



## Original article

## Do cave features affect underground habitat exploitation by non-troglobite species?

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## ABSTRACT

Many biospeleological studies focus on organisms that are exclusive inhabitants of the subterranean realm, but organisms that are not obligate cave-dwellers are frequent in caves, and may account for a substantial portion of biomass. Moreover, several taxa that are usually epigeous are regularly found inside caves, but for most of them it is unknown whether they accidentally enter them, or whether they actively select caves for specific environmental features. In this study we analysed the community of non-strict cave-dwelling organisms (amphibians, gastropods, spiders and orthopterans) in 33 caves from Central Italy, to assess how environmental factors determine community structure. Cave features strongly affected the distribution of the taxa considered. The combined effect of cave morphology and microclimate explained nearly 50% of the variation of community structure. Most of community variation occurred along a gradient from deep, dark and humid caves, to dry caves with wider entrances and extended photic areas. Most of species were associated with humid, deep and dark caves. Most of the non-troglobiont amphibians and invertebrates did not occur randomly in caves, but were associated to caves with specific environmental features. Analysing relationships between cave-dwelling species and environmental variables can allow a more ecological and objective classification of cave-dwelling organisms.

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## 1. Introduction

Many studies on the biology and ecology of underground environments focus on organisms that are exclusive cave inhabitants, which are often defined as troglonites or troglitic (Sket, 2008; Pipan and Culver, 2012). Troglonites are organisms that evolved specific adaptations to underground habitats, in which they spend their entire life cycle (Sket, 2008). However troglonites are not the sole components of fauna in cave ecosystems: organisms that are not obligate cave-dwellers are frequent in caves, may account for a substantial portion of biomass, particularly (but not exclusively) at limited distances from the cave entrance, and are extremely important for the functioning of cave ecosystem (Romero, 2009; Sendra and Reboleira, 2012). Bats represent a typical example of non-obligate cave dwellers that are extremely important for

underground environment: their guano play a fundamental role for several subterranean ecosystems.

Sket (2008) recently reviewed the historical classification of subterranean fauna, and proposed a standardized ecological nomenclature identifying three categories of non-obligate cave-dwellers: eutroglophiles, subtroglophiles and troglonexes. Eutroglophiles are epigeous species that are able to maintain permanent and self-sustaining subterranean populations. Subtroglophiles are species that are intimately associated to the cave environments, but requiring the epigean habitats during some period, or to complete some biological function (e.g., dispersal, feeding, reproduction...). Finally, troglonexes are organisms that normally live outside caves, but can sometimes be found in subterranean habitats, where they do not reproduce (Schiner, 1854; Vandell, 1964; Sket, 2008). Troglonexes are generally assumed to be not particularly important for understanding subterranean life or for the refinement of theoretical speleobiological questions (Sket, 2008). Actually, the term “troglonexene” is often considered as a synonym of accidental, suggesting that the presence of these organisms may be linked to passive mechanisms such as involuntary falls or trapping or to drift in the

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case of aquatic organisms. Troglomenes are thus frequently considered as chance guests of caves and supposed to enter them only sporadically (Schiner, 1854; Vandel, 1964; Sket, 2008).

The dichotomy between the true cave-dwelling organisms and the troglomenes remains abrupt in the classification of cave fauna (Vandel, 1964; Sket, 2008). This classification has recently been challenged by some authors, because it is considered too typologist (species often do not fit well the categories), and because it emphasizes the role of passive and accidental mechanisms to explain the occurrence in caves of usually epigeous species (Romero, 2009, 2011). The traditional classification of subterranean organisms gave rise to the notion that all “true” cave organisms should be blind and depigmented (Romero, 2009), while the distinctions between categories actually are complex and nuanced. As a matter of fact, several taxa are often and repetitively found in caves where nothing prevent them to exit (Romero, 2009), while many cave-dwelling organisms can exploit the epigeous environment under suitable climatic conditions, and particularly during night as in the case of some troglophilous orthopterans (e.g., the troglobiont salamander *Proteus aunguinus* (Schlegel et al., 2009)). It is important to note that hypogeous environments, such as caves, are not closed systems. Many organisms as well as abiotic elements such as water, air, and chemicals constantly move in and out of this environment (Culver and Pipan, 2009; Schneider et al., 2011). Even the deepest hypogeous karsts may be influenced by the organic matter percolating from the surface and other processes (Pipan et al., 2008; Stafford et al., 2008). In caves it is possible to find several taxa that apparently do not show specific adaptations to this environment, and that hardly fit the classical biospeleological categories (Romero, 2009).

For instance, several amphibian species are frequently found in underground environments (Fellers et al., 2010). Even if amphibians often remain underground for limited periods, they can have important roles in the trophic dynamics of caves (Peck, 1974; Fenolio et al., 2006), and they hardly fit the classical biospeleological categories. The lungless cave salamanders (genus *Hydromantes*) living in Mediterranean regions are an interesting example. These salamanders do not depend upon subterranean environments during cold and moist months (generally from autumn to spring), but caves and other underground environments play an essential role for their persistence during warmer months, when the external conditions become too harsh (e.g., dry, hot) (Salvidio et al., 1994; Cimmaruta et al., 1999; Lanza et al., 2006). In practice, even if these salamanders usually spend only a limited part of their life cycles underground, in some regions they can persist only where subterranean environments are available. Furthermore, only some caves are inhabited by these salamanders. Caves exhibit heterogeneous environmental features; salamanders select those with specific biotic and abiotic features, and this habitat selection processes determines patterns of species presence/absence and abundance (Ficetola et al., 2012, 2013). Caves can also allow the persistence of amphibian populations in karstic habitats with limited water at the surface, by offering stable pools and freshwater habitats for breeding (Manenti et al., 2009; Kohler et al., 2010; Manenti et al., 2011). Several species of epigeous amphibians are regularly found inside caves during some periods of the year (Bressi and Dolce, 1999), but for the majority it is unknown whether they accidentally enter caves, or whether they actively select caves on the basis of their environmental features.

A similar pattern also occurs for several species of non-trogliont invertebrates that are usually found in caves. Many trogliphile or troglomene species of Arachnids, insects and terrestrial gastropods can be often observed inside caves, especially during the dry season (Peck and Thayer, 2003; Shear, 2007; Vink and Duperre, 2011; Welter-Schultes, 2012; Manenti et al., 2013b).

However, very few studies have assessed why apparently epigeous organisms are regularly found in underground environments, and which environmental factors determine the structure of their communities in caves (Briggler and Prather, 2006).

The aim of this study was to analyse the environmental factors determining the composition and the structure of communities that occupy the less deep zones of caves (i.e., the first tens of meters of caves). In particular we challenge the idea that usually epigeous species, defined as troglomenes or accidentals organisms (Sket, 2008), are strays organisms for cave habitats, randomly responding to cave features. Furthermore, we evaluated whether identifying relationships between species and environmental variables can allow a more ecological classification of cave-dwelling species, considering the selection of specific environment features in addition to their adaptations of species.

## 2. Materials and methods

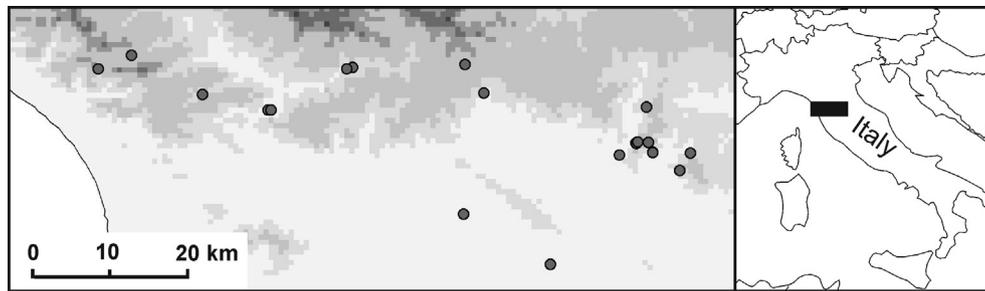
### 2.1. Study area

The study area is located in the Tuscan Apennines (between 44°06'20" N, 10°25'14" E and 43°45'19" N, 11°44'59" E) and consisted of 33 caves, specifically: four located in province of Florence (Calvana Mountains, Monte Morello), eight in province of Prato (Calvana Mountains), four in province of Pistoia (Pistoia Mountains), and 17 in the province of Lucca (Lucca Apennines and Apuan Alps) (Fig. 1). The area is characterized by a Mediterranean xeric climate and covered by mixed broadleaved forests (*Quercus cerris*, *Q. pueescens*, *Q. ilex*, *Q. suber*) alternated with grazed areas with typical calcifilous herbaceous cover (Festuco-Brometalia, *Alyssosedion albi*, *Juniperus communis*) (Regione Toscana, 2008).

We used the data of the Tuscany regional speleological register, and previously published data on biospeleological record to locate the caves and to record preliminary information of them (size, accessibility, hydrography). The altitudinal range was 91–890 m a.s.l. Most surveyed caves (28) are developed in limestone with abundant clay deposits. Some of caves surveyed in the Apuan Alps (2) were produced through fault displacements, related to tectonic movements, and are mainly developed in metamorphic schist rocks. Three of the surveyed caves were produced by human activities, two were underground storage areas, and one was a gallery built to drain a stream.

### 2.2. Cave surveys and environmental features

During the summer of 2012 (July–August), we surveyed caves as deeply as possible. We recorded nine features describing cave morphology, microclimate and ecosystem functioning, that can be important for their exploitation. Several environmental parameters of caves were measured at 6 m from the entrance. We selected this value because several cave-dwelling organisms already attain high abundance at this depth (Salvidio et al., 1994), and because the Italian Speleological Society recognizes as “caves” the cavities with spatial development of at least 5 m (Bonini et al., 1999). Using the same depth for all cavities enables a more objective comparison between caves with different features. We recorded maximum depth as the deepest point reached during exploration: this point corresponded the end of cave or with the depth at we could access without special equipment. We also recorded the presence of wet walls within the cave (y/n), maximum height and width at 6 m from the entrance (Ficetola et al., 2012). To estimate wall heterogeneity, we flattened a 1-m string against the cave wall in vertical direction, so that it followed the surface contours. We then measured the straight-line distance between the ends of the string for both right and left walls, and calculate the average (Camp and Jensen, 2007).



**Fig. 1.** Study Area within Italy. Dots identify cave location. Due to geographical proximity some localities appear superimposed. The shading represents altitude (resolution: 30 arc seconds), ranging from zero to 1830 m.

Furthermore, to characterize the microclimate and light availability in caves, we used a EM882 multi-function thermo-hygrometer and light-meter (PCE Instruments) to measure temperature, relative humidity, maximum and minimum illuminance at 6 m from the entrance.

### 2.3. Community surveys

We visited each cave at least twice, and assessed the presence of 11 different species of amphibians, arthropods and terrestrial gastropods that typically inhabit caves in the study area. To ensure consistency of results, in all the caves surveys were performed by the same researchers. We assessed the distribution of 4 species of amphibians: *Hydromantes italicus*, *Rana italica*, *Rana dalmatina* and *Bufo bufo*. *Hydromantes italicus* is the only amphibian of this community that is generally considered a troglophile species (sub-troglophile). Conversely, the other three species are typical epigeous species, whose occurrence in caves has occasionally been reported, without detailed information on the association with caves, and often considered as accidentals by previous studies (Bressi and Dolce, 1999; Lanza et al., 2006; Manenti, 2008). We also assessed the presence of three Arachnids taxa typically considered as troglophiles: *Meta menardi*, *M. (Metellina) merianae* and *Tegenaria* (Malthonica) sp. (Isaia et al., 2011). Among insects, we collected data on the occurrence of the Orthopteran *Dolichopoda letitiae*, a species endemic to the northern Apennines that is considered a scavenger and spends most of its life cycle underground (Allegrucci et al., 2005). We assessed three terrestrial gastropods: the snails *Oxychilus draparnaudi* and *Chilostoma planospira* and the slug *Limax* sp., whose occurrence has already been reported for some caves (Mazza et al., 2008). To assess species occurrence we used visual encounter surveys for all the caves surfaces. The sampling effort was similar for each cave with an effort of 4 min/m<sup>2</sup>. For each species, abundance was recorded as the maximum number of individuals detected within the cave during the two visits. Detection probability of large animals in caves is generally high, and previous analyses showed that two visits allow reliable assessment of the distribution of some of the considered species (amphibians: Ficetola et al., 2012; spiders: Manenti et al., unpublished).

### 2.4. Statistical analyses

We used redundancy analysis (RDA) to evaluate the relative role of cave features on the multivariate structure (i.e., species composition and abundance) of amphibian and invertebrate communities. RDA is a canonical analysis, combining the properties of regression and ordination techniques, that allows evaluating how much of the variation of the structure of one dataset (e.g., community composition in a cave; endogenous dataset) is explained by independent

variables (e.g., habitat features; exogenous datasets) (Borcard et al., 2011). As exogenous matrix, we used one matrix composed by the nine environmental features, and we used the matrices of abundance of amphibians and invertebrates as endogenous. We also combined the matrix of amphibians and invertebrates, for an analysis of the overall community. We calculated the amount of variation of community structure explained by cave features, and the significance of explained variance by performing ANOVA-like permutation tests (10,000 permutations) (Borcard et al., 2011). We used distance biplots of Principal Component Analysis (PCA) and of RDAs to visualize the relationships between community structure and environmental features. PCA and RDA plots provide complementary information. In PCA biplots, distances among objects approximate their Euclidean distances in the multidimensional space. PCA biplots therefore have the advantage of an accurate visualization distances among variables. The interpretation of RDA plots is similar: as in PCA plots, distances among centroids, and between centroids and individual objects approximate their Euclidean distances. In addition, in RDA plots the angles between response and explanatory variables reflect their correlation (a narrow angle indicates high correlation). Therefore RDA plots have the advantage of a more accurate representation of relationships between dependent and independent variables (Borcard et al., 2011).

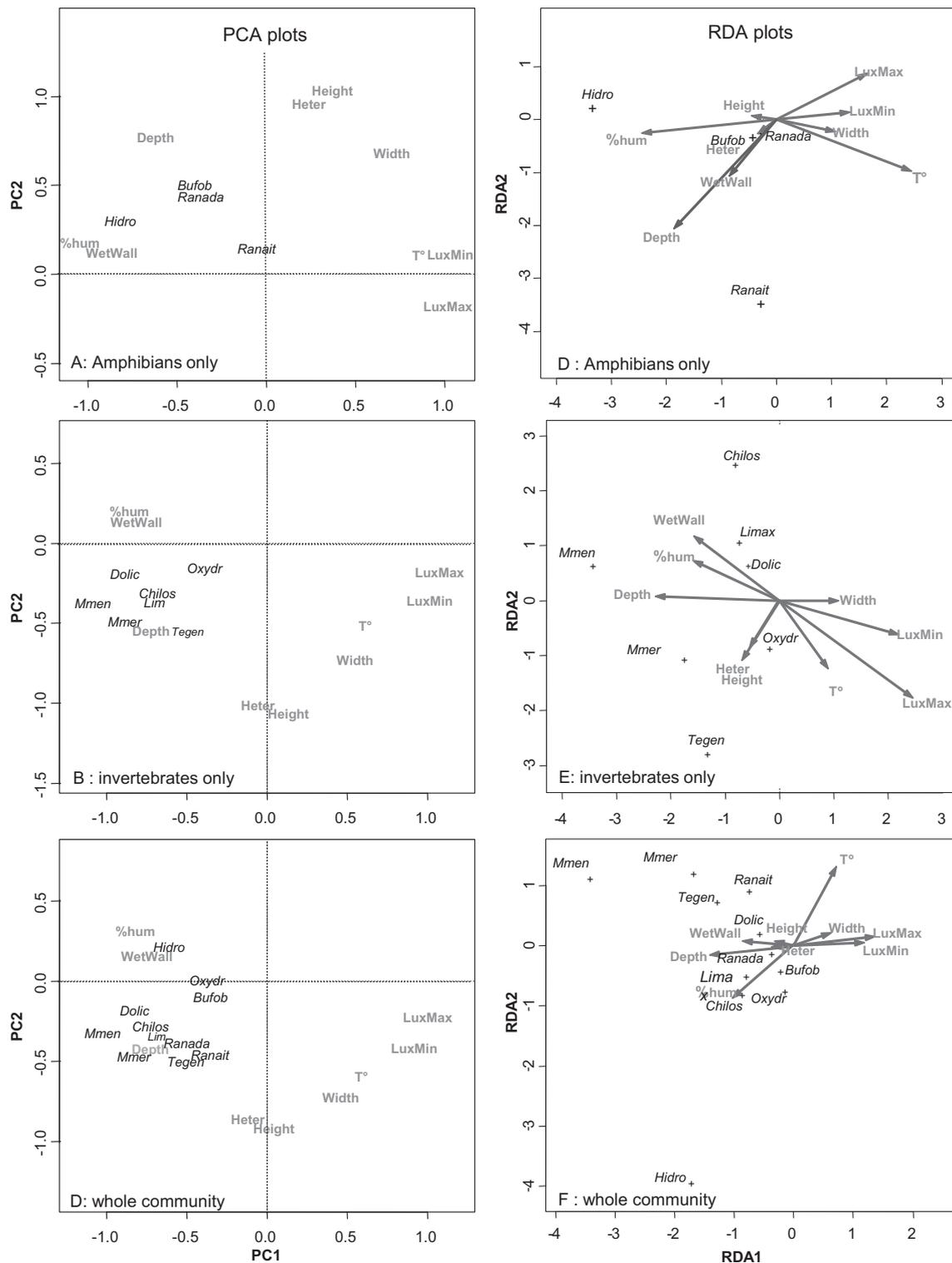
Prior to performing analyses, species abundance was square-root transformed. If necessary, environmental variables were transformed using logarithms (cave depth, height, width, and illuminance). RDAs was computed on standardized variables using the vegan package (Oksanen et al., 2012); we performed all statistical analyses in the R 2.14 environment (R Development Core Team, 2012).

## 3. Results

Within the 33 caves investigated, the most widespread amphibians were *Hydromantes italicus* (occurrence,  $O = 33.3\%$ ) and *R. italica* ( $O = 30.3\%$ ) that were recorded in one third of the caves surveyed. *R. dalmatina* ( $O = 9\%$ ) and *Bufo bufo* ( $O = 9\%$ ) were less frequent. The spider *M. menardi* was detected in more than 50% of the caves ( $O = 51.5\%$ ), while the other two arachnids considered were less frequent (*M. (Metellina) merianae*:  $O = 27.3\%$ ; *Tegenaria* sp.:  $O = 45.5\%$ ). For gastropods, the subtroglophile snail *O. draparnaudi* showed a lower occurrence ( $O = 9\%$ ) than the snail *C. planospira* ( $O = 27.3\%$ ) and the slug *Limax* sp. ( $O = 36.4\%$ ). The orthopteran *D. letitiae* was relatively frequent ( $O = 39.4\%$ ).

### 3.1. Amphibian community

Amphibian species showed limited distance in the PCA plots, indicating low Euclidean distances and therefore association with



**Fig. 2.** Plots of Principal Component Analysis (PCA, left panels) and of constrained Redundancy Analysis (RDA, right panels) showing the relationship between cave features and organisms. A) PCA, environmental features and amphibians; B) RDA, dependent matrix: amphibians; C) PCA, environmental features and invertebrates; D) RDA, dependent matrix: invertebrates; E) PCA, environmental features and amphibians; F) RDA, dependent matrix: overall community. See methods for differences between PCA and RDA plots. In RDA, constraining variables are represented by gray arrows and abbreviated as follows: %hum, relative humidity; T°, temperature; Depth, cave depth; Wetwall, wet walls; Heter, wall heterogeneity; Height, cave height; Width, cave width; Luxmin, minimum illuminance; Luxmax, maximum illuminance. Species are abbreviated as follows: Hidro, *Hydromantes italicus*; Ranait, *Rana italica*; Ranada, *Rana dalmatina*; Bufo, *Bufo bufo*; Dolic, *Dolichopoda letitia*; Chilos, *Chilostoma planospira*; Oxydr, *Oxychilus draparnaudi*; Tegen, *Tegenaria* sp.; Mmen, *Meta menardi*; Mmer, *M. merianae*, and Lim, *Limax* sp.

similar environments (Fig. 2a). Most of amphibians species were associated to deep caves with high relative humidity and presence of wet walls (Fig. 2a). RDA showed that the structure of amphibian community was significantly related to cave features (permutation test:  $P = 0.013$ ). The environmental variables considered explained 48.5% of variation of amphibian communities. The first RDA axis alone explained 36% of variance. This axis represented a gradient ranging from caves that were deep, humid, cold and receiving less light from outside (negative values of RDA axis 1 in Fig. 2b), to shallow caves that were dry, warm and receiving light from outside (positive values of RDA axis 1, Fig. 2b). The second RDA axis explained 11% of variance, and was mostly related to cave depth and to the presence of wet walls (negative values of RDA axis 2 in Fig. 2b). On the basis of RDA, *H. italicus* and *R. italica* were the species for which the distribution was best explained by environmental features. The abundance of *H. italicus* was strongly associated with negative levels of RDA axis 1, i.e., to the deepest, most humid, cold caves not receiving light from outside. *R. italica* was associated with negative values of RDA axis 2, i.e., to the deepest caves with presence of wet walls. The remaining two species (*B. bufo* and *R. dalmatina*) showed limited loadings along the first two RDA axes, suggesting less clear relationships between their distribution and the environmental features considered (Fig. 2b).

### 3.2. Invertebrate community

Most of invertebrate species showed limited distance in the PCA plots, indicating low Euclidean distances and therefore association with similar environmental features (Fig. 2c). RDA showed that the community structure of invertebrates was significantly affected by cave features (permutation test:  $P = 0.009$ ). Cave features explained a large proportion of variation of invertebrate communities (46.7%). The first RDA axis explained 38.8% of variance. This axis represented a gradient ranging from caves that were deep, humid cave with less light from outside (negative values of RDA axis 1 in Fig. 2d) to shallow, wide, dry caves with light (positive values of RDA axis 1, Fig. 2d). The second RDA axis explained only 4.4% of variance, and was mostly related to cave height and wall heterogeneity (negative values of RDA axis 2 in Fig. 2d). Most of species (particularly *Meta* spiders) were associated with negative values of RDA axis 1, i.e., deep, humid and dark caves. *Tegenaria* sp. was related to negative values of axis 1, but also to negative values of RDA axis 2. This suggests association with humid, high, deep caves with heterogeneous walls. The snail *C. planospira* was associated with positive values of axis 2, suggesting association with deep, humid caves with low heterogeneity (Fig. 2d).

### 3.3. Overall community

In the PCA plot, among-species distance was small even when considering the overall community. This confirms that most of species are associated with similar environmental features (Fig. 2e). RDA performed on the whole community confirms that cave features significantly affected its composition ( $P = 0.001$ ), and the environmental features considered explained nearly half of the variation (47.2%). The first RDA axis alone explained 31.7% of variance, representing a gradient from deep, humid caves receiving less light (negative values of RDA axis 1 in Fig. 2f) to shallow, wide, dry, warm caves receiving more light from the entrances (positive values of RDA axis 1, Fig. 2f). The second RDA axis explained 8.1% of variance, and was mostly related to temperature (positive values of RDA axis 2 in Fig. 2f). The results of the overall analysis generally confirmed the two partial analyses. *Meta* spiders were the taxa most strongly related to negative values of the RDA axis 1 (Fig. 2f),

while *H. italicus* was related to negative values of RDA axes 1 and 2 (i.e., humid and cold caves).

## 4. Discussion

Cave features strongly affected the distribution of both amphibians and invertebrates in the study area. In all the analyses, the combined effect of cave morphology and microclimate explained nearly 50% of the total amount of variation of community structure. Most of this variation was explained by a clear environmental gradient, which was identified as the first RDA component in all the analyses. This axis represented a gradient from deep, dark and humid caves to dry and luminous caves with wider entrances (e.g., Fig. 2f), and this gradient strongly affected community composition, as it accounted for most of explained variation in community structure. All the species considered were related to negative values of the first RDA axis, i.e., were more frequent and abundant in humid, deep caves and receiving no light from outside (Fig. 2). In other words, the non-troglobiont species of amphibians and invertebrates considered did not occur randomly in caves, but were in most of cases associated with caves having specific environmental features. This contrasts with traditional analyses that considered many of them as “trogloxenes”.

Among the species considered, only some (the salamander *H. italicus*, the spiders *Meta* and *Tegenaria*, the mollusk *Oxychilus draparnaudi* and the orthopteran *Dolichopoda laetitiae*) are generally considered as troglaphiles (subtroglaphiles; Di Russo et al., 1999; Allegrucci et al., 2005), while many others (the amphibians *R. italica*, *R. dalmatina*, *Bufo bufo*, the mollusks *Chilostoma planospira* and *Limax* sp.) are considered as troglloxenes, i.e., external species that occur in caves accidentally only (Bressi and Dolce, 1999; Sket, 2008; Welter-Schultes, 2012). However, these “trogloxenes” were frequent in the study caves, and the relationships between environmental features and some of these species were strong and analogous to those detected for the species that are considered to have greater cave affinities.

For instance, the frog *R. italica* has very few reported observations in caves, and these records are considered accidental and attributed to passive mechanisms (Bressi and Dolce, 1999). However, this frog was frequent, and was present in caves having specific features only, i.e., deep caves with wet walls. This association cannot be explained by random occurrence, and instead suggests some kind of selection for specific environmental features. Species–habitat relationships were similar for the salamander *Hydromantes strinatii*, which was strongly related the deepest, most humid caves. This salamander is considered a subtroglaphile species linked to underground habitats during dry season. Our results are similar to those found by recent studies on the closely related *H. strinatii*: these salamanders probably select caves with a specific microclimate, as only the most humid and cold caves contained conditions within their narrow physiological limits (Ficetola et al., 2012). It is not easy to disentangle the relative role of cave depth, air humidity and other features such as air temperature, occurrence of wet walls and light on amphibian distribution. These features are interdependent, as cave depth affects air circulation and microclimatic conditions of underground habitats; usually the deepest caves are more buffered against the external environment, with coldest temperatures and wettest conditions during summer. In amphibians, high humidity decreases dehydration rate, and exploiting the most humid and deep caves can allow better maintaining water balance (Wells, 2007).

The spider *M. menardi* was the most widespread species in the study caves, and showed a similar association with deep, humid and dark caves. This species has a complex life cycle: in early spring the hatched spiderlings are attracted by light and exit caves

dispersing outside till autumn, when they become photophobic and look for caves where they settle (Smithers, 2005). Cave depth can influence air circulation and facilitate cave location and exploitation for this spider. Moreover, although generally considered a specialist of the twilight zone nearby cave entrances, *M. menardi* can vary its position within caves according to seasonal microclimate changes (Manenti et al., unpublished), and the deepest caves are likely to provide more areas with suitable conditions. Similar considerations are likely for *M. merianae*, that has comparable ecological requirements, although is considered less specialized (Novak et al., 2010). The other spider examined, *Tegegnaria* sp., is often found in cave habitats (Isaia et al., 2011) and our study found that it was also correlated to cave height and walls heterogeneity. This species often builds webs in small holes located in walls and ceilings (Roberts, 2001). Cave morphology can be important in allowing shelters and prey detection.

The mollusks, *C. planospira* and *Limax* sp. were previously poorly reported for cave environments but were frequent in the wettest study caves. In particular *C. planospira*, is an endemic Italian species usually linked to humid and shady rocky limestone habitats (Welter-Schultes, 2012). Conversely, *Oxychilus draparnaudi* is often reported as a subtroglophile species with a certain level of specialization to cave life (Di Russo et al., 1999), still it occurred with the same frequencies of typically epigeous species. Relationships between *O. draparnaudi* and environmental features were not particularly strong, if compared with the other mollusks (Fig. 2d).

Only a few species, such as the amphibians *R. dalmatina* and *B. bufo* were close to the origin of the RDA axes in biplots (Fig. 2b), suggesting that they are not strongly affected by the environmental variables considered (Borcard et al., 2011). During their post-breeding activity, these amphibians are usually observed in natural habitats such as woodlands, or in semi-natural landscapes such as low intensity agricultural areas with natural elements (Ficetola et al., 2009; Manenti et al., 2013a). However, amphibian activity strongly depends on weather conditions, being for instance more intense during rainy periods (Mazerolle et al., 2007). When weather is not suitable for outdoor activity, these species require underground shelter, and caves can be an excellent shelter they may use during the prolonged periods with unsuitable weather that can occur in Mediterranean areas (Bonini et al., 1999; Manenti, 2008).

Most of studies on the biology and ecology of subterranean environments focus on troglobitic species (Culver and Pipan, 2009), while trogliphiles or troglonexes species occurring in caves are less studied. Usually they are just annotated in cave fauna checklists or reported in notes dealing with single species occurrence (Mazza et al., 2008; Barnes et al., 2009). The few studies performed on cave communities that considered trogliphiles organisms found an interesting stability of their composition along time and in the sector of the cave studied (Di Russo et al., 1999). Our analysis of the community living in the first zones of caves showed that most of species do not occur randomly in caves, but rather are strongly associated with environmental features corresponding to specific cave zones. The traditional classification of organisms found in caves [troglobites, trogliphiles (including eutroglobites and sub-troglobites) and troglonexes] was introduced by Schiner in the XIX century (Schiner, 1854), revised by Racovitza (1907), and recently updated by Sket (2008). This classification is based on the degree of dependence toward the subterranean environment, considering both morpho-physiological and behavioral traits. However, the biological relevance of the traditional classification has been recently challenged (Romero, 2009). This classification implies some degree of subjectivity, and does not take into account the complexity of ongoing ecological and evolutionary processes. For instance, a taxon that is at the beginning of the evolution toward cave dependence may be classified as “accidental” (Romero, 2009;

Romero, 2011). Our study suggests that several epigeous species, usually considered as troglonexes or accidentals according to the standard classification, are not strays organisms for cave habitats: their distribution is clearly linked to cave features, and follows patterns that are similar to the ones observed for more usual cave dwellers. Terms such as “accidentals” or “troglonexes” (literarily: cave foreigners) may not represent well the ecological processes determining the occurrence of these species in caves.

The study of relationships between environmental features of caves and the distribution of cave-dwelling organisms may help to complement the traditional classification. Also for species that are usually considered accidental/troglonexes, it is possible to analyze species–habitat relationships, to assess whether they occur randomly in caves, or whether they select those with specific environmental features. The identification of such habitat selection process would indicate a more active importance of cave environments also for the non-typical species. For instance, in our study case, the frog *R. italica* and the snail *C. planospira* showed high frequency and clear habitat association patterns, indicating that ecological processes are important in their exploitation of cave environments. Ecological analyses can thus allow us to go beyond the typological classification, and consider not only whether a species is frequent in caves or whether it shows troglomorphic features (Schiner, 1854; Romero, 2009; Romero, 2011), but also the ecological processes determining occurrence in caves. Cave features can affect the distribution not only of cave dependent fauna, as caves can provide important habitat also for some usually epigeous taxa. There is a need for a better knowledge of the ecological process acting in cave habitats and promoting cave exploitation, by integrating analyses performed at multiple levels, including the community level.

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