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The ecological niche of a specialized subterranean spider

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Keywords: *Troglohyphantes vignai*; Hypogean adaptation; Binomial GLMM; Food resources; Western Italian Alps; Disused mine

Abstract

Hypogean habitats offer unique opportunities for ecological studies because they are characterized by low abundance and diversity of organisms, they receive poor energy inputs, they are relatively stable from a climatic point of view and they are quite easily modeled. However, given the sometimes harsh conditions of the working environment as well as the complex accessibility of some caves, very few studies have investigated in detail the response of the subterranean species to different ecological factors. In this study, we investigated the ecological niche of the subterranean spider *Troglohyphantes vignai* Brignoli, 1971 (Araneae, Linyphiidae). We monitored over one year the local population of *T. vignai* occurring in a disused graphite mine in the Western Italian Alps. We placed sampling plots at progressive distances from the entrance and counted the individuals monthly. At each plot, we recorded the main biotic and abiotic parameters (i.e. temperature, humidity, prey availability, illuminance and structural complexity). The ecological niche of *T. vignai* was modeled through polynomial generalized linear mixed models. The environmental range where the probability of presence of *T. vignai* was higher ideally fitted a tradeoff between climatic stability and food availability, with higher preference for intermediate sections of the disused mine. No seasonal variations in the niche of *T. vignai* were detected. The methodology adopted here may be easily readapted in other hypogean sites, paving the way to a novel understanding of the ecological niche from an evolutionary perspective.

Introduction

When compared with epigeal ecosystems, subterranean environments are generally stable and show low abundance and diversity of organisms (Cardoso, 2012; Badino, 2010). Given the absence of light, hypogean habitats rely almost exclusively on exogenous energy inputs (Gers, 1998; Poulson & Lavoie, 2000), which are generally scarce. Although the ecological factors influencing hypogean habitats are generally well understood, the ecological niche of hypogean species has been rarely characterized. It appears likely that studies focusing on the niche of hypogean arthropods lagged behind their epigeal counterparts, not only because of the objective difficulties in working in underground habitats, but also because of the general low density of hypogean arthropods, which may represent a major impediment to data analysis.

Most of the recent studies about ecological niche of subterranean organisms focuses on specific model *taxa*, such as cave salamanders (e.g. Vignoli, 2008; Lunghi et al., 2015), carabids and cholevids beetles (Mammola et al., 2015) and hymenopterans (during their hypogean eco-phase; Novak et al., 2010a). Concerning spiders, a few authors focused on the niche of medium- to large-sized species occurring in the twilight zone [troglophiles *sensu* Sket (2008)], such as *Metellina meriana* (Novak et al., 2010b), *Meta menardi* (Novak et al., 2010b; Mammola & Isaia, 2014; Manenti et al., 2015; Chiavazzo et al., 2015) and *Meta bourneti* (Mammola & Isaia, 2014). The availability of trophic resources – as well as the competition for them – was pointed out as one of the main factors conditioning the presence and the abundance of troglophile spiders within the cave. An effect of the distance from the entrance, mainly interpreted as a *proxy* for the climatic isolation, was also observed (see also Novak et al., 2012; Tobin et al., 2013). As far as we are concerned, the environmental factors determining the specific ecological requirements of specialized subterranean spiders, have never been taken into consideration.

In this contribution, we investigate for the first time in literature, the ecological niche of the specialized subterranean spider *Troglohyphantes vignai* Brignoli, 1971 (Araneae, Linyphiidae) in the frame of a modern statistical framework.

The genus *Troglohyphantes* Joseph, 1881 (Araneae, Linyphiidae) is currently represented by 133 species, predominantly distributed in the European mountain ranges (WSC, 2015). In Italy the genus is represented by 36 species, 10 of them recorded in the Western Italian Alps (Isaia & Pantini, 2010; Isaia et al., 2011). Most of the species belonging to this genus shows adaptations to subterranean life, such as thinning of integuments, loss of pigmentation, heavy spination and reduction of the eye apparatus and are generally associated to dark, cool and humid habitats such as caves and other subterranean habitats (e.g. Brignoli, 1971, 1985; Deeleman-Reinhold, 1978; Pavlek & Ozimec, 2009).

T. vignai is a typical representative of this genus: since the description, all available records refer to wild caves and artificial subterranean systems (Brignoli, 1971, 1985; Pesarini, 2001; Arno & Lana, 2005; Isaia & Pantini, 2010; Isaia et al., 2010; Isaia et al., 2011). The species is endemic to the Western Italian Alps (NW Italy), being discontinuously distributed from the Cottian (Province of Torino) to the Maritime Alps (Province of Cuneo) (Isaia et al., 2011).

Here, we monthly surveyed a disused mine hosting a rich population of *T. vignai*, aiming at i) identifying the ecological factors driving the presence of this species in the subterranean habitat; ii) defining its ecological niche; iii) providing information about the life history of this species, so far unknown.

Material & Methods

Study site

The study was performed in a disused graphite mine in the nearby of the hamlet of Tornini, municipality of Pramollo, Chisone Valley, Cottian Alps, Italy [entrance at 7.199 E, 44.908 N (WGS84 reference system)]. Due to its regular shape and linear development, we were able to count spiders and measure the considered environmental parameters without difficulty and model the study site with high accuracy. The Tornini disused mine has an horizontal length of 56 m deep and an internal section of about 2 x 2.5 m. Moreover three collapsed side galleries (not investigated in the present study) depart from the main tunnel (Fig. 1). The main adit is about 2 x 1.5 m and opens in the vicinity of the paved road that cross the secondary valley of Pramollo within Chisone Valley (Cottian Alps, NW Italy): The disused mine opens in a mixed deciduous forest of chestnut (*Castanea sativa*) and beech (*Fagus sylvatica*). A secondary adit, partially obstructed by rocky debris, opens at few meters away from the main entrance and join the main tunnel after 19 m. The presence of two entrances causes a flow of cool air from one entrance to the other. Further than 19 m inside the main tunnel, the temperature never drops below 0 °C. The light reaches the internal tunnel up to 13 m from the entrance.

The disused mine hosts a diversified arthropod community, including a rich population of our model species *T. vignai*, as well as typical spiders of the twilight zone, such as *Meta menardi*, *Metellina merianae*, *Tegenaria* sp. and *Pimoa* sp. Furthermore, the cave is inhabited by cave crickets (*Dolichopoda* sp.) and several specialized subterranean arthropods such as the beetle *Doderotrechus ghiilianii isaiai*, diplopods (*Plectogona* sp.), chilopods (*Lithobius* sp., *Eupolybothrus* sp.) and springtails.

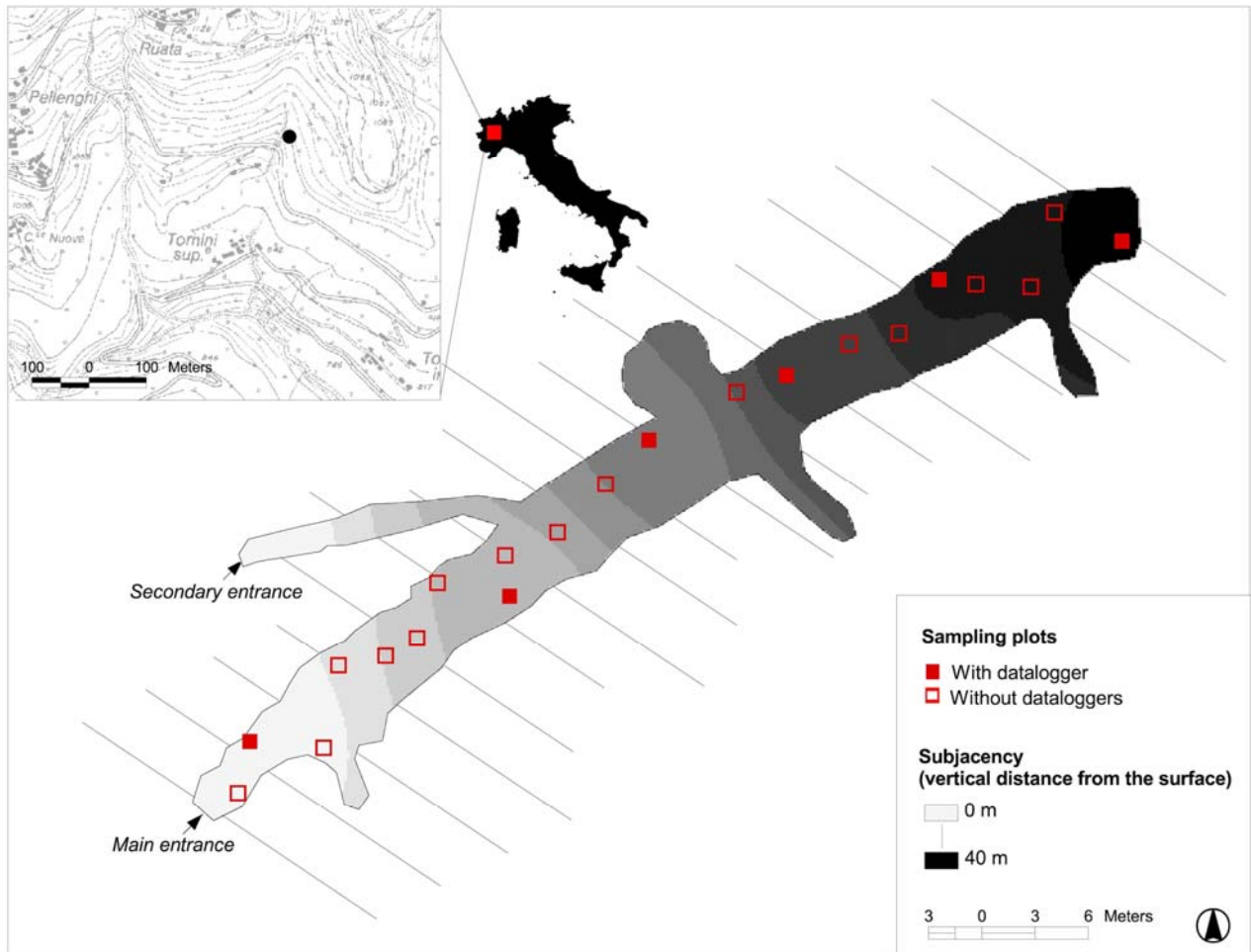


Fig. 1. Map of the study area. The position of the sampling plots is represented by twenty-one squares. The different sectors of the cave are coloured with different shades of grey representing the subajency (i.e. vertical distance from the surface; see e.g. Novak et al., 2012). The presence of temperature and relative humidity dataloggers is highlighted with bold squares.

Sampling design

The sampling design was readapted from Mammola & Isaia (2014) and Chiavazzo *et al.* (2015). Twenty-one sampling plots (squared areas of 1 x 1 meters) were allocated inside the main tunnel of the disused mine at progressive distances from the entrance, up to its end (56 m). Given the three-dimensionality of the investigated environment (see Bourne, 1976), we placed the sampling plots according their structural typology, i.e. on floors (n=7), walls (n=7) and roofs (n=7). The height of the sampling plots from the ground varied between 0 (floors), 0-2.5 (walls) and 2-2.5 (roofs) meters. As a proxy for the structural heterogeneity (spatial complexity), we measured the linear development of the plot, flattening a flexible measuring tape on the diagonal of the square (i.e. the longer the development, the higher the complexity) (see Camp & Jensen, 2007; Lunghi *et al.*, 2014).

We visited the study area once a month between November 2014 and October 2015 (12 total visits). During each visit, we counted the number of male, female and immature of *Troglohyphantes vignai* occurring at each sampling plot. During each survey, we also measured light intensity (lux) at each sampling plot by photometric probe LP 471 Phot (Delta OHM S.r.l.) (accuracy of 0.2 % ± 1 digit).

In addition, we recorded the presence of other arthropods occurring in the plots, identifying them up to the species level, whenever possible. These arthropods were classified as potential prey items of *T. vignai* on the base of: i) available data in literature (Deeleman-Reinhold, 1978; Isaia *et al.*, 2011); ii) body-size; iii) our field observations. In particular, we considered the following as potential prey items: flies (Dipterans), small sized beetles (Carabidae), small sized moths (Geometridae), silverfishes (Lepismatidae), springtails (Collembola), woodlouse (Isopoda), small sized centipedes and millipedes (Chilopoda and Diplopoda).

In order to characterize the microclimatic conditions occurring in the different sections of the disused mine, we placed six EL-USB-2+ temperature and relative humidity dataloggers (Lascar Electronics, Salisbury, United Kingdom) at 2, 15, 24, 36, 48 and 56 meters from the entrance (bold squares in Fig. 1). We programmed dataloggers to record temperature (T) and relative humidity (RH) every six hours for the whole sampling period (accuracy of ± 0.5°C for temperature and ± 2.0 % for relative humidity). For each sampling plot we calculated the mean temperature (T_{mean}), relative humidity (RH_{mean}) and the associated ranges (T_{max}-T_{min} = T_{range}; RH_{min}-RH_{max} = RH_{range}) of a period of 28 days centered on the day of the survey (from two weeks before to two weeks after the survey). For the sampling plots lacking dataloggers we used interpolated values (see next paragraph).

Data analysis

The phenology of *Troglohyphantes vignai* was graphically investigated via scatterplot (Lattice R package; Sarkar 2008), plotting counts of males, females and juveniles against time (monthly visits).

We defined the ecological niche of *T. vignai* through generalized linear mixed model (GLMM). The mixed procedure accounted for multiple observations from the same sampling plot, by specifying the sampling plot as random factor (see below). Given the low density of individuals *per* sampling plot (ranging from 1 to 3 individuals), we expressed counts as presence/absence within the sampling plot (i.e. Bernoulli distribution 0-1). We thus modeled the probability of presence and not abundance values. We selected the following covariates as potential explanatory variables of the presence of *T. vignai* in the plots: distance from the entrance (Dst; continuous variable), sampling season (Sea; categorical variables; levels: "Autumn", "Winter", "Summer", "Spring"), structural complexity (Complexity; continuous variable), illuminance (Light; continuous variable), abundance of prey items (Prey; continuous variable), structural typology (Type; categorical variables; levels: "Floor", "Vertical", "Roof"), mean monthly temperature and relative humidity, and associated ranges (Tmean; RHmean; Trange; RHrange, respectively; continuous variables).

Prior to model fitting, we explored the dataset following the standard protocol for data exploration proposed by Zuur *et al.* (2010). According to Zuur *et al.* (2009, 2010), the inclusion of outliers and highly correlated predictors in the regression analysis leads to misleading results (type I and II statistical errors). Accordingly, we used Cleveland dotplots and boxplots to assess the presence of outliers in dependent and independent variables. We investigated multi-collinearity among continuous covariates via Pearson correlation test (r) and variance inflation factors values (VIFs), setting the threshold for collinearity at $r > 0.7$ and $VIF > 3.0$. The collinearity between continuous and categorical variables was graphically evaluated with boxplots. The existence of possible non-linear responses of the continuous variables included in the model was investigated with the *gam* R command (Hastie, 2013). We ran the Bernoulli model using a complementary log–log link function (clog-log), as recommended in Zuur *et al.* (2009) for datasets with unbalanced set of zeros (absences) and ones (presences). The GLMM was fitted via the *glmer* R command (Bates *et al.*, 2014) in R environment (R development team, 2013).

Once we fitted the general model, we applied model selection (see Johnson & Omland, 2004), whereby model reduction was carried out on the full model by sequentially deleting terms (backward elimination) according to AICc values (Hurvich & Tsai, 1989; Burnham & Anderson, 2002). The process was carried on via the *drop1* R command, until a minimum adequate model of fixed effects remained - i.e. best model supported by observations that avoided overfitting (Howkins, 2004). Model validation was carried out following Zuur *et al.* (2009).

GIS processing

The raster image of our original planimetric drawing was projected “on the fly” in GIS environment, on which we drew the vector layer of the Tornini disused mine. For the interpolation we used an Inverse Distance Weighted function (IDW) using a sample of 12 plots (power 3) to estimate cell values and obtain the renderings of the dependent variable (probability surface of the presence of *T. vignai*) and main covariates considered in the analysis, namely mean annual temperature, relative humidity and associated ranges, illuminance and abundance of prey items.

Results

Life history

During the sampling period, we observed 126 individuals of *Troglohyphantes vignai*, of which 58 adults (17 males and 41 females) and 68 juveniles. Females occurred through the whole year, with a abundance peak from August to January. Males occurred discontinuously from August to January and were almost absent during the rest of the year. We never observed courtship or reproductive activities, nor laying of the cocoon. The annual sex ratio (M/F) was 0.41. Immatures were observed during the entire sampling period, with higher abundances in spring and summer (Fig. 2). During the study, in several occasions we observed *T. vignai* individuals feeding on Dipterans (Muscidae and Tipulidae) and diplopods (*Plectogona* sp.).

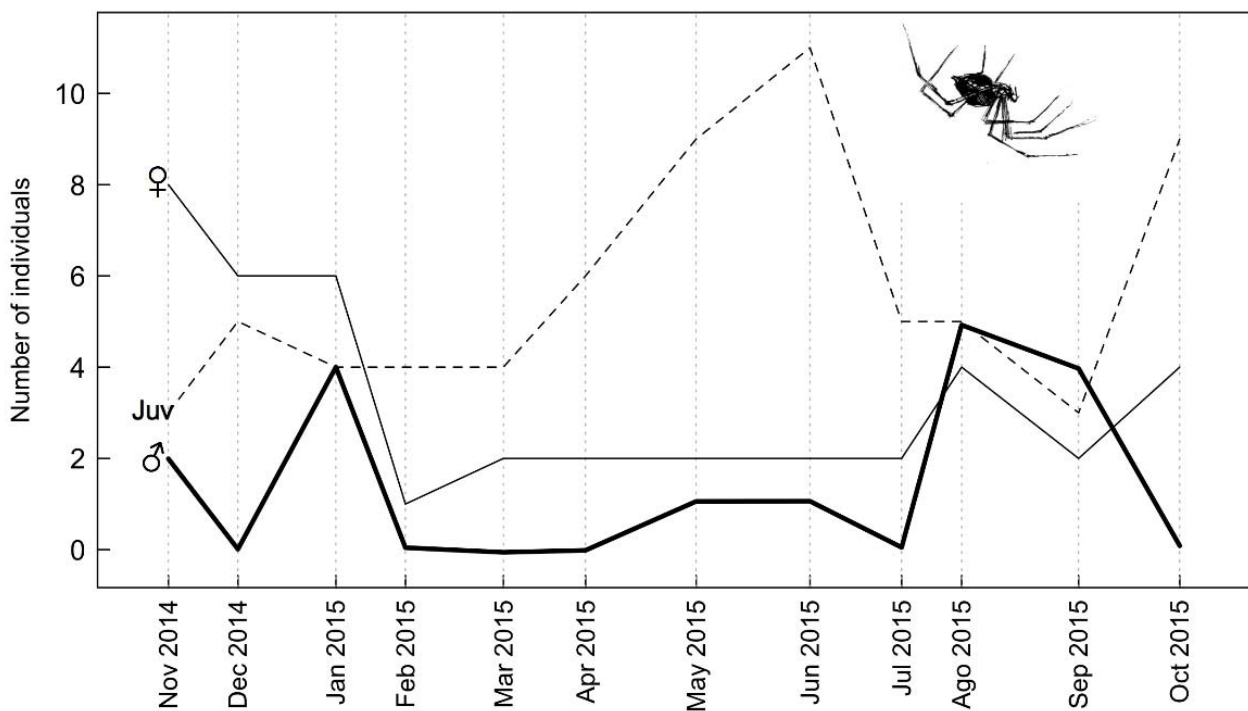


Fig. 2. Phenology of *Troglohyphantes vignai*. Abundance trends of adult males (♂), females (♀) and juveniles (Juv) in the sampling plots at the disused graphite mine of Tornini.

Ecological niche of *Troglohyphantes vignai*

In light of the data exploration (Zuur et al., 2010), a log-transformation ($\log x + 1$) was applied to illuminance to achieve homogenization (Zuur et al., 2009), and one outlier was removed from the

dataset. Both ranges of relative humidity and temperature were dropped from the analysis, being collinear with mean temperature (Pearson $R > \pm 0.7$). Temperature range was also dropped being negatively collinear with distance from entrance and positively with mean temperature (Pearson $R > \pm 0.7$). The categorical variable referring to the structural type and to the season were dropped from the analysis being collinear with complexity and prey availability, respectively.

As a result, we included distance (dst), illuminance (logLux), prey availability (Prey), structural complexity (Complexity) and mean temperature (Tmean) in the regression analysis. Additionally, we introduced a quadratic term (Dst^2) as covariate in the model in order to capture a non-linear effect of the distance from the entrance, detected during data exploration with the generalized additive model (approximate significance of the smooth term = edf: 2.113, F: 8.431, $p < 0.000$ ***). According to model selection (Tab. 1), the most appropriate model structure supported by the observations explaining the niche of *T. vignai* had the following (fixed) structure: $y \sim Dst + Dst^2 + Prey + Complexity$.

The probability of presence of the species was found to increase positively with increasing distance from the entrance (Dst Estimates $\beta \pm se$: 0.2852 ± 0.0494 , $p < 0.00$ ***) and negatively with squared distance from entrance (Dst^2 Estimates $\beta \pm se$: -0.0044 ± 0.0008 , $p < 0.00$ ***). The combination of the two effects resulted in a parabolic trend towards the dependent variable, namely the probability was higher for intermediate distances from the entrance of the mine. There was also an increase in the probability of presence of *T. vignai* with increasing abundance of prey items (Prey Estimates $\beta \pm se$: 0.3090 ± 0.0672 , $p < 0.00$ ***). Moreover, we detected a weak effect (close to significance) with structural complexity of the plot, with higher probability at increasing values (Complexity Estimates $\beta \pm se$: 0.0053 ± 0.0028 , $p = 0.06$ [*]). The combined effect of these variables on the probability of presence of *T. vignai* in the sampling plots is graphically illustrated in Fig. 3.

Tab. 1. Model selection. Model selection according to corrected Akaike criterion for finite sample size (AICc; Hurvich & Tsai, 1989; Burnham & Anderson, 2002). Models are ordered from the most to the less appropriate. Df = degrees of freedom; AICc = Corrected Akaike Information Criterion for finite sample size; $\Delta AICc$ = (AIC of the model) - (AIC of the best model); Akaike weight = $w_i(AIC)$ *sensu* Burnham & Anderson (2002). See text for abbreviations of the explanatory variables.

Model structure	Df	AICc	$\Delta AICc$	Akaike weights
$y \sim Dst + Dst^2 + Prey + Complexity$	6	240,14	0,00	0,47
$y \sim Dst + Dst^2 + Prey + Complexity + Tmean$	7	242,20	2,06	0,17
$y \sim Dst + Dst^2 + Prey + Complexity + logLux + Tmean$	8	244,03	3,89	0,07

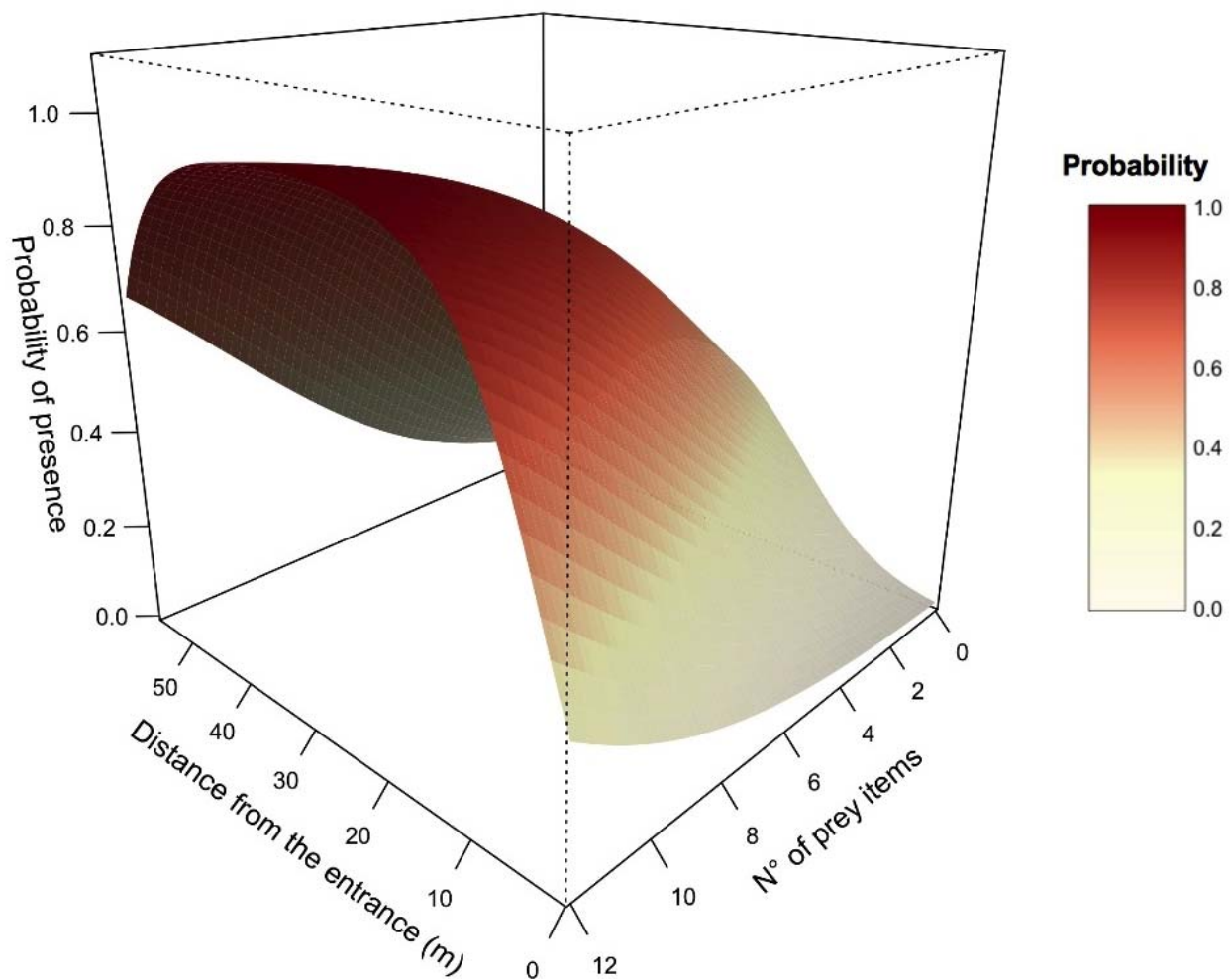


Fig. 3. Graphical representation of the ecological niche of *Troglodyphantes vignai*. Probability surfaces showing the relation among the three environmental variables retained after model selection (Tab. 1) and the probability of occurrence of *T. vignai* in the study area. Different combinations of the considered variables are shown: a) distance from the entrance and prey availability; b) prey availability and structural complexity; c) distance from entrance and structural complexity). In each plot the third variable is set at its mean value.

Discussion

The lack of solar radiation as well as the general scarce food supply represent strong limitations to life underground. Therefore, biotic subterranean communities are generally characterized by low diversity and low abundance. Compared to surface ecosystems, relationships between species are more simplified and competition is less severe. Cave dwelling organisms often show peculiar morphological, behavioral and physiological adaptations that enable them to survive the environmental conditions of the underground habitat. Adaptations (the so called “troglomorphism”) are generally convergent, and generally implies narrow ecological requirements that may result in clear niche partitioning, both from a spatial and temporal point of view. (Culver & Pipan, 2009; Romero, 2009). Despite their potentiality, subterranean organisms have been rarely used as models for the study and the definition of the ecological niche, and only general, non-quantitative, descriptive studies have been published and spiders do not represent an exception in this sense.

As for our model study, besides the cryophilic habits of the species and the general preference for moist and shaded habitats (Deeleman-Reinhold, 1978; Isaia & Pantini, 2010; Isaia *et al.*, 2010), very little is known about the ecological requirements of *Troglohyphantes* spiders, inhabiting the subterranean domain of most European mountain ranges.

Here, by means of advanced statistical procedure, we attempt to define quantitatively the niche of *T. vignai*, pointing out the combined effect of three main drivers conditioning the occurrence in this species in a subterranean ecosystem. According to our result, food availability, modeled as counts of available potential prey in the sampling plots, is the first factor conditioning the presence of *T. vignai* in our study site. The result appear sound, in accordance with the fundamental role played by the availability, the abundance and the typology of food resources in oligotrophic habitats (e.g. Culver & Pipan, 2009). External organisms entering the subterranean domain [troglonexes *sensu* Sket (2008)], basically represents the most important food resource for predators dwelling underground. The effect of the general decrease of prey density with increasing distance from the surface (e.g. Tobin *et al.*, 2013) is particularly evident for a sit-and-wait predator such as our model species. Indeed, the selection of prey-rich areas and maximizes food intake. Notably, a positive relation between the presence and abundance of various species of cave dwelling spiders and large aggregations of prey has been described before (e.g. Ficetola *et al.*, 2012; Mammola & Isaia, 2014; Manenti *et al.*, 2015). However, the numerical response of a predator through aggregation is generally mediated by other factors than the prey availability itself, such as competition or physiological tolerance.

In our case, the second important factor having an effect on the presence of *T. vignai* is the distance from the entrance. Interestingly, *T. vignai* selects intermediate distance, with an optimum between

15 and 40 m. Concerning other species of the same genus, Novak *et al.* (2012) reported a wider range of occurrence from 2 to 66 m for the subterranean specialized *T. diabolicus* in Slovenia. On the other hand, less specialized species such as *T. lucifuga* are usually collected in the vicinity of the cave entrance (Isaia & Pantini, 2010 and Isaia *et al.* 2010) . As already discussed in Chiavazzo *et al.* (2015), it is worth to remember that the parameter "distance from the cave entrance" has to be considered with caution. Indeed, this parameter can be regarded as a surrogate for several other variables having an effect on the general environmental and microclimatic conditions. In general, as well as in our case, the stability of both temperature and humidity increases with increasing distance from the entrance. Moreover, in our study area, the increase of the linear distance from the entrance corresponds to the parallel increase of the vertical distance from the surface (i.e. subjacency; see Fig. 1), a parameter that further contributes significantly in buffering the subterranean environment from the external conditions. Therefore, while selecting areas away from the entrance, individuals of *T. vignai* also select stable climatic conditions. This explanation is in accordance with the reduced physiological tolerance observed in specialized subterranean species (Romero 2009). In particular, the mean annual temperature range and the mean annual relative humidity range in our study area are progressively buffered from 15 to 40 m (from 3 to 0.5 °C and from 11 to 0.3 % , respectively). However, the lowest values (i.e. higher stability) are reached at the end of the tunnel.

Contrarily to what expected, light intensity and the distance from entrance were instead uncorrelated. Indeed, given the morphology of the mine adit, both dark and illuminated plots occurred near the entrance. Nevertheless, the range of occurrence of *T. vignai* was fully included in the dark zone.

When considering these argumentations altogether, it is possible to hypothesize that the environmental range where the probability of presence of *T. vignai* is higher (i.e. its spatial niche) ideally fits a tradeoff between the climatic stability from one side and prey availability from the other, with higher preference for intermediate sections of the disused mine. Accordingly, on one side, the selection of intermediate sectors of the tunnel represent an ideal compromise lying between the need to select climatically stable areas and the need to remain closer to the source of food (the epigean environment), thus avoiding competition. Indeed, in the vicinity of the entrance (epigean/hypogean ecotone) the availability of food resources is higher (Prous *et al.*, 2004, 2015), but so is the competition with other predators exploiting similar resources, such as *Meta* (Novak *et al.*, 2010b; Mammola & Isaia, 2014), *Metellina* (Novak *et al.*, 2010b) and other spider species censused in this work such as *Pimoa* sp. and *Tegenaria* sp. Moreover, given the stronger influence of the external climate, the entrance area may be unsuitable from a climatic viewpoint in different seasons. At the same time, although in the most distal sector of the disused mine (over 40 m) the

climatic stability is certainly suitable for *T. vignai*, in parallel the reduced abundance of prey items crucially limits the survival of the spiders. On the other hand, at intermediate distance *T. vignai* finds the best compromise (see Fig. 3).

Although it only approached statistical significance, structural complexity was also retained in the best model obtained via model selection (Tab. 1). Indeed, the probability of presence of *T. vignai* slightly increased with higher structural complexity. Our estimate for complexity reflects the presence of irregularities and crevices (i.e. three-dimensionality of the sampling plots). Likely, a higher structural complexity is favorable for building the horizontal sheet-web typical of Linyphiidae. On the contrary, a flat surface may not offer enough angularity to anchor the web. In confirmation of this hypothesis, it is worth to notice that Western Alpine are usually found among stony debris and in wall fissures (e.g. Isaia & Pantini, 2008; Isaia et al., 2010; Isaia & Pantini, 2010). In this respect, Deeleman-Reinhold (1978) observed that a free space of 5 cm or more is necessary to *Troglohyphantes* for building their web, since in cave dwelling species the size of the web ranges from 5 to 30 cm depending on the species and the size of the individual.

Finally, no seasonal variations in the niche of *T. vignai* were detected. In particular, interaction between the sampling season and other variables such as the distance from the entrance were not statistically significant, indicating that the spatial niche of *T. vignai* is stable through the year and seasonal migration towards the entrance or the deeper parts does not occur. On the other hand, the abundance of prey in the plots was seasonal dependent (higher in spring and summer), indicating an inhomogeneous availability of the prey items to *T. vignai* through the year, that leads to hypothesize a high resistance to starvation.

Observation on the life history

As far as we know, the only available information on the life cycle and natural history of *Troglohyphantes* spiders are found in Deeleman-Reinhold (1978), who observed natural populations and reared several individuals of different species in laboratory conditions (*T. croaticus*, *T. kordunlikanus*, *T. gracilis* and *T. diabolicus*). Accordingly, concerning sex ratios, females outnumber males at rates of 3:1, or more. Annual sex ratio in *T. vignai* aligned Deeleman-Reinhold's results. The longer life span of females and the high mortality rates of males after the last moult from subadults to adults (Deeleman-Reinhold, 1978) offer valid explanations for this trends. Notably, similar values of sex ratio were also reported by Gasparo & Thaler (2000) for other cave dwelling spiders, such as *Stalita taenaria* (Araneae, Dysderidae) and *Nesticus eremita* (Araneae, Nesticidae).

Although we never observed reproduction activities, it is possible to hypothesize that reproduction takes place from the end of summer onwards (Fig. 2), as observed in other cave-dwelling species of spiders (Smithers, 2005; Mammola & Isaia, 2014).

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