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Exploring the homogeneity of terrestrial subterranean communities at a local spatial scale

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Abstract. 1. Although caves are generally perceived as isolated habitats, at the local scale, they are often interconnected via a network of fissures in the bedrock. Accordingly, caves in close proximity are expected to host the same, or very similar, animal communities.

2. We explored the extent to which subterranean arthropod communities are homogenous at a local spatial scale of less than 1 km^2, along with which cave-specific environmental features result in a departure from the expected homogeneous pattern. We approached this question by studying richness and turnover in terrestrial invertebrate communities of 27 caves in a small karst massif in the Western Italian Alps.

3. Specialised subterranean species were homogeneously distributed among caves and were not influenced by seasonality. The only factor driving their distribution was the distance from the cave entrance, with deeper caves yielding a greater diversity of species.

4. Significant spatio-temporal turnover in species not specialised to subterranean life was observed. In summer, there was a significant homogenisation of the community and a more even distribution of species among sites; in winter, these species were missing or found exclusively at greater depths, where environmental conditions were more stable. Furthermore, caves at lower elevations yielded, on average, a greater diversity and abundance of these species.

5. This study demonstrated that the theoretical expectation of no turnover in community composition in caves in close proximity is not always met. Turnover can be mostly attributed to seasonal patterns and sampling depth; thus, our findings have implications for planning sampling and monitoring activities in caves.

Key words. Arthropods, beta diversity, community ecology, pitfall traps, spatial turnover, subterranean biology, temporal turnover, troglobiont.

Introduction

Ecologists and evolutionary biologists have frequently compared caves to islands (Culver, 1970; Snowman *et al.*, 2010; Esposito *et al.*, 2015; Fattorini *et al.*, 2016; Balogh *et al.*, 2020). In fact, from the perspective of a specialised subterranean organism, a cave is a patch of suitable habitat within a matrix of unsuitable habitats (Itescu, 2019; Mammola, 2019). It is understood that island-like properties of caves emerge mostly at broad geographical scales (Stoch & Galassi, 2010), wherever the extent of the study area is large enough to encompass geological discontinuities or other natural barriers limiting subterranean connectivity (see Fig. 2 in Mammola, 2019). For example, studies exploring the extent to which subterranean communities vary in their composition at continental scales have documented higher rates of turnover (β-diversity) than those typically

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observed in surface habitats (Zagmajster *et al.*, 2014; Mammola *et al.*, 2019). Yet, it is understood that β-diversity patterns are strongly scale dependent (Jarzyna & Jetz, 2018), meaning that the 'caves as islands' view rarely holds true at the local scale (Mammola, 2019).

According to a modern understanding of the subterranean realm, a cave is nothing but a human-accessible void in the ground. Subterranean organisms not only inhabit caves but can thrive in a large breadth of lightless habitats, including networks of fissures in the bedrock and shallow habitat pores not directly accessible to humans (Culver & Pipan, 2010; Giachino & Vailati, 2010; Mammola *et al.*, 2016; Pipan & Culver, 2017; Ficetola *et al.*, 2019). Indeed, we are starting to perceive caves as small 'windows' opening to a vaster world, the subterranean one, allowing us to catch a glimpse of what happens below our feet (Howarth, 1983; Uéno, 1987). If microcavernous habitats ensure subterranean habitat connectivity at the local scale, low values of β-diversity should be observed when studying biological communities of caves in close proximity. This pattern was recently confirmed by research exploring the spatial distribution of invertebrate species over the cross section of the Trnovski Gozd massif in Slovenia, demonstrating a limited distinction between shallow (0–50 m) and deep (up to 800 m) cave communities within this karst massif (Trontelj *et al.*, 2019).

The expectation of no community turnover among caves at restricted spatial scales is not, however, always met. Even when sampling caves in close proximity that theoretically should harbour the same fauna, slight or even conspicuous species turnover is observed. This may be the result of daily and seasonal changes in community composition (Lunghi *et al.*, 2017; Mammola *et al.*, 2017), of local habitat unsuitability due to a combination of specific environmental conditions (Jiménez-Valverde *et al.*, 2017), of competition dynamics that may lead to the exclusion of certain species from a given community (Mammola & Isaia, 2014), or even simply the consequence of imperfect detection (Ficetola *et al.*, 2018) when sampling such structurally complex environments (Wynne *et al.*, 2018, 2019).

Here, we seek to understand the extent to which habitat connectivity determines the homogenisation of subterranean invertebrate communities at local scales and which cave-specific environmental conditions may determine a departure from this expected pattern. We used a geographically restricted area, the cave system of Comba dell'Infernotto (Chesta & Elia, 2004), as a uniquely suited study site for this purpose, in that it hosts a great diversity of caves in an area of approximately 1 km^2. These caves encompass a wide range of environmental conditions and host a rich and diversified fauna, with several specialised subterranean species. Therefore, this system is well suited for exploring the ecological determinants of α- and β-diversity patterns at the local scale.

Our null hypothesis was that community composition is the same in all caves within the considered subterranean system. In other words, we expected to observe comparable levels of α-diversity in all caves and β-diversity values close to zero in pairwise comparisons among caves. We hypothesise that departures from such theoretical expectations should be linked to seasonal patterns in community composition and/or due to a combination of unsuitable local environmental conditions.

Material and methods

Study area

The study was carried out in the cave system of Comba dell'Infernotto (or Infernetto) (7.4°E, 44.2°N), in the municipality of Valdieri, Maritime Alps, Province of Cuneo, Piedmont, Italy (Fig. 1). With more than 40 caves and mines currently documented, this small karst area yields the greatest number of subterranean sites in the province of Cuneo (Chesta & Elia, 2004). This area is included within the boundaries of the Site of Community Importance IT1160056 'Alpi Marittime' (European Habitat Directive 43/92).

For this study, we selected 27 subterranean sites (Fig. 1) within the area of Comba dell'Infernotto, with a maximum distance of 1 km between sites. Other caves in this system were not investigated due to access difficulties. We sampled both caves and old abandoned mines in the same area, ranging from 4 to 861 m in length, from 0.5 to 35 m^2 in the size of the cave entrance, and from 1000 to 1200 m in the elevation of cave entrances (Table 1). All site entrances were in a dense beech forest (*Fagus sylvatica* L.).

Sampling design

We sampled invertebrates in caves using pitfall traps (diameter 9 cm, volume 40 ml). To minimize impacts on invertebrate populations, only one pitfall trap per site was used. We installed traps at the ground level, at the end of the cave for caves with length <10 m, and up to 40 m deep for longer caves. This ensured a balanced and homogenous coverage of distance from the entrances. We covered each trap with a flat stone to shelter it from percolating water (RůŽička, 1982). We filled traps with brine (supersaturated preserving solution of water and NaCl; Giachino & Vailati, 2010) and baited them with cheese.

To evaluate seasonal patterns in community composition, we trapped invertebrates once in summer, from June to September 2017, and once in winter, from November 2017 to April 2018. We were forced to overextend the winter sampling period (6 vs. 4 months in summer) due to a late snow melt. However, according to our previous experience, such unequal sampling does not corrupt the general outcomes as baited pitfall traps are mostly effective within 1–2 months from their installation, when the bait is still fresh (Mammola *et al.*, 2015, 2017).

We measured the linear distance from the cave entrance using an extendable tape. Moreover, we estimated the subjacency of each trap (i.e. the vertical distance from the surface) using Geographic Information System (GIS), marking the position of the trap on available geological surveys of Chesta and Elia (2004) and plotting the latter in plain view on a georeferenced topographical map. We derived subjacency for traps in caves below 10 m in length by direct measurements. We derived total cave length and maximal subjacency of each cave from Chesta and Elia (2004) or measured these parameters directly in the field

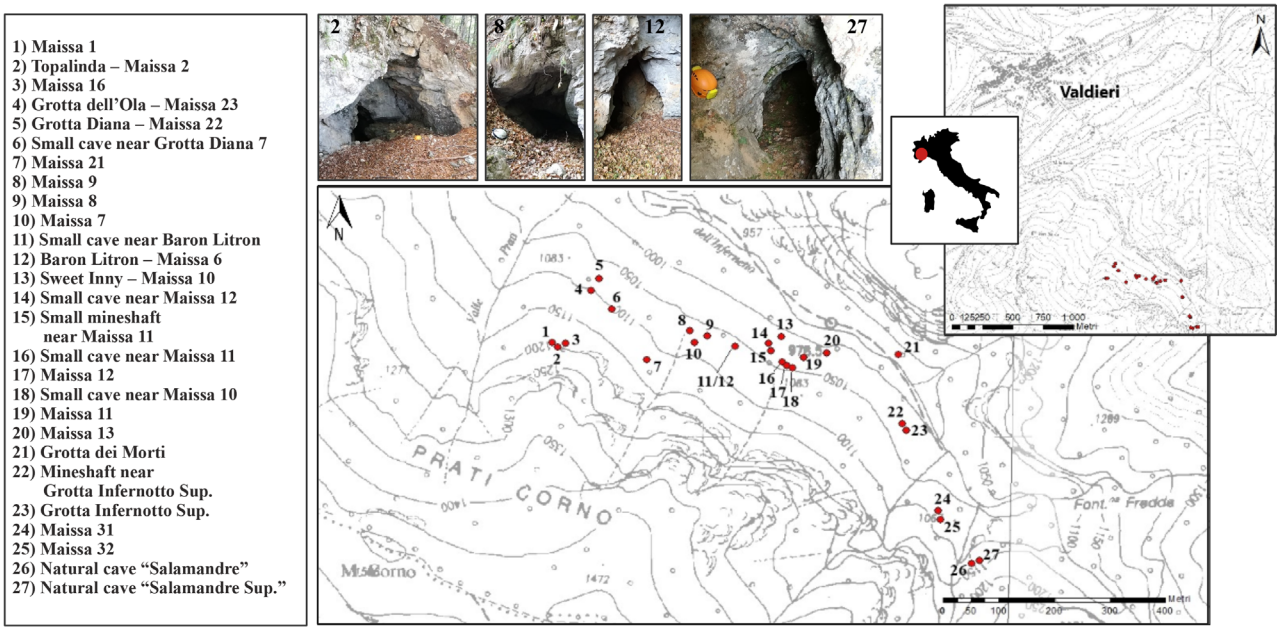

Fig. 1. Map of the study area. Dots show the distribution of the sampled caves on the left slope of the Comba dell'Infernotto (municipality of Valdieri, Province of Cuneo, Italy). Photographs illustrate examples of cave entrances. [Colour figure can be viewed at wileyonlinelibrary.com].

whenever this information was not available in speleological literature. We approximated the area of each cave entrance by multiplying its base by its height. For each cave, we also recorded, by eye, the presence of percolating water in the two seasons.

We measured temperature at each pitfall trap with EL-USB-2+ dataloggers (Lascar Electronics, Salisbury, United Kingdom), programmed to record a temperature measure (accuracy of ±0.5 °C) every 6 hours (00:00, 06:00, 12:00, 18.00) throughout the two sampling periods.

Species identification and ecological classification

Specimens were identified to the lowest possible taxonomic rank by experts of the different groups (see author contribution and acknowledgements for details). For the purpose of exploring subterranean diversity patterns, we assigned each species to two major ecological groups (Novak *et al.*, 2012; Niemiller & Zigler, 2013; Trontelj *et al.*, 2019): obligate subterranean species ('troglobionts'; Sket, 2008; Trajano & de Carvalho, 2017) and all other species ('non-troglobionts'; Novak *et al.*, 2012) (Appendix S1). We based this classification mainly on the expert opinion of different taxonomists involved in this work but also using data and morphological traits associated with subterranean life (loss of eyes and body pigment) from the literature.

Statistical analyses

All analysis were conducted in R (R Core Team, 2018). We used Poisson generalised linear models (GLMs) to explore factors driving alpha diversity (α) and the abundance of troglobiont and non-troglobiont species in our study sites. We followed the general protocol by Zuur and Ieno (2016) for conducting regression-type analyses, whereby we:

1. performed data exploration on the initial dataset, aiming to verify the presence of outliers, remove collinear predictors, and detect potential interactions among predictors (Zuur *et al.*, 2009);
2. constructed Poisson GLMs to test for significant relationships between the dependent variables and our explanatory predictors. We included potential interactions among predictors only if these were detected during data exploration (see point 1);
3. performed a step-wise model selection on each model with the *step1* function to obtain a minimum adequate model for each of the dependent variables, minimising the Aikaike Information Criterion value; and
4. validated each model with the aid of the package 'performance' (Lüdecke *et al.*, 2020). In this phase, we tested each model for over-dispersion and switched to a negative binomial distribution if models were over-dispersed (Gelman & Hill, 2007).

To investigate spatial and temporal turnover in community composition, we estimated pairwise β-diversity among caves and between the two seasons using the framework proposed by Carvalho *et al.* (2012) and Cardoso *et al.* (2014), whereby β-diversity is expressed as:

$$\beta_{\text{Total}} = \beta_{\text{Replacement}} + \beta_{\text{Richness}}.$$

Table 1. Main features of the investigated caves.

Code (Fig. 1)	Cave name	Cadastre code	Type	Elevation (m)	Pitfall distance from entrance (m)	Pitfall subjacency (m)	Total length (m)	Depth (m)	Entrance size (m^2)	Subjacency (m)	Longitude (°)	Latitude (°)
1	Maissa 1	1209 Pi	Natural	1186	16	16	37	−9	10	16	7.4050	44.2615
2	Topalinda – Maissa 2	1210 Pi	Natural	1179	36	30	334	−63	20	83	7.4052	44.2615
3	Maissa 16	1221 Pi	Natural	1169	4	7	12	6	4	3	7.4054	44.2615
4	Grotta dell'Ola – Maissa 23	1228 Pi	Natural	1105	4.5	2	6	−2	2.8	2	7.4060	44.2627
5	Grotta Diana – Maissa 22	1227 Pi	Natural	1048	19.1	14	39	−11	5	18	7.4061	44.2627
6	Small cave near Grotta Diana	n.c.	Natural	1111	3.1	8	4	0	2.7	8	7.4065	44.2622
7	Maissa 21	1226 Pi	Natural	1145	3	4	6	−2	2	4	7.4168	44.2614
8	Maissa 9	1217 Pi	Natural	1085	10.3	7	11	−1	2.5	7	7.4084	44.2617
9	Maissa 8	1216 Pi	Natural	1077	6.4	7	6	−2	1.2	9	7.4084	44.2618
10	Maissa 7	1215 Pi	Natural	1071	35	13	29	−11	1.3	13	7.4086	44.2618
11	Small cave near Baron Litron	n.c.	Natural	1063	5.5	3	10	−1	12	5	7.4093	44.2616
12	Barôn Litrôn – Maissa 6	1214 Pi	Natural/Mine	1063	16	38	861	−59	10	75	7.4093	44.2616
13	Sweet Inny – Maissa 10	1218 Pi	Natural	1045	14.3	13	116	−30	35	35	7.4098	44.2615
14	Small cave near Maissa 12	n.c.	Natural	1027	12	6	12	−7	1.5	6	7.4099	44.2613
15	Small mine shaft near Maissa 11	n.c.	Mine	1038	2.5	1	4	−1	0.5	1	7.4102	44.2617
16	Small cave near Maissa 11	n.c.	Natural	1051	3.5	2	5	0	26	1	7.4104	44.2613
17	Maissa 12	1219 Pi	Natural	1090	13.3	12	92	−20	2.6	14	7.4106	44.2613
18	Small cave near Maissa 10	n.c.	Natural	1037	3.5	2	8	3	3	2	7.4105	44.2617
19	Maissa 11	n.c.	Natural	1054	6.8	7	37	−20	0.8	22	7.4104	44.2613
20	Maissa 13	n.c.	Natural	1023	22	5	20	−4	3	5	7.4113	44.2619
21	Grotta dei Morti	1054 Pi	Natural	1023	19	15	84	−16	10	15	7.4131	44.2611
22	Mineshaft near Grotta Infernotto Superiore	n.c.	Mine	1041	5.5	4	6	−1	4.2	4	7.4113	22.2605
23	Grotta Infernotto Superiore	1055 Pi	Natural	1041	6.1	4	19	−1	2.5	12	7.4130	44.2609
24	Maissa 31	n.c.	Natural	1181	3.4	3	7	−2	3	3	7.4148	44.2580
25	Maissa 32	n.c.	Natural	1177	8.2	3	10	4	2	3	7.4148	44.2580
26	Natural cave "Salamandre"	n.c.	Natural	1100	3.6	4	7	−2	2.5	4	7.4144	44.2580
27	Natural cave "Salamandre Superiore"	n.c.	Natural	1110	2	5	10	2	1.5	5	7.4144	44.2580

n.c., mines or caves not included in the speleological cadastre; subjacency, vertical distance from the surface; Mammola *et al.*, 2017).

Table 2. Results of model selection.

Dependent variable	Model structure	AIC
Richness (α diversity) of troglobionts	Pitfall depth + Season + Elevation + Entrance size	129.24
	Pitfall depth + Elevation + Entrance size	127.46
	Pitfall depth + Elevation	126.17
	Pitfall depth	125.18
Abundance of troglobionts	Pitfall depth + Season + Elevation + Entrance size	264.60
	Pitfall depth + Elevation + Entrance size	262.62
	Pitfall depth + Elevation	261.17
	Pitfall depth	259.75
Richness (α diversity) of non-troglobionts	Pitfall depth × Season + Elevation + Entrance size	227.16
	Pitfall depth × Season + Elevation	225.15
Abundance of non-troglobionts	Pitfall depth × Season + Elevation + Entrance size	437.80
	Pitfall depth × Season + Elevation	435.82

For each dependent variable, models are listed from the least to the most supported.
AIC, Aikaike Information Criterion.

$\beta_{Richness}$ is the turnover in community composition explained by species loss/gain alone, and $\beta_{Replacement}$ is turnover in community composition explained by replacement of species alone. Thus, this framework allowed us to distinguish between these two processes (loss/gain vs. replacement) underlying changes in community composition. β-diversity was calculated with the *beta* function in the package 'BAT' (Cardoso *et al.*, 2015, 2020), using species abundances as input data. We graphically explored changes in β-diversity values among caves in the two sampling seasons using density plots. We used a Wilcoxon rank sum test with continuity correction to test if median $\beta_{Replacement}$ and $\beta_{Richness}$ values were significantly different between the two seasons for both troglobionts and non-troglobionts.

Results

α-*diversity and abundance of species*

Overall, we trapped 3026 specimens belonging to 17 arthropod orders, 12 molluscans, and 1 nematode (Appendix S1). Dipterans, both adults and larvae, were the most abundant organisms in our traps (1673 specimens), followed by coleopterans (616), diplopods (308), and acari (208). The pitfall trap placed in cave 11 (a small cave near Barôn Litrôn) was lost in summer, and therefore, this site was excluded from the analysis.

Due to malfunction, half of the dataloggers did not measure temperature correctly throughout the sampling period. As the removal of these missing data would have halved the sample size of the dataset, and considering that cave temperature was significantly associated with sampling season, we did not include any temperature-derived variable in the regression analysis. Furthermore, we found that the categorical variable 'presence of percolating water' was significantly associated with cave length. Cave length, cave maximum subjacency, and pitfall trap subjacency were also collinear with the distance of the pitfall from the entrance (all Pearson $r > 0.7$). Therefore, we included only the distance of the pitfall from the entrance, cave elevation, cave entrance size, and sampling season in the initial regression models. We successfully fitted and validated models for all four dependent variables. Poisson α-diversity models were not over-dispersed [obligates: dispersion ratio (DR) = 0.78; Pearson's $\chi^2 = 36.57$; $P = 0.86$; non-obligates: DR = 1.21; $\chi^2 = 55.56$; $P = 0.16$. Conversely, abundance Poisson GLMs were significantly over-dispersed (obligates: DR = 12.04; $\chi^2 = 565.73$; $P < 0.001$; non-obligates: DR = 35.74; $\chi^2 = 1643.84$; $P < 0.001$), and thus, we opted for a negative binomial distribution to model abundance. Results of model selection are presented in Table 2, while estimated regression coefficients and *P*-values are given in Table 3. α-diversity (Fig. 2a) and abundance of troglobionts (Fig. 2c) were best explained by the distance of the pitfall trap from the entrance; other variables had no significant effects and were dropped during model selection (Table 2). α-diversity (Fig. 2b) and abundance of non-troglobionts (Fig. 2d) were best explained by the distance of the pitfall trap from the entrance in interaction with the sampling season. Specifically, we observed higher α-diversity and abundance at lower depth in summer and at greater depth in winter. Moreover, abundance values were significantly lower in winter (Fig. 2c,d). Finally, there was an effect of elevation on α-diversity and abundance of non-troglobionts, with higher values at lower elevations (Table 2).

β-*diversity*

Results of β-diversity analysis are illustrated in Fig. 3. In troglobionts, the density of β_{Total} values across sites showed a bimodal concentration around 0 and 1, indicating the existence of two types of communities; β_{Total} values close to 0 corresponded to the comparisons between pitfall traps with similar depth and environmental conditions, and values close to 1 corresponded to the comparisons between pitfall traps installed close to versus far from the entrance. This bimodal distribution was more pronounced in summer than in winter (Fig. 3a). Nevertheless, $\beta_{Replacement}$ values were mostly concentrated towards 0 (Fig. 3b), indicating that community turnover in troglobionts was not due to a difference in species composition. There was a significant difference between $\beta_{Replacement}$ values for summer and winter ($W = 235950$, $P < 0.001$), whereas no significant

Table 3. Estimated regression parameters in the minimum adequate models.

Dependent variable	Variable	Estimated β ± SE	*P*-value	R^2
Richness (α diversity) of troglobionts	Intercept	−1.98 ± 0.50	–	0.50
	Distance from the entrance	0.85 ± 0.18	<0.001	
Abundance of troglobionts	Intercept	−3.10 ± 0.69	–	0.70
	Distance from the entrance	1.98 ± 0.28	<0.001	
Richness (α diversity) of non-troglobionts	Intercept	8.66 ± 1.54	–	0.87
	Distance from the entrance	−0.44 ± 0.12	<0.001	
	Season (Winter)	−3.12 ± 0.51	<0.001	
	Distance from the entrance × Season	0.97 ± 0.21	<0.001	
	Elevation	−0.01 ± 0.01	<0.001	
Abundance of non-troglobionts	Intercept	11.93 ± 2.82	–	0.91
	Pitfall depth	−0.38 ± 0.24	0.110	
	Season (Winter)	−6.34 ± 0.88	<0.001	
	Distance from the entrance × Season	1.54 ± 0.34	<0.001	
	Elevation	−0.01 ± 0.01	0.015	

R^2, Nagelkerke's pseudo-R^2 (Nagelkerke, 1991).

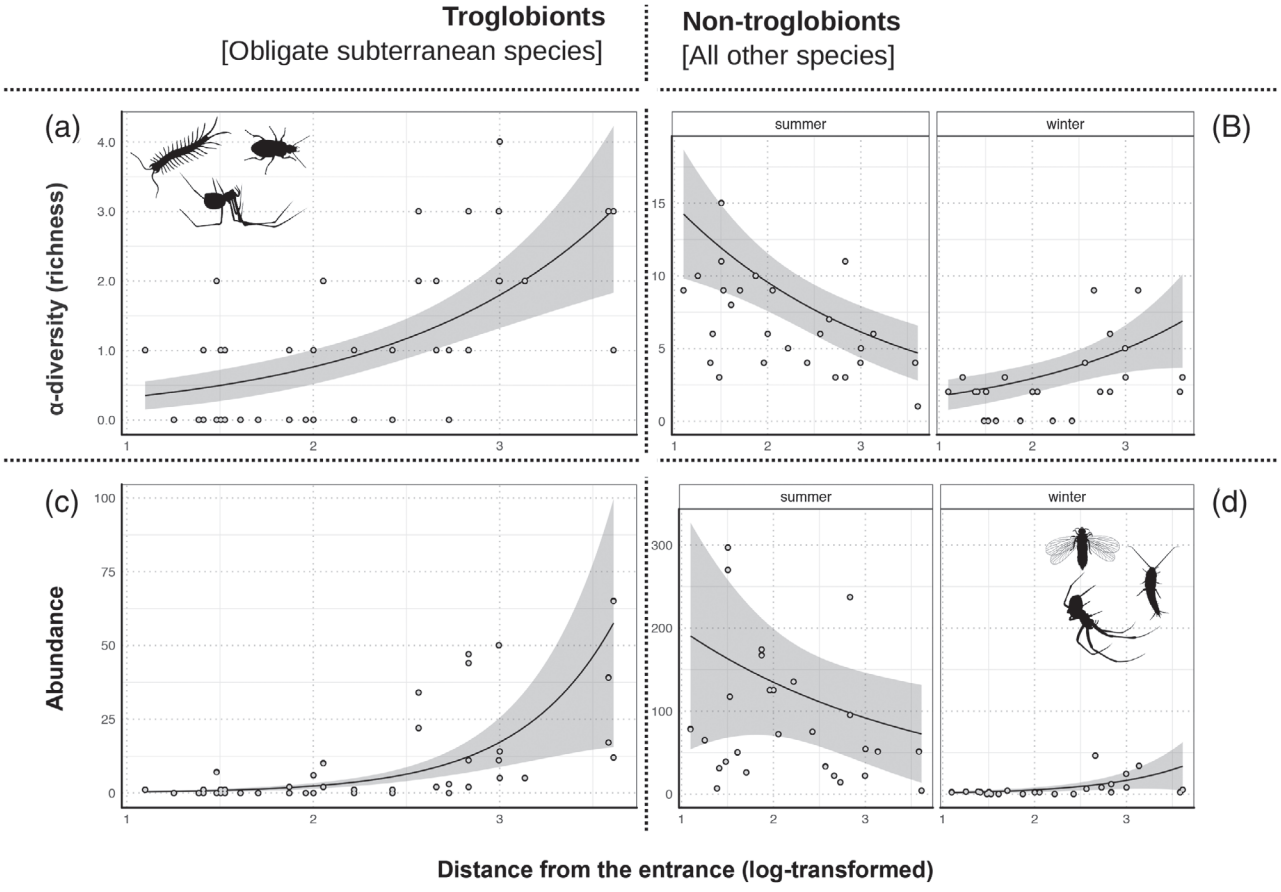

Fig. 2. Drivers of richness and abundance of species in the system of caves of Comba dell'Infernotto. Predicted relationships between the richness and abundance of troglobionts (a, b) and non-troglobionts (c, d) and the depth at which the pitfall trap was placed in each cave, based on the results of regression analysis. Note that, for non-troglobionts, there was a significant interaction between the depth of the pitfall trap and the sampling season; therefore, the predicted relationship is shown separately for each season. In all predictions of non-troglobionts, elevation is set at the mean values. Black lines are predicted values, while grey surfaces are 95% confidence intervals.

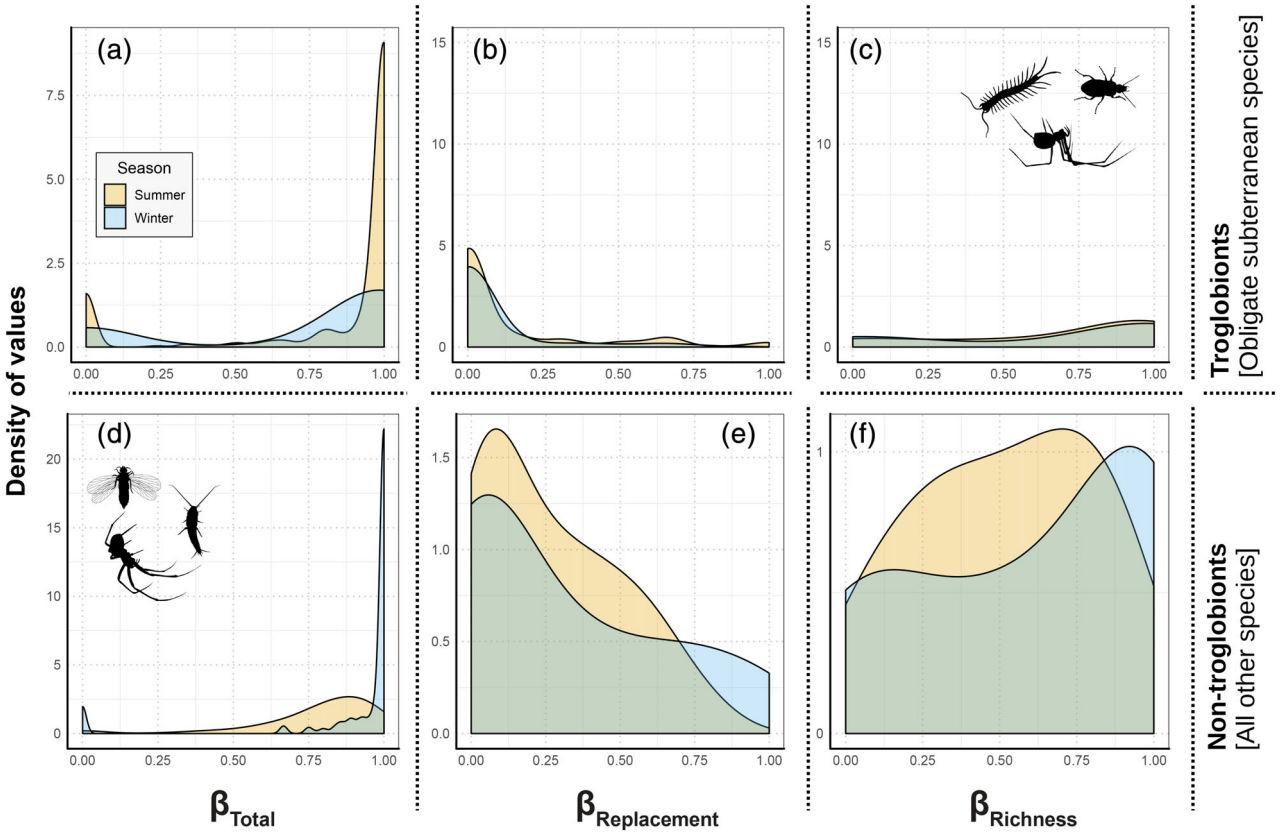

Fig. 3. Community turnover in the system of caves of Comba dell'Infernotto. Density of β-diversity values for troglobiont (a, b, c) and non-troglobiont (d, e, f) terrestrial arthropod communities in winter and summer samples. Total β-diversity is split in two components: $\beta_{richness}$ is the turnover in community composition explained by species loss/gain alone, and $\beta_{replacement}$ is turnover in community composition explained by replacement of species alone. [Colour figure can be viewed at wileyonlinelibrary.com].

differences between $\beta_{Richness}$ values in the two seasons were observed (W = 9418.5; $P = 0.22$; Fig. 3c).

We observed pronounced seasonal variations in the distribution of non-troglobionts across sites (Fig. 3d). In summer, there was a homogenisation of β-diversity values, indicating a more even distribution of species among sites (Fig. 3e,f). The richness component of β-diversity was found to fluctuate more across sites (Fig. 3f). Summer values were mostly concentrated either between 0.25 or between 0.75, whereas in winter the highest density of values was between 0.75 and 1. Observed differences between the two seasons were highly significant for $\beta_{Richness}$ (W = 156080; $P < 0.001$) and approached significance for $\beta_{Replacement}$ (W = 207350, $P = 0.05$).

Discussion

Our expectation that community composition should be equal across all the caves of the cave system of Comba dell'Infernotto was not entirely met. Although a pool of nine troglobiont species was consistently found in most caves (Appendix S1), we observed significant turnovers in species composition with the distance from the cave entrances. When considering non-troglobiont species, there was also substantial turnover in richness and community composition, which was mostly attributable to seasonality.

The main driver of α-diversity and abundance was the distance of the pitfall trap from the entrance. Pitfalls at greater distance from the cave entrance yielded greater diversity and abundance of troglobionts, independent from the sampling season. In our study site, a higher distance from the entrance (corresponding to greater values of subjacency) ensured the maintenance of more stable environmental conditions, including higher relative humidity and constant temperature (Fig. 4). These are the optimal microclimatic conditions for the specialised subterranean fauna, and indeed, subterranean habitats with grater environmental stability often support a more diverse and abundant subterranean arthropod community (Tobin *et al.*, 2013; Bento *et al.*, 2016; Mammola *et al.*, 2017).

In a few cases, troglobionts also occurred in close proximity to the surface, although in low numbers. This was not an unexpected pattern as it has been shown that obligate subterranean species within different cave systems may present a bimodal distribution, with peaks in richness and abundance in close proximity to the surface and deeper inside caves (Novak *et al.*, 2012; Kozel *et al.*, 2019). Yet, in the cave system of Comba dell'Infernotto, the predicted and observed abundance

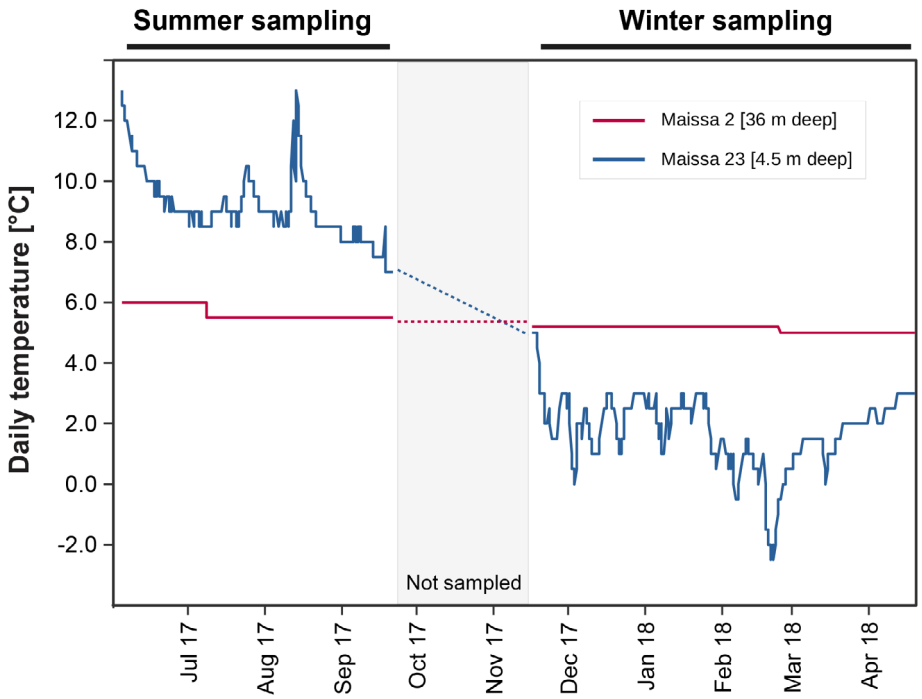

Fig. 4. Example of cave microclimate in the system of caves of Comba dell'Infernotto. Daily temperature was registered by two dataloggers, one placed at a depth of 36 m in Maissa 2 and one at 4.5 m in Maissa 23. [Colour figure can be viewed at wileyonlinelibrary.com].

in the vicinity of the surface was close to zero (Fig. 2d), which explains the non-significance of this pattern.

Although troglobionts were substantially unaffected by seasonal dynamics, the occurrence of non-troglobionts varied significantly between winter and summer in relation to the distance of the sampling plot from the cave entrance. In winter, we mostly collected these species far from the cave entrance, where environmental conditions are relatively stable through the year and where temperatures never drop below the freezing point (Fig. 4; see also Novak *et al.*, 2014). Winter abundance of non-troglobionts was generally low, following the general reduction of activity in surface habitats in winter and the typical dormancy pattern in most arthropods. In winter, we collected few external species in pitfall traps installed far from the entrance; these were mostly species overwintering in caves – a seasonal behaviour documented in several taxa (Chelini *et al.*, 2011; Lipovšek *et al.*, 2016, 2019; Balogová *et al.*, 2017; Mammola & Isaia, 2018).

On the other hand, in summer, we observed a massive colonization of the shallow sectors of caves by non-troglobionts (mostly external species). The importance of these species for the ecology of subterranean ecosystems is noteworthy as they provide significant inputs of carbon into the system (Novak *et al.*, 2013). Concomitantly, there was also a migration of non-troglobionts from deep toward shallow cave sectors. This pattern is often observed when studying spatial and temporal dynamics of temperate cave invertebrate communities (Tobin *et al.*, 2013; Lunghi *et al.*, 2017; Mammola & Isaia, 2018). In our case, the most abundant species involved in this migration was the predatory beetle *Sphodropsis ghiliani* (Schaum). In summer, this species seemingly moves into warmer, entrance sectors where the availability of prey is usually higher. The same migration pattern has been also observed for the same species in a cave of the north-western Italian Alps (Mammola *et al.*, 2015).

We also found higher richness and abundance of non-troglobiont species at lower elevations (Table 3). In the study area, the elevation difference determines a change in the average temperature of about 1 °C between lower (1000 m) and higher (1200 m) caves, which may in turn drive the observed biological pattern. Alternatively, the explanation for this relationship may be linked to gravitation-assisted patterns in the distribution of species. Trontelj *et al.* (2019) documented how the distribution of animals within karst massif can be influenced by gravity. They argued that '[…] *animals from a wider area of shallow subterranean spaces can be funneled towards deeper parts of vertical caves by flowing water or gravity*'.

Conclusions

Our results indicate that, at a spatial scale of less than 1 km^2, there is a single pool of subterranean specialised species that permanently occurs in the subterranean domain. This finding corroborates the idea that caves in close proximity are often interconnected by networks of subterranean habitat spaces (Giachino & Vailati, 2010; Trontelj *et al.*, 2019; Mammola, 2020). Yet, the theoretical expectation of no turnover in the community composition of these caves is not always met. In fact, there is a second pool of non-troglobiont species whose presence in the subterranean domain is scattered and influenced

by seasonality. Turnover is primarily attributable to active migrations of fauna from deep to superficial habitats and vice versa. From a methodological perspective, our results imply that sampling a few caves across different seasons should provide a general indication of the resident subterranean fauna of a certain area, keeping in mind that a large depth is essential for sampling troglobionts and that a greater diversity is generally expected at lower elevations within a karst massif.

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Author contributions

S. Mammola and M. Isaia conceived the study. S. Mammola, N. Chiappetta, and M. Isaia performed fieldwork. N. Chiappetta sorted specimens. M. Isaia identified spiders and harvestmen. D. Ž. Antić identified millipedes. M. Zapparoli identified centipedes. P. M. Giachino identified coleopterans and other insect orders. M. Isaia and N. Chiappetta performed GIS analyses. S. Mammola performed statistical analysis and wrote the first draft of the paper. All authors contributed to the writing and approved the final submission.

Data availability statement

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.12005934.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of taxa recorded in the system of caves of Maissa and their ecological classification.

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