Original article

Step back! Niche dynamics in cave-dwelling predators

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ABSTRACT

The geometry of the Hutchinson's hypervolume derives from multiple selective pressures defined, on one hand, by the physiological tolerance of the species, and on the other, by intra- and interspecific competition. The quantification of these evolutionary forces is essential for the understanding of the coexistence of predators in light of competitive exclusion dynamics. We address this topic by investigating the ecological niche of two medium-sized troglophile spiders (*Meta menardi* and *Pimoa graphitica*). Over one year, we surveyed several populations in four subterranean sites in the Western Italian Alps, monitoring monthly their spatial and temporal dynamics and the associated physical and ecological variables. We assessed competition between the two species by means of multi regression techniques and by evaluating the intersection between their multidimensional hypervolumes. We detected a remarkable overlap between the microclimatic and trophic niche of *M. menardi* and *P. graphitica*, however, the former —being larger in size— resulted the best competitor in proximity of the cave entrance, causing the latter to readjust its spatial niche towards the inner part, where prey availability is scarcer ("step back effect"). In parallel to the slight variations in the subterranean microclimatic condition, the niche of the two species was also found to be seasonal dependent, varying over the year. With this work, we aim at providing new insights about the relationships among predators, demonstrating that energy-poor environments such as caves maintain the potential for diversification of predators via niche differentiation and serve as useful models for theoretical ecological studies.

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1. Introduction

Since the formalization of the ecological niche as a hypervolume (Hutchinson, 1957), two main conceptualizations of the Hutchinson's niche has emerged (Soberón, 2007; Holt, 2009; Wiens, 2011). The first one is set at the interface of biogeography and ecology, and focuses on the species' bioclimatic range and on the elucidation of large-scale biogeographic patterns (e.g. Peterson et al., 2011). The second refers to a smaller scale, where the trophic resources and the species interactions become the most important factors shaping the geometry of the niche (Soberón, 2007).

The local scale is particularly important for the understanding of the ecological factors enhancing species coexistence and for the general assessment of competition for space and resources (May and MacArthur, 1972; Chesson, 2000; Chase and Leibold, 2003). In this framework, the multidimensional niche hypervolumes of

two species can be mathematically constructed using a set of *n* variables, and the competition can be assessed by calculating the overlap between the resulting geometrical solids (Hutchinson, 1957). However, from a mathematical standpoint, such estimation represents a challenging task, especially when dealing with hypervolumes with more than three dimensions (Blonder et al., 2014). Moreover, in complex ecosystems, confounding effects may increase the complexity in defining and quantifying the niche, including multi-species interactions, the intrinsic variability of the environmental conditions and the trophic availability.

Being characterized by highly predictable gradients in their environmental conditions, a simplified habitat structure and a low diversity and abundance of organisms (Romero, 2009; Culver and Pipan, 2009), hypogean ecosystems represent ideal ecological laboratories in this regard (Poulson and White, 1969). However, despite their potentiality, subterranean organisms have been rarely used as models for the advance of the niche theory (Howarth, 1981; Fišer et al., 2012; Mammola and Isaia, 2016), especially in the context of species coexistence at a local scale (Bourne, 1976; Poulson, 1977; Novak et al., 2010; Fišer et al., 2015).

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Intuitively, competition should be particularly evident in the case of top-level predators, such as cave-dwelling spiders, sharing the generally low availability of prey items typical of most subterranean ecosystems. Indeed, apex predators are likely to be down-regulated and close to carrying capacity (Haywarda et al., 2007), thus competition is expected to play a significant role in dimensioning their niche.

In this study, we focused on two species of medium-sized cave dwelling spiders, *Meta menardi* (Latreille) (Araneae, Tetragnathidae) and *Pimoa graphitica* Mammola, Hormiga, Isaia (Araneae, Pimoidae), often co-occurring in subterranean sites in the Western Italian Alps (Isaia et al., 2011) where they apparently exploit the same micro-habitats in the twilight zone (Mammola et al., 2016). Therefore, they represent an interesting model for the study of competition at the local scale.

Previous contributions (Bourne, 1976; Novak et al., 2010; Mammola and Isaia, 2014; Manenti et al., 2015) investigated the ecological niche of *M. menardi*, highlighting a general preference for the twilight zone of cool caves characterized by high relative humidity and prey availability, where they preferably colonize cave walls and roofs. Concerning *P. graphitica*, only the large-scale biogeographic patterns have been elucidated (Mammola et al., 2015a), while its micro-habitat preference remained unstudied.

We investigated the overlap between the spatial and temporal niche of the two model species by surveying monthly four hypogean sites hosting abundant populations of the two species. In a first step, we described the ecological niche of *P. graphitica* through multi-regression techniques, hypothesizing that i) the ecological factors driving its abundance are very similar to those of *M. menardi*, resulting in a substantial niche overlap.

Since adults of *Meta* are larger in size than *Pimoa* (Nentwig et al., 2016), we further hypothesized that ii) in face of the competition, *Meta* spiders are favored and effect the niche of *Pimoa*.

Thanks to the recent advances in the mathematical characterization of the niche (Blonder et al., 2014; Blonder, 2015), we were able to evaluate the niches of the two species as n-dimensional hypervolumes, and to quantify their reciprocal intersection (i.e. overlap). In light of the seasonal variation occurring in the twilight zone (Culver and Pipan, 2009), we also hypothesized that iii) the dimensionality of the two hypervolumes vary over the year, as well as their reciprocal overlap.

2. Material and methods

2.1. Study area

We set this study in four disused graphite mines located at the mouth of the Chisone Valley (Cottian Alps, Italy; Table 1). Rather than natural caves, we preferred artificial subterranean sites because of their shape and profile regularity, which facilitate the measurement of the considered environmental parameters and the census of the resident populations in light of statistical modelling (Mammola and Isaia, 2016).

The four study sites represent ideal habitat replicates, all of them being characterized by a horizontal main tunnel with an almost constant cross-section. All sites are colonized by mixed population of *Pimoa graphitica* and *Meta menardi*.

2.2. Data collection

We collected habitat variables adopting a sampling square methodology (see Bourne, 1976; Mammola and Isaia, 2014, 2016; Chiavazzo et al., 2015). In each site, we positioned squared sampling plots of 1 × 1 m inside the main tunnel at progressive distances from the mine adit, up to its end. In order to account for the three-dimensionality of the investigated environments (Bourne, 1976), we evenly distributed the sampling plots among the mine's floors, walls and roofs. Numbers of plots per site were proportional to the length of the mines (see Table 1).

As a proxy for 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 linear development, the higher the complexity; see Camp and Jensen, 2007). In our case, lower values of complexity were typically on floors, while the higher complexity was measured on walls and roofs, due to the irregularities of wall surfaces.

We monitored each study site once a month between November 2014 and October 2015 (12 total visits). During each visit, we counted the individuals of *P. graphitica* and *M. menardi* occurring in each sampling plot, as well as other arthropods co-occurring in the plot. The latter were classified as potential prey items on the basis of available data in the literature (Smithers, 1996, 2005; Novak et al., 2010; Mammola and Isaia, 2014; Mammola et al., 2016) and their body size. In particular, we classified the following as possible prey items: flies (Dipterans), beetles (Carabidae), moths (Geometridae), cave crickets (*Dolichopoda azami*) silverfishes (*Lepisma* sp.), small sized gastropoda (*Oxychilus* sp.), woodlouse (Isopoda), earthworms (Oligochetae), centipedes (Chilopoda), and millipedes (Diplopoda).

We characterized the local microclimatic conditions of the different study areas by means of 18 EL-USB-2+ temperature and relative humidity dataloggers (Lascar Electronics, Salisbury, UK), with a measurement range from −35.0 °C to 85.0 °C (±0.5 °C) for temperature and from 0 to 100% (±2.0%) for relative humidity.

We placed the dataloggers at progressive distances from the primary adit of each mine. We programmed dataloggers to record temperature (T) and relative humidity (RH) every six hours for the whole sampling period. For each sampling plot, we calculated mean temperature (Tmean), mean relative humidity (RHmean) and the associated ranges (Trange; RHrange) of a period of 28 days centred on the day of the survey. For the sampling plots lacking dataloggers we used interpolated values obtained in GIS environment, as explained in Mammola and Isaia (2016). During each survey, we also measured illuminance (lx) using a photometric probe (LP 471 Phot, Delta OHM S.r.l.; accuracy of 0.2% ± 1 digit).

2.3. Statistical analysis

2.3.1. Environmental drivers of Pimoa graphitica

We conducted all analysis in R (R Development Core Team, 2015). We characterized the ecological factors driving the abundance of *Pimoa graphitica* in its hypogean eco-phase (see

Table 1
Descriptive parameters of the investigated sites. Coordinates are given in UTM coordinate system (WGS84).

Site	Municipality	Hamlet	x	y	Main tunnel length	No of plots
Pons disused mine	Pons	Pons	356,674	4,980,578	50 m (accessible part)	18
Tornini mineshaft	Pramollo	Tornini	357,882	4,974,533	56 m	21
Fornaisa mineshaft	Inverso Pinasca	Fornaisa	360,922	4,976,010	21 m	14
Bonousso 1 mineshaft	S. Germano Chisone	–	359,315	4,973,683	34 m	17