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## Double dare: Climate change and volcanic activity threatens local populations of *Meta menardi* (Araneae, Tetragnathidae) in Sicily

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### ABSTRACT

*Meta menardi* (Latreille, 1804) and *M. bournetii* Simon, 1922 (Araneae: Tetragnathidae) are ubiquitous inhabitants of the twilight zone of most hypogean sites across Europe. The two species are broadly distributed in Italy, including Sicily, where they show a remarkable segregation along the altitudinal gradient of Mount Etna. Thanks to our recent sampling activities in this area, we create a georeferenced dataset allowing the application of Species Distribution Modelling aiming at evaluating the current and the future habitat in light of the impacts caused by climate change on the local populations. We predicted a relatively wide suitable area for *M. bournetii*, ranging from the sea level up to 1100 m a.s.l., whereas for *M. menardi* the suitable area encompasses a narrow mid altitude strip, extending halfway between the areas suitable for *M. bournetii*, and the highly unsuitable volcanic uplands, heavily disturbed by the volcanic activity. The averaged future predictions for 2070 under RCP 8.5 scenario, show that *M. bournetii* will expand its range upwards, in areas that are now suitable for *M. menardi*. In turn, predictions for *M. menardi* indicate an extreme reduction of the current strip of suitable habitat, likely determining its local extinction. Our findings are further corroborated by the analysis of the bioclimatic niche of the two species assessed via multidimensional Hutchinsonian hypervolume, being much smaller in *M. menardi* compared to of *M. bournetii*. In light of our results, it seems likely that having wider climatic preference, *M. bournetii* will substitute *M. menardi* in most of its current range in Sicily. Future interventions aiming at the conservation of *M. menardi* on Mount Etna are strongly advised.

### 1. Introduction

Subterranean ecosystems are extremely stable environments compared to their surrounding external ones (Poulson and White, 1969; Howarth, 1993). Species thriving in these habitats often show pronounced sensitivity to even small environmental changes, especially pertaining temperature and humidity (e.g., Barr and Kuehne, 1971; Howarth, 1980; Mammola et al., 2019; Nicolosi et al., 2021). Thus, there is concern about the possible effect of climate change on subterranean coenosis, also in the light of their reduced physiological tolerance (e.g., Novak et al., 2014) and poor dispersal ability (e.g., Cardoso, 2012; Mammola et al., 2015), which prevents them from shifting their distributional range towards newly appearing patches of suitable habitat (Mammola et al., 2018).

Cave-dwelling invertebrates with poor subterranean adaptations have instead retained the ability to disperse effectively outside the caves in certain phases of their life cycle. This is well-exemplified by the troglophile cave-dwelling *Meta* spiders (Araneae:

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Tetragnathidae), ubiquitous inhabitants of the twilight zone of most hypogean sites across Europe. Despite widely distributed in subterranean habitats, *Meta* spiders show broad ranges of distribution compared to specialised subterranean spiders (Deltshev, 2011; Koponen, 1993; Mammola and Isaia, 2017), which can be explained in the light of their life cycle (Mammola and Isaia, 2014), including an epigeal and a hypogean ecophase. Indeed, after the first molt, spiderlings move towards the cave entrance and disperse via ballooning outside (Tercats, 1972; Smithers and Smith, 1998; Smithers, 2005). Thanks to this airborne dispersal, they can travel over long distances, thus colonizing sites that are far apart from each other. After three or four moults the spiders colonize hypogean sites and grows until adulthood is reached. The selection of hypogean sites is likely driven by climatic preference, with *Meta bourneti* preferably dwelling in warm hypogean sites (above 9 °C) and *M. menardi* selecting cool hypogean sites (5–9 °C) (Isaia et al., 2007; Mammola and Isaia, 2014). Such preference is reflected in the distribution of the two species, the first being particularly abundant in Southern Europe and widely distributed in the Mediterranean basin (Nentwig et al., 2022), from Europe to Georgia and North Africa (World Spider Catalog, 2022) and the latter being distributed in the Palaearctic region, reaching northward the Scandinavian Peninsula and eastward Ukraine and Turkey (World Spider Catalog, 2022).

Within caves, the ecological requirements of *Meta menardi* and *M. bourneti* are very similar, being both strongly bound to the twilight zone and selecting sites with higher abundance of prey (Mammola and Isaia, 2014). However, when the microclimatic conditions in a cave are favourable for *M. menardi* –narrow ranges of low temperature and high humidity– *M. bourneti* is apparently excluded by competition (Mammola and Isaia, 2014). However, the narrow climatic preferences of *M. menardi* makes it particularly vulnerable to increasing temperature due to climate change, which, on the contrary, is expected to favour the expansion of *M. bourneti* (Mammola and Isaia, 2017). Recent observations on Mount Etna lava tubes (Nicolosi et al., 2023b) pointed out for the first time the presence of an isolated population of *M. menardi* in Sicily. Here, in accordance with its preference for colder and wetter sites seen in Mammola and Isaia (2014), the species uniquely occurs in cool caves above 1200 m a.s.l., but unexpectedly disappear in caves located in the volcanic uplands over 1600 m. In accordance with its preference for drier and warmer sites, *M. bourneti* spans from the coastline up to a maximum altitude of 1200 m, where it possibly come into contact with *M. menardi*. However, not even here, the two species have ever been observed to coexist within the same hypogean site (see also Brignoli, 1971, 1979; Gasparo and Thaler, 2000; Milner, 2013; Ribera, 1978).

Considering the dispersal ability and the expected increasing trend of temperature, *Meta bourneti* and *M. menardi* are likely to increase the possibility of coming into contact on Mount Etna, representing an intriguing scenario to study their possible interaction.

Given that the two species have never been observed to coexist within the same hypogean site (Brignoli, 1971, 1979; Gasparo and Thaler, 2000; Isaia et al., 2011; Mammola and Isaia, 2017; Milner, 2013; Ribera, 1978), a negative interaction is highly expected. We hypothesize that the ongoing effects of climate change will impact their distribution patterns of the two species along the altitudinal gradient of Mount Etna by reducing habitat suitability for *M. menardi* and by favouring the upshift of *M. bourneti*. Moreover, the potential upshift of *M. menardi* could be hindered by the high frequency of volcanic events in the Etna uplands. Considering these dynamics, a comprehensive understanding of the factors influencing the distribution of *Meta* spiders living on Mount Etna is therefore required to establish appropriate management plans for their conservation – especially the highly isolated Sicilian population of *M. menardi* -, both at local and global scale. In this regard, this research aims at i) characterising the main bioclimatic factors driving the presence of the two species on Mount Etna; ii) investigating the environmental factors explaining the bioclimatic segregation of the two species; iii) predicting the future rearrangements of the two species ranges under future warming scenarios in the study area.

## 2. Material and methods

### 2.1. Study area

Mount Etna (Sicily, S-Italy) is an active volcano that spans 3350 m in elevation in Eastern Sicily, 20 km north of the city of Catania (37° 45'03.0"N, 14° 59'35.59"E). The volcano formed at the beginning of the Quaternary (Branca et al., 2008, 2011), and, according to Branca and Del Carlo (2004), is one of the most active volcanoes in the world.

The volcano covers an area of approximately 2100 km<sup>2</sup> which almost coincides with the Regional Park of Mount Etna (EUAP0227). The high frequency of volcanic activities, both effusive and explosive, as well as the opening of eruptive fissures on the flanks (e.g., Calvari et al., 1994), causes continuous modifications of the slopes, especially in the summit areas (Bisson et al., 2021). Due to its geographical, geological and climatic isolation, Mount Etna hosts a high floral and faunistic diversity (Caruso, 1999; Nicolosi et al., 2023a; Sabella and Nicolosi, 2023; Sciandrello et al., 2020). The vegetation is frequently affected by volcanic activities causing dramatic changes in structure, density, cover, floristic composition, species richness and diversity (Poli and Grillo, 2000).

Over 200 lava tubes are censused on the volcano (Centro Speleologico Etneo, 1999), opening at different altitudes and showing an extremely diversified range of ecological and microclimatic conditions. Caves closer to the sea coast are generally warm and dry, whereas caves opening near the summit are cold and humid. Although lava tubes are normally associated with *pahoehoe* lavas, on Mount Etna they formed in both “aa” and “*pahoehoe*” flows (e.g., Calvari, 1998), further increasing the extraordinary geodiversity of this area.

### 2.2. Species distributional data

Presence data of *Meta bourneti* (18 occurrences) and *M. menardi* (17 occurrences) on Mount Etna are issued from our previous contribution (Nicolosi et al., 2023b). Moreover, for this work we included a few more occurrences and 35 absence points obtained from recent field activities. Data cover a period of three years (2019 and 2021). After spatially thinning this dataset using a 1-km distance

parameter in the R package *spThin* (Aiello-Lammens et al., 2015), 49 unique data points remained. The distance between data points was set at 1 km taking as reference the highest spatial resolution of bioclimatic layers available from WorldClim data ([www.worldclim.org](http://www.worldclim.org)) (30 arc-seconds, corresponding to an approximate distance of 1 km).

### 2.3. Data extraction

We extracted the land use in a buffer of 50 m radius centred on the sampling site from regional digital maps (available at [www.site.regione.sicilia.it](http://www.site.regione.sicilia.it)) using QGIS (Quantum Gis Development 2023).

We calculated the percentage of vegetated areas, lava fields and anthropogenic use. The category “vegetated areas” incorporates land uses referring to natural vegetation, including woodlands, shrublands and prairies, while “anthropogenic use” included both agricultural and urban areas. “Lava fields” refers to those areas covered with recent lava flows and not covered by vegetation.

Cave temperature (T) was monitored in 2021–2022 using Hygrochron™ devices (accuracy:  $\pm 0.5$  °C) placed inside the cave. Measurements were taken every 12 h and the devices were retrieved after 12 months. Data from the Hygrochron™ devices were used to generate values of mean annual cave temperature, which was then related to the mean temperature values extracted from WorldClim data ([www.worldclim.org](http://www.worldclim.org)) for 1970–2000 and 2021–2040 series (resolution 30 s), using linear regression models – `lm` command in the ‘stats’ R package (R Development Team). The best fit of real vs WorldClim temperature data was obtained with the 1970–2000 data (see [Supplementary material, Table S1](#)), which was considered as the most suitable time series to represent the current climatic conditions.

We downloaded the average data for the years 1970–2000 of 19 bioclimatic variables with a spatial resolution of 30 s. These variables, derived from monthly mean temperature and rainfall patterns, are considered ‘biologically meaningful’ (see O’Donnell and Ignizio, 2012 for further details). They thus reflect a more accurate relationship with species-specific physiological constraints than simple monthly averages (Hijmans et al., 2005). For each sampling site, we extracted the value of each bioclimatic variable using the function “extract” from the package *raster* (Hijmans, 2015) in the R software (R Core Team, 2022).

Lava ages were obtained from the Geological map of Mount Etna (scale 1:50,000; Branca et al., 2011) and from the geodatabase of the Istituto Nazionale di Geofisica e Vulcanologia, Osservatorio Etneo (INGV-OE, <http://geodb.ct.ingv.it/geoportale/>).

The frequency of volcanic events (lava flows and pyroclastic events) was obtained by subdividing the study area into six altitudinal belts of 500 m each, and calculating the number of lava flows or pyroclastic events per year occurring in each belt in the time frame 1970–2000. The boundaries of each lava flow were extracted from the geo-database of the above-mentioned Geological map of Mount Etna. In addition, we used the historical catalogue of Branca and Del Carlo (2004) to include lava flows hidden by subsequent pyroclastic products. Data were plotted using a GIS platform (ArcGIS <https://www.esri.com/en-us/home>).

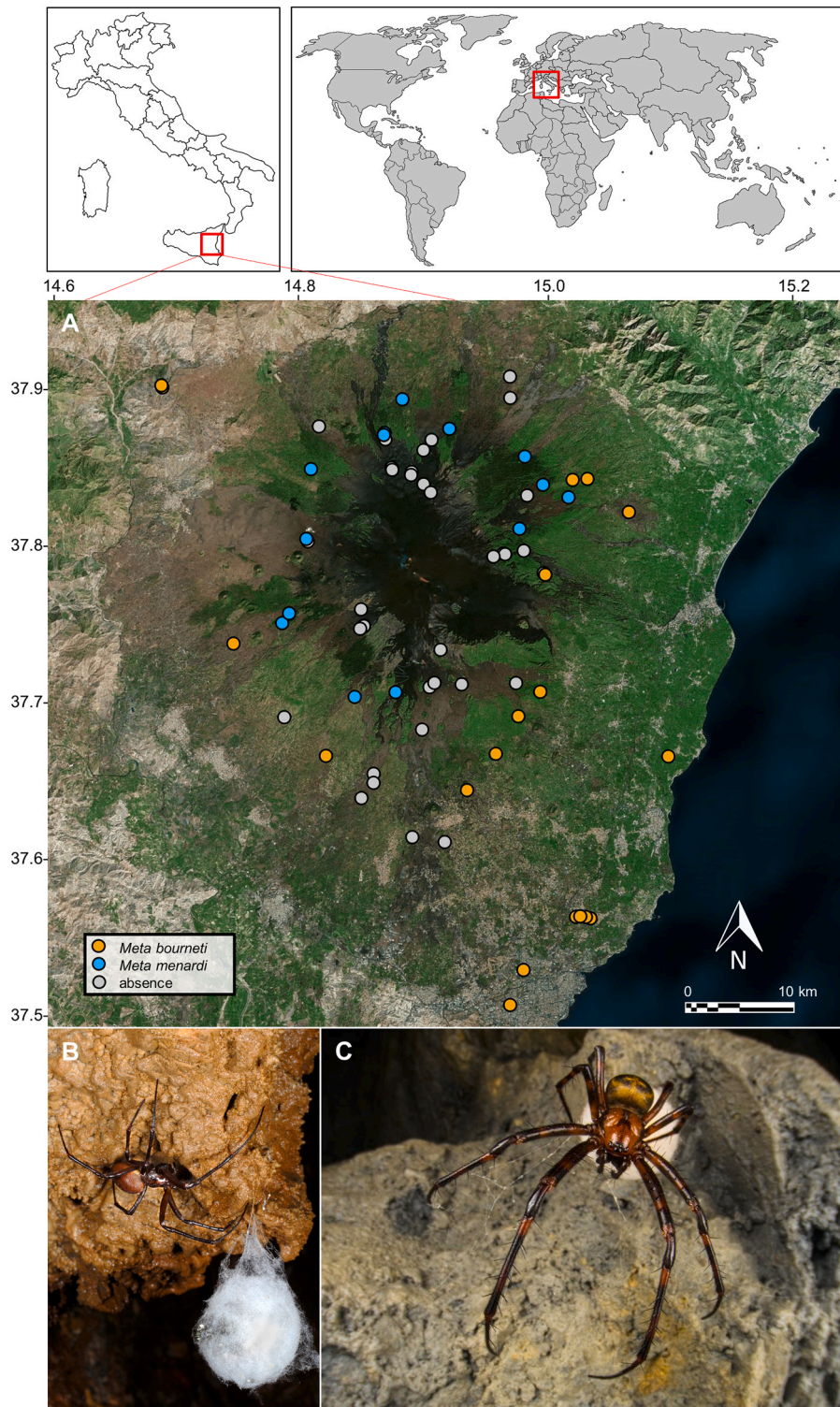
### 2.4. Statistical analyses

We performed all statistical analyses in R (R Core Team, 2022). In a first step, we reduced collinearity among bioclimatic variables and elevation by performing a Principal Component Analysis (PCA) using the ‘`princomp`’ function from the base stats package in R. Based on the scree plot (Fig. S1), we retained the first three axes (hereafter PC1, PC2 and PC3) that explained > 95% of the total variance (PC1 = 80.5%; PC2 = 10.2%; PC3 = 6.10%). Then, we tested the PCA axes for multicollinearity land use variables, lava age and frequency of volcanic events with the R Pearson test (Fig. S2). Being all variables highly correlated ( $|R| > 0.5$ ), we retained only the three PCA axes and the land use variable “vegetated areas” for the analyses of the ecological niche of the two species.

In a second step, we explored the factors driving the occurrence of the two species on Mount Etna lava caves using regression-type analyses (Zuur and Ieno, 2016). We performed a Generalised Linear Model (GLM) by using the `glm()` function in the stats-package in R by specifying a binomial distribution and a clog-log link for each species. We considered the presence of *Meta bournetii* or *M. menardi* as dependent variables (y), while PC1, PC2, PC3 and the land use variable “Vegetated areas” were used as independent ones. The structure of the models (in R notation) was:

$$y \sim \text{PC1} + \text{PC2} + \text{PC3} + \text{Vegetated areas}$$

Based on the results obtained from the previous analysis, we investigated the bioclimatic niches of the two species to highlight potential differences in their bioclimatic requirements. To perform this analysis, we calculated their multidimensional hypervolume *sensu* Hutchinson (1957) via the *hypervolume* R package (Blonder, 2015) based on the first three axes of the PCA, namely the variables showing a significant effect either on a species or the other. This approach quantifies the multidimensional Hutchinsonian hypervolume of a species based on a kernel density estimation procedure (KDE) performed on the standardised values of the environmental variables recorded in sites where the species is present (see Blonder et al., 2014). The hypervolumes of the two species were calculated with the `hypervolume.gaussian` R command (Blonder, 2015). Following the approach proposed by Blonder et al. (2014), we standardised the choice of bandwidth for each variable through a Silverman estimator (Silverman, 1992) and we set a threshold that included 100% of the total probability density. The overlap between the hypervolumes of the two species was obtained via the `hypervolume_set` and `hypervolume_overlap_statistics` R commands respectively (Blonder, 2015). Overlap statistics include the Jaccard and Sorensen similarity indices, ranging from 0 to 1 (0 = no overlap; 1 = complete overlap).



**Fig. 1.** Satellite image showing all occurrence records for *Meta bourneti* and *M. menardi* on Mount Etna (S-E Sicily). The spiders *M. bourneti* (B) (Photo: M. Isaia) and *M. menardi* (C) (Photo: E. Biggi) and on cave walls.

## 2.5. Species Distribution Models (SDM)

### 2.5.1. Environmental predictors

Based on the previous analysis, we modelled the current distribution of *Meta bournetii* and *M. menardi* in the study area based only on bioclimatic variables. We employed 19 bioclimatic variables at a resolution of 0.5' to represent current climatic conditions (www.worldclim.org). Subsequently, we selected only the uncorrelated bioclimatic variables from the initial set of variables ( $VIF < 5$ ), Temperature Annual Range (BIO07), Mean Temperature of Wettest Quarter (BIO08), Precipitation of Wettest Quarter (BIO16), Precipitation of Warmest Quarter (BIO18), Precipitation of Coldest Quarter (BIO19). Data layers at the same spatial resolution were obtained for future scenarios (2070). The data available here are climate projections from the general circulation model (GCM) CCSM4 that were downscaled and calibrated (bias corrected) using WorldClim 1.4 as baseline climate. For CMIP5 we used the representative concentration pathway (RCP) with a low and high-emission (respectively RCP 2.6 and 8.5) scenario, which corresponds to the pathway with the lowest and the highest greenhouse gas emissions (Wayne, 2013).

### 2.6. Modelling procedures

Modelling was carried out in the R 4.2.1 statistical programming environment (R Core Team, 2022). For both species, we conducted three commonly used Species Distribution Models (SDMs) with default parameters for presence-absence data, utilizing the 'sdm' package (Naimi and Araújo, 2016). We then selected the models that exhibited the highest levels of performance. Models included a regression method (generalised linear models, GLM; McCullagh and Nelder, 2019), a machine learning method (random forests, RF; Breiman, 2001) and a classification method (flexible discriminant analysis, FDA; Hastie et al., 1994). For modelling, the occurrence points of one species were considered as true absence of the other species, and vice versa.

We performed model validations using the bootstrapping replication approach with the 'sdm' package developed by Naimi and Araújo (2016). To assess model performance, we employed the area under the Receiving Operator Curve (AUC) and the true skill statistic (TSS; Allouche et al., 2006). The AUC value ranges from 0 to 1 (Fielding and Bell, 1997), with 0.50 indicates a model performance equivalent to random chance and 1.0 indicating perfect discrimination (Swets, 1988). TSS, a threshold-dependent metric, varies between -1 and 1, with 1 representing perfect model performance and values less than or equal to zero indicating performance no better than random (Allouche et al., 2006). To assess model performance, we calculated the mean AUC and TSS across fifty replicates of each algorithm for all species.

Each SDM fitted using the current climate data was projected into the future climate scenarios. The mean habitat suitability was calculated for each current and the two 2070 climate-model scenarios. We subsequently compared the habitat suitability for both current and 2070 future predicted climate scenarios under the CMIP5 (RCP 2.6 and 8.5) to show changes in habitat suitability for both species.

The 'sdm' package was used to combine the distribution maps using the "ensemble" function to produce consensus 'ensemble' maps based on weighted AUC values (Naimi and Araújo, 2016). Ensemble prediction is a process of synthesising integrating multiple individual models to provide robust estimates of potential species' distributions (e.g., Araújo and New, 2007; Marmion et al., 2009; Meller et al., 2014; Poulos et al., 2012; but see Crimmins et al., 2013; Zhu and Peterson, 2017). Binary maps were created where pixels exceeding a certain threshold indicated the presence of *Meta* spiders under various climate projections, while pixels falling below the threshold signified the absence of *Meta* spiders across all models. Subsequently, these maps were utilized to calculate the percentage of occurrence for both species in both present and future scenarios using QGIS (Quantum Gis Development 2023).

## 3. Results

The database used for the analysis included 34 presence sites of *Meta* species (19 presence for *M. bournetii* and 15 presences for *M. menardi*) and 35 absence sites (Fig. 1).

A list of the investigated lava caves and species detected is reported in Table S2. According to our results, 22 out of 69 sampling sites fall into recent volcanic areas (<500 years) (Table S2), being all absence data. *Meta bournetii* and *M. menardi* occurred exclusively in vegetated habitats and, in particular, in those sites dominated by arboreal (26 out of 34) or shrubby (8 out of 34) vegetation (Table S2). Moreover, *Meta menardi* occurred only in caves above 1200 m a.s.l. (mean  $\pm$  SD = 1379  $\pm$  207 m) while *M. bournetii* occurred at lower altitudes (646  $\pm$  380 m). None of the species occurred over 1600 m and they were never found together in the same caves (Fig. 1, Table S2).

### 3.1. Frequency of volcanic events (1970–2000)

The volcanic events on Mount Etna occur frequently at the summit craters whereas flank eruptions take place at intervals of years (Branca and Carlo, 2005). Accordingly, when considering the number of events during the period 1970–2020, we registered the highest frequency on the 3000–3300 altimetric belt (28), gradually decreasing in belt at lower altitudes (Fig. S3; Table S3).

As a result of a higher number of events, the percentage of lava covering the summit areas was higher compared to the lower ones. In particular, the 3000–3300 and 2500–3000 belts showed 36.91% and 35.62% values of lava coverage, respectively. However, when considering the presence of exposed pyroclastic deposits on the summit area, the percentage drastically increased, reaching 100% and 70%, respectively (Table S3).

### 3.2. PCA and generalised linear models

The PCA analysis highlighted a clear separation between sites colonised by *M. menardi* and *M. bournetii* (Fig. S4) that was confirmed by the results of the PERMANOVA ( $F_{2,66} = 21.7$ ;  $P < 0.001$  \*\*\*).

The generalised linear mixed model pointed out that PC1 to play a significant role in predicting the presence of *M. bournetii* (Table 1, Estimate  $\beta \pm$  SD:  $0.58 \pm 0.16$ ,  $P < 0.001$  \*\*\*). For *M. menardi*, we recovered a significant negative response to PC1 ( $-0.56 \pm 0.25$ ,  $P = 0.025$  \*) and PC2 ( $-0.99 \pm 0.45$ ,  $P = 0.025$  \*) and a significant positive response to PC3 ( $1.21 \pm 0.56$ ,  $P = 0.031$  \*). No effect due to vegetation was recovered by our analysis. The results of GLM are given in Table 1.

### 3.3. Hypervolumes

The analysis of the niche hypervolumes showed a greatest four-dimensional hypervolume for *M. bournetii* (1461.0), whereas for *M. menardi* the dimension was around 45-fold smaller (31.4). The visual inspection of the overlap between the two hypervolumes (Fig. 2) showed that the bioclimatic niche of *M. menardi* was almost completely comprised into that of *M. bournetii*, as demonstrated by the unique fractions of the two hypervolumes (Jaccard = 0.03, Sorensen = 0.07; unique fraction *M. bournetii* = 0.97; unique fraction *M. menardi* = 0.01).

### 3.4. SDM - Model performance

The performance of SDMs using different evaluation techniques is presented in Table 2. Most of the individual models performed well in respect to all evaluation metrics. The AUC values for predictive accuracy exceeded 0.80 in all cases, while TSS values ranged from 0.69 to 0.84 (Table 2). For *M. bournetii* the RF model showed the highest AUC with 0.9, followed by GLM (0.84) and FDA (0.82), while for *Meta menardi* the RF showed the highest AUC with 0.94, followed by FDA (0.83) and GLM (0.82). (Table 2).

### 3.5. SDM - Environmental variables and response curves

The relative influence of predictors across models is shown in Fig. 3. For *Meta bournetii*, the temperature of the wettest quarter (BIO08) contributed most to all models, with respectively 71.6% (GLM), 25.8% (RF) and 51.3% (FDA). For *Meta menardi*, the Temperature Annual Range (BIO07) contributed most to the GLM model (52.0%), whereas the Precipitation of Warmest Quarter (BIO18) had the top contribution on the RF (14.8%) and FDA (55.2%) models (Fig. 3).

### 3.6. Current and future distribution of *Meta* spiders in Sicily

The ensemble models for both species agreed with the known distribution of the two species on Mount Etna (Fig. 4). The current suitable area for *Meta bournetii* was predicted from the sea level up to an altitude of approximately 1100 m along all the slopes of the volcano (Fig. 4). The current suitable area for *Meta menardi* was predicted along a narrow strip on Mount Etna, between 1000 and 1600 m a.s.l.

The averaged future prediction under the RCP 2.6 and 8.5 scenarios in the year 2070 shows in both cases a gain in habitat suitability for *Meta bournetii* along the uplands of Mount Etna, respectively of + 17.39% and + 21.56% (Table 3). The species is expected to extend its distribution up to approximately 1600 m a.s.l. on the southeastern side, and at slightly lower elevations on the northern slope of the volcano, interfering with sites that are currently colonised by *Meta menardi* (Fig. 4). For both future scenarios (RCP 2.6 and 8.5) a complete loss of habitat suitability for *M. menardi* on Mount Etna is predicted (Fig. 4 and Table 3).

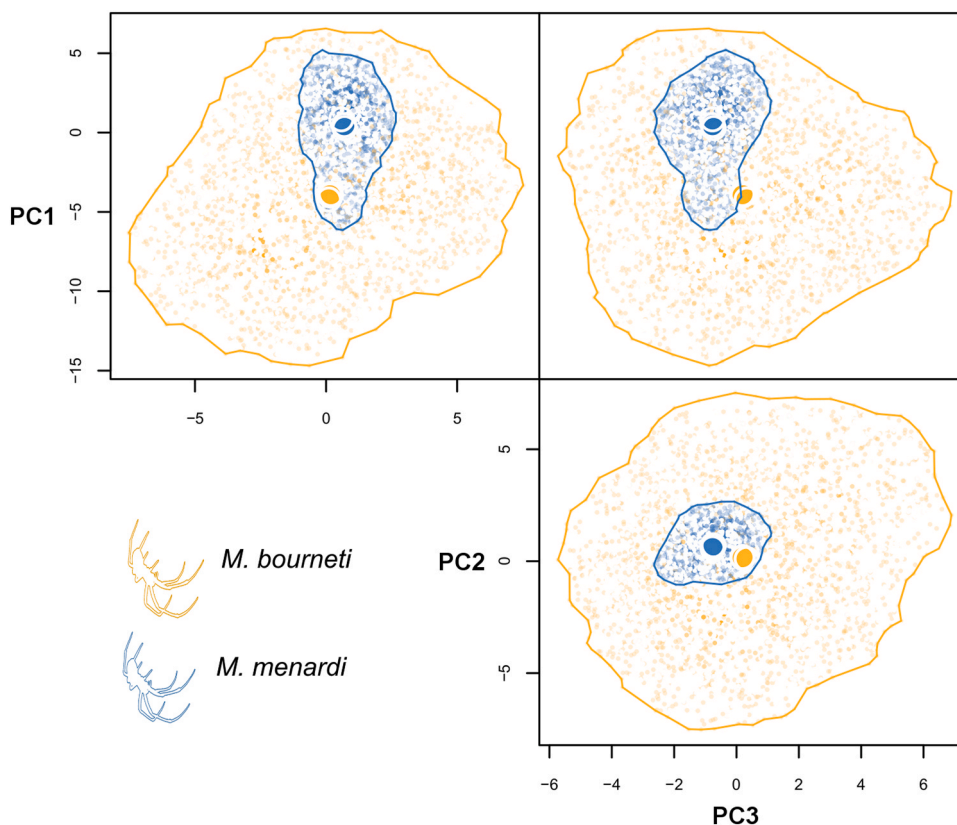
## 4. Discussion

Cave microclimate and the related environmental factors proved to be particularly important in determining habitat preference and

**Table 1**

Estimated regression parameters (Estimated  $\beta \pm$  S.E.) of the Generalised Linear Model (GLM) investigating the factors predicting the presence of *M. bournetii* and *M. menardi* on Mount Etna.

Species	Model	Variables	Estimated $\beta \pm$ S.E.	z	P-value
<i>M. bournetii</i>	$y \sim$ PC1 + PC2 + PC3 + Vegetated areas	Intercept	-2.41 $\pm$ 0.65	-3.71	< 0.001 ***
		PC1	0.58 $\pm$ 0.16	3.60	< 0.001 ***
		PC2	-0.18 $\pm$ 0.22	-0.83	0.405
		PC3	0.34 $\pm$ 0.24	1.40	0.160
		Vegetated areas	0.17 $\pm$ 0.35	0.48	0.633
		<i>M. menardi</i>	$y \sim$ PC1 + PC2 + PC3 + Vegetated areas	Intercept	-3.04 $\pm$ 0.85
PC1	-0.56 $\pm$ 0.25	-2.24		0.025 *	
PC2	-0.99 $\pm$ 0.45	-2.24		0.025 *	
PC3	1.21 $\pm$ 0.56	2.15		0.031 *	
Vegetated areas	0.83 $\pm$ 0.45	1.83		0.067.	



**Fig. 2.** Pair plots showing the estimated three-dimensional hypervolumes of *Meta* spiders on Mount Etna (orange = *M. bournetii*; light blue = *M. menardi*). The colored points for each taxon reflect the centroids (large points), original observations (intermediate points) and the stochastic points sampled from the inferred hypervolume (small points).

**Table 2**

Evaluation metrics of model performance for *Meta menardi* and *M. bournetii*, including AUC (Area Under the Curve), PCC (Percent Correctly Classified), Sensitivity, Specificity, and TSS (True Skill Statistic) for each model algorithm (Generalized Linear Model [GLM], Random Forests, [RF], and Flexible Discriminant Analysis [FDA]).

Species	Method	AUC	COR	TSS	Deviance
<i>M. menardi</i>	GLM	0.82	0.48	0.69	1.36
	RF	0.94	0.73	0.84	0.58
	FDA	0.83	0.49	0.71	0.98
<i>M. bournetii</i>	GLM	0.84	0.54	0.73	3.81
	RF	0.90	0.65	0.79	0.75
	FDA	0.82	0.48	0.67	1.30

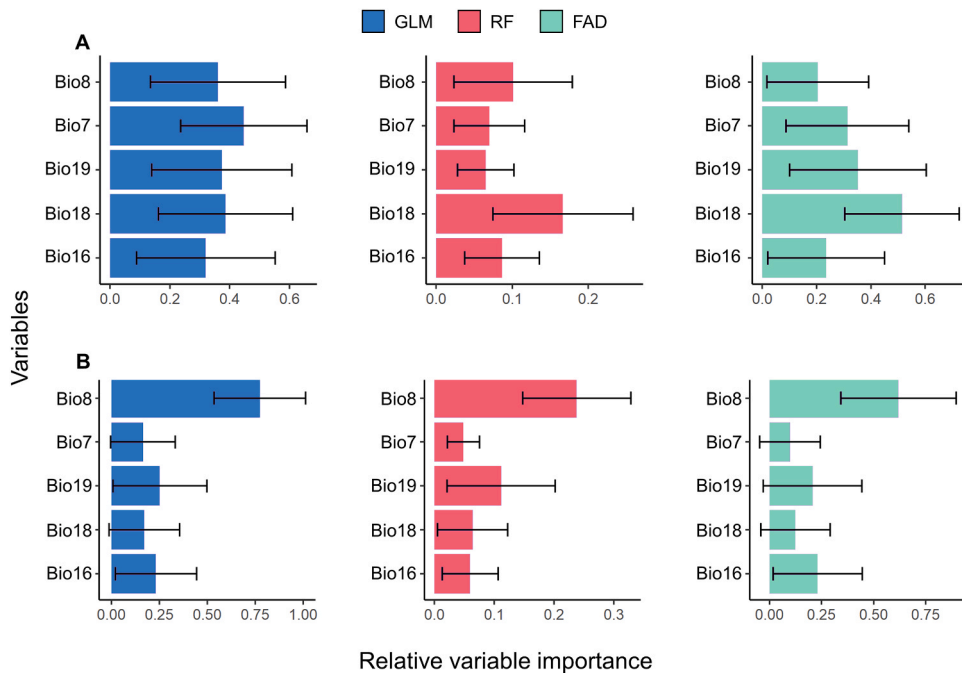
niche segregation in *Meta* spiders, as proved for the Italian (Mammola and Isaia, 2014; Mammola, 2017; Brignoli, 1971) and British (Mammola, 2017) populations of the two species. Similar trends are also apparent in the Pyrenean region, where occurrence data refer to *M. bournetii* preferably found in caves below 900 m a.s.l., and *M. menardi* in caves above 900 m a.s.l. (Ribera, 1978).

In accordance with the predicted trade-off between latitude and altitude postulated by Mammola et al. (2021) –i.e. *M. bournetii* colonising caves at higher elevations at lower latitudes–, in our study area *M. bournetii* shows a higher upper altimetric limit (1200 m) compared to higher latitudes (see Mammola et al., 2021). In parallel, the same would be expected for *M. menardi*, but on Mount Etna such upshift seems to be hampered, possibly due to the volcanic activity preventing the colonisation of volcanic uplands.

Such intriguing setting (see Nicolosi et al., 2023b) served as the impetus for our current study. Our primary objectives were to provide a comprehensive explanation of the factors influencing this pattern on Mount Etna and to gain insights into the future of the local populations of these two species. This involved offering predictions regarding potential shifts in their ranges in response to future warming scenarios in the study area, thereby highlighting the potential impact of climate change on their populations.

Our detailed analysis emphasized the significant role of climatic factors in segregating these two species. Furthermore, our modelling approach allowed us to anticipate their fate, considering the possible interactions driven by ongoing climatic changes on the volcano.





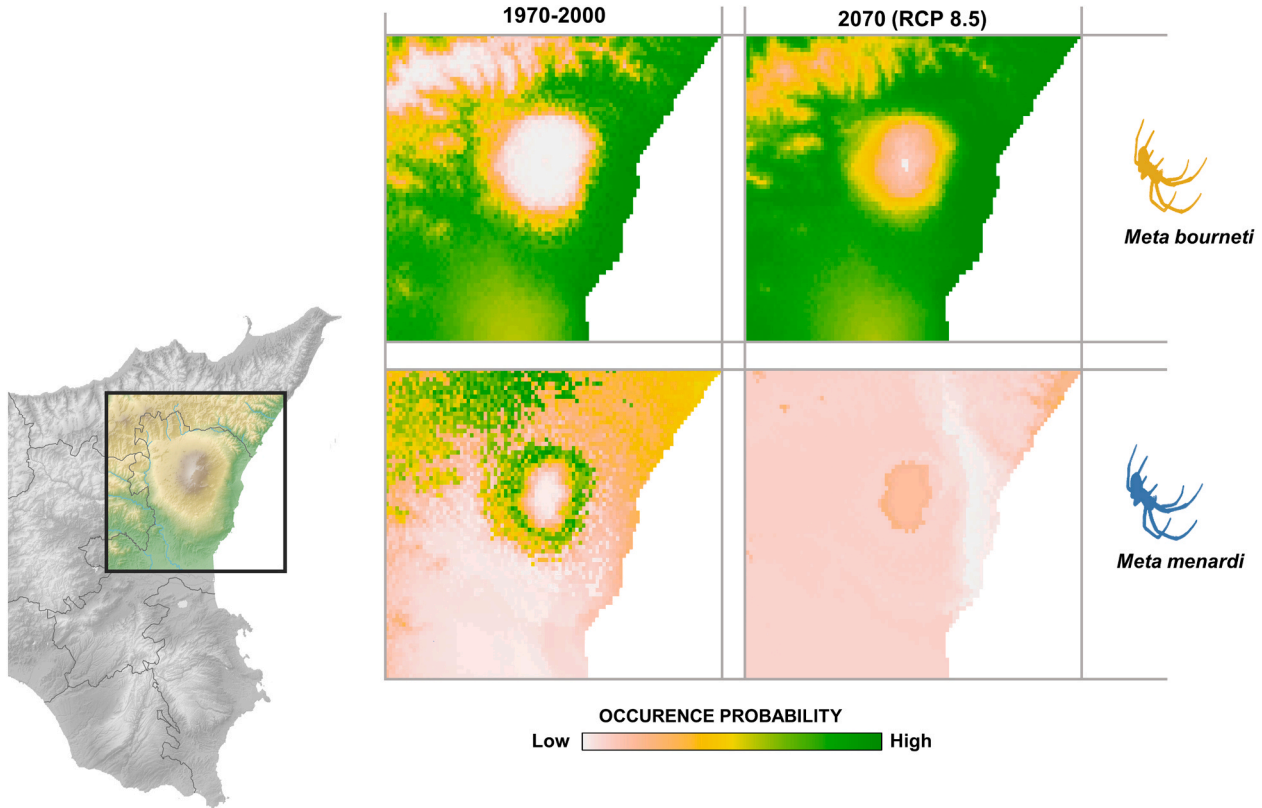
**Fig. 3.** Environmental variables used to create the species distribution model and their percentage contribution to model performance for *Meta bournetii* (A) and *M. menardi* (B). The variables including in the models are: BIO07: Temperature Annual Range, BIO08: Mean Temperature of Wettest Quarter, BIO16: Precipitation of Wettest Quarter, BIO18: Precipitation of Warmest Quarter, BIO19: Precipitation of Coldest Quarter. The response curves of *M. bournetii* and *M. menardi* were similar across models (Fig. S5).

Mount Etna is a remarkable biotope in Europe, which is threatened by both natural and anthropogenic disturbances. The study area is particularly sensitive to climate change, as species migration upwards on mountains is generally limited (Thuiller, 2007). Moreover, stochastic events have been documented to affect subterranean habitats and/or species, including floods (Pacioglu et al., 2019) and earthquakes (Fattorini et al., 2018), which are common in our study area. Indeed, as an active volcano, effusive and explosive eruptions are frequent events, producing lava and pyroclastic flows that can reach long distances (up to 17 km) (Calvari and Pinkerton, 1998; Del Negro et al., 2016, 2020). These events are major natural disturbances with varied and complex consequences for both plants and animals (Del Moral and Grishin, 1999), which, coupled with the ongoing climatic alterations could be highly detrimental to the local biodiversity, thus including *Meta* spiders.

The results of regression analysis pointed to a major role of the bioclimatic variables in predicting the presence of *Meta* spiders on Mount Etna. More specifically, all variables considered at first, including lava coverage and frequency of volcanic events, were all highly correlated with bioclimatic parameters, leading to an easier and more straightforward interpretation of the factors explaining the segregation of the two species. Moreover, none of the species occur in recent lava fields, confirming the unsuitability of this habitat for these species. Such pattern is probably due to the great number of volcanic events and related high coverage of recent volcanic products in the summit areas (15 events in the altimetric belt 1500–2000, approximately where *M. menardi* reaches the limit of its range). Moreover, volcanic activities also prevent the establishment of the vegetation (Poli and Grillo, 2000), which is known to play a key role in facilitating the dispersion of the epigeal juvenile stages of this species (Smithers, 2005).

The PCA based on microclimatic variables suggested a clear segregation between *Meta bournetii* and *M. menardi*. Temperature-related variables seem to favour the occurrence of *Meta bournetii*, but the species seems negatively influenced by precipitation-related variables, indicating a preference of the species for warmer and drier sites. On the other side, precipitation-related variables seem to favour the occurrence of *Meta menardi*, colonising sites at higher elevation, where temperature is lower and the amount of precipitation is generally higher. Similarly, caves presenting higher humidity seem to favour the presence of *Meta menardi* in the Pre-alpine region in Lombardy (Italy) (Manenti et al., 2015). This pattern was explained by Mammola and Isaia (2014) in the Italian Western Alps, who demonstrated a conditional differentiation of the niche among *M. menardi* and *M. bournetii*, with the first being more competitive at narrow ranges of cooler temperature and higher relative humidity and *M. bournetii* limited in a low number of caves climatically unsuitable for *M. menardi*.

In accordance with Mammola and Isaia (2017), we show how the niche hypervolume of *Meta menardi* is almost entirely comprised in that of *M. bournetii* (Fig. 3). However, *Meta menardi* shows a remarkably smaller bioclimatic niche compared to *Meta bournetii*. This suggests a certain niche overlap in subterranean habitats (Mammola and Isaia, 2014; Mammola and Isaia, 2017; Nentwig et al., 2022; Smithers, 2005), although *M. bournetii* exhibit a wider preference in terms of microclimatic requirements. Accordingly, the hypervolume of *M. bournetii* was found to be 45-fold wider than that of *M. menardi*, suggesting a much narrower ecological preference in respect to *M. bournetii* (see also Mammola and Isaia, 2014; Mammola and Isaia, 2017; Novak et al., 2010).



**Fig. 4.** Predicted current (1970–2000) and future (2070) distribution under the high-emission scenario RCP 8.5 for *Meta bournetii* and *M. menardi* on Mount Etna. All predictions are based on an ensemble of GLM, RF and FDA models.

**Table 3**

Percentage of presence across the study area during Current 1970–2000, Future 2070 RCP 2.6 and Future 2070 RCP 8.5 (see Fig. 4). Values in square brackets indicate percentage variation in respect to the Current scenario.

	Current (1970–2000)	Future (2070) - RCP 2.6	Future (2070) - RCP 8.5
<i>M. bourneti</i>	51.54%	62.39% (+17.39%)	65.71% (+21.56%)
<i>M. menardi</i>	15.36%	0.13% (−99.15%)	0 (−100%)

The suitable areas predicted by the models agreed with the observed current range distribution on Mount Etna. For *Meta bourneti*, the current suitable habitats are predicted along all slopes of the volcano, from the sea level up to 1100 m. The Mean Temperature of Wettest Quarter emerged as the main driver of the distribution of *M. bourneti*, in accordance with the scarce tolerance to low temperatures mentioned in Mammola and Isaia (2014) and Manenti et al. (2015).

For *Meta menardi*, the present distribution was predicted along a narrow altitudinal strip, extending halfway between the suitable area of *M. bourneti* and the unvegetated volcanic uplands. A notable contribution of the Precipitation of Warmest Quarter and a slight contribution of the Temperature Annual Range were detected when considering the habitat suitability of *M. menardi*, indicating its preference for humid areas, especially in the warmer months, and its low tolerance to higher temperature variations, as previously documented for this species (Mammola and Isaia, 2014; Manenti et al., 2015).

The averaged future predictions from the three climatic models for 2070 showed that both species will be affected by climate change. *Meta bourneti* is likely to be favoured by the increase of temperature and to expand its distribution toward new suitable areas above 1500 m, possibly coming in interaction with *Meta menardi* (Fig. 4, Table 3).

At the same time, predictions for *Meta menardi* indicate that most caves on Mount Etna will become climatically unsuitable for the species in the near future, leading to the abandonment of the currently inhabited sites, which, in turn, will become climatically suitable for *M. bourneti*.

Unfortunately, due to the unsuitability of the volcanic uplands and the high frequency of volcanic events, an upshift of *M. menardi* will be very unlikely, reducing drastically the occurrence of suitable sites for this species on Mount Etna (Fig. 4, Table 3).

Considering that both species generally colonise the outermost sectors of caves (Mammola et al., 2016), they will likely react to climatic change in a relatively short time-scale (Mammola and Isaia, 2017). Interestingly, in 2021, we were able to detect the first replacement of *Meta menardi* by *M. bourneti* in “Grotta di Piano Noce” (1195 m a.s.l), located at the boundary between the suitable areas of the two species. Despite being an isolated event, it seems likely that the replacement of *Meta menardi* by *M. bourneti*, and their upward migration, will occur in the short term. However, the potential expansion in the summit areas of the volcano will be limited by environmental factors characterising the volcanic uplands.

## 5. Conclusions

Caves in Sicily harbour a wide subterranean biological diversity with distinctive characteristics and significant biogeographic importance (e.g., Caruso, 1982; Sendra et al., 2019; Sabella et al., 2019, 2020; Nicolosi et al., 2023a).

Considering future climate scenarios, our research illustrates the predicted drastic reduction of the current suitable habitat of *M. menardi*, coupled with the environmental peculiarity of Mount Etna volcanic caves, leading to its regional extinction. These findings provide valuable insights into the regional consequences of a global issue. Although the implications of climate change are often discussed from a global perspective, it is crucial to acknowledge that its impact manifest more rapidly at regional and local scales. This is particularly pronounced in areas of high sensitivity, such as islands (Courchamp et al., 2014) and mountain tops (Thuiller et al., 2005), where local species are among the first to face the risk of extinction. Local populations of many species cannot shift their climatic niches rapidly enough to prevent extinction (Román-Palacios and Wiens, 2020), making the implementation of prevention strategies to reduce impacts of global climate change on a national and global scale difficult (Prabhakar et al., 2009).

Our work demonstrates that the extinction risk for *M. menardi* in Sicily as a consequence of global warming is extremely high. We regard the Sicilian population of *M. menardi* as a matter of regional conservation concern due to global warming. The conservation of the small population of *M. menardi* on Mount Etna is therefore crucial, as peripheral populations may harbour genotypes and phenotypes important for adaptation in a changing environment (Forsman, 2014). Future investigations in this direction and management activities at the local level would be therefore necessary to establish an appropriate management plan for the conservation of *M. menardi* in Sicily. For instance, management activities could include appropriate reforestation plans aiming to favour colonisation processes of the younger lava substrates.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02699](https://doi.org/10.1016/j.gecco.2023.e02699).

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