 95% confidence intervals (**gray stripe**) between length of femur IV and habitat suitability of each monitoring site derived from the Ecological Niche Model presented in Mammola *et al.* (2019) (see Material and Methods for further details).

in Table 3. The femur IV length ranged from 5.590 mm (Col de Mallemort) to 7.510 mm (Serriére de la Lombarde). In the locality with smallest femurs, Mongioie – Bocchin dell'Aseo where the mean femur IV length was 5.778 mm (n = 5), the habitat suitability index was 0.170. The site with the longest femurs IV was Serriére de la Lombarde, with a mean length of 7.288 mm (n = 5). This site had a high habitat suitability index, corresponding to 0.737.

Only in seven sampling sites we were able to collect cocoons, and their finding was generally rare. The cocoon size ranged from 6.915 mm (Passo della Gardetta) to 12.545 mm (Serriére de la Lombarde). The site with the largest average cocoon size was Col du Trem (11.467 mm; n = 2), whereas the locality with the smaller average cocoon size was Passo della Gardetta (8.407 mm; n = 4).

Results of the regression analyses, highlighted relationship very close to statistical significance (P-value = 0.0516) between the length of the femurs IV and the habitat suitability predicted by the model (Fig. 4). No significant relationship was observed between habitat suitability and cocoon size, possibly due to the low sample size.

Specimens collected at Grande Séolane showed an unexpected great length of the femur IV. Accordingly, when excluding this observation, the significance of the regression improves, reaching a P-value of 0.0202.

DISCUSSION

In this work, we provide an updated frame of the knowledge on the biology of *Vesubia jugorum*, with original information on its distribution, habitat characterisation, life history and conservation.

Vesubia jugorum occurs almost exclusively in rocky areas at high elevations, such as rocky debris, boulder fields and scree, mostly from 2000 m upwards (Tongiorgi 1969; Mammola *et al.* 2016, 2019). More specifically, when considering the current dataset of occurrences, the known altitudinal range spans from 1800 (Pian della Casa, Rifugio Regina Elena, Valdieri) to 3010 m a.s.l. (top of Mount Corborant, Vinadio). Specimens are generally observed wandering on the rocks or sheltering under stones (Mammola *et al.* 2016) and occasionally in prairies at the edge of alpine screes. According to Tongiorgi (1969), individuals are most active at night, while they shelter under stones during the day. Our observations generally confirm these data; moreover, we also observed individuals basking in full sun at high elevations.

Considering the harsh condition of the habitat, the growing season seems likely limited to 5-6 months per year, corresponding to the snow-free periods of maximum intake of solar energy, which is fundamental for increasing metabolic rate in poikilothermic invertebrates. It seems plausible that the spider overwinters under the snow for 6-7 months (Fig. 3), when conditions at the interface snow-soil remain stable around 0°C and the metabolic rate of the spider possibly decreases (Danks 2006; Knapp & Řeřicha 2020).

In light of the number of instars required to complete the development and to reach adulthood, as seen in large entelegyne spiders (Eason & Whitcomb 1965; Eason 1969; Dolejš *et al.* 2014), and the duration of the growing season (approximately three instars per growing season), it is expected that maturity is reached at least after four seasons. Multi-annual life cycles are common in spiders having a long overwintering period (Pickavance 2001; Hammel 2005; Høye & Forchhammer 2008). It seems likely that, similarly to other Lycosids, males reach adulthood at the 10th instar, and females at 11th or 12th. After mating, males die (generally at the end of summer). Females overwinter once more, and die the following year, presumably at the age of five years. The presence of females with cocoons at the beginning of the growing season, before the appearance of males, suggests that females store sperm in their receptacula during overwintering, and then lay eggs when the temperature increases, as seen on other Lycosids (Eason & Whitcomb 1965; Dolejš *et al.* 2010). The cocoon construction is similar to that reported for other Lycosids (Eason 1964; Engelhardt 1964; Eason & Whitcomb 1965). The ability to produce more than one egg sac seen in laboratory-reared females is widespread in wolf spiders, not only in the temperate zone but also at higher altitudes and latitudes (see for example Buddle 2000; Pickavance 2001; Høye *et al.* 2020; Viel *et al.* 2022). As seen in Mammola *et al.* (2019), average clutch size is positively correlated with the average female size.

The generalist predatory habit of *Vesubia jugorum* is coherent with the general opportunistic habit found in most high alpine spiders, dwelling in habitat with limited resources. The hunting behaviour, with the adoption of the "full leg basket" technique, is common in lycosoid spiders, which hunt without web (see Eggs *et al.* 2015). Feeding behaviour is similar to that of other wolf spiders (Nyffeler & Benz 1988; Nyffeler & Breene 1990): *V. jugorum* was observed masticating the prey organisms with the chelicerae, maximizing food assimilation and thus increasing the total energy extracted from each prey item. The cannibalism as well has been observed in other wolf spiders (Samu *et al.* 1999; Anthony 2003; Buddle *et al.* 2003).

Under laboratory conditions, adult females fed while carrying egg sacs or pulli, differently from other burrowing species of lycosids (e.g. in the genus *Trochosa* C. L. Koch, 1847; see Engelhardt 1964), generally fasting after laying eggs. Together with the presence of a small opening in the silken walls of the retreat (Tongiorgi 1969), this may suggest that females leave their retreats during the egg sac-guarding and pulli-carrying period.

As the result of the samplings carried out during the "Explor'Nature Colmars-les-Alpes 2021" and "Explor'Nature Valdeblore 2022", five new localities have been discovered. The new occurrences in Colmars-les-Alpes extended the known limits of the species geographic distribution towards south-west, in an area predicted as suitable by the species distribution models but never investigated before. Occurrences in Valdeblore were highly expected, being located close to the center of the distribution range, in a highly suitable area, according to the models.

All the new findings here reported validate the distribution limits in projecting the potential current geographic distribution of *Vesubia jugorum*, confirming the importance of these tools to overcome gaps in spatial data in threatened species.

Ecological Niche Modelling presented in Mammola *et al.* (2019) points out a specific relationship between some climatic feature and the probability of presence of *Vesubia jugorum.* In particular, timing, duration and thickness of seasonal snow coverage seems to play a major role in determining the distribution of the species by possibly influencing the duration of its growing season. Accordingly, observational data seems to support that the development of *V. jugorum* occurs during a relatively short snow-free period in summer and early autumn (Mammola *et al.* 2016). During the rest of the year, the individuals most likely survive under stones in the upper layers of the rocky debris, which are insulated by a deep blanket of snow (see, e.g. Zhang 2005). According to the interpretation of the statistical models, habitat quality for *V. jugorum* declines in areas where the mean annual number of days of snow cover during the year is < 40, which is typical for lower elevations. In addition, habitat quality declines where the mean annual number of days of snow coverage is > 100, a condition occurring either above 2800-3000 m within the core of the species distribution or at northern latitudes within the species range.

Climatic evidence inferred from statistical models finds support in our data derived from temperature data-loggers positioned under stones in suitable areas for one year. The fast and high accumulation of snow at the beginning of the cold season, affects the ground climatic regime by insulating it from cold temperatures and variations occurring above ground, generating ideal conditions for the survival of ground arthropods at the snow-ground interface during winter. More specifically, the insulation effect of thick snow cover, has a significant influence on the ground thermal regime, and increase with increasing snow depth due to the thermal resistance of the snowpack (Zhang 2005; Luetschg *et al.* 2008). If, on one hand, during the cold season from November to June, the stable climatic conditions at the snow-ground interface allow protection from the extreme winter temperatures and their variations, on the other hand, the early snowmelt occurring in the area and the consequent rapid temperature increase of the ground temperature lengthen the duration of the snow-free period, thus allowing a longer growing season for the species (Mammola *et al.* 2019).

Best available knowledge and updated information on the ecology and the distribution of this species are fundamental to provide an updated insight on the conservation status of this species. In the conservation context of the endangered species, monitoring is a fundamental tool to detect trends in populations and distribution, and to measure the impacts of threatening processes (Legge *et al.* 2018).

The results of the monitoring baseline phase confirmed the relationship between climatic suitability and femur size suggested by Mammola *et al.* (2019). Specimens with largest femur IV occurred in localities where the predicted habitat quality was highest (Fig. 4), confirming the use of this trait for monitoring purposes. Only at Grande Séolane specimens showed an unexpected great length of femur IV despite the low value of the predicted habitat quality. Interestingly, ongoing molecular analysis have highlighted issues and raised questions concerning the population of Grande Séolane, revealing a lack of shared haplotypes with the neighbouring populations and a genetic pattern which is hardly explainable in the framework of the current and historical population dynamics proposed for *V. jugorum* (a forthcoming paper by Milano *et al.*).

The use of the femur IV in our work rather than the femur I (as done in Mammola *et al.* 2019) does not seem to bias the significance of the relation. In predatory arthropods, specimens with greater body size have greater predatory efficiency and a higher benefit in terms of reproductive success and performance, compared to smaller ones. Therefore, populations having smaller specimens can be considered of higher concern in a conservative perspective. Body size in predatory arthropods determines their ability to thrive and the proportion of resources that they can allocate for reproduction (Jakob *et al.* 1996; Sokolovska *et al.* 2000). A positive relationship between body size and reproductive success has been reported in several spider species (Marshall & Gittleman 1994), including wolf spiders (Anderson 1990; Uetz *et al.* 2002; Ameline *et al.* 2018).

The size of the cocoon is a universal proxy of fitness, as a larger cocoon corresponds generally to a greater number of eggs (Marshall & Gittleman 1994; Bowden *et al.* 2013). However, in our case, we could not recover a significant relationship between cocoon size and habitat suitability, possibly due to low sample size (a similar issue was encountered in Mammola *et al.* [2019]).

Our approach to the monitoring turned out to be a practical and non-invasive tool for the assessment of the species health, and the morphological traits measured during the monitoring programme proved to be reliable proxies for the overall body size and for the reproductive success of the species. The results obtained during this first step of the monitoring (the "zero status"), provided baseline information on the status of the populations, and will be compared with the results of the future monitoring campaign, planned for 2024, to detect potential population decline over time and to inform suitable response measures and coordinate conservation policies.

CONCLUDING REMARKS AND PERSPECTIVES

Despite the research carried out in these years and the abovementioned advances in the knowledge of this species, several aspects still remain unknown, especially the ones inherent in the life cycle of this species, from post-embryo stages to adults. As a consequence, rather than based on direct measures, the life-span and the number of instars of the specimens have been estimated on the basis of the observed duration of the instars and of the information available in literature for other large entelegyne spiders. Laboratory rearing aiming to observe the growing pattern in captivity would be welcome to confirm our – inferred, but reliable – hypothesis.

In addition, there is uncertainty on the overwintering behaviour and on the seasonal movements of the specimens. According to literature data and field observations, no specimens have been found from the beginning of October (see Maurer & Thaler 1988) onwards, both in rocky areas and in other adjacent habitats.

During our laboratory experiments, we were not able to trigger any winter dormancy in laboratory conditions: specimens collected in late summer and placed in climatic chamber at low constant temperatures (0-1°C) did not enter dormancy, but remained active for 40-60 days and died afterwards, leaving open the question about overwintering behaviour in this species.

Another key aspect that needs further investigations is the courtship behaviour. Lycosids are known for their complex pre-copulatory behaviour, in which visual, vibratory and chemical signals are involved in sexual communication. Despite numerous attempts, the laboratory observations did not provide significant results. Males have been observed approaching the females and performing drumming against the substrate using the palps, but with no significant reactions elicited in the females. It seems likely that laboratory conditions where the mating was attempted, were not able to reproduce the basic conditions to ensure the mating.

Future studies are thus required to better clarify several aspects of the ecology and life history of this species, and additional samplings are needed to gain a further better understanding of the species distribution. In this regard, given that part of this species distribution falls within protected areas, training initiatives designed to provide to the staff of the parks and to volunteers a basic knowledge to detect and identify the species, could represent a valid contribution in collecting species occurrence information, and could help to attract more conservation attention to this species – one of the biggest wolf spiders in Europe – as seen for other charismatic species occurring in the Alps.

In light of its ecology, *Vesubia jugorum* has been recognized as a suitable model for the study of the effect of the climatic changes on the alpine biome (Isaia *et al.* 2016; Mammola *et al.* 2019). Accordingly, enhancing awareness on the threats affecting this very emblematic species, may contribute to its conservation and may promote the general perception of the effects of climate change on the alpine ecosystems.

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Paper V

Associations between habitat quality, body size and reproductive fitness in the alpine endemic spider *Vesubia jugorum*

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Photo credit: Emanuele Biggi

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Abstract

Aim: In theory, the highest-quality habitat across a species' range should support individuals with the highest fitness, making it possible to evaluate the outputs of species distribution models (SDMs) by exploring the relationship between habitat quality and functional traits related to species' fitness. However, this relationship has been tested almost exclusively in plants. We investigated the degree to which morphological and reproductive traits of an alpine spider varied along a gradient of habitat quality projected via SDMs.

Location: South-western Alps (France and Italy).

Time period: 2007–2018.

Major taxa studied: *Vesubia jugorum* (Arachnida: Araneae: Lycosidae).

Methods: We used climatic, topographical and geomorphological variables at a resolution of 250 m to model habitat quality for *V. jugorum*, with multiple algorithms (generalized additive models, boosted regression trees and maximum entropy models). We collected spiders in the field and measured their body size and egg-case size (a functional trait related to reproductive success). We tested the relationship between functional traits and habitat quality with linear mixed models.

Results: All SDM algorithms we tested fit the data well, with similar explanatory ability. Models revealed a positive relationship between the probability of presence and cumulative precipitation and percentage of rock. An additional important variable in the SDMs was duration of snow coverage, with optimal projected habitat quality between 40 and 100 days/year with snow. Modelled habitat quality was positively associated with maximum body and egg-case size.

Main conclusions: Our work provides evidence of a positive association between projected habitat quality and traits of a terrestrial invertebrate. A model that fits the data well potentially can be used to predict variations in species' traits, thus offering an experimental test of SDM projections with field-collected data. We encourage SDM users to incorporate data on functional traits into their modelling fitting exercises.

Keywords: alpine fauna, Alps, ecological niche modelling, functional biogeography, functional traits, model accuracy, model evaluation, mountaintop species, species distribution model, spiders

1. Introduction

Species distribution models (SDMs) are a family of statistical methods that investigate the relationship between occurrence data and environmental variables, with the general goal of projecting a spatially explicit probability surface that represents the potential distribution or the ecological niche of a given species (Peterson et al., 2011). Over the last three decades, development of correlative SDMs has been rapid (Lobo, Jiménez-Valverde, & Hortal, 2010; Zimmermann, Edwards, Graham, Pearman, & Svenning, 2010). These models make it possible to transfer current distribution models in space and time (Yates et al., 2018), with applications to global change biology (Dormann, 2007; Hijmans & Graham, 2006; Pearson & Dawson, 2003), invasion biology (Peterson, 2003; Peterson & Vieglais, 2001) and conservation studies (Guisan et al., 2013).

Whilst the usefulness of SDMs in ecology and biogeography has been widely acknowledged (Peterson et al., 2011), some have argued that the potential of these statistical tools still is not fully expressed (e.g., Araujo & Guisan, 2006; Benito Garzón, Robson, & Hampe, 2019; Hällfors et al., 2016). More than ten years ago, Guisan and Thuiller (2005) foresaw that SDMs may offer "more than simple habitat models", for instance by incorporating or addressing biotic interactions, migration processes, dispersal limitations and population dynamics (Araujo & Luoto, 2007; Boulangeat, Gravel, & Thuiller, 2012; Franklin, 2010; Thuiller, Albert, Dubuis, Randin, & Guisan, 2009; Violle, Reich, Pacala, Enquist, & Kattge, 2014; Zimmermann et al., 2010). An additional possibility is to investigate the relationship between projected habitat quality for a given species and variation in the species' functional traits. In other words, given the assumption that habitat quality is positively correlated with fitness (Nagaraju et al., 2013; Thuiller et al., 2009; Wittmann, Barnes, Jerde, Jones, & Lodge, 2016), SDMs potentially can be validated by checking whether the areas projected to have the greatest habitat quality are occupied by individuals or populations with higher than average fitness. For instance, Wittmann et al. (2016) found a positive correlation (r = 0.5) between the growth rate of a wild grass carp [*Ctenopharyngodon idella* (Valenciennes, 1844)] and habitat quality for the species as projected by a maximum entropy model.

The few studies that have explicitly tested the relation between habitat quality and species traits mainly focused on plants (Benito Garzón et al., 2019; Elmendorf & Moore, 2008; Nagaraju et al., 2013; Pollock, Morris, & Vesk, 2012; Smith, Alsdurf, Knapp, Baer, & Johnson, 2017; Thompson & McCarthy, 2008; Thuiller, Lavorel, Midgley, Lavergne, & Rebelo, 2004; Thuiller et al., 2009; Wright, Davies, Lau, McCall, & McKay, 2006) and occasionally vertebrates (fishes: Larson, Olden, & Usio, 2010; Michel, Chien, Beachum, Bennett, & Knouft, 2017; Wittmann et al., 2016; salamanders: Lunghi et al., 2018). Results of these studies were heterogeneous: a positive relationship between habitat quality and species fitness – measured with different proxies – has not been found in all species (Elmendorf & Moore, 2008; Larson et al., 2010; Thuiller et al., 2009) or ecotypes tested (Wittmann et al., 2016; Wright et al., 2006).

Here, we provide what we believe to be the first such analysis of an arthropod. Under the assumption that the functional traits of a specialist are more effective for thriving in a given set of environmental conditions (Devictor et al., 2010), and that specialists are more sensitive to climatic variations than generalists (Clavel, Julliard, & Devictor, 2011), we focused on a species restricted to mountaintops. First, we used SDMs to investigate species–environment relationships and project habitat quality across the species' range. Second, we investigated the degree to which functional traits measured in individuals collected across the species' range varied along the gradient of projected habitat quality. We hypothesized that there is a positive, significant relationship between habitat quality predicted by SDMs and the morphological and reproductive traits of the species.

2. Material and methods

2.1. Species and study area

We focused on the alpine endemic spider *Vesubia jugorum* (Simon, 1881), one of the largest wolf spiders (Lycosidae) in Europe. *V. jugorum* exclusively occupies rocky areas such as boulder fields and scree at high elevations (subnival and nival zones, from 2,000 to more than 3,000 m; Mammola, Milano, Cardoso, & Isaia, 2016; Tongiorgi, 1969; see Supporting Information Appendix S1). This species, classified as Endangered by the International Union for Conservation of Nature (Isaia & Mammola, 2018), has a small distributional range, encompassing the Ligurian and Maritime Alps, the southern part of the Cottian Alps, and the Provence Alps. Most of the species' range falls within the boundaries of national parks, sites of community importance, and special protection areas, including Parco Naturale Alpi Marittime and Parco Naturale del Marguareis in Italy and Parc National du Mercantour in France (Mammola et al., 2016). In these areas, elevation ranges from *c.* 300 to 3,297 m (Mount Argentera, the highest peak). The climate is Mediterranean in the south and more continental in the north (climatic details in Patsiou, Conti, Zimmermann, Theodoridis, & Randin, 2014).

2.2. Species distribution modelling

2.2.1. Occurrence data

We assembled data on 101 presences of *V. jugorum* (Figure 1) on the basis of recent field surveys (2010–2018) and data from the literature (reviewed in Mammola et al., 2016). The few records published before 2007 were included in the analyses only if our recent surveys detected the species in the same locations. Full details about assembly of the data and field methods are in Supporting Information Appendix S2. To minimize spatial sampling heterogeneity, we aggregated data at the resolution of the environmental predictors (250 m) to avoid inflation of the number of presences. It can be difficult to obtain large sample sizes of endangered species in complex terrain. Although we fully explored the known distributional range of the species, we acknowledge that the sample size is small, and that the ultimate strength of the inference may be affected as a result.

2.2.2. Environmental predictors

We used climatic, topographical and geomorphological variables at a resolution of 250 m as predictors (Table 1). Consistent with recent literature (Brandt et al., 2017; Fourcade, Besnard, & Secondi, 2018; Saupe et al., 2012), we selected the initial set of predictors on the basis of our knowledge of the species' biology (i.e., variables likely to be associated with habitat quality for *V. jugorum*), and only then culled the variables with statistical inference.

To represent the climate of the Maritime Alps in which the species occurs (Patsiou et al., 2014), we selected three climatic variables reflecting continentality: mean annual temperature, annual temperature range and cumulative annual precipitation. Temperature variables were produced by statistical downscaling data from the ALADIN-Climat general circulation model provided by the French National Meteorological Research Center (1976–2005; Herrmann, Somot, Calmanti, Dubois, & Sevault, 2011). Full details of the downscaling procedure are in Supporting Information Appendix S3.

Considering the association of snow cover with the distribution of high-elevation species (Niittynen & Luoto, 2018), and the expected influence of snow cover duration on the development of *V. jugorum* (Mammola et al., 2016), we generated a variable representing snow coverage. We downloaded the MODIS Terra "MOD10A2.006" time series from the National Snow & Ice Data Center, for January 2002 through December 2017. These data have a resolution of 500 m (Masuoka, Fleig, Wolfe, & Patt, 1998). We extracted the "eight days snow cover" data in raw format. For each eight days (synthesis), we summed the number of days with snow (0 to 8). Then, we calculated the mean annual days/year of snow over the 16-year period.

Given that *V. jugorum* occurs almost exclusively in rocky lands (Mammola et al., 2016; Tongiorgi, 1969), we generated a raster representing the distribution of this land cover type. We downloaded Landsat Enhanced Thematic Mapped Plus (ETM+) (27 July 2000) and Operational Land Imager (OLI) (27 August 2014) multispectral rasters, at a resolution of 30 m, from the United States Geological Survey (USGS) interface. We identified rocky surfaces by applying a normalized difference vegetation index (NDVI) threshold (< 0) and selecting pixels with negative values of NDVI on both dates as rocky (Fretwell, Convey, Fleming, Peat, & Hughes, 2011).

Considering that *V. jugorum* inhabits topographically complex areas (Mammola et al., 2016), we estimated roughness and slope exposure (aspect). Topographical variables distinct from elevation may be useful in representing non-climatic aspects of a species' niche (Title & Bemmels, 2017). We derived the variables from the Shuttle Radar Topography Mission (SRTM) digital elevation model raster (resolution of 90 m), available from the USGS (Reuter, Nelson, & Jarvis, 2007). We estimated roughness by calculating, for each pixel, the difference between the highest and lowest elevation in a square of 7 × 7 pixels. For aspect, we characterized a north–south exposure index.

To avoid collinearity among predictors, we calculated pairwise Pearson correlations and applied a standard $r > |0.70|$ threshold for removal of variables (Dormann et al., 2013).

2.2.3. Calibration area

We calibrated and projected SDMs within the spatial extent hypothesized to fall within the long-term dispersal and colonization potential for the species over its evolutionary history (Barve et al., 2011). Because we had no data on gene flow or dispersal, we assumed a low dispersal potential by masking the study area to 6.0 to 8.0° latitude and 43.5 to 44.5° longitude. Given that the species occupies high elevations, we further excluded areas below 1,500 m (Figure 1).

2.2.4. Modelling methods

There exists a large suite of algorithms for modelling the distribution of species (Peterson et al., 2011). Qiao, Soberón, and Peterson (2015) suggested the use of evaluation metrics to assess the performance of potentially competing SDM algorithms, and selecting the best-performing algorithm given the occurrence data. Accordingly, we assessed the relative performance of three main categories of SDM algorithms: regression [generalized additive models (GAMs)], regression trees [generalized boosted regression models (GBMs)] and machine learning [maximum entropy (MaxEnt)].

We fitted GAM with the *gam* R function (Hastie, 2017). We created 1,000 pseudoabsence points, which we randomly extracted from across the study area. We fitted an initial model that included all non-collinear environmental variables, estimating the optimum amount of smoothing for each variable by generalized cross-validation. When the effect of a variable was linear [estimated degrees of freedom (edf) ≈ 1], we removed the smoothed term and introduced the parametric term. We reduced the full model by sequentially removing terms on the basis of the Akaike's information criterion (AIC), until a minimum model with only significant terms remained.

We considered models with ΔAICs lower than 2 as equivalent (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

We constructed GBMs with the *gbm* R function (Ridgeway, 2017) and by following the general protocol by Elith, Leathwick, and Hastie (2008). We used the ‘2°far’ method to extract a number of absence points equal to the number of presence points (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). We specified a Gaussian distribution, and used the *gbm.perf* R function (Ridgeway, 2017) to estimate the optimal number of trees for cross-validation. We evaluated each variable's contribution to the final model on the basis of relative influence.

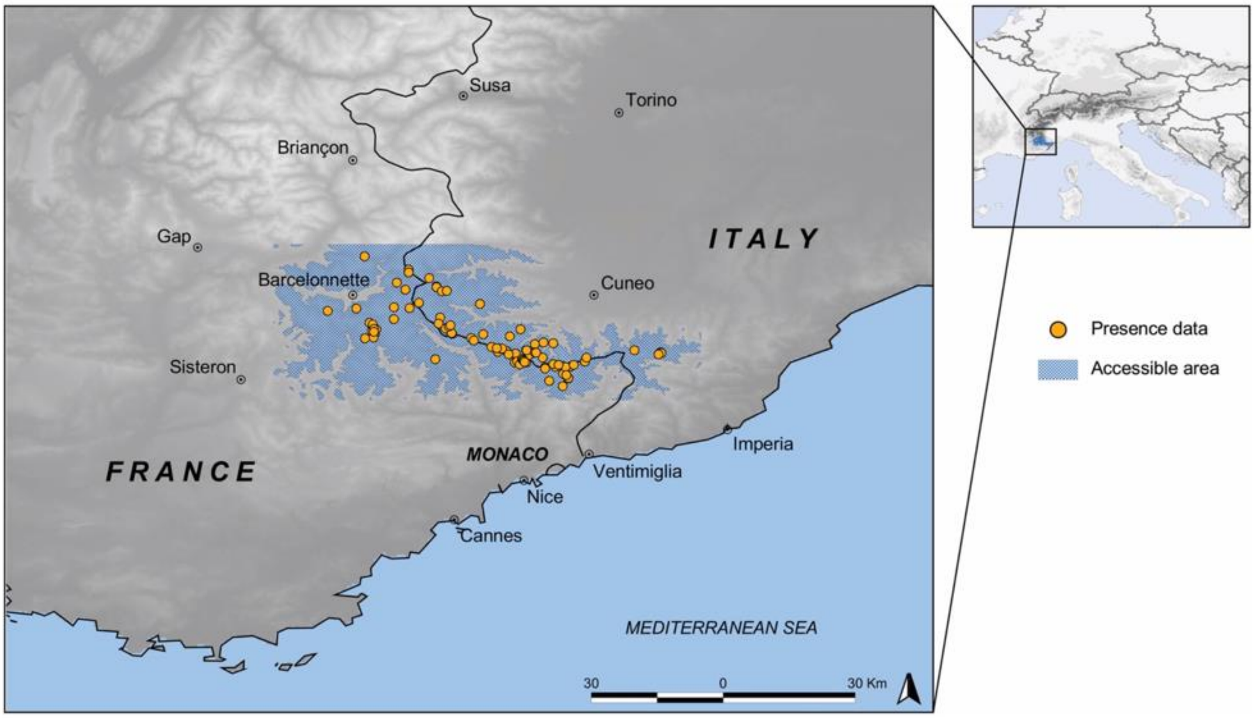

Fig. 1. Presences of *Vesubia jugorum*

We constructed MaxEnt models with the *maxent* function in the "dismo" R package (Hijmans, Phillips, Leathwick, & Elith, 2014). To calibrate the model, we used 1,000 background points (Phillips & Dudik, 2008). Given that our dataset included < 100 occurrences, we specified feature classes and regularization multiplier manually rather than using default settings (Morales, Fernández, & Baca-González, 2017). We estimated the most suitable configuration of these two parameters via the *ENMevaluate* function in the "ENMeval" R package (Muscarella et al., 2014). We evaluated the variables' contribution to the final model on the basis of permutation importance.

For each algorithm, we ran 50 bootstrap replicates, retaining a random partition of 20% of the points from each run. We estimated the predictive ability of the three models with the Boyce index in the "ecospat" R package (Broennimann, Di Cola, & Guisan, 2018). This is considered to be the most appropriate metric when there are few reliable absence records (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006). We generated a final model with the complete data and the best-performing models. We projected the model into the study area to represent the current distribution of *V. jugorum*.

2.3. Analysis of functional traits

2.3.1. General considerations

We investigated the degree to which functional traits of individuals of *V. jugorum* across their distributional range varied along the gradient of habitat quality projected by SDMs. We considered a functional trait as a morphological feature, measured at the individual level, which reflects individual performance (Violle et al., 2007). The body size of a predatory arthropod determines its ability to thrive and the proportion of resources that it can allocate to reproduction. Therefore, body size is a proxy measure of fitness (Jakob, Marshall, & Uetz, 1996; Sokolovska, Rowe, & Johansson, 2000). A direct relationship between body size and reproductive success has been demonstrated in a number of spider species (Marshall & Gittleman, 1994), including wolf spiders (Ameline et al., 2018; Anderson, 1990; Uetz, Papke, & Kilinc, 2002). We also measured egg-case (cocoon) size, another indirect measure of fitness (Bowden, Høye, & Buddle, 2013; Marshall & Gittleman, 1994).

2.3.2. Data acquisition

We obtained specimens for morphological analysis from 40 locations across the species' range. Given that the size of juveniles ($n = 29$) varies by an order of magnitude, and that we captured few males ($n = 9$), we included only adult females ($n = 102$) in the analysis.

We measured five morphological traits related to body size: femur, tibia and metatarsus length, and carapace length and width (details in Supporting Information Appendix S4). We used both leg and carapace measures because they are well correlated with the overall body size of spiders (Elgar, Ghaffar, & Read, 1990; Hagstrum, 1971) and their sizes in adults are fixed. We made measurements with a Leica M80 stereoscopic microscope (up to 60 × magnification; Leica Microsystems, Switzerland). To standardize data acquisition, we derived measurements from digital pictures taken with a Leica EC3 digital camera and calculated with Leica LAS EZ 3.0 software. Again, we acknowledge that sample sizes were limited. However, measurement of leg segments and other body parts of *V. jugorum* in the field, especially when multiple measurements are needed, is challenging given the complex terrain and high mobility of the spider. Therefore, we decided to take measurements in the laboratory, but limited the number of individuals we sampled.

The cocoon of wolf spiders is attached to the spinnerets at the rear of the spiders' bodies. We observed and captured 17 females that were carrying their cocoons. We estimated cocoon diameter in the field with a digital calliper and then released females. We classified cocoon size in five equal intervals of 1 mm, ranging from 8.5 to 13.5 mm.

2.3.3. Relationship between habitat quality and morphological traits

We used the coordinates at which each measured specimen was captured to extract the projected value of habitat quality from the SDM. We assessed multicollinearity among morphological traits with a pairwise Pearson r correlation, setting the threshold for collinearity at $r > |0.70|$ (Dormann et al., 2013). We tested the relationship between morphological traits and projected habitat quality with linear mixed models (LMMs) that we fitted in the "nlme" R package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). This mixed method allowed us to address the fact that because we measured multiple individuals from the same populations, we violated the models' assumption of spatial independence. We included the sampling location as a random factor. We expressed the variance explained by the fixed terms in the regression models as marginal *R*2. We validated each model by constructing standard validation plots on the basis of the model residuals and fitted values (Zuur et al., 2009), and investigated possible nonlinearities in the residuals with the *gam* R command (Hastie, 2017).

To visualize the spatial pattern of variation in functional traits, we tested the linear relationship between the traits and the longitude and latitude of the occurrences. We used the same model and mixed structure explained above. In both models, we introduced quadratic terms (longitude2, latitude2) to capture nonlinear parabolic patterns in the residuals that we detected during model validation.

Given the small sample size of cocoons, it was not possible to fit a stable LMM to estimate the relationship between cocoon size and projected habitat quality. Instead, we used a Pearson's *r* correlation to assess this relationship, with the null hypothesis of no correlation between cocoon size and habitat quality (*r* = 0). We report both 95% confidence intervals of the coefficient of correlation and a *p*-value based on a *t* test.

Table 1. Initial set of variables used to construct the species distribution models, and their relative strength of association with presence of the species. Estimated parameters and variable contributions are given only for variables that were not collinear (Table 2). For the generalized additive model (GAM), estimated β- and *p*-values are given for the linear terms (n.s. = not statistically significant; eliminated during model selection), whereas estimated degrees of freedom (edf) and *p*-values are given for the smoothed term (snow). For the generalized boosted regression model (GBM) and the maximum entropy (MaxEnt) model, we report the variables' relative influence and permutation importance.

Variable	**Description**	**GAM**	**GBM**	**MaxEnt**
Snow	Mean annual number of days with snow coverage	edf = 3.86, χ2 = 12.90, p < 0.001	18.7	40.7
Rock	Percentage of rocky lands in the raster pixel	β ± *SE* = 0.01 ± 0.01, *p* < 0.001	49.6	23.8
Precipitation	Cumulative annual precipitation (mm)	β±SE=2.70±0.61, p < 0.001	21.3	34.9
T_range	Temperature annual range (°C)	n.s.	6.5	0.4
T_mean	Mean annual temperature (°C)	–	–	–
Elevation	Elevation in metres	n.s.	–	–
Roughness	Difference between the highest and lowest elevation	n.s.	1.7	0.2
Aspect	Slope exposure (°)	n.s.	2.5	0.0

Table 2. Pairwise Pearson *r* correlations between environmental predictors. Non-collinear variables included in the model are in boldface. See Table 1 for explanations of variable names

	Snow	Rock	Precipitation	T_Range	T_Mean	Elevation	Roughness	Aspect
Snow	–							
Rock	0.6	–						
Precipitation	–0.1	–0.1	–					
T_Range	–0.3	–0.1	–0.4	–				
T_Mean	–0.7	–0.6	–0.3	–0.1	–			
Elevation	0.7	0.6	–0.2	–0.1	–1.0	–		
Roughness	–0.1	0.3	–0.1	0.5	–0.2	0.1	–	
Aspect	–0.1	0.1	0.1	0.1	0.1	0.1	0.1	–

3. Results

3.1. Species distribution model and projected distribution

After removing duplicate occurrences and invalid records (see Supporting Information Appendix S2), we used 89 occurrences to generate the SDMs. We selected six non-collinear variables for constructing the models: snow coverage, percentage of rock, cumulative precipitation, annual temperature range, roughness and aspect (Table 2). The outputs of the three SDM algorithms were similar, although there were some differences between the most important variables identified by MaxEnt and by GBM algorithms (Table 1). All models indicated a positive relationship between the probability of presence and cumulative precipitation. The probability of presence also increased as the percentage of rock and snow cover increased. The probability of presence increased in areas with > 40 mean annual number of days with snow, and steeply decreased at 100 days (Supporting Information Appendix S5). Temperature and topographical variables explained negligible variations in the distribution of *V. jugorum* (all MaxEnt permutation importance < 1; all GBM relative influence < 5; no significant terms in any GAM).

The Boyce index indicated that all SDM algorithms we tested fit the data well, with similar explanatory ability (all Boyce indexes > 0.80; median of the 50 bootstraps). Therefore, as recommended in the literature (Araujo & New, 2007; Guisan & Thuiller, 2005), we used an ensemble of the three model projections – the median value weighted by the index value – to represent the species distribution (Figure 2a). Overall, the ensemble model's projections of habitat were consistent with the known distribution of *V. jugorum* (Mammola et al., 2016), with the highest-quality areas corresponding to the Mercantour-Argentera massif at the border between Italy and France. This area was projected to be a largely continuous area of habitat quality, which may facilitate connectivity among local populations. Two additional areas of habitat, more fragmented than the latter, were projected at the eastern and north-western corners of the species' known range (Ligurian and Cottian Alps, respectively).

3.2. Relationship between habitat quality and morphological traits

All of the morphological traits of female *V. jugorum* that we measured were variable (Supporting Information Appendix S4). There was a high degree of correlation among all leg segments (all Pearson $r > 0.90$) and between leg and carapace length and width (all Pearson $r > 0.70$; Supporting Information Appendix S4). Therefore, we arbitrarily selected femur length as a representative measure of body size (Figure 2a). We found a positive, significant relationship between femur length and habitat quality as projected by the model (estimated $\beta \pm SD = 1.19 \pm 0.24$; $p < 0.001$; $R2 = 0.31$), with larger individuals in high-quality areas (Figure 2b). Because femur length and carapace size were positively correlated, we obtained the same positive linear trend by constructing a LMM with carapace width as the dependent variable (estimated $\beta \pm SD = 0.73 \pm 0.20$, $p < 0.001$).

Cocoon size was also positively correlated with habitat quality ($r = 0.62$, 95% Confidence Interval = 0.20–0.85; $t = 3.07$, $p < 0.01$; $n = 17$; Figure 2c).

Femur length increased significantly as longitude increased (estimated β ± *SD* = 23.55 ± 8.05; $p < 0.01$) and decreased as a quadratic function of longitude (estimated β ± *SD* = –1.64 ± 0.56; $p < 0.01$); *V. jugorum* with the longest femurs were collected at intermediate longitudes, between 7 and 7.5° (*R*2 = 0.15; Figure 3a). Femur length also increased significantly as latitude increased (estimated β ± *SD* = 741.98 ± 317.04; $p = 0.02$) and decreased as a quadratic function of latitude (estimated β ± *SD* = –8.39 ± 3.58; $p = 0.02$); individuals with the longest femurs were collected at relatively southern latitudes, between 44.1 and 44.3° (*R*2 = 0.22; Figure 3b).

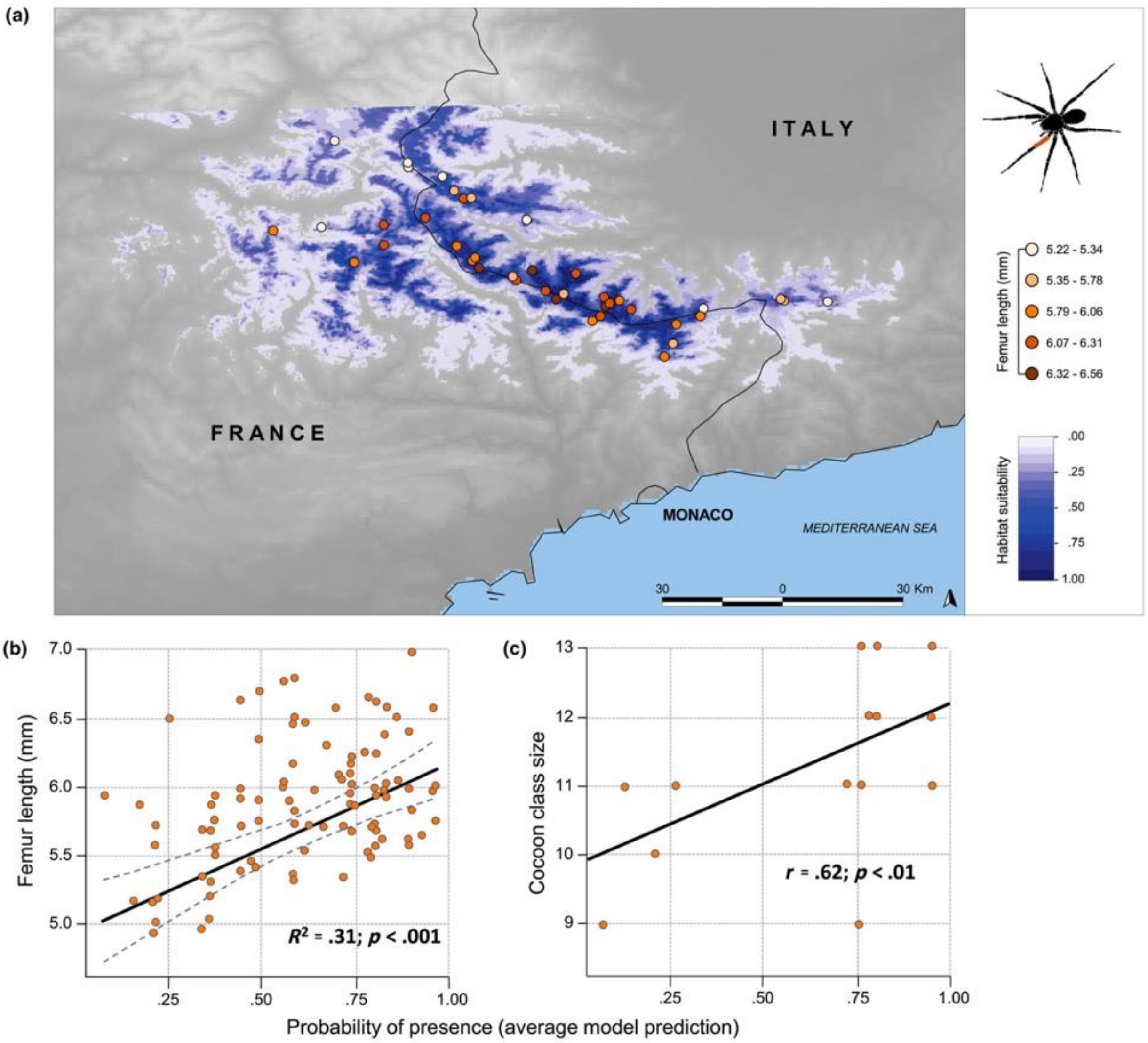

Fig. 2. Species distribution and relationship between projected habitat quality and functional traits. (a) Projected habitat quality for *Vesubia jugorum*. (b) Predicted linear relationship (solid line) and 95% confidence interval (dotted lines) between habitat quality and femur length, derived from the linear mixed model. Only fixed effects are shown. (c) Relationship between cocoon size and projected habitat quality. The black line represents the positive linear trend according to the Pearson correlation. Due to the proximity of values, some points are superimposed

4. Discussion

4.1. Interpretation of the SDMs

Overall, SDM fits to the data were good, suggesting that the distribution of *V. jugorum* can be adequately predicted on the basis of land-cover and climatic variables. Topographical variables explained little variation in the distribution of the species (Table 1). The projected distribution of habitat was similar to the projected distribution of relictual populations of other species in the same area, such as the plant *Saxifraga florulenta* Moretti (Saxifragaceae) (Patsiou et al., 2014). Areas projected to have high habitat quality for *V. jugorum* are characterized by high local precipitation. As expected when modelling the habitat of species with restricted distributions (e.g., Sardà-Palomera & Vieites, 2011; Warren et al., 2001; Williams et al., 2009), landcover types – here, the percentage of rocky lands – further contributed to the explanatory ability of the SDMs. In the study area, the percentage of rocky lands is positively correlated with elevation: rocky areas occur at higher elevations, whereas grassland and scrubland at lower elevations limit the distribution of the species. The high level of direct solar radiation in rocky habitats may affect diurnal thermoregulation. Arthropods, including *V. jugorum*, that occur in cold mountain environments with high levels of solar radiation often are dark in colour. Melanism helps to raise body temperature more rapidly, while protecting against ultraviolet radiation (Mani, 2013).

The third important variable in the SDMs was duration of snow coverage (Supporting Information Appendix S5). Development of *V. jugorum* occurs during a relatively short snow-free period in summer and early autumn (Mammola et al., 2016). During the rest of the year, the individuals most likely survive in the upper layers of the rocky debris, which are insulated by a deep blanket of snow (see, e.g., Zhang, 2005). A substantial decline in the projected habitat quality occurred where the mean annual number of days of snow cover was < 40, which is typical for lower elevations. A decline in projected habitat quality also occurred where the mean annual number of days of snow coverage was > 100. Such conditions occur either above 2,800–3,000 m within the core of the species' distribution or at northern latitudes within the study area. Late summer snowmelt may decrease the duration of the developmental season.

4.2. Relationship between functional traits and habitat quality

As far as we are aware, our work provides the first evidence of a positive relationship between projected habitat quality and functional traits of a terrestrial invertebrate. Body and cocoon size of *V. jugorum* were positively related with habitat quality as approximated via an ensemble of three SDM projections. The largest individuals, and females with the largest cocoons, occurred in the core of the species' distribution (Pulliam, 2000), where the amount of predicted high-quality habitat was greatest. This area, between 7.0–7.5° longitude and 44.1–44.3° latitude, roughly corresponds to the emergence of hercynian massif of Argentera, in the palaeo-European basement of the external domain (see fig. 2 in Corsini, Ruffet, & Caby, 2004). This area encompasses the highest peaks and the oldest geological substrates in the south-western Alps, reflecting the complex biogeographical history and refugia of this mountain range during glaciations (e.g., Patsiou et al., 2014).

In these areas (habitat quality > 0.8), femur length roughly ranged from 5.75 to 7 mm. Conversely, in low quality marginal areas (habitat quality < 0.25), from 4.9 to 5.9 mm. Greater body size may imply a greater predatory efficiency and higher performance, increasing the fitness of individuals living in high quality areas. However, despite the significance of the relationship, the sample size was relatively higher in areas where projected habitat quality was greater (Figure 2a), which may affect the ultimate strength of our inference.

Strong relationships between body size and elevational or latitudinal climate gradients are common in ectothermic invertebrates (Atkinson, 1994; Mousseau, 1997), including spiders (Ameline et al., 2018; Entling, Schmidt-Entling, Bacher, Brandl, & Nentwig, 2010). Our results are consistent with the observed general inverse relationship between body size of spiders and habitat quality in marginal areas (Joqué, 1981). In adult female spiders, carapace size is also correlated positively with the dimensions of the egg clutch (Marshall & Gittleman, 1994). Therefore, body size is an indirect measure of the expected number of offspring. This relationship may indicate an increase in reproductive outputs as habitat quality increases. Although our results were based on a limited number of cocoons (*n* = 17), they were consistent with the latter hypothesis (Figure 2c).

Given that *V. jugorum* is endangered (Isaia & Mammola, 2018), measuring variation in its morphological traits may be a practical, non-invasive means of assessing population health through time and as climate changes.

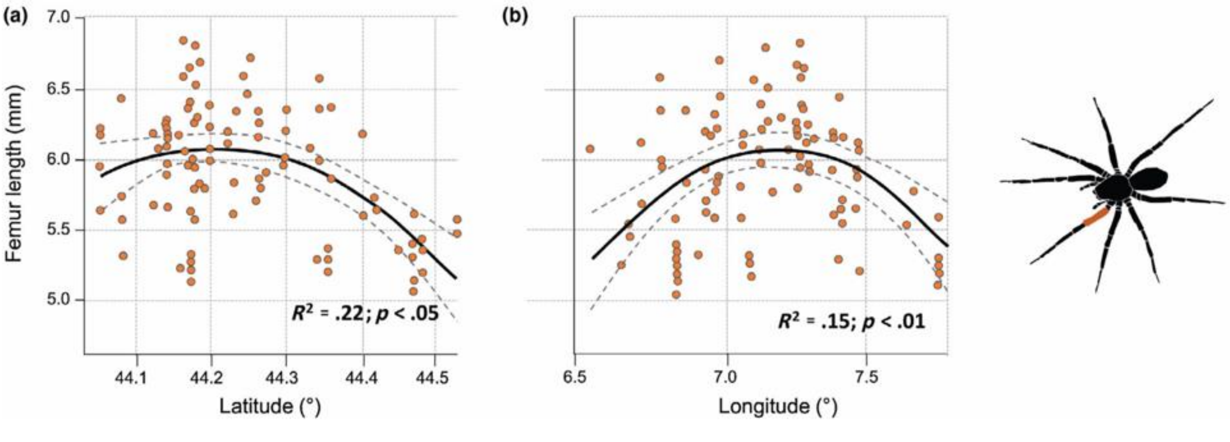

Fig. 3. Predicted variation in femur length. Predicted relationship (solid line) and 95% confidence intervals (dotted lines) between femur length and latitude (a) and longitude (b), derived from the linear mixed models. Only fixed effects are shown. Due to the proximity of values, some points are superimposed

4.3. Biological realism of SDMs and evaluation of model performance

Our results contribute to the debate about the biological realism of SDM projections and the possibility of evaluating model accuracy and fit with field data. Although the projection of an SDM may be satisfactory, the link between model projections and biological processes often is difficult to test (Guisan & Thuiller, 2005). SDMs are usually constructed with distribution data from online repositories (e.g., the Global Biodiversity Information Facility) and a standard set of variables (e.g., the BIOCLIM data; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Fick & Hijmans, 2017), and are rarely validated with field-collected data. Our study suggests that it is possible to correlate SDM projections with functional traits that serve as proxies for fitness.

To the extent that a model that fits the data well potentially can be used to predict variations in species traits, this approach offers an experimental verification of SDM projections grounded in field-collected data. This is relevant because the ability of conventional statistical metrics to evaluate the predictive ability of SDMs often has been questioned (e.g., Bahn & McGill, 2013; Fourcade et al., 2018; Wenger & Olden, 2012), highlighting a general paucity of objective criteria for discriminating among competing SDMs. Although we acknowledge that data on functional traits across a species' distribution are often rare, especially for widespread species, and that such analyses are time-consuming, we strongly encourage SDM users to incorporate functional data – either morphological, physiological or genetic – into their modelling fitting exercises.

Integration of correlative analyses of species distributions and functional traits has been advocated (Benito Garzón et al., 2019; Michel et al., 2017; Thuiller et al., 2009; Wittmann et al., 2016) to bridge biogeography and functional ecology (Violle et al., 2014). Nevertheless, there have been few attempts to relate SDM predictions and functional traits, and these focused on a limited number of plant and vertebrate taxa. Integrating biogeography and functional ecology likely would benefit both disciplines, increasing their applicability in ecological research and providing a way to assess the accuracy of our models.

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Conflict of interest

None declared.

Author contribution

FM, MI and SM conducted fieldwork. FM performed laboratory activities. JA and MV assembled remote sensing data and performed statistical downscaling. SM planned the statistical approach, performed the analysis and wrote the first draft of the manuscript. MI suggested the line of enquiry and supervised the work. All authors contributed significantly to the writing of the manuscript by means of comments and additions to the text.

Data accessibility

Data supporting this study – occurrences of *Vesubia jugorum* and measures of morphological traits – are available in the Dryad Digital Repository (Mammola, Milano, Vignal, Andrieu, & Isaia, 2019).

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Paper VI

Understanding past and future response to climate change of the IUCN endangered spider *Vesubia jugorum* (Araneae, Lycosidae).

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Photo credit: Emanuele Biggi

In preparation

Abstract

Pleistocene climatic fluctuations are considered as an important factor shaping distributional patterns and genetic structures of endemic species in the Southwestern Alps. Understanding how cold-adapted species responded to past climatic oscillations provides useful insights on the potential future effects of climate change on alpine ecosystems. *Vesubia jugorum* is an endemic spider occurring in the high-altitude rocky areas of the Southwestern Alps, assessed as Endangered by the IUCN Red List due to its restricted geographic range, its sensitivity to global warming and its continuing decline. Here, we combined species distribution modelling and phylogeographic inferences to investigate the evolutionary history and the present distribution pattern of *V. jugorum*, and to predict bioclimatic suitability both in the past (Last Glacial Maximum, LGM) and under future (2021–2040) climate scenarios. The present-day suitable area was mostly coincident with the known geographic distribution, and mainly centred in the Maritime Alps. The projection of the potential distribution of *V. jugorum* into past climatic conditions showed a distribution range smaller compared to the present one, and mostly restricted to the southern part of the Maritime and Ligurian Alps, which was devoid from glaciers. The analyses of the mitochondrial DNA sequences showed high level of genetic differentiation of the populations, particularly relevant in the Maritime Alps, providing evidence that this area could host the most ancient and isolated populations of *V. jugorum*, and could have acted as a refugium for the species during Pleistocene glacial-interglacial phases. Future forecasts showed significant shifts in the bioclimatic range towards higher altitude and latitudes, with a general decrease in the current suitability particularly remarkable in the central and south-eastern parts of the distribution range. Our results suggested that Maritime Alps are important in terms of long-term persistence of the species, and therefore represent valuable areas for the conservation of *V. jugorum*.

Keywords: Alpine spiders, Climate change, mitochondrial DNA, Pleistocene glaciations, phylogeography, Shared Socioeconomic Pathways (SSPs), species distribution model, *Vesubia jugorum*.

1. Introduction

Climate changes strongly influence the distribution and the evolution of species in space and time. Quaternary glaciations, for example, induced multiple episodes of expansion and contraction of the species' ranges in the Alps (Hewitt, 2004), shaping their current distributional patterns and genetic structures and generating specific areas of endemism (Bennett, 1990; Comes & Kadereit, 1998; Hewitt, 2004). Similarly, future warming scenarios are expected to influence species distribution range in a great number of alpine species (Walther et al., 2002). High-mountain habitats are expected to be particularly vulnerable to temperature variations, with warming rates approximately doubling the global average (Böhm et al., 2001). The rapid increase in temperature, and the consequent change in climatic suitability, will prompt latitudinal and altitudinal range shifts in species distributions, resulting in a reduction of range size for mountaintop and dispersal-limited species (Parmesan, 1996; Root et al., 2003).

The "Expansion-Contraction" model has been proposed to describe the responses of organisms to Pleistocene climate change (Hewitt, 1996, 1999; Taberlet et al., 1998), and proved to be useful for predicting the impact of future climate change on species (Gates, 1993). According to this model, small populations of cold-adapted species survived in southern glacial refugia during cooling periods, and re-populated higher latitudes through northward range expansions during postglacial warming. Such a cyclic climatic shift throughout the Pleistocene implies the repeated fragmentation and isolation of populations in glacial refugia, with strong effects on the genetic structure of the species (Comes & Kadereit, 1998; Hewitt, 1996, 2000; Schönswetter et al. 2005; Tribsch & Schönswetter, 2003). Consequently, populations persisting in glacial refugia have relatively long and stable demographical history, resulting in higher levels of genetic diversity when compared to populations established in recently colonized areas (Hewitt, 2000).

Due to the mild effects experienced during the Quaternary glaciation, Southwestern Alps acted as refugium for a remarkable number of species during ice ages (Casazza et al., 2005, 2016; Diadema et al., 2005; Guerrina et al., 2015; Minuto et al. 2006; Patsiou et al., 2014). Indeed, Southwestern-Alpine refugial area are regarded as one of the major hotspots of biodiversity in Europe, characterized by high levels of endemism and by the presence of divergent intraspecific phylogeographic lineages (Casazza et al., 2005, 2016; Médail & Quézel, 1997). The impact of past and future climatic conditions and the role of refugia in range dynamics are well documented for endemic plants of the Southwestern Alps (*e.g.* Casazza et al., 2005, 2016; Diadema et al., 2005; Guerrina et al., 2015; Médail & Quézel, 1997; Minuto et al. 2006; Patsiou et al., 2014; Szövényi et al., 2009; Zecca et al., 2017), but have been rarely considered in high-mountain animal species.

In this study, we focused on the alpine endemic spider *Vesubia jugorum* (Simon, 1881), a large wolf spider (Araneae, Lycosidae) inhabiting high-altitude rocky areas in the Southwestern Alps (Mammola et al., 2016, 2019; Milano et al., 2023; Tongiorgi, 1969). Previous research based on species distribution modelling demonstrated the sensitivity of this species to global warming, with a significant expected future reduction of its bioclimatic range (Isaia et al., 2016). On the basis of its small distributional range and the projected continuing decline, *V. jugorum* has been classified as Endangered by the International Union for Conservation of Nature (IUCN) (Isaia & Mammola, 2018). Accordingly, a long-term monitoring programme based on the relationship between habitat quality and the individual performance of *V. jugorum*, measured by means of functional traits correlated with habitat suitability (Mammola et al., 2019; Milano et al., 2023), has been designed for evaluating the ongoing impact of climate change on the species survival and for detecting changes in populations.

Here, we adopted a multidisciplinary approach to investigate the biogeographic events that shaped present day population structure of this species and to infer effects of past and future climate change on species distribution and genetic diversity. Accordingly, we integrated Species Distribution Models (SDMs) with phylogeographic analyses to elucidate the evolutionary history and the present distribution pattern of *V. jugorum*. In addition, we investigated the evolution of two continuous morphological characters (femur and carapace lengths), aiming at assessing the relevance of these functional traits in the reconstruction of the evolutionary history of the lineages in *V. jugorum* and their role in the future monitoring programme.

In particular, we hypothesize that: 1) past climatic changes played a key role in shaping the distributional pattern and the genetic structure of the populations of *V. jugorum*; 2) that the ongoing climate change will further cause relevant impacts on this cold-adapted species. Our results point at providing key information useful for the conservation and management of this endangered endemic species, highlighting the role that climate had played in the evolutionary diversification of *V. jugorum* and that will likely play for its long-term persistence.

2. Material and Methods

2.1. Genetic analyses

2.1.1. Sampling and Data acquisition

Specimens of *Vesubia jugorum* were hand-collected at 12 localities scattered across the known distributional range in the South-western Alps, in summer 2016, 2017 and 2018. Samples were selected to represent the overall potential intraspecific diversity (see Table 1 for sampling details). Specimens were stored at -20°C and for each of the 12 localities four specimens were used for genetic analyses, for a total of 48 samples (Table 1).

For the morphological analysis we included only adult females, due to the variation in the size of juveniles and to the low number of males collected. We measured two morphological traits related to body size: the length of the carapace and of the femur IV. We used these measures since they are well correlated with the overall body size of spiders (Elgar et al., 1990; Hagstrum, 1971; Mammola et al., 2019) and their size in adults is fixed. The measurements were carried out through Leica M80 stereoscopic microscope (60 × magnification). To standardize data acquisition, we derived measurements from digital pictures taken with a Leica EC3 digital camera, and we calculated them with Leica LAS EZ 3.0 software (Leica Microsystems, Switzerland).

2.1.2. DNA extraction, amplification and sequencing

One leg was removed from each specimen for DNA extraction. Whole genomic DNA was extracted using the NucleoSpin® Tissue kit (Macherey-Nagel GmBH) following the manufacturer's protocol.

A 625 bp region and a 1,025 bp region of the mitochondrial cytochrome c oxidase subunit I (COI) gene, were amplified by polymerase chain reaction (PCR). We utilized the primer pairs LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′; Folmer et al., 1994) and HCO2183R2 (5′-CCAAAAAATCAAAATARATGYTG-3′; De Busschere et al., 2010), and C1-J-1751 (5′-GAGCTCCTGACATAGCATTCCC-3′; Simon et al., 1994) and C1-N-2776 (5′-GGATAATCAGAATATCGTCGAGG-3′; Hedin & Maddison, 2001). Additionally, portions of the nuclear H3 and 28S rRNA genes were amplified for a subset of specimens following Colgan et al. (1993) and Hedin & Maddison (2001). However, illegible or highly polymorphic chromatograms were obtained in most cases, and the two nuclear regions were therefore omitted from further analyses.

PCR amplifications were carried out in 12.5 μL reaction volume in a final concentration of 1 μL of DNA sample with 1.25 μL of dNTP, 1.25 μL *Taq* buffer, 0.5 μL $MgCl_2$, 0.125 μL *Taq* polymerase and 0.125 μL of each primer. PCR amplification included an initial denaturation of 10 min at 94°C followed by 39 cycles of 30 s at 94°C, annealing at 47°C for 30 s, and extension at 72°C for 90 s; finally, a final elongation step at 72°C for 5 minutes was conducted. The final products were purified using ExoSAP-IT™ PCR Product cleanup reagent (Thermo Fisher Scientific) prior to sequencing. PCR products were sequenced bidirectionally at Macrogen, Inc. (http://www. macrogen.com) with ABI 3730xl DNA Analyzer (Applied Biosystems: Carlsbad, CA, USA). Geneious 6.1.6 was used to assemble the obtained chromatograms and to check for the presence of open reading frames (translation table 5).

Sequences were aligned using MAFFT 7.110 (Katoh & Standley, 2013) with the E-INS-i option, after adding the two outgroups *Pardosa laura* (GenBank accession number: NC025223) and *Lycosa oculata* (GenBank accession number: KC550670).

Table 1. Samples included in the analyses, with information on the sampling locality, coordinates, and altitude, haplotype and haplogroup coding, femur and carapace length.

Sample	Locality	Coordinates	Altitude (m)	Haplotype	Haplogroup	Carapace size (mm)	Femur size (mm)	Sex
BDA1	Italy: Bocchin dell'Aseo	44.1745 N 7.7926 E	2295	V1	3	5.3125	7	Female
BDA3	Italy: Bocchin dell'Aseo	44.1745 N 7.7926 E	2295	V1	3	5.25	7.375	Female
BDA4	Italy: Bocchin dell'Aseo	44.1745 N 7.7926 E	2295	V1	3	5.125	7.25	Female
BDA5	Italy: Bocchin dell'Aseo	44.1745 N 7.7926 E	2295	V1	3	5.28125	7.34375	Female
CC1	Italy: Colle della Ciriegia	44.14183 N 7.28315 E	2543	V2	1	6.1875	6.96875	Female
CC2	Italy: Colle della Ciriegia	44.14183 N 7.28315 E	2543	V3	1	6.15625	6.8125	Female
CC3	Italy: Colle della Ciriegia	44.14183 N 7.28315 E	2543	V4	1	6.21875	7.6875	Female
CC5	Italy: Colle della Ciriegia	44.14183 N 7.28315 E	2543	V5	1	6.25	7.46875	Female
CDC2	France: Col de la Cayolle	44.26256 N 6.73233 E	2459	V6	2	–	–	Juvenile
CDC5	France: Col de la Cayolle	44.26256 N 6.73233 E	2459	V6	2	–	–	Juvenile
CDC6	France: Col de la Cayolle	44.26256 N 6.73233 E	2459	V6	2	5.6875	7.71875	Female
CDC7	France: Col de la Cayolle	44.26256 N 6.73233 E	2459	V7	2	5.9375	–	Female
CM1	France: Col de Mallemort	44.4749 N 6.85327 E	2560	V8	2	5.0625	6.4375	Female
CM2	France: Col de Mallemort	44.4749 N 6.85327 E	2560	V8	2	5.3125	6.84375	Female
CM4	France: Col de Mallemort	44.4749 N 6.85327 E	2560	V8	2	5.59375	7.75	Female
CM6	France: Col de Mallemort	44.4749 N 6.85327 E	2560	V8	2	–	–	Juvenile
CV2	France: Col de Vars	44.5345 N 6.68947 E	2355	V9	2	4.71875	6.40625	Female
CV3	France: Col de Vars	44.5345 N 6.68947 E	2355	V9	2	–	–	Male
CV4	France: Col de Vars	44.5345 N 6.68947 E	2355	V9	2	–	–	Juvenile
CV5	France: Col de Vars	44.5345 N 6.68866 E	2376	V9	2	5.46875	7.46875	Female
GSL1	France: Grande Séolane	44.33181 N 6.55209 E	2520	V10	3	–	–	Juvenile
GSL3	France: Grande Séolane	44.33355 N 6.55124 E	2547	V11	3	–	–	Juvenile

GSL4	France: Grande Séolane	44.33355 N 6.55124 E	2547	V11	3	–	–	Juvenile
GSL5	France: Grande Séolane	44.33355 N 6.55124 E	2547	V10	3	5.90625	7.96875	Female
MBG1	France: Mont Bégo	44.08065 N 7.44597 E	2617	V12	3	5.3125	7.3125	Female
MBG2	France: Mont Bégo	44.08065 N 7.44597 E	2617	V12	3	6.40625	7.9375	Female
MBG3	France: Mont Bégo	44.08065 N 7.44597 E	2617	V12	3	5.71875	7.3125	Female
MBJ1	France: Mont Bégo Bas	44.08118 N 7.44774 E	2565	V13	3	–	–	Juvenile
OS1	Italy: Oserot	44.4052 N 6.97709 E	2500	V8	2	–	–	Female
OS2	Italy: Oserot	44.40522 N 6.97708 E	2508	V8	2	–	–	Juvenile
OS5	Italy: Oserot	44.40522 N 6.97708 E	2508	V14	2	–	–	Juvenile
OS6	Italy: Oserot	44.40522 N 6.97708 E	2508	V8	2	–	–	Juvenile
PSA1	Italy: Passo Sant'Anna	44.222 N 7.09572 E	2396	V11	3	6.09375	7.59375	Female
PSA2	Italy: Passo Sant'Anna	44.222 N 7.09572 E	2396	V11	3	–	–	Male
PSA3	Italy: Passo Sant'Anna	44.2224 N 7.09513 E	2394	V11	3	6.1875	7.75	Female
PSA5	Italy: Passo Sant'Anna	44.222 N 7.09572 E	2396	V11	3	–	–	Female
SL1	France: Serrière de la Lombarde	44.19823 N 7.1604 E	2337	V11	3	6.0625	8.0625	Female
SL2	France: Serrière de la Lombarde	44.19823 N 7.1604 E	2337	V11	3	5.96875	7.375	Female
SL3	France: Serrière de la Lombarde	44.19823 N 7.1604 E	2337	V11	3	6.0625	7.84375	Female
SL4	France: Serrière de la Lombarde	44.19823 N 7.1604 E	2337	V11	3	6.21875	8.03125	Female
VAG1	France: Vallon de l'Agnel	44.124 N 7.45273 E	2350	V15	3	5.65625	7.1875	Female
VAG2	France: Vallon de l'Agnel	44.124 N 7.45273 E	2350	V15	3	6.15625	7.71875	Female
VAG4	France: Vallon de l'Agnel	44.124 N 7.45273 E	2350	V15	3	–	–	Juvenile
VAG5	France: Vallon de l'Agnel	44.124 N 7.45273 E	2350	V15	3	–	–	Female
VDC1	Italy: Vallone del Chiapous	44.17694 N 7.32638 E	2307	V16	1	5.96875	7.59375	Female
VDC2	Italy: Vallone del Chiapous	44.17694 N 7.32666 E	2318	V17	1	5.96875	7.3125	Female
VDC3	Italy: Vallone del Chiapous	44.17833 N 7.32277 E	2324	V18	1	–	–	Male
VDC6	Italy: Vallone del Chiapous	44.17694 N 7.32638 E	2307	V18	1	6.25	7.6875	Female

2.1.3. Genetic analyses

Descriptive statistics (n° of haplotypes, haplotype diversity, nucleotide diversity) of each sampling locality and haplogroup were calculated with DnaSP 6 (Rozas et al., 2017). To better visualize the geographic structure, a median-joining haplotype network was built using the software PopART 1.7 (Leigh & Bryant, 2015), with haplotypes colored according to sampling localities.

Pairwise genetic distances within and between sampling localities were calculated as % uncorrected *p*-distances with 1000 non-parametric bootstrap replicates in MEGA X (Kumar et al., 2018) and were represented as a heatmap with the 'ggplot2' package (Wickham, 2016) in the R Statistical Software (R Core Team, 2021). Similarly, genetic distances were calculated within and between haplogroups. Genetic distances were plotted against geographic distances, the latter calculated from sampling coordinates using the packages 'geosphere' and 'ggplot2' (Wickham, 2016, Hijmans et al. 2017). A Mantel test (Mantel, 1967) was then performed to evaluate a correlation between genetic and geographic distance matrices, using the package 'vegan' (Oksanen et al., 2013).

Phylogenetic inference was performed using maximum likelihood (ML) and Bayesian inference (BI). ML analyses were performed using RAxML 8.2.12 (Stamatakis, 2014) under a GTR substitution model and with 1000 non-parametric bootstrap replicates. For BI analyses, the best substitution models and partitions were determined with PartitionFinder 1.1.1 (Lanfear et al., 2012), using the Bayesian Information Criterion (partition by codon: pos1=TrN+I, pos2=HKY, pos3=HKY). Before reconstructing the phylogenetic hypothesis, the marginal likelihood estimations of the clock and non-clock models were obtained with MrBayes 3.2.7 (Ronquist et al., 2012), resulting in the clock model being highly supported ($2\log(B_{12}) = 548.4$) (Kass & Raftery, 1995). BI was performed with the software BEAST 1.8.2 (Drummond et al. 2012), setting a coalescent tree prior and a strict clock. The substitution rate was obtained from literature, since no reliable fossil records or well-dated biogeographic events were available for calibrating the tree, and was set to 0.01679 substitutions per million years, as obtained by Piacentini & Ramirez (2019) for the COI gene in the family Lycosidae. Three independent replicate analyses were run for 100 million generations, sampling every 10,000th and were then combined using LogCombiner 1.8.2 (Drummond et al., 2012), setting a burn-in of 25%. Stationarity for effective sampling size and unimodal posterior distribution were checked with Tracer 1.6 (Rambaut et al., 2014), and a maximum clade credibility tree was obtained using TreeAnnotator 1.8.2 (Drummond et al., 2012).

In order to assess the presence of cryptic species, a DNA-based species delimitation technique was applied. Specifically, the single-threshold Generalized Mixed Yule Coalescent (st-GMYC) method (Pons et al., 2006) was run in the R environment using the packages 'apes' (Paradis et al., 2004) and 'splits' (Ezard et al., 2009) and the ultrametric Bayesian tree as input.

Finally, the evolution of the two continuous morphological characters (carapace and femur length), was assessed by ancestral state reconstruction. Only female specimens were kept for these analyses, whereas males, juveniles and specimens not measured were pruned from the ultrametric Bayesian tree. The ancestral states were estimated and visualised using the functions *fastAnc* and *contMap* in the R package ‘phytools’ (Revell, 2012), respectively. Moreover, to account for uncertainty in ancestral node reconstructions, the 95% confidence intervals for each node were mapped on the relative traitgrams using the function *phenogram*.

2.2. Ecological Niche Modelling

We conducted all analyses in R (R core team, 2021). We computed Ecological Niche Modelling to predict the present, past and future distribution of our model species. In constructing and reporting species distribution models, we followed the ODMAP (Overview, Data, Model, Assessment and Prediction) protocol (Zurrell et al., 2020), a tool designed to maximise reproducibility and transparency of distribution modelling exercises (Appendix S1).

We assembled data on 107 presences of *V. jugorum* on the basis of the available data in literature (Mammola et al., 2019) plus recent field surveys gathered during this study (2019–2021). To avoid overrepresentation of certain regions as a result of sampling heterogeneity, we performed spatial thinning using the function *thin* in the ‘red’ R package (Cardoso, 2017). We thinned occurrences through 100 iterations setting a maximum distance of 0.5%. We calibrated and projected models within the spatial extent hypothesized to fall within the long-term dispersal and colonization potential for a given species over its evolutionary history (the ‘M area’; Barve et al., 2011). Considering the distribution range and the low dispersal potential of this species (Mammola et al., 2019), we approximated the extent of the study area by masking the bioclimatic layers to 6.0 to 8.0° latitude and 43.9 to 46° longitude.

The toponomastics and classification of the different sectors and sub-sectors of the Alps follows the partition of the Alpine chain (SOIUSA; Marazzi, 2005).

We modelled the current distribution range of the species using a combination of climatic and topographic variables. We extracted the standard 19 bioclimatic variables for “present” conditions (1970–2000) and elevation data from WorldClim 2 (Fick & Hijmans, 2017), all at a spatial resolution of 30 arc-seconds. We performed a Principal Components Analysis on the predictor variables to generate new axes that summarized variation in fewer, independent dimensions, thereby minimizing multicollinearity among variables.

Given the lack of reliable absence data, we constructed species distribution models using a presence-background algorithm (MaxEnt), with the function *maxent* in the ‘dismo’ R package (Hijmans et al., 2014). Considering the sample size of our occurrence datasets, we fitted the MaxEnt models with default settings (Morales et al., 2017). We evaluated model performance with the Boyce index (Boyce et al., 2002) using the *ecospat.boyce* function in the 'ecospat' R package (Broennimann et al., 2018). This is an appropriate metric when lacking absence data (Hirzel et al., 2006). We ran 50 bootstrap replicates, retaining a random partition of 20% of the points from each run to assess predictive performance. Once the model had been validated, we generated a final model using the full set of occurrence models and projected it into recent climate. We then projected the results into ancestral and future climatic conditions, in order to estimate variations in the distribution ranges relative to past and future climate changes.

We obtained downscaled and calibrated Paleoclimatic data for the Last Glacial Maximum (~21,000 years ago) at 2.5 arc-minutes, from the Earth System Model based on Model for Interdisciplinary Research on Climate (MIROC-ESM).

To predict the potential consequences of future climate, we used a new set of integrated emission scenarios, combining the Representative Concentration Pathways (RCPs) with specific socioeconomic and technological development, *i.e.* the Shared Socioeconomic Pathways (SSPs), as discussed in O'Neill et al. (2016) and in van Vuuren et al. (2014). The Shared Socioeconomic Pathways are reference pathways describing plausible alternative trends in the evolution of society and ecosystems over a century timescale (O'Neill et al., 2014). We selected a sustainable (RCP2.6, SSP1) and a fossil-fuelled (RCP8.5, SSP5) development scenario. We projected these scenarios in a range of 20-year-period outcome (2021–2040), with a spatial resolution of 30 arc-seconds. Among available Coupled Model Intercomparison Project Phase 6 (CMIP6) climate models, we used the IPSL-CM6A-LR climate model (Boucher et al., 2020).

3. Results

3.1. Population structure

The final alignment of the analysed portion of the COI gene consisted in 1184 bp, including 48 specimens of *Vesubia jugorum* from 12 localities, corresponding to 18 haplotypes. Conversely, the sequencing of H3 and 28S rRNA genes resulted in highly polymorphic and poor-quality chromatograms, as also observed in previous studies (Murphy et al., 2006; Piacentini & Ramirez, 2019), and nuclear data were therefore not used in further analyses.

The genetic diversity indices calculated for each locality and haplogroup are summarized in Table 2. Total haplotype (h) and nucleotide (π) diversity across all specimens was 0.918 and 0.015 ± 0.001, respectively. Group 1 exhibited the highest haplotype ($h=0.964$) and nucleotide ($\pi=0.00666 \pm 0.0009$) diversity, whereas in Group 2 and Group 3 both haplotype and nucleotide diversity were lower (see Table 2).

Table 2. Genetic indices for each sampling locality, haplogroup, and for the overall dataset, with information on number of haplotypes (H), haplotype diversity (h), and nucleotide diversity (π).

Sampling locality	Number of sequences	N	Haplogroup	h	π (sd)
Bocchin dell'Aseo (BDA)	4	1	3	0	0 (0)
Colle della Ciriegia (CC)	4	4	1	1	0.00293 (0.00074)
Col de la Cayolle (CDC)	4	2	2	0.5	0.00088 (0.00047)
Col de Mallemort (CM)	4	1	2	0	0 (0)
Oserot (OS)	4	2	2	0.5	0.00088 (0.00047)
Col de Vars (CV)	4	1	2	0	0 (0)
Grande Séolane (GSL)	4	2	3	0.667	0.00117 (0.00036)
Passo Sant'Anna (PSA)	4	1	3	0	0 (0)
Serrière de la Lombarde (SL)	4	1	3	0	0 (0)
Monte Bego (MBG)	3	1	3	0	0 (0)
Monte Bego Basso (MBJ)	1	1	3	0	0 (0)
Vallon de l'Agnel (VAG)	4	1	3	0	0 (0)
Vallone del Chiapous (VDC)	4	3	1	0.833	0.00147 (0.00053)
Haplogroup 1	8	7		0.964	0.00666 (0.0009)
Haplogroup 2	16	5		0.75	0.00467 (0.00057)
Haplogroup 3	24	6		0.779	0.00311 (0.00025)
Overall dataset	48	18		0.918	0.01501 (0.001)

The haplotype network showed three main haplogroups (Fig. 1), separated by 15–22 steps. Group 1 showed the highest diversity, with 7 different haplotypes found in two close localities (CC and VDC). Conversely, in Group 2 and Group 3 haplotypes from nearby localities clustered together or were separated by only a few steps (1–4). Generally, the haplotypes were exclusive to single sampling localities, except V8 and V11, which were shared across localities. Specifically, V8 was found in individuals from two closely located localities (CM and OS; Fig. 1), whereas V11 was shared by two very close (PSA and SL) and one more distant (GSL) localities (see Fig. 1). Moreover, in Group 3, several haplotypes from distant localities were found to be very similar, separated by a few substitutions (*i.e.*, 1–4).

The overall mean intraspecific distance in *V. jugorum*, calculated as % uncorrected *p*-distance, was 1.5 ± 0.2%. The pairwise distances between sampling localities ranged from 0 to 2.9% (Fig. 2a and Table S1). The distances within the three haplogroups were 0.7 ± 0.2% in Group 1, 0.5 ± 0.1% in Group 2, and 0.3 ± 0.1% in Group 3. Group 1 showed the highest genetic distance from the other two haplogroups, 2.6 ± 0.4% and 2.4 ± 0.4% from Group 3 and Group 2, respectively. Conversely, the genetic distance between Group 2 and Group 3 was lower (1.9 ± 0.3%).

The relationship between genetic and geographic distance was shown in Fig. 2b. A slight positive correlation between genetic and geographic distance among the populations was detected by the Mantel test (r = 0.13, p-value = 0.007).

3.2. Phylogenetic tree

Phylogenetic reconstructions based on ML and BI yielded similar results, even though nodal support was generally higher in the BI tree (Fig. 3). *Vesubia jugorum* was split in three main clades, corresponding to the three haplogroups found in the haplotype network. One clade included two populations from geographical adjacent localities, occurring in the central portion of the Maritime Alps (CC and VDC). A second clade, further divided into three well-supported clades, included the northern populations with the exception of GSL (CDC, CM, CV and OS). A third clade grouped the remaining populations from the eastern (BDA, MBG and VAG) and central (PSA and SL) portion of the species' distribution range, along with the westernmost population GSL.

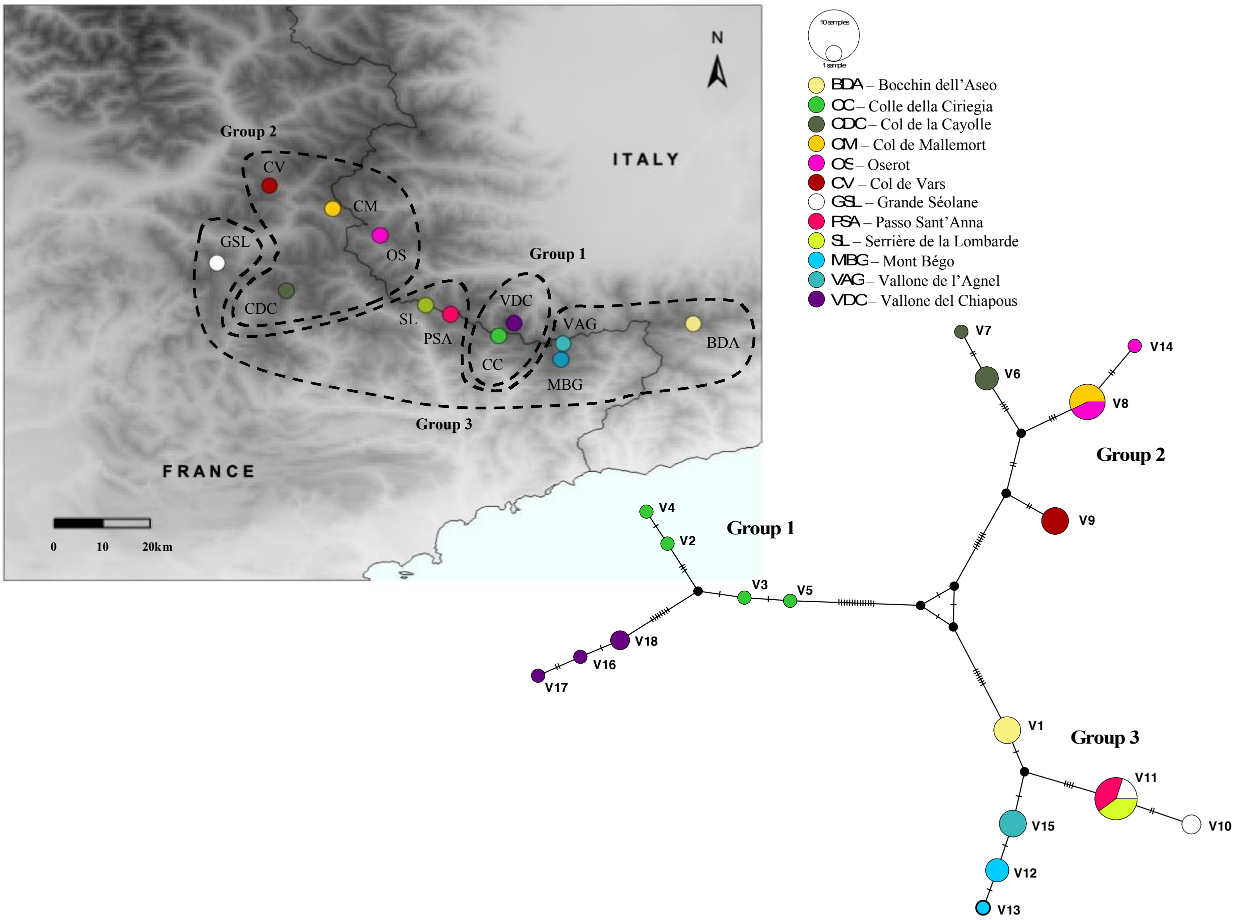

Fig. 1. Haplotype network of the investigated populations. Codes in the map indicate localities (see legend), alphanumeric codes in the networks refer to haplotypes. The size of each circle is proportional to the number of sampled individuals with each haplotype (see scale above the legend).

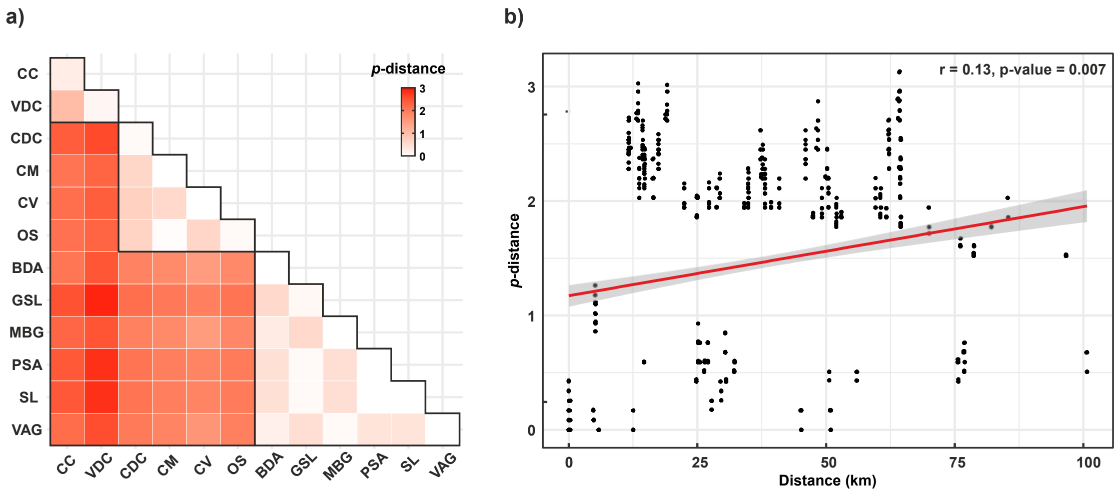

Fig. 2. Genetic distances and isolation-by-distance plot. a) Heatmap showing the pairwise % uncorrected *p*-distances within and between sampling localities, with darker colours indicating higher distances. Black outlines show the intra-haplogroup distances. b) Genetic distances plotted against geographic distances, with the interpolation line in red.

The estimated time of the diversification of the extant lineages of *V. jugorum* according to the COI was 0.87 million years ago (95% HPD = 0.62–1.17 million years ago), and the split between Group 2 and Group 3 occurred 0.62 million years ago (95% HPD = 0.4–0.87 million years ago). The basal split of the two populations in Group 1 (CC and VDC) traced back to 0.34 million years ago (95% HPD = 0.19–0.55 Ma). In Group 2, the northernmost population (CV) originated approximately 0.22 Ma (95% HPD = 0.12–0.35 Ma), and the diversification of the remaining lineages occurred 0.15 Ma (95% HPD = 0.07–0.22 Ma). In Group 3, the isolated population of the Ligurian Alps (BDA) formed a separated lineage approximately 0.17 Ma (95% HPD = 0.08–0.28 Ma), while the eastern populations (MBG and VAG) diverged from the remaining populations at 0.12 Ma (95% HPD = 0.06–0.21 Ma).

The st-GMYC analysis revealed that the null model (*i.e.*, the entire sampling belong to a single species) could not be rejected (likelihood ratio=5.0319, p-value=0.08), indicating that the dataset is likely composed of populations from a single species. Finally, the ancestral state reconstructions of the carapace and femur length were mapped on the phylogenetic hypothesis as shown in Fig. 4. However, the relative traitgrams with the 95% confidence intervals of the reconstructed ancestral states mapped for each node revealed a large uncertainty, especially in the deeper nodes (Fig. S1). Despite that, regarding the femur size, the largest values were found in group 1, starting from the ancestor of CC and VDC samples, and in group 3, even if with the exception of BDA specimens and some MBG and VAG specimens (Fig. S1a). On the other hand, an increase in carapace size is only seen starting from the ancestor of the SL, PSA, and GSL samples (group 3), with some other large size carapaces scattered across the tree (Fig. S1b).

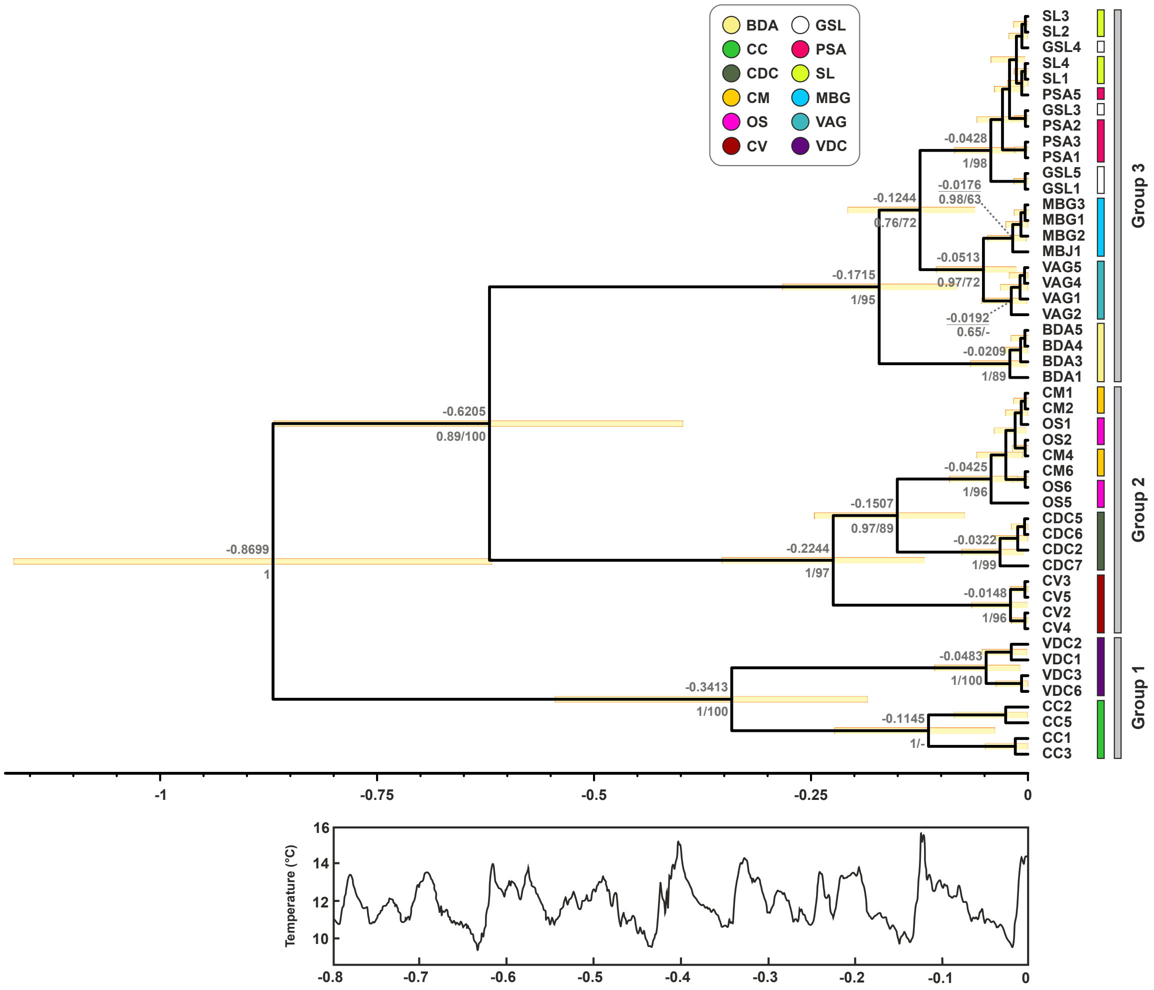

Fig. 3. Time-calibrated Bayesian tree based on the COI region. Numbers above nodes show the estimated divergence times, whereas numbers below nodes shows Bayesian posterior probabilities and maximum likelihood bootstrap values, respectively. Yellow bars at nodes indicate the 95% HPD confidence intervals of the divergence times. Colored bars at tips represent the sampling localities, as shown in the legend. Below the tree is the surface temperature for the last 800,000 years (Hansen et al., 2013) and for the last 1 million years (modified from Candy & Alonso-Garcia, 2018).

3.3. Species distribution models and model performance

After spatial thinning, we kept 84 occurrences for *Vesubia jugorum* to generate the species distribution models. We retained the first four principal components, which cumulatively explained around 95% of the overall variance in the dataset. The Boyce index indicated that the distribution models had high explanatory ability (Boyce index > 0.77; median of the 50 bootstraps).

3.3.1. Current potential distribution

The present-day suitable area estimated by the model was mostly coincident with the known geographic distribution of *Vesubia jugorum* (Fig. 5a).

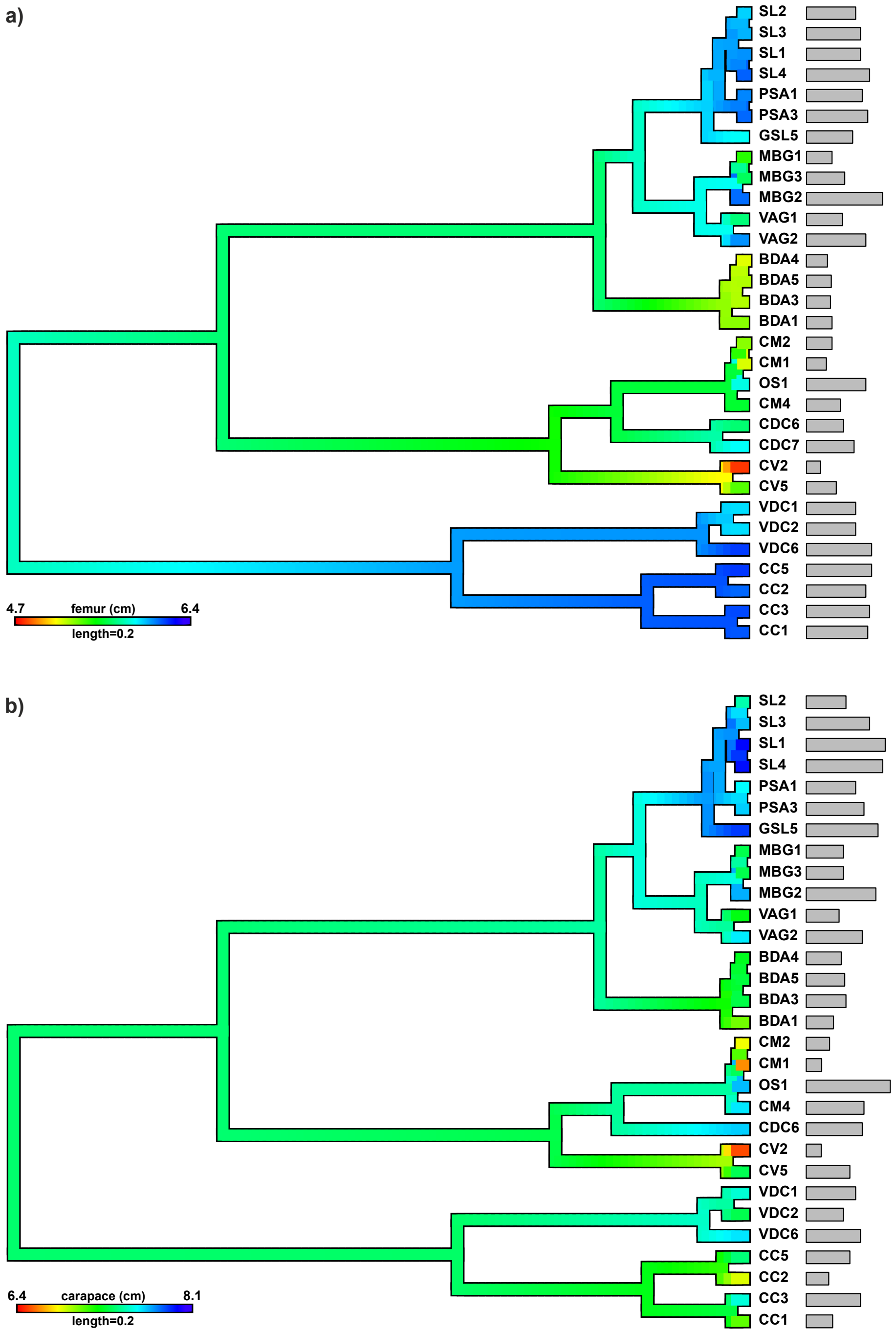

Fig. 4. Ancestral state reconstructions for the continuous characters a) femur and b) carapace length. Boxes at the right of tips represent the exp-transformed values for each specimen.

The potential distribution range was centred in the Maritime Alps, and ranged from the southern Cottian Alps down to the Ligurian Alps. Current predictions identified suitable areas in montane areas across the border between Italy and France.

The most suitable and unfragmented areas corresponded to Argentera-Mercantour Massif, in the central portion of the Maritime Alps. Another suitable, isolated area, was predicted in the southernmost part of the species' range, in the area corresponding to the Marguareis-Mongioie Massif, in the Ligurian Alps. Additional suitable areas were detected in the south-western limits of the known distribution, across the Provence Alps.

Northwards, the predicted range extended beyond the known limit of the species range, in the high Varaita Valley and in the northern edge of the high Ubaye Valley, across the margin between Alpes-de-Haute-Provence and Haute-Alps departments (Fig. 5a). In these regions, the degree of habitat suitability was lower in respect to the south.

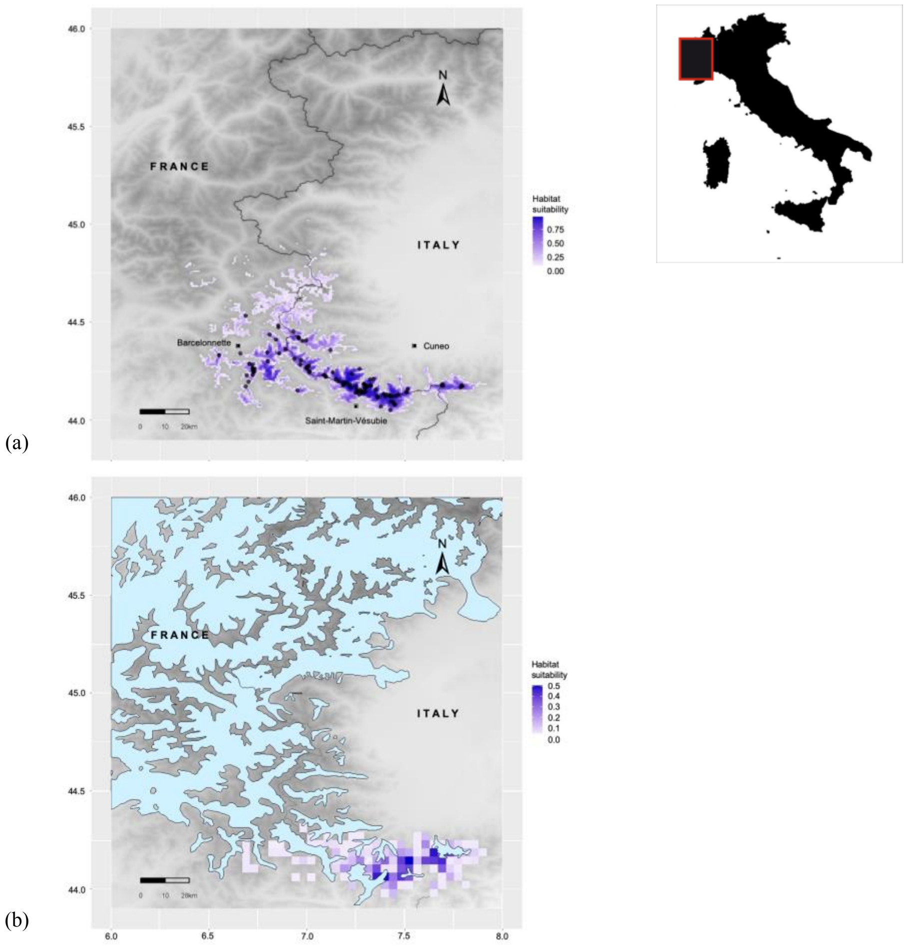

Fig. 5. Maps of the bioclimatic suitability for *Vesubia jugorum* projected at the present climate (a) and during the Last Glacial Maximum (b). The predicted species distribution is shown in blue. Limits of the ice cover in the Last Glacial Maximum (Ehlers et al., 2011) are reported for Pleistocene projections (light-blue shapes in the lower map).

3.3.2. Past projected distribution

The projection of the potential distribution of *Vesubia jugorum* into the past climatic conditions, showed a different range in respect to the present-day one (Fig. 5b). The potential past distribution was found to be smaller than today, and limited to areas which were devoid from glaciers. The northern portion of the current range was likely unsuitable during the Last Glacial Maximum, and the distribution of this species was restricted to an area corresponding to the south-eastern part of the current distribution. In particular, the Marguareis-Mongioie and the Argentera-Mercantour massifs provided areas of high suitability, namely the two areas where the current suitability is higher nowadays.

3.3.3. Future projected distribution

Future forecasts, obtained by projecting the habitat suitability under sustainability (SSP1-RCP2.6) and fossil-fuelled development (SSP5-RCP8.5) scenarios, showed significant shifts in the bioclimatic range towards higher altitude and latitudes (Fig. 6).

In both future scenarios, a general decrease in the current suitability was observed, particularly remarkable in the central and south-eastern parts of the distribution range. By contrast, an increase in suitable habitat in the north of the range, with the appearance of new suitable areas, was predicted.

According to the SSP1-RCP2.6 scenario, a decrease in the suitability was observed all over the current range. The reduction in the availability of future suitable areas will be even more significant in the Ligurian Alps, where the remaining patch of suitable habitat is expected to be more isolated from the rest of the population. In the Maritime and southern Cottian Alps, despite experiencing fewer changes in suitability, a general thinning of the suitable areas was observed, suggesting a general shift towards higher altitude. Conversely, an increase in habitat suitability in the northern Cottian Alps, and a slight north-westward shift of the suitability, was predicted.

On the other hand, the SSP5-RCP8.5 scenario indicated a more significant contraction of the current distribution and a general lower suitability with respect to the currently suitable areas, with a more marked shift of the suitable range toward north, in the northern Cottian and in the Graian Alps. Many areas of currently available suitable habitat in the Maritime Alps are not predicted to retain their high suitability, and an increasing isolation of the central current range from the newly northern suitable areas was expected. The extent of suitable area in the Ligurian Alps was expected to reduce further, as well as the isolated patched occurring south-west of the current distribution, in the Provence Alps.

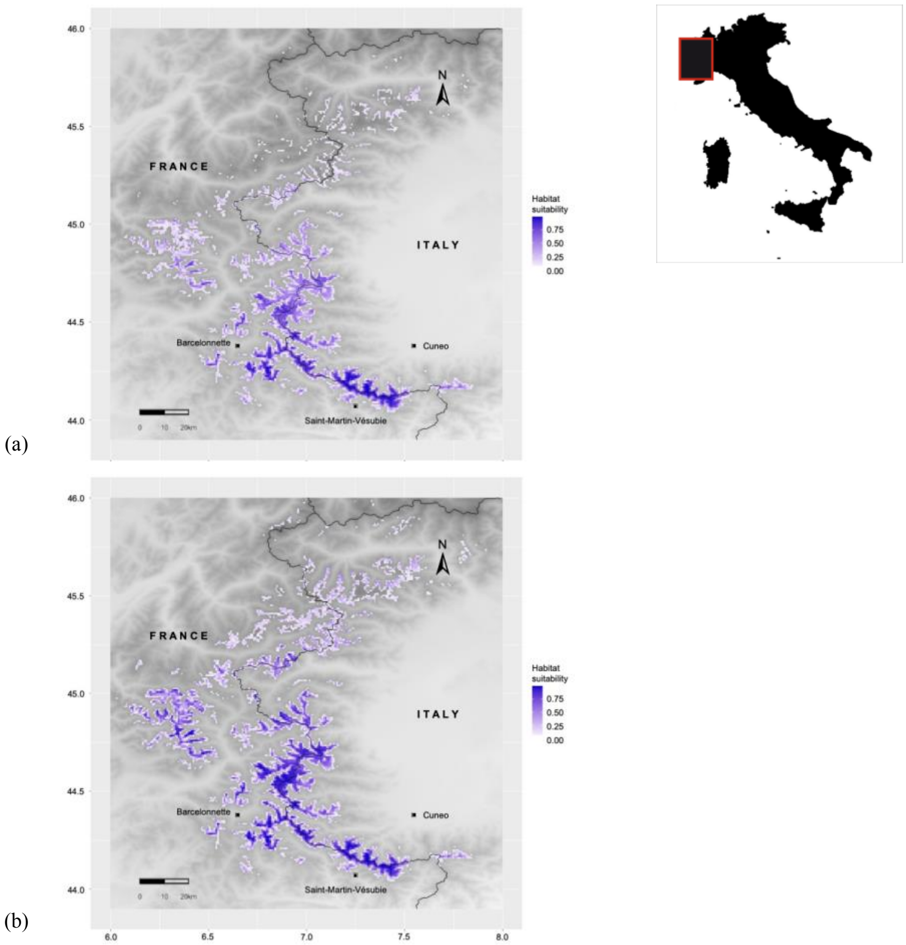

Fig. 6. Maps of the predicted distribution range of *Vesubia jugorum* in 2021–2040 according to (a) a sustainable and (b) a fossil-fuelled development scenario.

4. Discussion

According to our results, Pleistocene climatic oscillations, played an important role in shaping the current distributional pattern and the genetic diversity of *Vesubia jugorum*. As seen in other Alpine endemic species (Brunetti et al., 2019; Comes & Kadereit, 1998; Schmitt, 2009; Tribsch, 2004; Tribsch & Schönswetter, 2003), extreme variation of climate in Alpine habitats and movements of ice masses during Quaternary glacial cycles (Ehlers et al., 2011) possibly played a major role in expanding and contracting the distribution of this wolf spider.

Species distribution models projected in the Last Glacial Maximum (LGM), showed that past bioclimatic suitability of *V. jugorum* was smaller in range compared to present, and mostly centred in the south-eastern part of the current distribution, namely the Maritime and Ligurian Alps. These areas, which remained largely free from glaciers through time (Ehlers et al., 2011), served as a refugium for many species during Pleistocene glaciations (Casazza et al., 2016; Diadema et al., 2005; Guerrina et al., 2015, 2022; Minuto et al., 2006; Patsiou et al., 2014; Szövényi et al., 2009).

Reasonably, this could also be the case for *V. jugorum*, experiencing suitable conditions in this area from LGM to present. Tentatively, populations inhabiting the northern valleys of the Southwestern Alps before LGM most likely disappeared due to ice shield advance or persisted in peripheral refugial areas and unglaciated mountain peaks ('nunataks') in the interior of the Pleistocene ice shields. This pattern, led to the diversification of geographically isolated lineages, that during the warmer interglacial phase re-colonized areas previously unsuitable or covered by glacial masses (post-glacial colonization hypothesis, *sensu* Guerrina et al., 2021). The colonization of the northern portions of the range and the plausible re-establishment of connections among populations sheltered in isolated mountain refugia would have enabled gene flow dynamics. At the same time, it is likely that the southernmost populations survived *in situ* via short altitudinal shifts, following their climatic optimum (long-term stability hypothesis, *sensu* Guerrina et al., 2021). Our hypothesis is paralleled by other studies on cold-adapted endemics in the Alps, suggesting that endemic species survived in refugia during the glaciations (Schönswetter et al., 2002, 2003, 2004, 2005; Tribsch & Schönswetter, 2003).

Such scenario is congruent with the phylogenetic reconstruction that we obtained for the species lineages. Southern populations remained isolated from the rest of the range, evolving higher level of genetic differentiation. Conversely, northern populations showed low levels of genetic differentiation, compatible with a scenario of more recent colonization, followed by a short period of glacial isolation, thus preventing the accumulation of among-populations genetic differentiation. As a result, the species exhibits a weaker phylogeographic structure and lower genetic diversity in formerly glaciated areas than in unglaciated regions, retracing the patterns observed for other alpine species (Casazza et al., 2016; Schönswetter et al., 2006). Accordingly, numerous studies provide substantial evidence that putative refugial populations harbour higher levels of genetic diversity than populations subjected to repeated cycles of range contractions and post-glacial colonization (see *e.g.* Comes & Kadereit, 1998; Excoffier & Ray, 2008; Hewitt, 2000).

According to our phylogenetic reconstruction, the initial diversification of the lineages of *V. jugorum* that we recovered with our sampling traced back to ca. 0.87 Mya. This time period may be approximately related to the glacial period occurring between 0.90 and 0.85 Mya (Rodrigues et al., 2017), when the cooler conditions and the ice shields would have caused an overall contraction of the wide ancestral distribution, prompting the species to find refuge in the southern latitudes, at the periphery of the Pleistocene glaciers, and in isolated refugia scattered across the species' distribution. We hypothesize a glacial cycle-driven extinction of ancestral northern populations during cooler periods, followed by the expansion of populations which survived in climatic refugia during warmer periods. When the glaciers retreated and new areas became available, these populations may have expanded their range. Conversely, the populations occurring in the central portion of the Maritime Alps, in the area corresponding to the Argentera massif, probably migrated to higher altitudes following their climatic optimum and remained isolated from the other populations, causing the basal split observed in the phylogenetic tree.

The structure of the tree suggests that such populations have been isolated from the others for a quite long time. Indeed, the high levels of haplotype diversity observed in some cases (CC and VDC, Group 1), would provide evidence that this area of Southwestern Alps could be the centre of origin for the extant lineages of *V. jugorum*, and could have acted as a refugium for the species during Pleistocene glacial-interglacial phases. Additional indirect evidence come in the light of the geomorphology of the area. The Argentera massif is geologically isolated, characterized by high altitudes (up to 3,300 m) and characterised by very narrow and deep valleys with high differences in height (up to 2,000 m) between the valley floors and the mountain tops, which may justify a loss of genetic continuity and effective barriers to gene flow within populations. The high geographic structuring of these populations is confirmed by the positive correlation between geographic and nucleotide distances resulting from the Mantel test, even if based on a single mitochondrial marker. Further glacial-induced isolations may have led to the split between Group 2 and Group 3, occurring ca. 0.62 Mya. Support to this hypothesis is provided by the presence of a deep structuring in space, likely because of low levels of gene flow between localities or between the three haplogroups. During the following glacial-interglacial cycles, further diversification within these haplogroups may have originated.

Interestingly, a divergent and private haplotype (V9) was found in the Col de Vars (CV). Col de Vars is located in the northernmost portion of the range of *V. jugorum*, in a region with a very low level of habitat suitability (see Mammola et al., 2019). It is possible that this divergent haplotype could be the remnant of a former wider population of *V. jugorum*, probably the result of a Pleistocene colonization, that survived to the habitat contraction during glacial expansion, isolated from the remaining southern populations.

The genetic affinities between GSL and the remaining localities of the Group 2, in particular SL and PSA, is hard to explain. GSL, PSA and SL share one haplotype (V11). This fact suggests the possibility that gene flow between these three populations occurred in the last 50,000 years. The establishment of corridors of suitable habitat at lower elevation between Provence and Maritime Alps could have promoted the colonization of the Grande Séolane by south-eastern lineages during glaciations. Alternatively, this population may have originated from a first colonization from southeast, followed by isolation from the nearest lineages of the Group 3. The estimated time of divergence of the populations occurring at the south-eastern edge of the range in the Marguareis-Mongioie Massif (BDA), in the Ligurian Alps, from the other southern populations occurred approximately 0.17 Mya.

The model we used to explain population dynamics in *Vesubia jugorum* is similar to the one invoked to explain diversification in other alpine species, based both on molecular analyses and species distribution models (Bettin et al., 2007; Guerrina et al., 2022; Schönswetter et al., 2002). However, given the large confidence intervals around the time estimate of the basal splits, it is difficult to point out the precise climatic conditions that exactly determined the phylogenetic patterns within the species. Despite that, our modelling projections indicate a similar pattern, at least for later stages, as inferred by the molecular analyses, supporting our observations.

Future forecasts based on different emission scenarios showed significant shifts in the bioclimatic range, both towards higher latitudes and altitudes. This confirms the estimations made by Isaia et al. (2016). Based on both SSP1-RCP2.6 and SSP5-RCP8.5 future scenarios, an increase in suitable habitats in the north of the range, with the appearance of new suitable areas far beyond the known limit of the species distribution, is observed. By contrast, an overall decrease of habitat suitability is predicted for the central and south-eastern parts of the current distribution range, with a general shift towards higher altitudes. We predict that some of the southern and western peripheral portions of the distributional range will remain isolated, potentially leading to genetic drift. In particular, a general decline of suitable areas in the Ligurian Alps, as well as the appearance of isolated patches in south-west of the current distribution, mainly in the Provence Alps, is expected. This implies a substantial reduction of the current genetic diversity in these populations, which poses concerns to their long-term survival. Loss of genetic diversity is considered extremely detrimental from a conservation point of view, since low levels of diversity are generally correlated with reduced adaptive potential (Allendorf & Luikart, 2007). We regard such peripheral populations as the most threatened by the ongoing climatic change.

The most relevant factors potentially influencing the future colonization of newly appeared suitable areas are represented by species' dispersal ability and by habitat connectivity. *Vesubia jugorum* is strongly linked to high-altitude rocky lands (Milano et al., 2023). Unfavourable habitat conditions in the lowlands, in addition to the presence of biogeographical barriers between Southwestern Alps and northernmost mountain ranges, limit the potential for colonisation of new areas of climatically suitable habitat. Future scenarios showed a progressive lack of connection between the current suitable areas and the areas that are predicted to become suitable in the next future. In addition to the lack of habitat connectivity, the limited dispersal ability is a further factor which could influence the future ability of this species to cope with climate change. The results of our phylogeographic analyses showed a strong population structure and a limited gene flow even between geographically close populations, corroborating our suspects about the vulnerability of this species.

The phylogenetic history of this species, in association with the presence of biogeographical barriers delimiting the current species range and the putative dispersal ability of the species, let us to conclude that the possibility of the species to disperse and colonise new suitable areas within the next years has to be considered highly improbable. These general considerations have implications for conservation genetics, highlighting areas where conservation efforts should be concentrated. Maritime and Ligurian Alps, where most of the Pleistocene refugia are localized, are indeed worth of special conservation attention since they support most of the current genetic variation. In this context, the preservation of genetic diversity in these areas is required for achieving a long-term conservation of the species.

As far as the evolution of morphological traits (femur and carapace lengths) is concerned, we tried to understand whether functional traits do or do not reflect phylogeny and could be informative in the reconstruction of the evolutionary history of the lineages in *V. jugorum*. Ancestral state reconstruction revealed a large uncertainty in the character evolution and a scattered pattern across the tree, likely suggesting multiple convergent evolution of these traits in different populations. The similar values found in phylogenetically divergent groups, would suggests that the trait variation we examined is mainly driven by environmental gradients, such as traits responses to abiotic conditions, rather than by evolutionary trajectories. Thus, it is more likely that femur and carapace length has evolved as a result of an environmental stress response. The positive response of these functional traits to the habitat quality, as already suggested by Mammola et al. (2019), and their independence from genetically-based long-term adaptation, confirms the reliability in their use for monitoring purposes. On these bases, variations in functional traits of *V. jugorum* represent a reliable tool for investigating long-term adaptation to environmental conditions.

5. Conclusion

Combining species distribution modelling and mitochondrial phylogeography, the present study explores the responses of *Vesubia jugorum* to the late Quaternary climate changes by determining the patterns of population genetic structure, demographic history and the distribution shifts. We assume that the time slice used in our projections (LGM, present and future) is able to capture, at least to some degree, the key climatic conditions across the entire Pleistocene. Tentatively, during the climatic oscillations that took place in the last 1 million years, *V. jugorum* underwent alternations of contractions-expansions in its geographic range, similar to the pattern predicted since the last 21,000 years by our models. Additionally, we provide further information for the conservation and management of this endangered endemic species, highlighting the role that Pleistocene refugia may have played in the evolutionary diversification of the species and that will play for its long-term persistence.

In a context of changing climate, in which endemic cold-adapted species are suffering a dramatic contraction of their range due to the ongoing global warming, investigating the dynamics of range shifts throughout the broad temporal spectrum of *V. jugorum* can provide useful information for the general conservation of alpine endemic species. Moreover, our results will contribute to a better understanding of the complex factors that shape the evolutionary history of endemic species in glacial refugia and their conservation implications.

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Paper VII

Species conservation profiles of the endemic spiders *Troglohyphantes* (Araneae, Linyphiidae) from the Alps and the north-western Dinarides

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Species Conservation Profiles

Species conservation profiles of the endemic spiders *Troglohyphantes* (Araneae, Linyphiidae) from the Alps and the north-western Dinarides

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Abstract

Background

The genus *Troglohyphantes* Joseph, 1882 (Araneae, Linyphiidae) includes 131 species, mainly distributed across the main European mountain ranges. The Alps and the north-western Dinarides account for 66 species, most of them showing narrow or even point-like distributions. The majority of *Troglohyphantes* spiders dwell in subterranean habitats including caves, mines, soil litter, rocky debris and other moist and shaded retreats. Despite being intensively studied from taxonomic, ecological and biogeographic standpoints, knowledge on the status of conservation and on the potential risk of extinction of these spiders is lagging. To date, only three species have been included in the global IUCN Red List, but their status has not been updated ever since their last assessment in 1996. The aim of this contribution is to assess the Alpine and north-western Dinaric species of the genus *Troglohyphantes* and to re-assess the species previously evaluated, according to the last version of the IUCN Red List Categories and Criteria.

New information

Amongst the 66 species here considered, 62 had sufficient data to allow the quantification of their Extent Of Occurrence (EOO) and Area Of Occupancy (AOO). Most of the species have a narrow distribution range, with an estimated EOO < 20,000 km^2 and AOO < 2,000 km^2, meeting the thresholds for the inclusion in the threatened categories. Five species have a more widespread distribution (EOO > 20,000 km^2), extending across multiple countries. The quality of the data on distribution of four species was not sufficient to provide a reliable estimation of the distribution range.

A continuing decline in EOO, AOO and habitat quality was inferred for 30 species. The majority of them were subterranean specialised species, with a reduced thermal tolerance and a low dispersal ability. Accordingly, changes in subterranean microclimatic conditions due to climate change represent a major threat for these species. Land-use change and habitat alteration were identified as additional relevant threats for several species.

A considerable proportion of the species here assessed was found in protected areas and in sites of the Natura 2000 network. In addition, 14 species are formally protected by national and sub-national legislation. At present, 25 species are listed in the regional Red Lists.

Long-term monitoring programmes, management plans for both the species and their habitats, expansion of the extant protected areas and designation of new ones, should be considered as the most effective approaches to species conservation.

Keywords

climate change, IUCN, cave, Red List, subterranean species, Linyphiidae, troglobiont, karst, spiders

Introduction

The Alps and the Dinarides are known for their wide variety of habitats and they have been recognised as one of the major biodiversity hotspots in Europe (Nagy et al. 2003, Condé and Richard 2005). The combination of topographical, geomorphological and long-term climatic factors allowed the development of a very diverse and unique fauna, including spiders (Nentwig et al. 2022). Spiders (Arachnida, Araneae) are a mega-diverse group of arthropods comprising more than 50,000 currently described species (World Spider Catalog 2022). They are considered one of the most successful groups of organisms in terms of abundance, evolutionary radiation, biomass, functional roles and ecological plasticity (Turnbull 1973, Coddington and Levi 1991, Cardoso et al. 2008, Coddington et al.

2009, Foelix 2011, Jocqué et al. 2013, Nentwig 2013, Garrison et al. 2016, Mammola et al. 2017a, Dunlop et al. 2018) and they have colonised all terrestrial habitats, including subterranean ones (Mammola et al. 2018a).

Spiders have undergone a remarkable diversification in subterranean habitats (Mammola and Isaia 2017, Mammola et al. 2018a, Mammola et al. 2019b), including deep soil strata in forest, shallow voids in mountain screes and deep caves (Mammola and Isaia 2017); therein, they play an important functional role as apical predators in the subterranean food webs (Parimuchová et al. 2021).

The genus *Troglohyphantes* (Araneae, Linyphiidae) is predominantly distributed in the main European mountain ranges, including Pyrenees, Alps, Dinarides and Carpathians (Deeleman-Reinhold 1978, Pesarini 2001, Deltshev 2008, Isaia et al. 2011, Isaia et al. 2017, Mammola et al. 2018b). Currently, 131 species are described (Nentwig et al. 2022), most of them occurring in Europe. Their distribution is often restricted to very narrow areas, sometimes to just one or a few localities (Deeleman-Reinhold 1978, Isaia et al. 2011, Isaia et al. 2017, Mammola et al. 2018a).

Species of the genus *Troglohyphantes* generally show a remarkable preference for subterranean habitats (sensu Culver and Pipan 2019). They mainly occur in cold, wet and dark habitats, such as caves, bunkers, mines, but also in Shallow Subterranean Habitats (SSH, sensu Culver and Pipan 2019), including soil and leaf litter, rocky debris and other moist and shaded retreats (Fage 1919, Deeleman-Reinhold 1978, Isaia et al. 2010, Isaia et al. 2011, Isaia et al. 2017, Mammola et al. 2018a).

Troglohyphantes spiders display different levels of subterranean habitat specialisation. Species found in both caves and surface habitats are often able to withstand ecological variations, while others are almost exclusively found in caves and are characterised by behavioural, physiological and morphological adaptations to the stringent conditions of the subterranean habitat (Deeleman-Reinhold 1978, Isaia et al. 2017, Mammola et al. 2020, Mammola et al. 2022a). These adaptive traits include reduction or loss of eyes and cuticular pigmentation, thinning of the integument, heavier spination, appendage elongation, reduction in the metabolic rate leading to higher resistance to starvation, alteration of the circadian rhythm, reduction in fecundity, slower development, delayed maturation and extended longevity when compared with their surface relatives (for a review, see Mammola and Isaia 2017). Detailed descriptions and quantification of functional traits of *Troglohyphantes* spiders (hypogean affinity, upper thermal limits, conservation status and legal protection) are available with open access in the World Spider Trait database (Pekár et al. 2021).

As demonstrated by means of ecological niche modelling and physiological experiments (Mammola et al. 2018a, Mammola et al. 2019a), the increased specialisation to subterranean habitats seen in *Troglohyphantes* spiders, resulting from a long evolutionary history in a thermally stable environment, is accompanied by the concomitant narrowing of their thermal tolerance. While most species living close to the surface or in shallow subterranean environments have retained their ability to withstand temperature variations, specialised subterranean species of *Troglohyphantes* have lost such thermoregulatory mechanisms and are, therefore, particularly vulnerable to potential subterranean climatic variation induced by climate change (Mammola et al. 2019b).

Anthropogenic global warming is expected to significantly influence and modify the underground climate (Badino 2004, Domínguez-Villar et al. 2014), ultimately affecting subterranean biocoenosis and ecosystems (Mammola et al. 2019c, Sánchez-Fernández et al. 2021). This pressure is exacerbated by land-use change and habitat alteration, both subterranean and at the surface, which are, in general, regarded as the major threats to spider communities (Borges et al. 2016, Borges et al. 2019, Branco and Cardoso 2020, Milano et al. 2021, Mammola et al. 2022b). In addition, most of the occurrence localities of *Troglohyphantes* are highly isolated from each other, hindering the – already very poor – dispersal ability of these species (Cardoso et al. 2011, Mammola et al. 2015, Mammola and Isaia 2016).

Accordingly, recent analyses focusing on Western Italian Alps pointed towards a future decline in habitat suitability for specialised subterranean *Troglohyphantes* spiders and hypothesised potential high risk of local extinction for the most restricted endemic species (Mammola et al. 2018a). This prediction finds further confirmation in recent studies quantifying upper thermal limits of the western alpine species (Mammola et al. 2019a) showing very low ranges of thermal tolerance, especially for the most adapted species.

All in all, the existing wealth of threats facing subterranean biota (Mammola et al. 2022) and the ecological and biogeographical peculiarities of the *Troglohyphantes* spiders, strengthens the importance of considering these species in international and national conservation measures. Here, we aim to assess the Alpine and the north-western Dinaric species of the genus *Troglohyphantes* according to the International Union for Conservation of Nature (IUCN) Red List Criteria.

Methods

We compiled a comprehensive dataset with georeferenced records of the 66 species of *Troglohyphantes* occurring in the Alps and the north-western Dinarides, based on scientific literature, grey literature and unpublished records. We performed spatial analyses in R (R Core Team 2021), with the package 'red' – IUCN red-listing tools (Cardoso 2017), using either observed occurrences or estimated ranges. The package includes functions to calculate the Extent of Occurrence (EOO) and the Area of Occupancy (AOO), to map species ranges and to perform species distribution modelling.

In this work, we calculated EOO and AOO as follows:

- for species with low levels of subterranean adaptation (sensu Mammola et al. 2019a, hereinafter "non-specialised species"), with at least 15 records and for which we do not have full confidence about range limits, we modelled the range via species distribution modelling. Due to the lack of reliable absence data for our model species, we constructed a species distribution model using a standard presence-background algorithm (MaxEnt), with the function maxent in the 'dismo' R package (Hijmans et al. 2021). We modelled the distribution of the species using a combination of present-day climatic data and altitude above sea level (Fick and Hijmans 2017) at a spatial resolution of 30 arc-seconds (approximately 1 km at the Equator). As recommended in the literature (Peterson et al. 2011, Saupe et al. 2012, Merow et al. 2013), we calibrated species distribution models within a geographic area that we hypothesised has been accessible to the species. Considering the low dispersal potential of *Troglohyphantes* spiders (Mammola et al. 2018a), we approximated this area by buffering each occurrence by a diameter of 60 km. For a few species for which the density of records was low and scattered across the known distribution range (i.e. when the maximum distance between two neighbouring records exceeds 60 km), we assumed this area by buffering each occurrence record by 100 km. We performed a Principal Components Analysis on the predictor variables to generate new axes that summarised variation in fewer dimensions, thereby avoiding collinearity amongst covariates. To avoid overfitting, we retained the first four principal components. One hundred models were run for each species, using both coordinates and the associated spatial error. For each modelled distribution, we calculated EOO and AOO using specific functions in 'red' and reported their lower and upper confidence limits and the consensus values, calculated as all the cells predicted to be suitable for the species in at least 97.5%, 2.5% and 50% of the runs, respectively. These values are respectively reported as three consequent numbers in the relative sections "Extent of occurrence" and "Area of occupancy".

- for high and intermediate subterranean specialised species (sensu Mammola et al. 2019a, hereinafter "subterranean specialised") with narrow distribution ranges, we classified EOO and AOO as "observed" (in this respect see Mammola and Leroy 2017). For non-specialised species with less than 15 records, due to the unreliability of the distribution predicted by models with limited known occurrences, we based EOO and AOO on the “observed” distribution, with comments on the relative uncertainty about range limits. Particular cases are treated individually in each species profile. We used the minimum convex polygon encompassing all observations to calculate EOO and the 2 x 2 km cells known to be occupied to calculate AOO. When EOO was smaller than AOO, it was made equal as per the IUCN guidelines (IUCN Standards and Petitions Committee 2019);

We checked and validated the final maps and related values with our own expert opinion. We also produced KMLs maps using the 'red' function "kml".

We calculated the generation length of the species on the basis of the ecological information available in literature. Deeleman-Reinhold (1978) observed that subadults of *Troglohyphantes* species may moult up to 14 months after their collection. However, some non-specialised species passed through two moults in 5 months. Accordingly, we estimated a minimum generation length of two years for non-specialised species and four years for subterranean specialised species.

The nomenclature used in this work refers to the latest version of the World Spider Catalog (2022). All the species traits are sourced from the World Spider Trait database (Pekár et al.

2021). The toponomastics and classification of the different sectors and sub-sectors of the Alps follows the partition of the Alpine chain (SOIUSA, Marazzi 2005).

Species Conservation Profiles

Troglohyphantes achillis Isaia & Mammola, 2022

Species information

Taxonomy

Kingdom	Phylum	Class	Order	Family
Animalia	Arthropoda	Arachnida	Araneae	Linyphiidae

Taxonomic notes

In Mammola et al. (2018a) and Mammola and Isaia (2016), this species was treated as *T. vignai* (partim). Being a subterranean specialised species, results of ecological niche modelling used to project future habitat suitability in Mammola et al. (2018a) are equally applied to this species.

Region for assessment:

- Global

Figure(s) or Photo(s):

Fig. 1

Figure 1. doi

Troglohyphantes achillis Isaia & Mammola, 2022. Photo credit: Emanuele Biggi.

Reviewers

Marc Milne

Paulo Borges

Editor

Pedro Cardoso

Geographic range

Biogeographic realm:

- Palearctic

Countries:

- Italy

Map of records (Google Earth):
Suppl. material 1

Basis of EOO and AOO: Observed

Basis (narrative)

Caves in Western Alps have been extensively sampled, allowing us to define EOO and AOO of this species with reasonable confidence.

Min Elevation/Depth (m): 990

Max Elevation/Depth (m): 1414

Range description

This species is known from a few localities of the Chisone and Germanasca Valleys, in the Northern Cottian Alps, (north-western Italy) (detailed occurrences and relative references in Suppl. material 67).

Extent of occurrence

EOO (km2): 57

Trend: Decline (inferred)

Justification for trend

As seen in Mammola et al. (2018a) for other subterranean specialised *Troglohyphantes* species of the Western Alps, climate change is expected to affect the distribution of this species in the future. Given the reduced thermal tolerance of this organism and its low dispersal ability (Mammola et al. 2019c, Isaia et al. 2022), a reduction of its geographic distribution range is expected in the future.

Causes ceased?: No

Causes understood?: Yes

Causes reversible?: No

Area of occupancy

AOO (km2): 16

Trend: Decline (inferred)

Justification for trend

As seen in Mammola et al. (2018a) for other subterranean specialised *Troglohyphantes* species of the Western Alps, climate change is expected to affect the distribution of this species in the future. Given the reduced thermal tolerance of this organism and its low dispersal ability (Mammola et al. 2019c, Isaia et al. 2022), a reduction of its geographic distribution range is expected in the future.

Causes ceased?: No

Causes understood?: Yes

Causes reversible?: No

Locations

Number of locations: 1

Justification for number of locations

The habitat where this species occurs is affected by changes in subterranean microclimatic conditions due to climate change, which is expected to impact the whole population (Mammola et al. 2018a).

Trend: Stable

Population

Number of individuals: Unknown

Trend: Decline (inferred)

Justification for trend

In view of the reduced thermal tolerance of this species (Isaia et al. 2022), alterations of the microclimatic conditions of the habitat due to climate change are expected to impact the whole population of this species.

Basis for decline:

- (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat

Causes ceased?: No

Causes understood?: Yes

Causes reversible?: No

Subpopulations

Number of subpopulations: 4

Trend: Decline (inferred)

Justification for trend

Due to the subterranean adaptation and the narrow physiological tolerance of this species, hampering dispersal through non-subterranean habitats (see Mammola et al. 2015 about high genetic structuring in this species), each locality reasonably hosts a single highly isolated subpopulation. Accordingly, we identified four subpopulations, all likely to be impacted by climate change.

Habitat

System: Terrestrial

Habitat specialist: Yes

Habitat (narrative)

This species has been collected among the floor debris and on the walls of the twilight zone, in natural caves and mine prospects located at the medium alpine montane belt, from 1,000 up to 1,400 m above sea level, characterised by mean annual temperature values ranging from 6.1 to 8.9°C (Isaia et al. 2022). See Mammola and Isaia (2016) for a characterisation of the ecological niche of the species and additional information on its preferred habitat.

Trend in extent, area or quality?: Decline (inferred)

Justification for trend

As seen in Mammola et al. (2018a) for other species of *Troglohyphantes* of the Western Alps, a drastic decline in the habitat suitability of *T. achillis* as a consequence of climate change is expected.

Habitat importance: Major Importance

Habitats:

- 7. Caves and Subterranean Habitats (non-aquatic)

Ecology

Size: 3 mm

Generation length (yr): 4

Dependency of single sp?: No

Ecology and traits (narrative)

According to thermal tolerance tests, *T. achillis* shows intermediate thermal tolerance, reaching 50% mortality at temperature values 5°C above its cave temperature (Isaia et al. 2022). Females are present all year round, while males are found in small numbers in spring or early autumn and almost disappear in winter; annual sex ratio estimated on a population in a mine in the Chisone valley is 2.4:1 in favour of females (Mammola and Isaia 2016). See Mammola and Isaia (2016) and Isaia et al. (2022) for additional information on the ecological preferences of this species.

Threats

Threat type: Future

Threats:

- 11.1. Climate change & severe weather - Habitat shifting & alteration
- 11.2. Climate change & severe weather - Droughts
- 11.3. Climate change & severe weather - Temperature extremes

Justification for threats

This species is potentially exposed due to its extremely narrow geographic distribution range. As seen for other species of the genus *Troglohyphantes* of the Western Alps (

Mammola et al. 2018a), climate warming is expected to reduce the currently suitable habitat for this spider. Moreover, in view of its reduced thermal tolerance (Isaia et al. 2022), this species has a limited dispersal ability, which represents an additional concern in face of the ongoing increase of temperature.

Conservation

Conservation action type: In Place

Conservation actions:

- 1.1. Land/water protection - Site/area protection
- 1.2. Land/water protection - Resource & habitat protection

Justification for conservation actions

One of the records of this species is located within the Special Area of Conservation and Special Protection Area of the Orsiera Rocciavré (SAC/SPA IT1110006).

Other

Use type: International

Ecosystem service type: Important

Research needed:

- 1.2. Research - Population size, distribution & trends
- 1.3. Research - Life history & ecology
- 1.5. Research - Threats

Justification for research needed

Research on basic information such as distribution, ecology, life cycle and possible threats throughout the range are needed.

Troglohyphantes albopictus Pesarini, 1989

Species information

Taxonomy

Kingdom	Phylum	Class	Order	Family
Animalia	Arthropoda	Arachnida	Araneae	Linyphiidae

Region for assessment:

- Global

Reviewers

Marc Milne

Paulo Borges

Editor

Pedro Cardoso

Geographic range

Biogeographic realm:

- Palearctic

Countries:

- Italy

Map of records (Google Earth):
Suppl. material 2

Basis of EOO and AOO: Observed

Basis (narrative)

This spider was collected in very few localities. Its low level of subterranean specialisation, together with the observed high altimetric range of its known distribution, possibly reflects a higher dispersal capacity when compared to subterranean specialised species. Consequently, it may be possible that the present known range of this species is underestimated.

Min Elevation/Depth (m): 22

Max Elevation/Depth (m): 1661

Range description

Troglohyphantes albopictus is restricted to the Colli Euganei, the Colli Berici and the Prealps of Veneto (north-western Italy) (detailed occurrences and relative references in Suppl. material 67).

Extent of occurrence

EOO (km2): 2306

Trend: Stable

Justification for trend

This species is not strictly relegated to deep subterranean habitats, being collected both in epigean and shallow subterranean habitats. It is plausible that anthropogenic climate change may affect the habitat suitability of this species. However, in view of the relatively wide thermal tolerance and the relatively high dispersal ability of non-specialised *Troglohyphantes* species (Mammola et al. 2019a), the distribution range of *T. albopictus* is not expected to undergo significant reduction in the near future. A deeper study on the current distribution of this species and on the potential impacts of climate change is required.

Causes ceased?: Yes

Causes understood?: Yes

Causes reversible?: Yes

Area of occupancy

AOO (km2): 44

Trend: Stable

Justification for trend

This species is not strictly relegated to deep subterranean habitats, being collected both in epigean and shallow subterranean habitats. It is plausible that anthropogenic climate change may affect the habitat suitability of this species. However, in view of the relatively wide thermal tolerance and the relatively high dispersal ability of non-specialised *Troglohyphantes* species (Mammola et al. 2019a), the distribution range of *T. albopictus* is not expected to undergo significant reduction in the near future. A deeper study on the current distribution of this species and on the potential impacts of climate change is required.

Causes ceased?: Yes

Causes understood?: Yes

Causes reversible?: Yes

Locations

Number of locations: Not applicable

Justification for number of locations

No known threats to this species.

Trend: Stable

Population

Number of individuals: Unknown

Trend: Stable

Justification for trend

There are no currently known threats to the species.

Causes ceased?: Yes

Causes understood?: Yes

Causes reversible?: Yes

Subpopulations

Number of subpopulations: Unknown

Trend: Unknown

Habitat

System: Terrestrial

Habitat specialist: Yes

Habitat (narrative)

The species was collected both in epigean and shallow subterranean habitats. The record from Colli Berici was collected in a damp wood, in the vicinity of a small stream. No additional information about the habitat was provided.

Trend in extent, area or quality?: Stable

Habitat importance: Major Importance

Habitats:

- 1.4. Forest - Temperate
- 7.2. Caves and Subterranean Habitats (non-aquatic) - Other Subterranean Habitats

Ecology

Size: 3.9 mm

Generation length (yr): 2

Dependency of single sp?: No

Ecology and traits (narrative)

Not much is known about the ecology and life history of *T. albopictus*. This spider shows minor specialisation to subterranean life (Mammola et al. 2022a).

Threats

Threat type: Past

Threats:

- 12. Other options - Other threat

Justification for threats

The existence of threats is unknown for this species.

Conservation

Conservation action type: In Place

Conservation actions:

- 1.1. Land/water protection - Site/area protection
- 1.2. Land/water protection - Resource & habitat protection

Justification for conservation actions

Troglohyphantes albopictus has been recorded within several protected areas (EUAP0243 Parco Regionale dei Colli Euganei and SAC/SPA IT3260017 Colli Euganei - Monte Lozzo - Monte Ricco, SAC/SPA IT3210040 Monti Lessini - Pasubio - Piccole Dolomiti Vicentine, SAC/SPA IT3230022 Massiccio del Grappa).

Other

Use type: International

Ecosystem service type: Important

Research needed:

- 1.2. Research - Population size, distribution & trends
- 1.3. Research - Life history & ecology
- 1.5. Research - Threats

Justification for research needed

Research on basic information such as distribution, natural history, ecology and possible threats of the species would be needed.

OMISSIS: pp. 16 – 321.

In the original paper, the Result section is composed by 66 Species Conservation Profiles. For practical reasons, we here reported the Species Conservation Profiles of the first two species as examples.

Here follows the Discussion (p. 321).

Discussion

In this work, we assessed the extinction risk of 66 species of spiders belonging to the genus *Troglohyphantes* occurring in the Alps and in the north-western Dinarides (Fig. 16) according to the IUCN Red List Criteria (IUCN 2001, IUCN 2012). In most cases (62 out of 66 species), the data in hand allowed us to calculate the Extent Of Occurrence (EOO) and the Area Of Occupancy (AOO).

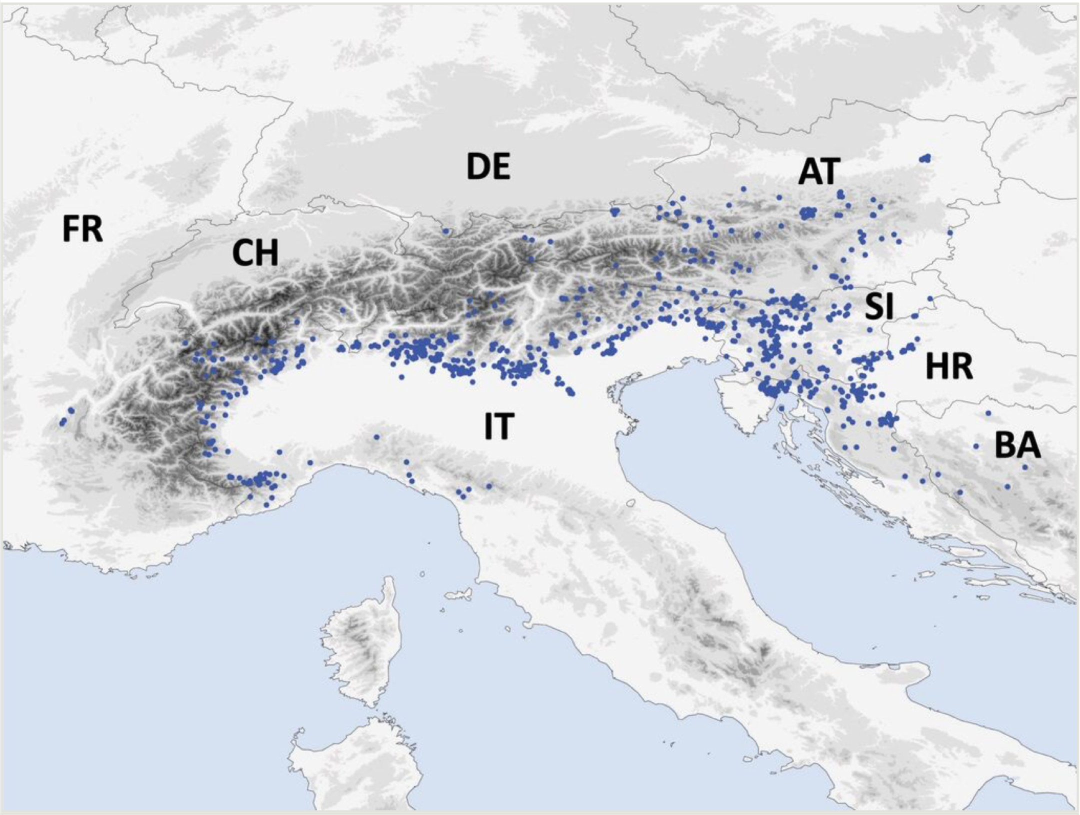

Figure 16. doi

Map of the Alps and the north-western Dinarides, showing all records of *Troglohyphantes* spiders considered in this work. AT = Austria; BA = Bosnia and Herzegovina; CH = Switzerland; DE = Germany; FR = France; HR = Croatia; IT = Italy; SI = Slovenia.

For 46 species, we derived geographic information, based on the known occurrences. In other cases (16 species), the number of occurrences allowed the application of Species Distribution Models. Four species were missing critical information to assess their status, being known on one or very few specimens or never being recorded after their original description (*T. cavadinii*, *T. comottii*, *T. cruentus* and *T. pavesii*).

Most of the species considered have a very narrow distribution range (14 species occurring in only 1–2 localities), with an estimated EOO < 20,000 km^2 and AOO < 2,000 km^2, meeting the thresholds for the inclusion in the threatened categories (Fig. 17). Only five species are more widespread, with an estimated EOO > 20,000 km^2 (Fig. 17).

Twenty species cover more than one country (seven of them more than two), whereas most of the species are restricted to one single country: 30 species occur only in Italy, 11 in Slovenia, three in Croatia, one in Austria and one in France (Fig. 18).

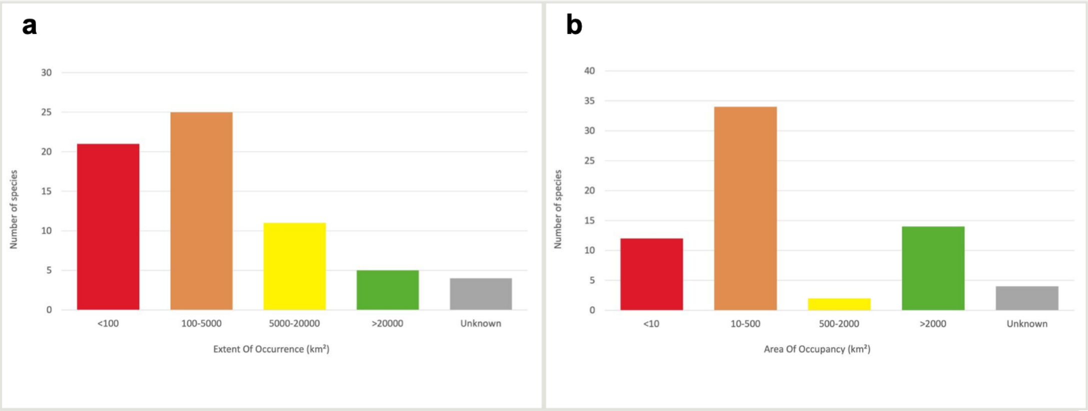

Figure 17.

Geographic range measures of the *Troglohyphantes* species assessed in this study: **a** Extent Of Occurrence (EOO) and **b** Area Of Occupancy (AOO).

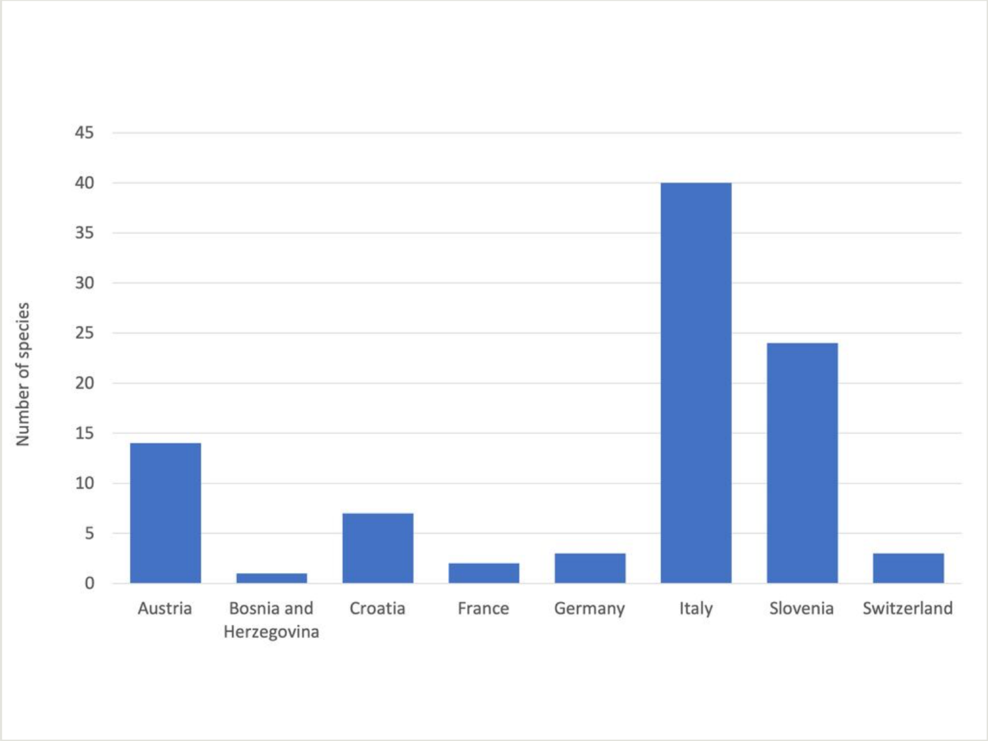

Figure 18. doi

Number of the *Troglohyphantes* species considered by country.

Trends in EOO, AOO and habitat quality were considered to be stable for 30 species (Fig. 19). These show minor adaptation to subterranean life, being mainly found in the vicinity of the cave entrance or in shallow subterranean habitats and for which no current major threats are known. It seems likely that these species are more able to withstand ecological variations and higher temperature increases compared to highly adapted subterranean species (Mammola et al. 2019a).

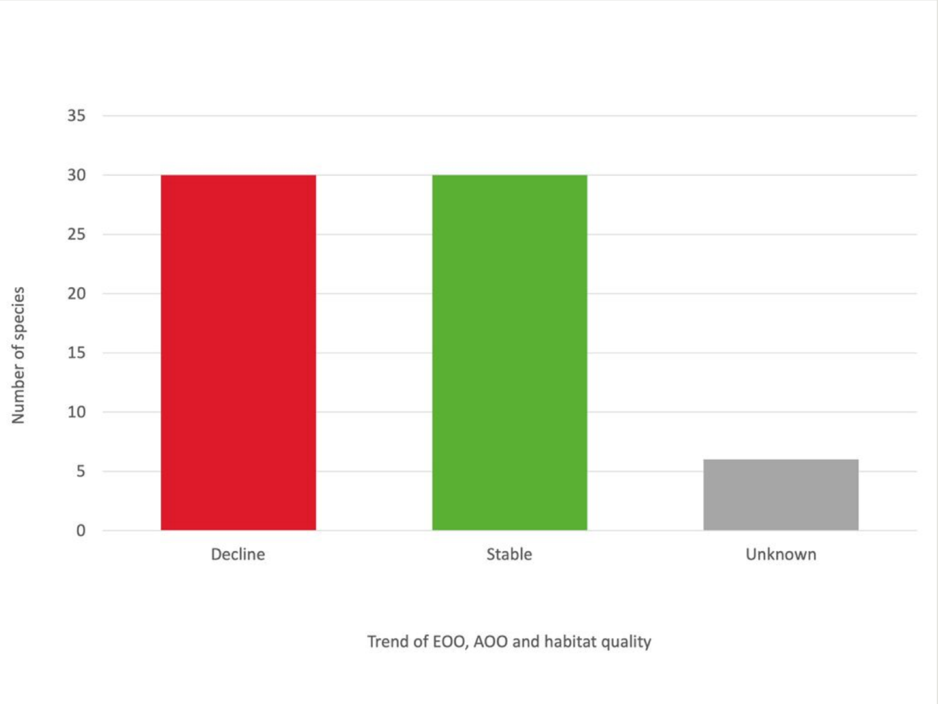

Figure 19. doi

Trend of Extent Of Occurrence (EOO), Area Of Occupancy (AOO) and habitat quality of the *Troglohyphantes* species considered.

Although most of the species showing poor adaptation to subterranean life have relatively low extinction risk in view of their relatively wide thermal tolerance and the relatively high dispersal ability, there are a number of species with a very restricted distribution, requiring further research attention and protection measures.

For 30 species, we inferred a decline in the EOO, AOO and habitat quality (Fig. 19). The majority of them are subterranean specialised species, thus showing fine-tuned thermal tolerance to the constant and narrow temperature ranges of the subterranean habitat (Mammola et al. 2019a). In a climate change perspective, this ecological feature turns out to be a strong limitation, preventing subterranean adapted species to accommodate changing conditions by dispersal or to persist *in situ* (Mammola et al. 2018a, Mammola et al. 2019b). Subterranean habitats are more sensitive to perturbation than other habitat types. Anthropogenic global warming is expected to significantly influence and modify the underground climate (Badino 2004, Domínguez-Villar et al. 2014, Mammola et al. 2019b). Considering their high sensitivity to the potential subterranean climatic variation induced by climate change, a reduction in the extent of the distribution of *Troglohyphantes* specialised species is expected, as demonstrated by Mammola et al. (2018a) for the species of the Western Alps.

Quarrying activities represented the major threat to one species, *T. exul*, a highly adapted subterranean species occurring in a single cave, for which the nearby quarries are expected to cause critical damage to cave habitat, altering microclimate and decreasing overall habitat quality.

Habitat loss and land-use change due to urbanisation and infrastructure development are also considered to be important drivers of increased extinction risk in cave animals, although they were identified as the main reason for the declining AOO and EOO for two species only (*T. latzeli* and *T. liburnicus*). Urban development can impact habitats through physical degradation and fragmentation, pollution by solid and liquid municipal waste and railway and road construction, leading to drastic declines in natural populations.

The main factor in the decline of *T. tauriscus* was identified as forestry and silvicultural practices, which is expected to lead to a loss of habitat suitability in some subpopulations across the species' range.

The high input agricultural activities represent the main threat for *T. spatulifer*, a species restricted to an isolated forest patch embedded in an intensively-managed agricultural landscape.

Forestry and intensive agricultural activities are also expected to negatively affect the habitat quality of other *Troglohyphantes* species in several areas, but it remains unclear whether they may represent major threats to the survival of these species.

For several subterranean species, a secondary impact has been recognised to be driven by tourism in caves. Cave tourism can have several impacts on the cave environment, such as physical modifications to cave habitats, marked fluctuations in temperature, changes in relative humidity and carbon dioxide concentrations and the possible accumulation of litter left by tourists in the cave (Fernandez-Cortes et al. 2011). These impacts negatively affect the subterranean ecological processes with cascade effects on all trophic levels.

The main threats to *Troglohyphantes* species are summarised in Fig. 20.

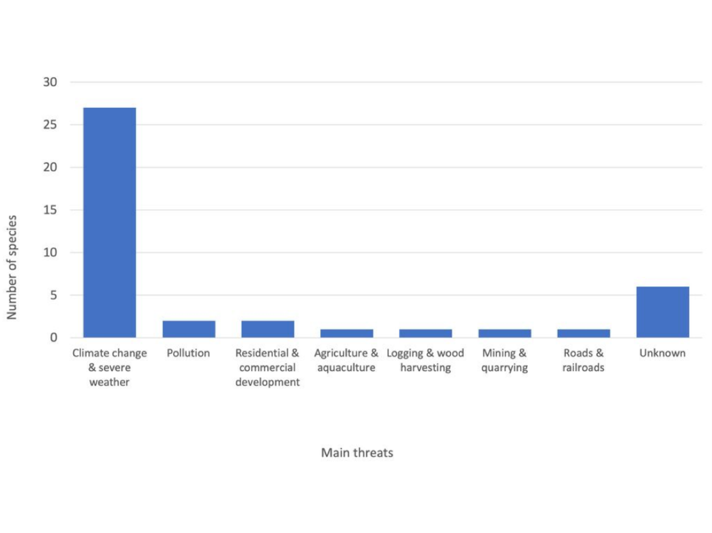

Figure 20. doi

Main threats to the *Troglohyphantes* species assessed in this study.

A considerable proportion of the species assessed has been found in protected areas and in sites of the Natura 2000 network. More than 80% of the species (53) here considered had at least one record in a site belonging to the Natura 2000 network and many of the subterranean occurrences have been collected in sites identified as Annex I habitats “Caves not open to the public” (Habitat 8310). However, most of the species assessed have a narrow distribution range that seldom overlaps with protected areas and many habitats of high conservation value for the *Troglohyphantes* species are poorly represented in the Natura 2000 network. Therefore, several species do not benefit from the Habitats Directive.

In addition, only 14 species (21%) are mentioned in national and sub-national legislation (Austria and Croatia). Almost all of them (13 species) have been listed in the 59th Regulation of the Carinthian State Government of 2015 (LGBl. Nr. 59/2015) and are fully protected from capture, collection, killing and disturbance according to the Carinthian Nature Conservation Act 2002 (LGBl. Nr. 79/2002). One species, *T. liburnicus*, is strictly legally protected in Croatia according to the Nature Protection Act (Official Gazette 70/05, NN 139/2008).

Of all species considered in this study, 25 (38%) are mentioned in regional Red Lists. Fifteen species are listed in the Red List of Slovenia (Uradni list RS št. 82/02 in 42/10) and considered potentially threatened due to their rarity (category R). Eight species are assessed in the Red List of endangered spiders for Carinthia (Komposch and Steinberger 1999), seven of which are considered extremely rare in the region (category R) and one is assessed as generally threatened (category G). Three species are listed in the category R of both the national Red List of spiders of Germany (Blick et al. 2016) and the regional Red List of Bavaria (Blick and Scheidler 2004). One species is assessed as Vulnerable in the Red Book of Croatian Cave Dwelling Fauna (Ozimec et al. 2009).

Three species (*T. gracilis*, *T. similis* and *T. spinipes*) are listed as Vulnerable in the IUCN Red List, based on their restricted geographical distribution (World Conservation Monitoring Centre 1996a, World Conservation Monitoring Centre 1996b, World Conservation Monitoring Centre 1996c). However, they were assessed before the publication of the new IUCN standards (version 3.1, 2001) and their evaluation is outdated and hard to compare with the assessments provided in this work.

One of the main shortfalls in the conservation of *Troglohyphantes* species is the general lack of biological information. As pointed out for spiders in Europe (Milano et al. 2021) and more generally for invertebrates (Cardoso et al. 2011), the majority of species are poorly known and the information is usually limited to their geographic distributions. Reliable data on population size are not available for any species of *Troglohyphantes* and their trends were mainly inferred by the decline in EOO and AOO. This makes the determination of the conservation status of these species difficult, with the risk of providing incomplete assessments and leaving many endangered species out from conservation planning and conservation priorities.

Long-term monitoring of species populations would be essential to provide key information on the population dynamics and their trends when assessing the species conservation (Mammola et al. 2022). Given the limited resources available for conservation and the need to maximise their allocation, monitoring the health of populations through a trait-based approach, such as the estimation of the stenothermic profiles of the species in relation to the variations of cave temperatures (Mammola et al. 2019b, Isaia et al. 2022) or the measurement of the species performance via morphological traits (Mammola et al. 2019a, Milano et al. in press), could help to reduce the knowledge gap (Lowe et al. 2020).

According to the threats identified for *Troglohyphantes* species, active management of the habitats more sensitive to perturbation is considered a priority for the conservation of the species. Subterranean specialised species, in particular, could benefit from general effective measures aiming at preserving the subterranean ecosystems (see Mammola et al. 2019c and Mammola et al. 2022). Although the protection of these habitats cannot limit the impact of climate change, the prevention or reduction of additional stress can increase the resilience of habitats and species to the effects of climate change.

Spiders have already been shown to be efficient and effective bioindicators in many terrestrial ecosystems (Bonte et al. 2002, Scott et al. 2006). Given their adaptations to the stringent conditions of the hypogean habitat (Deeleman-Reinhold 1978, Isaia et al. 2017, Mammola et al. 2019a, Mammola et al. 2020) and their vulnerability to microclimatic variations (Mammola et al. 2019b), subterranean specialised *Troglohyphantes* species could be potentially used as adequate bioclimatic indicators.

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Paper VIII

Taxonomy, ecology and conservation of the cave-dwelling spider *Histopona palaeolithica*, with the description of *H. petrovi* sp. nov. (Araneae: Agelenidae)

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Photo credit: Emanuele Biggi

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Abstract

The spider genus *Histopona* Thorell, 1869 (Araneae: Agelenidae) includes several species that exhibit a preference for subterranean conditions, being occasionally or exclusively found in caves, crevices and similar habitats. Within the genus, the species displaying the highest level of subterranean adaptation is possibly *H. palaeolithica* (Brignoli, 1971). This species was described based on a female collected in 1967 in a cave on the Western Ligurian shore (Italy), but had never been recorded thereafter. Our recent biospeleological surveys at the type locality failed to recover the species, possibly because the cave has been impacted by the expansion works of a large quarry. However, we found a new population in a cave opening a few hundred meters away from the type locality. As a result of this finding, we provide the first description of the male, as well as a re-description of the female. We also describe a new species of *Histopona* based on a female specimen that was collected in a cave in Montenegro, and was previously attributed to *H. palaeolithica*. In light of the rarity of these specialized stenoendemic species, we provide general information on their ecology and conservation status, as well as information useful for assessing their extinction risk based on International Union for Conservation of Nature (IUCN) guidelines.

Keywords: Endemism, extinction risk, Mediterranean, subterranean fauna, systematics

1. Introduction

The genus *Histopona* Thorell, 1869 (Araneae: Agelenidae) currently includes 22 species primarily distributed in the Central-Eastern Mediterranean basin (World Spider Catalog 2019). According to the latest overview of European subterranean spiders (Mammola et al. 2018), at least 15 of these species exhibit a preference for subterranean conditions, being occasionally or exclusively found in caves, crevices and similar habitats (Brignoli 1971, 1972, 1977a, b; Deltshev 1978; Deeleman-Reinhold 1983; Gasparo 2005; Deltshev & Petrov 2008; Bolzern et al. 2013). These ecological preferences parallel the appearance of morphological adaptations to the subterranean environment (i.e., troglomorphism; see Christiansen 2012), which in *Histopona* primarily pertains to size, loss of pigmentation and eye regression (Deeleman-Reinhold 1983). More specifically, the size of the anterior median eyes (AME) appears to be conspicuously reduced in the subterranean species, compared to their surface-dwelling relatives; for instance, a conspicuous reduction of the AME is found in *H. bidens* (Absolon & Kratochvíl, 1933), *H. dubia* (Absolon & Kratochvíl, 1933), *H. palaeolithica* (Brignoli, 1971) and *H. thaleri* Gasparo, 2005 (Absolon & Kratochvíl 1933; Kratochvíl 1938: 16, figs. 20, 24; Brignoli 1971; Gasparo 2005).

Within the genus, the species with the highest level of troglomorphism is possibly *H. palaeolithica* (Brignoli, 1971). This species was described on the basis of one female and one juvenile collected in 1967 by Augusto Vigna Taglianti in the Arma delle Arene Candide cave (Liguria, Italy). According to the original description (Brignoli 1971: 128), this species has only six eyes, because the AME are replaced by two small spots of black pigment (Fig. 1a). The species had never been collected after the original description and the male is as yet undescribed (Mammola et al. 2018; Pantini & Isaia 2019). With the aim of filling this taxonomic gap, between 2015 and 2018 we conducted repeated biospeleological searches at the type locality and in several caves in the nearby area. While our extensive surveys at the type locality failed to recover the species, we found a new population in a cave opening a few hundred meters away from the type locality.

As a result of this finding, we provide the first description of the male of *H. palaeolithica*, as well as a re-description of the female based on specimens collected in the new locality. In parallel, we provide the description of a new species of *Histopona*, based on the record of a female specimen from the Golubova pećina cave in Montenegro, which was formerly attributed to *H. palaeolithica* by Naumova et al. (2016). In light of the rarity of these species, we give general information on their ecology and conservation status, including details allowing for the assessment of their extinction risk according to the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (IUCN 2001, 2012).

2. Methods

Most specimens were stored in 75% ethanol in the Marco Isaia collection at the Department of Life Sciences and Systems Biology, University of Torino (Italy). A few specimens were further preserved in absolute ethanol for future DNA analysis, and exemplar specimens were deposited at the Museo Civico di Scienze Naturali ‘‘E. Caffi’’ (Bergamo, Italy). The holotype of the new species here described is lodged at the National Museum of Natural History Bulgarian Academy of Sciences (Sofia, Bulgaria). Specimens were examined using a Leica M80 stereoscopic binocular. Measurements are in millimeters (mm), and acquired using a Leica M80 stereoscopic microscope (up to 60x magnification). Measurements were taken from digital pictures made with a Leica EC3 digital camera, and calculated with the Leica LAS EZ 3.0 software (Leica Microsystems, Switzerland). All measurements are given in mm. Speleological cadastral codes of the caves are shown in squared brackets [‘regional code’ and ‘number’], and coordinates of localities are given in WGS84 datum, in decimal degrees.

Abbreviations.—AER = anterior eye row; ALE = anterior lateral eyes; ALS = anterior lateral spinnerets; AME = anterior median eyes; AOO = Area of Occupancy; d = dorsal; EOO = Extent of Occurrence; Fe = femur; MCSNB = Museo Civico di Scienze Naturali ‘‘E. Caffi’’ di Bergamo; Me = metatarsus; MI-coll = Marco Isaia collection; MSNV = Museo di Storia Naturale di Verona; NMNHS = National Museum of Natural History, Bulgarian Academy of Sciences, Sofia; p = prolateral; Pa = patella; PER = posterior eye row; PLE = posterior lateral eyes; PLS = posterior lateral spinnerets; PME = posterior median eyes; PMS = posterior median spinnerets; r = retrolateral; RTA = retrolateral tibial apophysis; Ta = tarsus; Ti = tibia; v = ventral.

TAXONOMY

Family AGELENIDAE C. L. Koch, 1837

Genus *Histopona* Thorell, 1869

Histopona palaeolithica (Brignoli, 1971)

(Figs. 1–2)

Cicurina (Chorizomma) palaeolithica Brignoli, 1971: 128, figs. 89, 90.

Histopona palaeolithica (Brignoli): Brignoli, 1977a: 952. Brignoli, 1977b: 38, figs. 13, 16. Deeleman-Reinhold, 1983: 336, figs. 20, 21.

Type material.—Holotype female. ITALY: Liguria (SV): Arma delle Arene Candide [Li 34], 44.162338N, 8.328318E, promontory Caprazoppa, Finale Ligure, 25 November 1967, A. Vigna Taglianti (MSNV; includes 1 juvenile specimen).

Other material examined.—ITALY: Liguria (SV): 4 ♀, Pozzo delle Cento Corde [Li 137], 44.163068N, 8.318228E, promontory Caprazoppa, Campi di Orso, Borgio Verezzi, 23 December 2016, D. Alterisio, M. Isaia, S. Mammola (MI-coll.); 1 ♀, 1 juvenile, same data except 6 March 2017, M. Isaia, S. Mammola (MCSNB); 2 ♀, 2 juveniles, same data except 20 April 2017, M. Isaia (MI-coll.); 2 ♀, 3 juveniles, same data except 18 October 2017, M. Isaia, S. Mammola (MI-coll.); 2 ♀, 1 ♂, same data except 2 June 2018, E. Biggi, M. Isaia, S. Mammola (MI-coll.).

Diagnosis.—Males of *Histopona palaeolithica* are best diagnosed by the shape of the tegulum and the positions of the origin and the distal tip of the embolus. Compared to the species of *Histopona* assigned to the *myops*-, *strinatii*- and *torpida*-groups (see Deeleman-Reinhold 1983 for species-group designations), the embolus is shorter, but it is longer in respect to the italica-group. Additional diagnostic characters are the shape of the conductor and the cymbium, the latter being less elongated compared to the *myops*-group and more elongate compared to the *torpida*- and *italica*-groups.

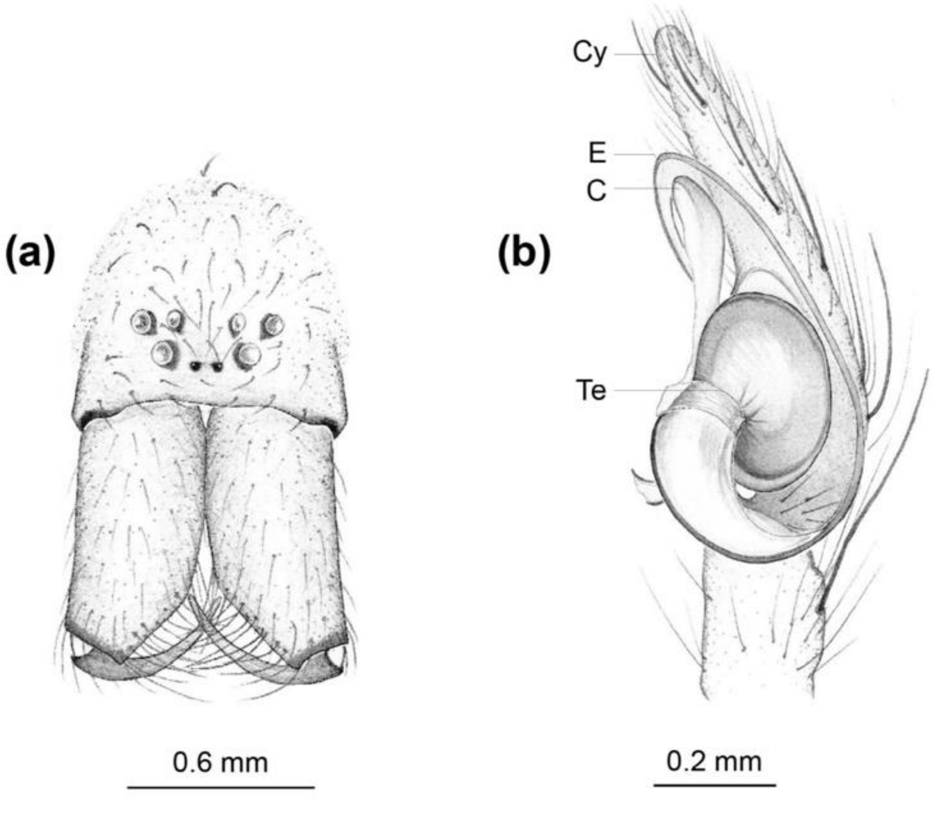

Fig. 1a–b. *Histopona palaeolithica* (Brignoli, 1971), male from Pozzo delle Cento Corde [Li 137] collected 2 June 2018: a, head region, frontal view; b, right palp, prolateral view. Abbreviations: C = conductor; Cy = cymbium; E = embolus; Te = tegulum. Illustrations by Elena Pelizzoli.

Description (male).—Measurements (n = 1; specimen from Pozzo delle Cento Corde [Li 137] collected 2 June 2018): Total length 4.98 (including spinnerets). Cephalothorax 1.77 long, 1.32 wide. Prosoma yellow-brown. Sternum yellow-brown, without pattern. Head region of the same color, 0.70 wide. PER 0.37 wide, AER 0.25. Eye diameter: AME 0.01 (no corneal lens is visible), ALE 0.06; PME 0.04; PLE 0.06. Both eye rows recurved in dorsal view. AME reduced to a small spot of pigment, other eyes normally developed (Fig. 1a). Clypeus height under AME 0.07, under ALE 0.09. Chelicerae: 0.62 long, 0.31 wide. Labium as long as wide or moderately wider than long. Sternum 1.08 long, 0.84 wide. Gnathocoxa ratio (width to length) 0.57. Chelicerae with 3 teeth on promargin and 5 teeth on retromargin. Opisthosoma 2.48 long (including spinnerets), grey-white without pattern. Colulus reduced, only two hairy plates are visible. Legs: I 6.83 (Fe 1.81) (Pa 0.52) (Ti 1.68) (Me 1.66) (Ta 1.16); II 6.03 (Fe 1.60) (Pa 0.42) (Ti 1.44) (Me 1.45) (Ta 1.12); III 5.82 (Fe 1.54) (Pa 0.39) (Ti 1.34) (Me 1.47) (Ta 1.08); IV 7.57 (Fe 1.88) (Pa 0.55) (Ti 1.84) (Me 2.13) (Ta 1.17); same color as prosoma, all trochanters notched. Chaetotaxy: I (Fe 2d, 1p, 1r) (Pa 2d) (Ti 2d, 2p, 1r, 2v) (Me 2p, 2r, 4v); II (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 1r, 4v) (Me 2p, 5v); III (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 2r, 3v) (Me 5d, 2p, 2r, 5v); IV (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 2r, 5v) (Me 2d, 3p, 2r, 3v) (Ta 1r). PLS longer than all others, distal segment as long as basal segment. PMS as long as ALS.

Palp (Figs. 1b–d): 2.02 (Fe 0.65) (Pa 0.21) (Ti 0.19) (Ta 0.87). RTA with a sclerotized dorsal branch, distally pointed; lateral branch forming a finger-shaped appendix; ventral branch forming a stout appendix, protruding ventrodistally. Cymbium elongated, similar to the species included in the *strinatii*-group, less elongated than in the *myops*-group, more elongated than in *torpida*- and *italica*-groups. Ratio bulb length (laterally from cymbium base to conductor tip) to cymbium length 0.68. Tegulum ring-shaped, ending in a filiform embolus originating at 7 o'clock position, with distal tip between 4 and 5 o'clock position. Embolus shorter than in *myops*-, *strinatii*- and *torpida*-groups, longer than in the *italica*-group. Conductor lamella-like, distally broadly rounded. Connection of conductor and tegulum membranous, band-like. Median apophysis and tegular apophysis absent.

Description (female).—Measurements (n = 1; specimen from Pozzo delle Cento Corde [Li 137] collected 20 April 2017). Total length 4.86 (including spinnerets). Cephalothorax 2.07 long, 1.35 wide. Prosoma yellow-brown. Sternum yellow-brown, without pattern. Head region of the same color, 0.83 wide. PER 0.32 wide, AER 0.25. Eye diameter: AME 0.02 (no corneal lens is visible), ALE 0.06; PME 0.03; PLE 0.07. Both eye rows recurved in dorsal view. AME reduced to a small spot of pigment, other eyes normally developed. Clypeus height under AME 0.08, under ALE 0.10. Chelicerae 0.79 long, 0.41 wide. Labium as long as wide or moderately wider than long. Gnathocoxa ratio (width to length) 0.60. Chelicerae with 3 teeth on promargin and 5 teeth on retromargin.

Sternum 1.14 long, 0.97 wide. Opisthosoma 2.78 long (including spinnerets), grey-white without pattern. Colulus reduced, only two hairy plates are visible. Legs: I 7.21 (Fe 2.00) (Pa 0.66) (Ti 1.71)

(Me 1.64) (Ta 1.20); II 6.61 (Fe 1.77) (Pa 0.70) (Ti 1.51) (Me 1.55) (Ta 1.08); III 6.36 (Fe 1.81) (Pa 0.62) (Ti 1.35) (Me 1.57) (Ta 1.01); IV 7.15 (Fe 2.13) (Pa 0.64) (Ti 1.39) (Me 2.12) (Ta 0.87); same color as prosoma, all trochanters notched. Chaetotaxy: I (Fe 2d, 1p, 1r) (Pa 2d) (Ti 2p, 4v) (Me 2p, 3r, 3v); II (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2p, 4v) (Me 2p, 2v); III (Fe 2d, 2p, 1r) (Pa 2d) (Ti 1d, 2p, 2r, 5v) (Me 2d, 3p, 3r, 1v); IV (Fe 2d, 2p, 1r) (Pa 2d) (Ti 1d, 2p, 3r, 4v) (Me 1d, 2p, 2r, 4v) (Ta 1r). PLS longer than all others with distal segment as long as basal segment. PMS as long as ALS. Palp: 2.31 (Fe 0.72) (Pa 0.27) (Ti 0.48) (Ta 0.84); chaetotaxy: (Fe 3d) (Pa 2d) (Ti 2d, 4p, 5r). Epigyne and vulva (Figs. 2a–c): epigynal plate 0.24 long, 0.30 wide, poorly sclerotized, subtriangular, marsupium-like, with a small undivided epigynal valve arising from the posterior margin (sensu Deeleman-Reinhold 1983) covering the copulatory openings. Copulatory ducts paired leading to the paired genital pouch, anteriorly straight or convex, directing into poorly sclerotized and pigmented rounded receptacula; fertilization ducts very short (Fig. 2c).

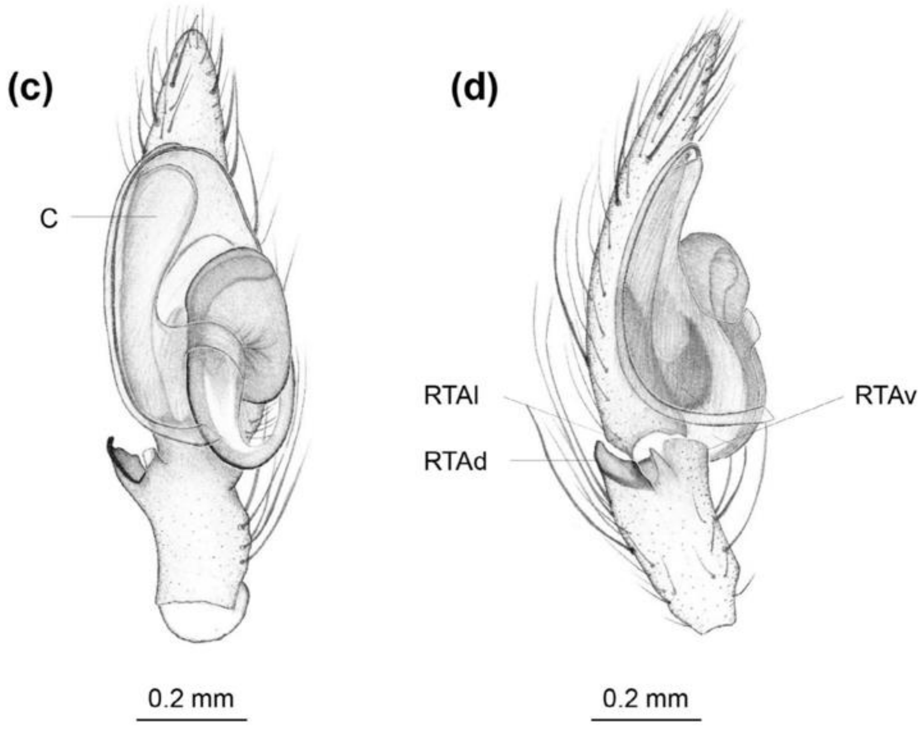

Fig. 1c–d. *Histopona palaeolithica* (Brignoli, 1971), male from Pozzo delle Cento Corde [Li 137] collected 2 June 2018: c, right palp, ventral view; d, right palp, retrolateral view. Abbreviations: C = conductor; RTAd = dorsal branch of RTA; RTAlv = lateral branch of RTA; RTAv = ventral branch of RTA. Illustrations by Elena Pelizzoli.

Distribution, sampling notes and ecology.—*Histopona palaeolithica* is restricted to subterranean habitats in the promontory of Caprazoppa (291 m elevation), located at ca. 0.5 km from the Mediterranean (Ligurian) shore. One population was reported in literature (Brignoli 1971) from the type locality, the Arma delle Arene Candide [Li 34] cave. A second population is herein documented for the Pozzo delle Cento Corde [Li 137] cave. Both caves open in stretches of Mediterranean scrubland.

Between 2015 and 2016, we conducted six visits to Arma delle Arene Candide, a 667 m long cave with restricted access due to the presence of remarkable paleontological remains (Mussi 2005; Catasto Spelologico Ligure 2018). In spite of our sampling efforts, including pitfall trapping inside the cave and in its surroundings, we were unable to find specimens of *H. palaeolithica*. In recent years, part of the cave was destroyed by the extension works of a large quarry. We believe that a secondary entrance, which was opened as a consequence of the mining activities, caused the alteration of air circulation patterns, changing local microclimatic conditions including the drying of the cave, which now results in an abundant presence of dust. According to the original collector, at the time of the collection of the type material (1967), the climatic conditions of the cave were remarkably different from the current ones, with high humidity and mud on the floor rather than dust (A. Vigna Taglianti, pers. comm. 2016). We hypothesize that these environmental alterations are likely to be the main cause of the extinction of the local population of *H. palaeolithica* in the cave. It is worth noting that the cave is also the type locality of four other arthropod species (Conci 1952), including the arachnids *Leptoneta crypticola franciscoloi* Caporiacco, 1950 (Araneae: Leptonetidae) and *Chthonius (Ephippiochthonius) concii* Beier, 1953 (Pseudoscorpiones: Chthoniidae), which were similarly never found during our surveys.

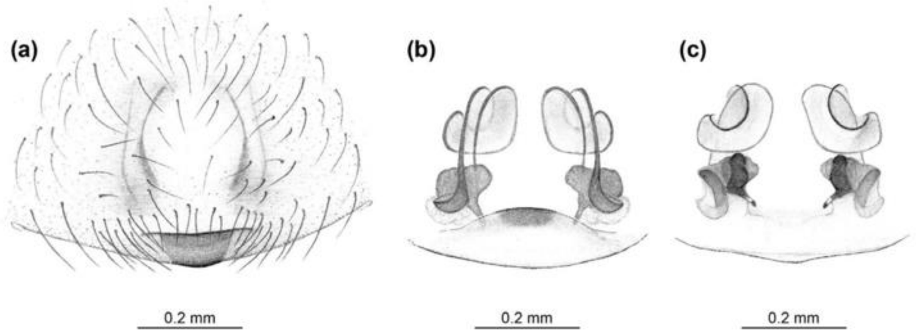

Fig. 2. *Histopona palaeolithica* (Brignoli, 1971), female from Pozzo delle Cento Corde [Li 137] collected 20 April 2017: a, epigyne, ventral view; b, epigyne cleared, ventral view; c, vulva, dorsal view. Abbreviations: Cd = copulatory duct; Ev = epigynal valve; Fd = fertilization duct; Gp = genital pouch; R = receptaculum. Illustrations by Elena Pelizzoli.

Conversely, individuals of *H. palaeolithica* are locally abundant in the Pozzo delle Cento Corde [Li 137] cave. This is a small vertical cave, whose entrance (1 3 1.5 m) opens at the base of the limestone cliff of the ''Falesia delle Cento Corde'' climbing site. The cave has a drop of -24 m and a total planimetric development of 36 m (Catasto Spelologico Ligure 2018). Individuals of *H. palaeolithica* were primarily found at the base of the first pit (-10 m), especially among the humid debris on the floor of the first room (10 × 10 × 4 m). Pozzo delle Cento Corde is a dry cave with a ground temperature ranging from approximately 21 °C in the entrance area to 17°C in the innermost sections (these climatic data based on winter temperature measurements by Motta & Motta 2017). In the first room, where most individuals were collected, ground temperature ranges from 19.2 to 20.9°C and relative humidity from 60 to 70% (Motta & Motta 2017).

Aside from caves, *H. palaeolithica* probably lives in interstitial habitats, such as narrow fissures in limestone rocks or under deep stones. The species spins a 5–7 cm wide sheet web, lacking a funnel (Fig. 3). The spider stands on top of the web (Figs. 3a–c). Females are abundant throughout the year, while males appear to be rare; five visits between 2016 and 2018 were necessary to find a single male specimen.

Conservation status and basic information for an IUCN Red List assessment.—Range description, Area of Occupancy (AOO) and Extent of Occurrence (EOO): the species is endemic to the Caprazoppa promontory (min–max elevation 0–291 m). In spite of our exhaustive searches in caves on the Western Ligurian shore (Riviera di Ponente), and more specifically in the area of Borgio Verezzi and Finale Ligure, including the type locality (Arma delle Arene Candide), we only found a population of *H. palaeolithica* in the Pozzo delle Cento Corde cave. The estimated EOO and AOO are both extremely small, less than 1 km^2. We infer a decline in both EOO and AOO as a result of quarrying activities. Dispersal ability for this species is not known, but since this is a highly specialized cave-dwelling species with restricted range, it is assumed that it has a very low dispersal capacity.

Locations: Despite significant targeted surveys and search effort, the only location known for this species is the Pozzo delle Cento Corde cave. As a result of changes in local microclimatic conditions due to quarrying activity, we consider the population of the type locality, Arma delle Arene Candide cave, locally extinct. The whole area of the Caprazoppa promontory is currently subject to quarrying activities, which are likely to represent a major threat to the species' survival.

Threats: The species is potentially exposed due to its extremely narrow geographic distribution range and its presumably low dispersal capacity. Given the general low tolerance to habitat changes of subterranean organisms, it is suspected that quarrying activities in the area may interfere with the species' survival. Secondary impacts could derive from tourism, due to the high number of climbers and hikers in the area. Moreover, the cave opening is easily accessible and located at the base of the climbing site. Even if climbing activities do not present a direct threat to the species' survival, the possible accumulation of litter thrown by tourists into the cave could cause changes in the cave environment and decrease habitat quality.

Conservation actions: In light of the mentioned threats, it is worth considering the extinction risk of *H. palaeolithica*. As very little is known about the biology and life history of this species, to date it is not possible to provide any precise management actions. However, the inclusion of this species on the IUCN Red List represents an important starting point for its conservation. As seen for other subterranean systems of conservation concern for red listed and legally protected species, *H. palaeolithica* could benefit from effective protection with adequate legislation aiming to preserve the Caprazoppa promontory from future expansion of quarrying activities. In addition, a strict code of conduct and specific guidelines for touristic, speleological and other activities inside and outside the Pozzo delle Cento Corde cave should be implemented.

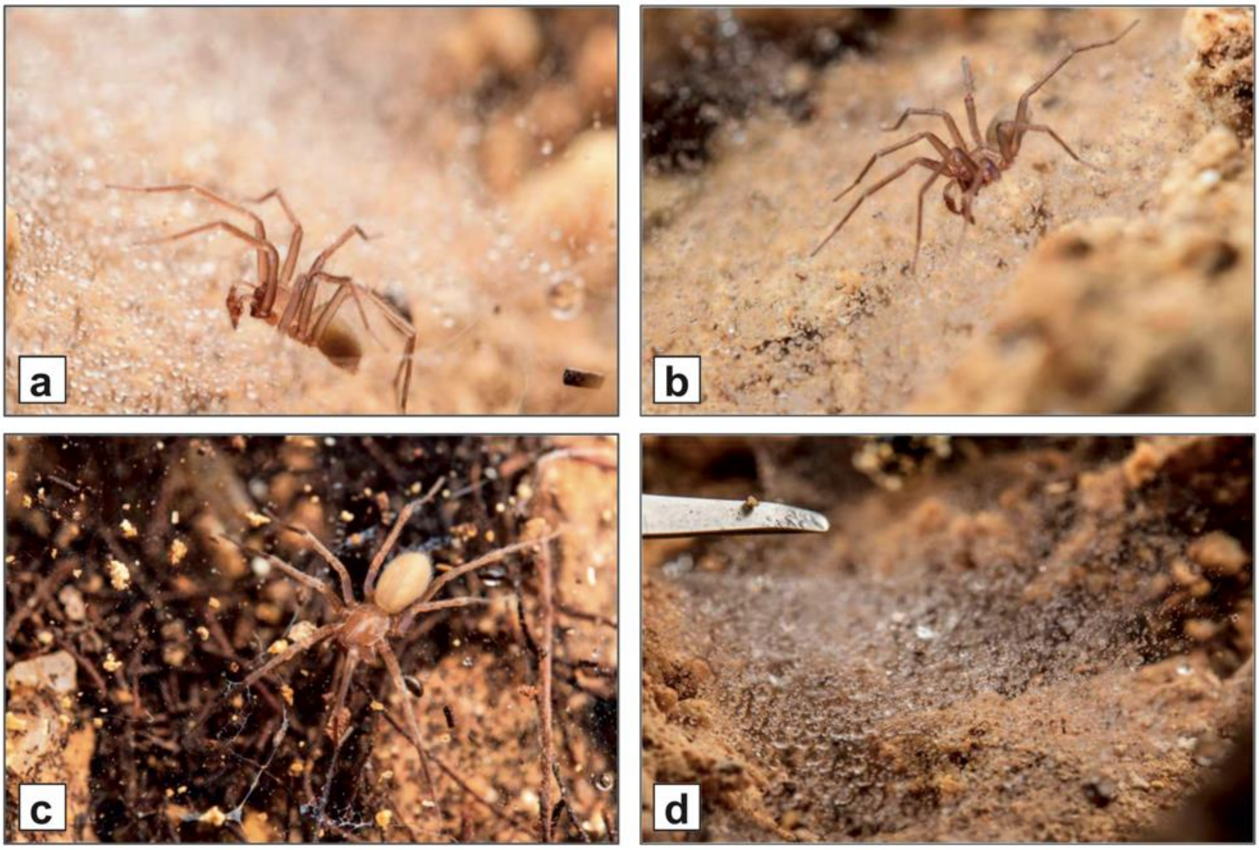

Fig. 3. *Histopona palaeolithica* (Brignoli, 1971), male from Pozzo delle Cento Corde [Li 137] collected 2 June 2018: a–c, habitus; d, shape of the web. Photo credits: Emanuele Biggi, used with permission.

Histopona petrovi Isaia & Mammola, sp. nov.

http://zoobank.org/?lsid1⁄4urn:lsid:zoobank.

org:act:F271C5DA-3C09-4BBA-B6B4-B9291F1B00ED

(Fig. 4)

Histopona palaeolithica Brignoli: Naumova et al., 2016: 432 (misidentified specimen from Golubova Pećina cave).

Type material.—Holotype female. MONTENEGRO: Bar: Golubova Pećina cave, 42.218N, 19.138E, Seoca village, Virpazar district, 12 August 2006, B. Petrov, S. Lazarov (NMNHS).

Etymology.—The species is dedicated to the Bulgarian zoologist and alpinist Boyan Petrov (1973–2018), one of the collectors of the type material. Boyan disappeared climbing his tenth eight-thousand meter peak in Himalaya, the Shishapangma (8,027 m).

Diagnosis.—*Histopona petrovi* sp. nov. is best diagnosed by the shape of the vulva (viewed dorsally), in particular by the shape of the spermathecae, which are conspicuous, tubular and arc-shaped (Fig. 4d). In comparison with *H. palaeolithica*, they are much more sclerotized and pigmented. The undivided valve of the epigyne arising from the posterior margin is also diagnostic, being trapezoidal rather than subtriangular, slightly curved in the middle and more pronounced than in *H. palaeolithica* (almost protruding when seen from above or from the side) (Figs. 4b,d).

Description (female).—Measurements (n = 1, holotype). Total length 4.58 (including spinnerets). Cephalothorax 1.95 long, 1.37 wide. Prosoma yellow-brown. Sternum yellow-brown, without pattern. Head region of the same color, 0.84 wide. PER 0.35 wide, AER 0.22 wide. Eye diameter: AME 0.01 (no corneal lens is visible), ALE 0.04; PME 0.03; PLE 0.06. Both eye rows recurved in dorsal view. AME reduced to a very small spot of pigment, other eyes normally developed (Fig. 4a). Clypeus height under AME 0.11, under ALE 0.13. Chelicerae 0.89 long, 0.38 wide. Labium as long as wide or moderately wider than long. Sternum 1.03 long, 0.96 wide. Gnathocoxa ratio (width to length) 0.42. Chelicerae with 3 teeth on promargin and 5 teeth on retromargin. Opisthosoma 2.43 long (including spinnerets), grey-white without pattern. Colulus reduced, only two hairy plates are visible. Legs: I 7.70 (Fe 2.01) (Pa 0.66) (Ti 1.84) (Me 1.85) (Ta 1.34); II 7.05 (Fe 1.86) (Pa 0.60) (Ti 1.68) (Me 1.76) (Ta 1.15); III 6.82 (Fe 1.73) (Pa 0.58) (Ti 1.60) (Me 1.72) (Ta 1.19); IV 9.06 (Fe 2.32) (Pa 0.51) (Ti 2.31) (Me 2.50) (Ta 1.42); same color as prosoma, all trochanters notched. Chaetotaxy: I (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 1r, 2v) (Me 2p, 2r, 4v); II (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 2r, 3v) (Me 4p, 3v, 3r); III (Fe 2d, 1r) (Pa 2d) (Ti 2d, 2p, 3r, 3v) (Me 3d, 4p, 2r, 4v); IV (Fe 2d, 2p, 1r) (Pa 2d) (Ti 2d, 2p, 3r, 5v) (Me 2d, 3p, 3r, 6v) (Ta 1r). PLS longer than all others, with distal segment as long as basal segment. PMS as long as ALS. Palp: 4.92 (Fe 0.62) (Pa 0.30) (Ti 0.60) (Me 0.94) (Ta 2.46); chaetotaxy: (Fe 3d) (Pa 2d) (Ti 2d, 5r, 4p). Epigyne (Figs. 4b,c) and vulva (Fig. 4d): epigynal plate 0.30 long, 0.39 wide, poorly sclerotized, trapezoidal, marsupium-like, with an undivided epigynal valve (sensu Deeleman-Reinhold 1983) arising from the posterior margin and covering the copulatory openings, similar in shape to the small undivided valve of *H. palaeolithica*, but bigger and slightly curved in the central part. When seen from above or from the side, the valve is protruding (more than in *H. palaeolithica*). Copulatory ducts paired leading to the paired genital pouch, directing into the heavily sclerotized and pigmented arc-shaped receptacula, not visible in dorsal view, but clearly visible after epigyne dissection, in dorsal view; fertilization ducts short but visible (Fig. 4d).

Distribution, sampling notes and ecology.—*Histopona petrovi* sp. nov. is known from only a single specimen collected in the Golubova Pećina cave. This is a narrow cave of about 100–150 m, opening at an elevation of 440 m in rocky habitats. The specimen was collected in the dark zone, about 40 m deep, under a stone. Cave internal temperature is around 14°C (Stoev & Enghoff 2008). Based on the morphological troglomorphism, in particular the depigmentation and AME reduction, we regard *H. petrovi* sp. nov. as a subterranean adapted species and likely a troglobiont (as defined in Mammola & Isaia 2017). Further information on the natural history and ecological preferences are required to confirm this observation.

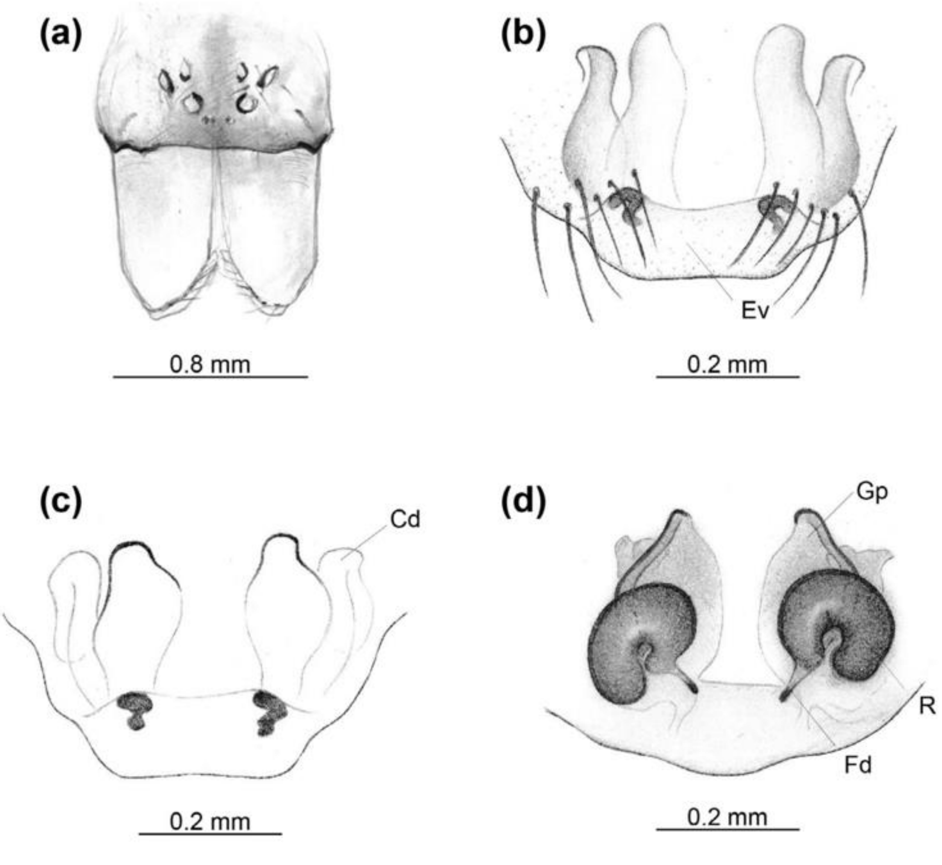

Fig. 4. *Histopona petrovi* Isaia & Mammola sp. nov., holotype female from Golubova Pećina: a, head region, frontal view; b, epigyne, ventral view; c, epigyne cleared, ventral view; d, vulva, dorsal view. Abbreviations: Cd = copulatory duct; Ev = epigynal valve; Fd = fertilization duct; Gp = genital pouch; R = receptaculum. Illustrations by Stefano Mammola and Elena Pelizzoli.

Conservation status and basic information for an IUCN Red List assessment.—*Histopona petrovi* sp. nov. is currently known from only a single cave. There is currently no information on the species' distribution, ecology or natural history, hindering the possibility of a direct or an indirect assessment of its risk of extinction. The Red List category ''Data Deficient'' (DD) should be therefore used in the event of a formal IUCN assessment. Basic research is needed to estimate the conservation status and the possible threats affecting this species.

3. Discussion

Histopona palaeolithica and *H. petrovi* sp. nov. exhibit somatic characters that justify their generic placement in *Histopona* (see Deeleman-Reinhold 1983; Bolzern et al. 2013). These include the eye arrangement, elongated sternum (i.e., reaching backwards between coxae IV), notched trochanters, leg spination (i.e., two dorsal spines on Fe II and two or more prolateral spines on Mt I), reduced colulus and absence of an abdominal or leg pattern. This interpretation also fits the case of the newly discovered male of *H. palaeolithica*, showing typical characters also in the male genitalia, namely more than one palpal tibial apophysis, an elongated cymbium and a long and thread-like embolus.

Based on morphological characters referring to female and partly to male genitalia, Deeleman-Reinhold (1983) classified the extant species of *Histopona* into five species-groups. Authors describing new *Histopona* species after 1983 kept using this classification by adding species to the extant groups or, in one case (*H. breviemboli* Dimitrov, Delshev & Lazarov, 2017), suggesting that the species could not be placed in any of the extant groups (Dimitrov et al. 2017). Excluding the latter species, the extant groups are the: *torpida*-group (7 species, from Central Europe to Caucasus); *myops*-group (7 species, Balkans), *strinatii*-group (2 species, Greece), *italica*-group (3 species, Italy) and *palaeolithica*-group (2 species, including *H. palaeolithica* from Italy and the newly described *H. petrovi* sp. nov. from Montenegro) (Fig. 5). Due to the absence of a male, Deeleman-Reinhold (1983) placed *H. palaeolithica* in a separate and self-standing group based on female characters, namely the peculiar small and undivided epigynal valve, a character shared with the monotypic genus *Hadites* Keyserling, 1862 and with some species of *Malthonica* Simon, 1898.

When considering our new findings, the male of *H. paleaolithica* exhibits some affinity with the species included in the *myops*- and *strinatii*-groups (i.e., male palp with conductor, but no apophysis on the radix). *Histopona petrovi* sp. nov. could also be placed in the *palaeolithica*-group based on the presence of a relatively small and undivided epigynal valve. From a morphological point of view, both species in the *palaeolithica*-group seem, to a certain extent, also related to *Hadites tegenarioides* Keyserling, 1862, described on the basis of one female and juvenile males from the island of Hvar (Croatia), approximately 180 km north from Golubova Pećina, along the Adriatic shore (Fig. 5), and whose taxonomical status appears in need of revision. However, in the absence of a proper morphological or molecular phylogenetic analysis, the delimitations of the species-groups and the phylgenetic position of *H. palaeolithica* and *H. petrovi* sp. nov., as well as their affinities to the genus *Hadites*, remain speculative.

The morphological peculiarity of *H. palaeolithica* is mirrored by its geographic distribution at the western periphery of the range of the genus, and by the lack of closely related species in the same area (Fig. 5). Other than for *H. torpida* (C.L. Koch, 1837) and *H. luxurians* (Kulczyński, 1897), which show wider distributions in Europe and Eastern Europe, respectively, the genus *Histopona* is represented by mid- or small-ranged species, most of them distributed in south-eastern Europe. Congeneric species occurring in Italy are represented by species included in the *italica*-group (i.e., *H. leonardoi* Bolzern, Pantini & Isaia, 2013, *H. fioni* Bolzern, Pantini & Isaia, 2013 and *H. italica* Brignoli, 1977 from the Alps and Apennines; see Bolzern et al. 2013), *H. torpida* (C.L. Koch, 1837) (*torpida*-group), with recent records in north-eastern Italy (Isaia et al. 2007; Ballarin et al. 2011; Hansen 2011; Trotta & Cherubini 2017) and old, poorly reliable records on the Italian and the French slopes of the Maritime Alps (Thorell 1875; Calloni 1889; Berktau 1890).

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This paper is dedicated to the memory of Prof. Augusto Vigna Taglianti (1943–2019), esteemed Italian zoologist and good friend of many of us. We are grateful for the major contribution he gave to the knowledge of the Italian fauna and for being a constant source of inspiration for the whole Italian scientific community, especially for the young zoologists. The finding of *H. palaeolithica* was indeed stimulated by the information he shared with us about the collection site of the type series of this species.

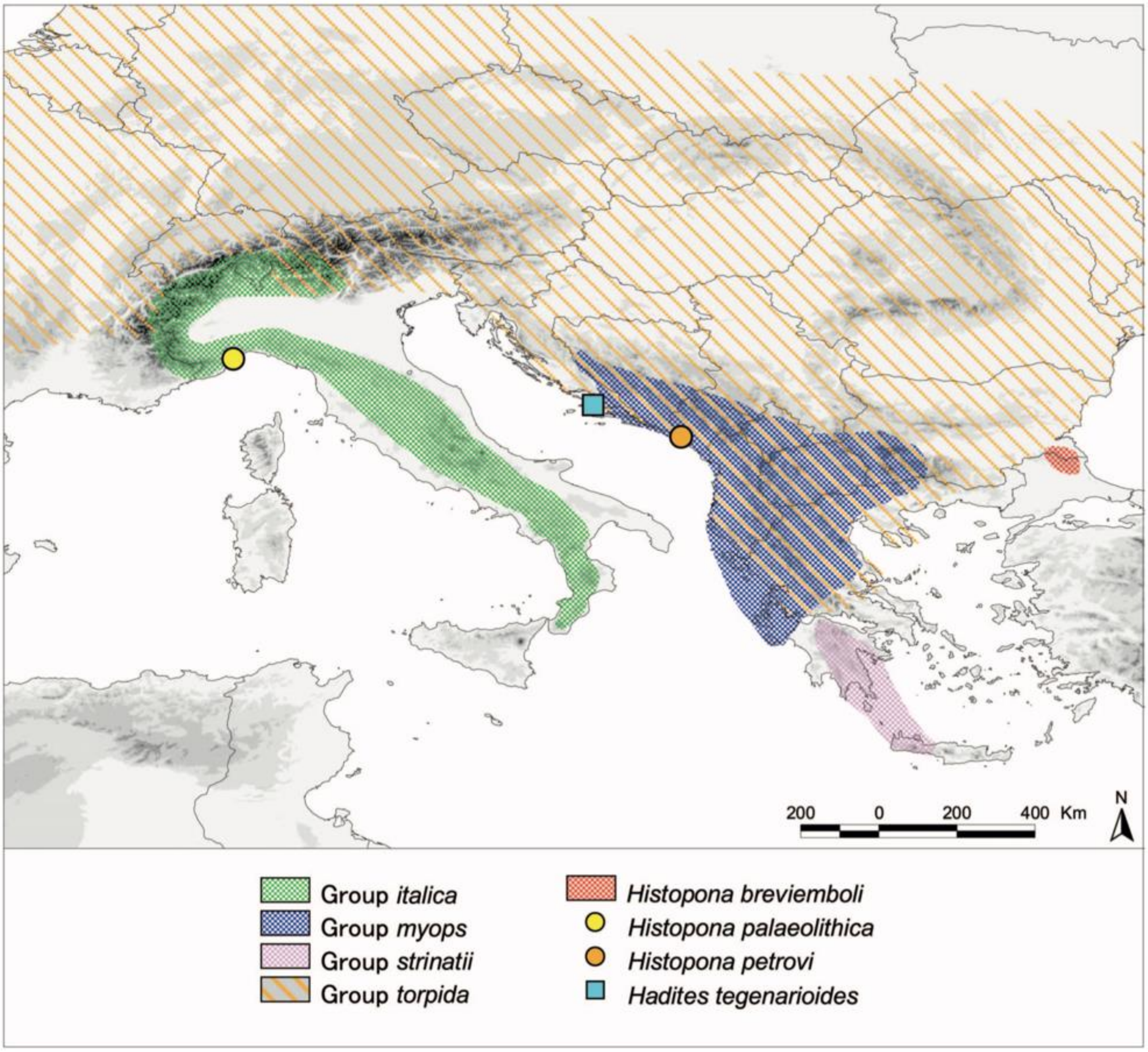

Fig. 5. Map of south-eastern Europe, showing the distribution range of the genus *Histopona* and the related species *Hadites tegenarioides* Keyserling, 1862, with reference to the species groups proposed by Deeleman-Reinhold (1983).

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