Distribution of Terrestrial Cave-Dwelling Arthropods in Two Adjacent Prealpine Italian Areas with Different Glacial Histories

Leonardo Latella[1], Nicoletta Verdari[1], and Mauro Gobbi[2,*]

[1]Sezione di Zoologia, Museo Civico di Storia Naturale of Verona, Lungadige Porta Vittoria 9, Verona I-37129, Italy.
    E-mail:leonardo.latella@comune.verona.it
[2]Sezione di Zoologia degli Invertebrati e Idrobiologia, Museo delle Scienze, Via Calepina 14, Trento I-38122, Italy

Leonardo Latella, Nicoletta Verdari, and Mauro Gobbi (2012) Distribution of terrestrial cave-dwelling arthropods in two adjacent Prealpine Italian areas with different glacial histories. *Zoological Studies* **51**(7): 1113-1121. The aim of this study was to investigate the distribution of cave-dwelling arthropod communities in 2 adjacent karst areas with different glacial histories. Endemic and obligate cave-dwelling faunas were recorded in 60 caves located in 2 adjacent Prealpine areas (in Veneto, northeastern Italy): the Baldo and Lessinia Mountain groups were compared. During the last glacial period, the Baldo Mountain group was completely surrounded and isolated from the Lessinia group by the Adige glacier, while the Lessinia was only partially surrounded. The effect of glacial isolation, both geographically (cave locations) and elevationally (cave elevation), on the faunal distribution was tested using the number of troglobiont and endemic species collected in each area. The Lessinia hosts a higher number of troglobiont species and a lower number of endemic species compared to those of the Baldo area. Furthermore, results indicated that the similarity in species assemblages in caves was not driven by their geographic location, but by colonization patterns caused by isolation created by the Adige glacier during the last ice age. This suggests that the geographic isolation of the Baldo area during Quaternary climatic fluctuations determined the species which colonized the caves and consequently prevented multiple colonizations during warm periods. Glacier-induced isolation during the last ice age can therefore be considered one of the main factors which determined terrestrial arthropod colonization of caves in the Prealps area.
http://zoolstud.sinica.edu.tw/Journals/51.7/1113.pdf

Key words: Troglobionts, Quaternary, Glacier, Endemism, Alps.

Characterizing patterns and gradients in species distributions and diversity is crucial for assessing impacts of past, current, and future environmental changes on biodiversity (Rahbek 2005, Field 2009). The climate during the last ice age forced species to change their distribution ranges. Many species which were probably widely distributed throughout Central Europe during the ice ages can survive today only in alpine or relict tundra areas (Coope and Wilkins 1994). As a consequence of global warming at the end of the last glacial period, thermophilic species expanded and colonized Central Europe (Hewitt 1999), while cold-stenotherm ones shifted to higher latitudes, higher elevations, and/or to caves (Holsinger 2000, Humphreys 2000). This process is still occurring at a global scale due to the changing climate (Parmesan 1996, Gobbi et al. 2011). While the effects of climatic change on faunal colonization during the Quaternary are quite well-described on a large spatial scale, they are still poorly understood at the local scale and should be investigated in detail.

During the last glacial period, the Italian Alps were covered by glacier tongues except at the top of the highest mountains (Hughes et al.

*To whom correspondence and reprint requests should be addressed. Tel: 39-349-6356319; 39-0461-270372. Fax: 39-0461-270376.
  E-mail:mauro.gobbi@mtsn.tn.it

2006). In contrast to the Alps, Prealpine areas were only partially covered by glaciers (Sauro 1973, Bassetti and Borsato 2007). This favored the colonization of ice-free zones by invertebrates from moist and cold habitats, like forest litter and soil, alpine grasslands, and talus areas. During interglacial periods, as glaciers retreated, populations became isolated in the highest parts of the Prealpine mountains or took refuge in cold, moist interiors of caves (Latella and Sauro 2007 2011). Surface populations became extinct or isolated, and there was therefore little or no gene flow to cave communities, boosting the evolution of 'troglobiont' (cave-adapted) species. This is known as the climatic relict hypothesis (Sbordoni 1982, Humphreys 2000, Assmann et al. 2010, Hampe and Jump 2011).

The main challenge for taxonomists and biogeographers is to explain why some areas contain more species or greater endemism than others (Baselga 2008, Field 2009, Schuldt and Assmann 2009, Barbosa et al. 2010). Our research therefore attempted to analyze the effect of isolation during the last glacial period on the number of troglobiont arthropods in 2 nearby, isolated karst areas in the eastern Italian Prealps. The following hypotheses were tested: (1) species assemblages and distributions in 2 nearby areas were a result of different degrees of past glacier-induced isolation; and (2) caves located at higher elevations have the highest number of troglobiont

and endemic species because they were isolated for longer periods, compared to those at lower elevations.

MATERIALS AND METHODS

Study area

The 2 selected study areas are located in the western part of the Veneto Prealps (south-eastern Italian Alps) (Marazzi 2005). They belong to 2 mountain groups: the Baldo-Altissimo group (called Baldo hereafter) (with a surface area if 398 km² and a maximum elevation of 2200 m) and Lessinia Mountains (called Lessinia hereafter) (with a surface area of 1403 km² and a maximum elevation of 1865 m) (Fig. 1). The caves investigated in this work ranged in elevation from 322 to 1741 m in Baldo and from 150 to 1575 m in Lessinia (Fig. 1A, B).

The Baldo is surrounded by the Loppio Valley on the northern side, the Adige Valley on the eastern side, Quaternary frontal moraines formed by the Garda glacier on the southern side, and Garda Lake on the western side. This mountain range (Dolomia Principale, Calcari Grigi, Calcari oolitici di S. Vigilio, Rosso Ammonitico, Scaglia Rossa, and Maiolica) is predominantly formed by carbonate rocks, which are particularly important for the development of karst phenomena (Pasa
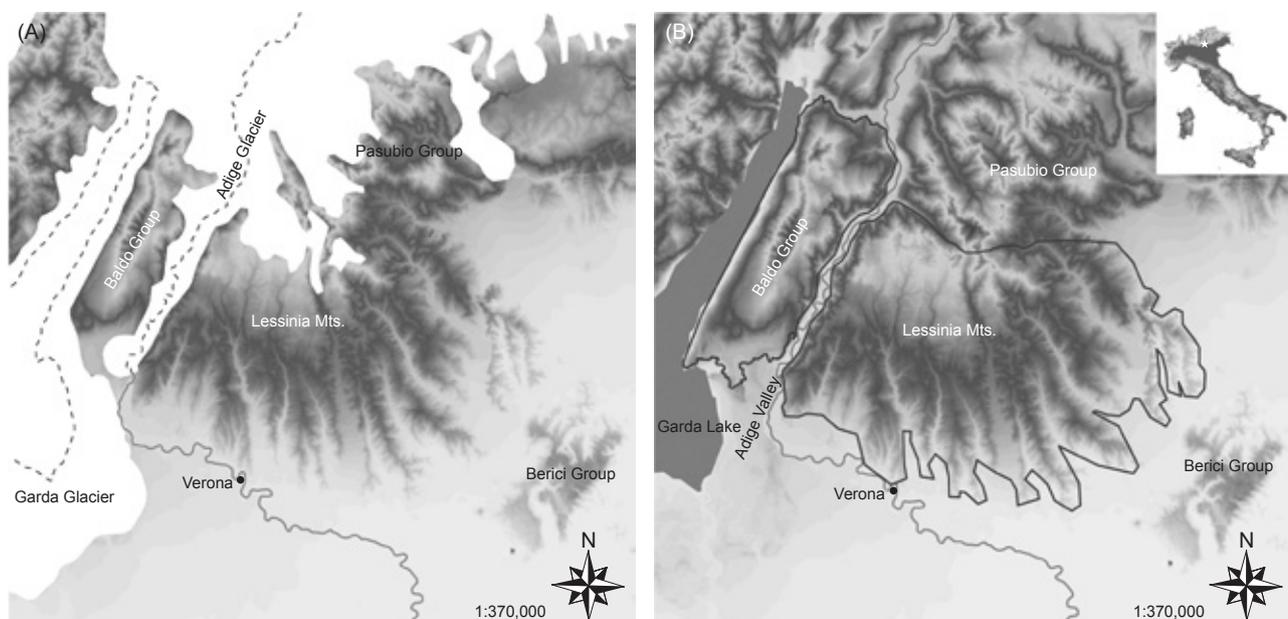

Fig. 1. Two study areas (Baldo and Lessinia) (A) during the last glacial period and (B) today.

1954, Zorzin 2011).

The Lessinia is bordered by the Adige Valley to the west and the Leogra Valley to the east and northeast. The Val dei Ronchi separates the range from the Pasubi-Carega Group to the northwest. Lessinia includes the western Lessinia Mountains (between the Adige and Illasi Valleys) and eastern Lessinia Mountains (between the Illasi and Leogra Valleys). The western Lessinia Mountains (Dolomia Principale, Calcari grigi, Rosso Ammonitico, Scaglia Rossa, and Maiolica) mainly consist of carbonate rocks; some areas of the eastern Lessinia Mountains are prevalently composed of volcanic rocks developed during the Venetian Tertiary volcanic province magmatism (Sauro 1973) where no cave formations exist.

During the Quaternary, the 2 areas (Baldo and Lessinia) were separated by the Adige glacier; today they are separated by the Adige River valley (Fig. 1A, B).

The 1st surveys of the subterranean habitats of Lessinia and Baldo date back to the 1st 1/2 of the 8th century. A remarkable increase in biospeleological studies occurred from the 1930s (Latella 2005), and since then, numerous studies have been undertaken investigating systematic and biogeographical aspects of the cave faunas (Ruffo 1938, Caoduro et al. 1994, Latella and Sauro, 2007). In total, 60 caves (N_{Baldo} = 17; $N_{Lessinia}$ = 43) and 41 species (S_{Baldo}= 6; $S_{Lessinia}$ = 35), previously sampled, were investigated in this study (Fig. 2).

Fig. 2. Distributions of caves and the geographical position of the Lessinia cells.

Investigated taxa

The present distributions of terrestrial cave-dwelling invertebrate assemblages provide insights into the past connectivity and paleogeography of adjacent karst areas (Culver et al. 2006, Latella and Sauro 2007). Presence-absence matrices of troglobionts for the 2 investigated study areas were generated from the existing database "Fauna delle Grotte del Veneto (Cave fauna of Veneto)", property of the Museo Civico di Storia Naturale di Verona. We considered endemic troglobionts species for each of the study areas and troglo-bionts with wider distributions. The species included in the matrix belong to 9 taxa listed below (see Table 1 for the list of species):

Palpigrades (Arachnida; Palpigradi; Eukoeneniidae); 1 species with 2 subspecies; Pseudoscorpions (Arachnida; Pseudoscorpiones: Chthoniidae and Neobisiidae); 3 genera and 7 species; Harvestmen (Arachnida; Opiliones; Ischyropsalididae); 1 species; Spiders (Arachnida; Araneae; Linyphiidae); 1 species; Woodlice (Arachnida; Isopoda; Trichoniscidae); 2 genera and 2 species; Millipedes (Diplopoda: Polydesmidae, Craspedosomatidae, and Julidae); 3 genera and 6 species; Springtails (Entognatha; Collembola: Onychiuridae and Entomobryidae); 2 genera and 2 species; Crickets (Insecta; Orthoptera; Raphidophoridae); 1 species; and Beetles (Insecta; Coleoptera: Carabidae and Cholevidae); 3 genera and 8 species of Carabidae Trechinae, and 5 genera and 11 species of Cholevidae Leptodirinae.

Statistical analyses

To avoid any positive correlation between the number of sampled caves and the number of collected troglobionts species, the Lessinia was divided in 3 areas of equal size and shape, similar to that of the Baldo, and with a comparable number of caves (Lessinia_1 = 14, Lessinia_2 = 15, Lessinia_3 = 14) (Fig. 2). Species accumulation curves were calculated, based on Mao Tau values to compare sampling completeness in the 4 different cells (Lessinia_1-3 and Baldo) (Dole-Olivier et al. 2009). Troglobiont richness in each cell was estimated using the following species richness estimators: the incidence-based coverage estimator (ICE) and Chao2 (Colwell and Coddington 1994, Chazdon et al. 1998, Hortal et al. 2006).

A generalized linear model (GLM) multivariate test, a technique which performs an analysis of variance (ANOVA) for experiments with more than 1 dependent variable (Gotelli and Ellison 2004), was used to test the effect of cave elevation and geographic location on the number of troglobiont species in each cell. The number of troglobiont species (expressed as frequency and percentage values) were transformed to arcsine $(frequency/100)^{0.5}$ to normalize the distribution, while the geographic position was expressed as a categorical variable based on the 4 main areas: Baldo, and Lessinia_1-3.

A cluster analysis using Ward's minimum variance method (Everitt et al. 2001) was run on the species-cave matrix to classify caves based on their species compositions.

Species accumulation curves and ICE and Chao2 estimators of species richness were computed using Estimates 7 (Colwell 2004); the GLM was performed using SPSS vers. 13.0 (SPSS, Chicago IL, USA), and the cluster analysis using PAST (Paleontological Statistics vers. 2.15, Hammer et al. 2001).

RESULTS

In total, 40 troglobiont species and subspecies were recorded (Table 1), 19 of which were endemic to one of the 2 study areas: 3 species are endemic to Baldo and 17 species to Lessinia. Only 2 species were common to both Baldo and Lessinia: *Balkanoroncus boldorii* (Pseudoscorpiones), known from Prealpine caves of Lombardy and Veneto, and *Ischyropsalis strandi* (Opiliones), endemic to Veneto and Trentino Alto Adige caves.

A comparison of the ICE and Chao2 indices showed that the number of observed troglobiont species in the Baldo corresponded to the number of estimated species (Table 2). In contrast, there was little agreement between the observed and estimated numbers of species in the Lessinia, with ICE and Chao2 numbers approximately 30% greater than the recorded species richness (Table 2).

The accumulation curves calculated for both the overall Lessinia and the 3 cells (Lessinia_1-3) showed a gradual increment and never reached the asymptote even when all caves were included; whereas the Baldo's curve reached the asymptote (Fig. 3).

The GLM analysis showed no significant differences in numbers of troglobionts for elevation (p = 0.79) or geographic location (p = 0.21) (Table

Table 1. List of terrestrial troglobiont species recorded in the study area

Recorded species	Mt. Baldo	Lessinia Mts.
PALPIGRADI		
Eukoenenia austriaca peregrina (Condè, 1989)		a
Eukoenenia austriaca stinyi (Strouhal, 1936)		a
ARANEAE		
Troglohyphantes exul Thaler, 1987		a
PSEUDOSCORPIONES		
Chthonius (C.) *lessiniaensis* Schawaller, 1982		a
Chthonius (*Ephippiochthonius*) *pieltaini* Beier, 1930		a
Neobisium (*Blothrus*) *torrei* (Simon, 1881)		a
Roncus leonidae leonidae Beier, 1942		a
Roncus leonidae ruffoi Gardini, 1991*		a
Balkanoroncus boldorii (Beier, 1931)	a	a
OPILIONES		
Ischyropsalis strandi Kratochvil, 1936	a	a
ISOPODA		
Androniscus degener Brian, 1926		a
Troglocyphoniscus osellai Caruso, 2000*		a
DIPLOPODA		
Trogloiulus boldorii Manfredi, 1940	a	
Trogloiulus mirus Manfredi, 1931		a
Typhloiulus tobias Berlese, 1886		a
Serradium hirsutipes (Strasser, 1981)		a
Serradium semiacquaticum Enghoff, Caoduro, Adis & Messner 1997*		a
COLLEMBOLA		
Onychiuroides hauseri (Dallai, 1975)		a
Pseudosinella concii Gisin, 1950		a
ORTHOPTERA		
Dolichopoda laetitiae laetitiae Minozzi, 1920		a
COLEOPTERA		
Orotrechus cfr. *vicentinus**		a
Orotrechus pominii Tamanini, 1953*		a
Orotrechus vicentinus juccii Pomini, 1940*		a
Orotrechus vicentinus martinellii Daffner, 1987*	a	
Orotrechus vicentinus vicentinus (Gestro, 1907)*		a
Italaphaenops dimaioi Ghidini, 1964*		a
Lessinodytes caoduroi Vigna Taglianti, 1982		a
Lessinodytes pivai Vigna Taglianti & Sciaky, 1988*		a
Boldoria baldensis (Muller, 1928)*	a	
Neobathyscia fabianii (Dodero 1904)*		a
Neobathyscia lessinica Muller 1934*		a
Neobathyscia mancinii Jeannel, 1924*		a
Neobathyscia mancinii ruffoi Piva, 2008*		a
Neobathyscia affinis Piva, 1984		a
Neobathyscia pasai Ruffo, 1950*		a
Halbherria zorzii (Ruffo, 1950)*		a
Halberria pivai Giachino & Vailati, 2005*		a
Halbherria vericoi Piva 1984*		a
Aphaotus martinellii Giachino & Vailati, 2005*	a	
Lessiniaella trevisioli Pavan, 1941*		a

*Endemic species.

3). On the other hand, the Baldo and Lessinia differed in the frequencies of endemic species ($p = 0.0001$), but not in troglobiont species ($p = 0.20$) (Table 3). The Baldo exhibited a higher frequency of endemic species compared to Lessinia's cells and the overall Lessinia value (Fig. 4).

The cluster analyses showed a clear separation between the Baldo (B) and Lessinia caves (L1, L2, and L3), the presence of 1 Baldo

cave within Lessinia's clusters was due to the presence of only 1 troglobiont (*Ischyropsalis strandi*), which was widespread in all areas (Fig. 5). Caves in the Baldo were more similar in composition than those of the Lessinia.

DISCUSSION

Our work demonstrates that caves in 2 neighboring Prealpine karst areas, with different glacial coverage during the last glacial period, differed in the frequencies of subterranean arthropods.

When comparing the Baldo and Lessinia, the former was characterized by fewer troglobionts, which are mostly endemic to Baldo. On the other hand, the Lessinia had a higher species richness
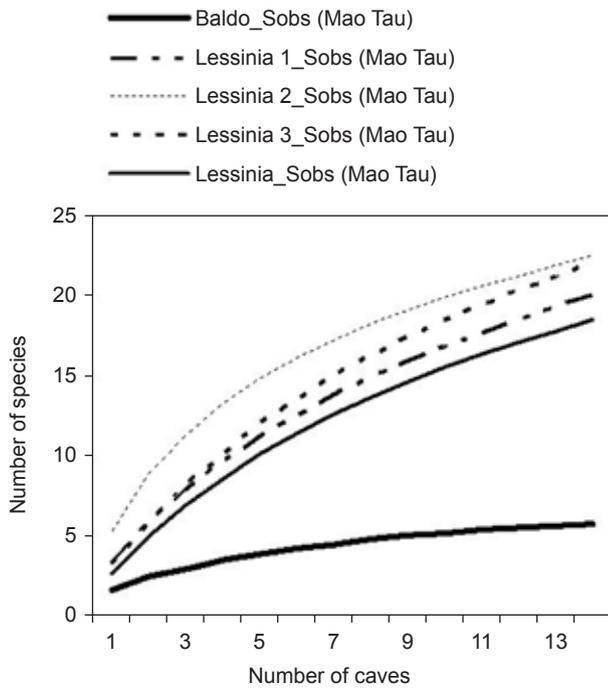

Fig. 3. Species accumulation curves. Numbers of troglobionts species plotted against the number of caves.
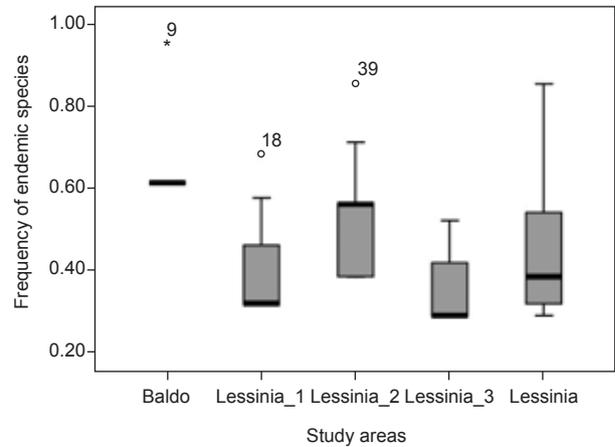

Fig. 4. Box-plot of the frequency of endemic species in each area (Baldo, Lessinia cells, and the overall Lessinia). Boxes represent the interquartile range (Hspread), and the median is the horizontal line in the box; the lines extend from the lowest to the highest value within 1.5 Hspread from the end of the box. Circles represent outliers (values between 1.5 and 3 Hspread). *Extreme cases (values of > 3 Hspread).

Table 2. Observed and estimated values of species richness (ICE, incidence-based coverage estimator; and Chao2) for troglobiont diversity in the sampled areas

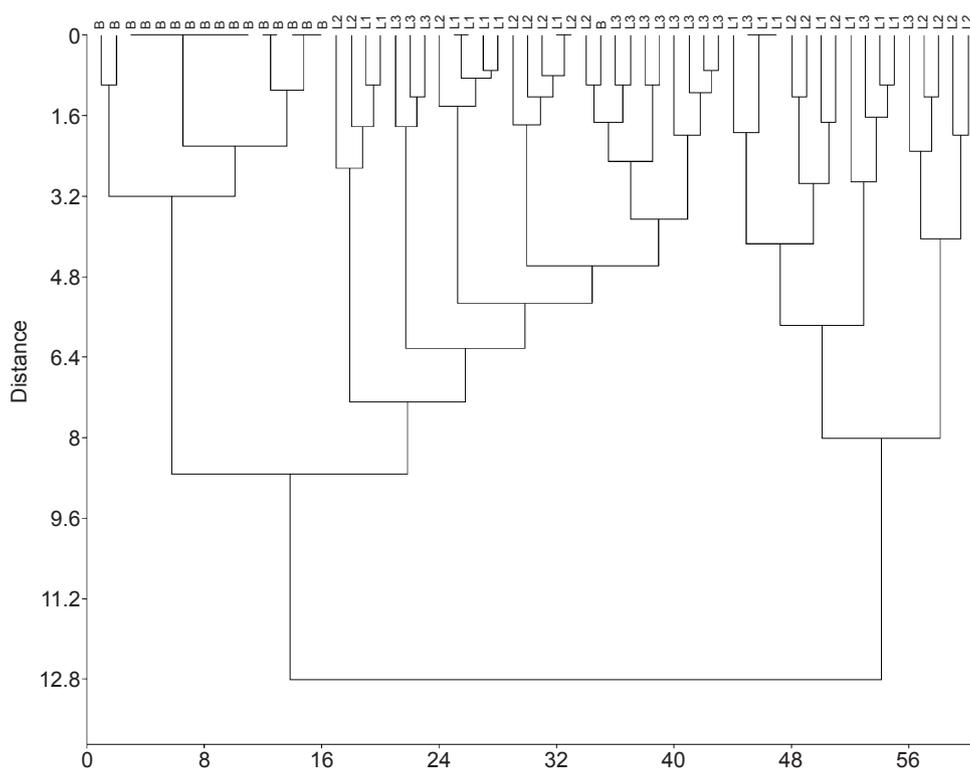| Area	No. of species recorded	Estimated no. of species	
		ICE	Chao2
Baldo	6	6.5	6.1
Lessinia	38	52	53.3
Lessinia_1	20	32.9	29.2
Lessinia_2	23	30.3	28.8
Lessinia_3	24	32.6	33.2

Fig. 5. Dendrogram clustering caves with the same assemblage compositions (B, Baldo; L1, L2, L3, Lessinia cells 1-3). The dendrogram groups the sites into clusters based on similarity in species assemblage compositions; the y-axis indicates the distance which separate sites which are joined into a higher-level cluster.

Table 3. Results of the multivariate generalized linear model (significant *p* values are in boldface), and the post-hoc test calculated using the frequency of endemic species (alpha indicates the type I error rate, i.e., the probability of incorrectly rejecting a true statistical null hypothesis). *d.f.*, degrees of freedom; *F*, Fisher's F-ratio

Source	Dependent variable	Type III sum of squares	*d.f.*	Mean square	*F*	*p* value
Model	Frequency of troglobionts	0.15	4	0.054	1.181	0.329
	Frequency of endemic species	0.807	4	0.202	14	**0.0001**
Elevation	Frequency of troglobionts	0.003	1	0.003	0.068	0.795
	Frequency of endemic species	0.047	1	0.047	3.232	0.078
Geographic location	Frequency of troglobionts	0.194	3	0.065	1.24	0.205
	Frequency of endemic species	0.427	3	0.142	9.892	**0.0001**

Post-hoc test on the frequency of endemic species.
Tukey's B

Geographical location	*n*	Subset for alpha = 0.05		
		1	2	3
Lessinia_3	14	0.346		
Lessinia_2	14	0.412		
Lessinia_1	15		0.531	
Baldo	17			0.635

Means for groups in homogeneous subsets are displayed.

than the Baldo in each of its 3 cells, but the frequency of endemics was lower. The species richness estimators of troglobionts showed, according to Christman and Culver (2001) and Culver et al. (2006), that higher species richness in Lessinia may have been the result of a larger number of available caves during colonization.

Our results indicate that sites located at higher elevations did not necessarily have the highest frequency of troglobiont or troglobiont-endemic species. Speciation in ice-free areas did not occur during the last glaciation at these high-elevation sites. To achieve speciation, it is likely that a longer ice-free period is required at these elevations (Barr and Holsinger 1985).

A taxonomic comparison of troglobionts at Baldo and Lessinia showed that species compositions of these 2 areas significantly differed. Although the geographic distance between Lessinia_1 and Lessinia_3 was similar to that between Baldo and Lessinia_1, Baldo and Lessinia_1 exhibited assemblages with different species compositions. This suggests that similarities between assemblages were not linked to the distance between the investigated areas with caves, but to colonization patterns induced by the past glacial separation of the 2 areas, and Baldo's isolation.

Glacial-induced isolation is considered a main variable determining frequencies of endemic and troglobiont species (Habel and Assmann 2009). Climatic and environmental changes occurring during the Pleistocene in the Baldo and Lessinia triggered colonization of subterranean environments in these 2 groups of mountains by the ancestors of the present troglobiont taxa (Barr and Holsinger 1985). We further propose that geographic isolation of the Baldo and climatic fluctuations during the Quaternary caused the caves to be colonized by some species, but hindered multiple colonization events. In contrast, during the Pleistocene ice age stadial, the Lessinia area was never totally isolated from adjacent areas; it remained connected with the neighboring Prealps and lowlands, allowing repeated invasions and subsequent adaptations of these species to cave environments. This hypothesis explains the much-higher number of endemic species in the Baldo, compared to the Lessinia, and stresses the importance of past local glacier fluctuations in the evolution of endemic species. Our results agree with the hypothesis that the distribution of cave fauna is a consequence of colonizations, isolations, and adaptations to cave environments,

which occurred during past climate fluctuations (Christmas and Culver 2001, Juan and Emerson 2010).

In conclusion, we demonstrated that the effect of glacial-induced isolation at the local scale is extremely important in understanding diversity patterns of obligate cave-dwelling fauna. Local-scale studies give a more-detailed description of the past faunal colonization scenario in topographically complex areas such as the Alps. Moreover, invertebrate subterranean faunas are important for biogeographic analyses, as they provide examples of evolutionary mechanisms and speciation occurring in isolation at the local scale.

REFERENCES

Assmann T, A Casale, C Drees, JC Habel, A Matern, A Schuldt. 2010. Review: the dark side of relict species biology: cave animals as ancient lineages. *In* T Assmann, JC Habel, eds. Relict species: phylogeography and conservation biology. Berlin and Hidelberg: Springer-Verlag, pp. 91-103.

Barbosa AM, D Fontaneto, L Marini, M Pautasso. 2010. Is the human population a large-scale indicator of the species richness of ground beetles? Anim. Conserv. **13:** 432-441.

Barr TC, JR Holsinger. 1985. Speciation in cave fauna. Ann. Rev. Ecol. Syst. **16:** 313-337.

Baselga A. 2008. Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography. **31:** 263-271.

Bassetti M, A Borsato. 2007. Evoluzione geomorfologica e vegetazionale della bassa valle dell'Adige dall'ultimo massimo glaciale: sintesi delle conoscenze e riferimenti ad aree limitrofe. Studi Trentini Sci. Nat. Acta Geol. **82:** 31-42.

Caoduro G, G Osella, S Ruffo. 1994. La fauna cavernicola della regione veronese. Mem. Mus. Civico Storia Nat. Verona (II serie) sezione Sci, Vita (A: Biol,) **11:** 1-144.

Chazdon RL, RK Colwell, JS Denslow, MR Guariguata. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica, pp. 285-309. *In* F Dallmeier and JA Comiskey, eds. *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies*. Parthenon Publishing, Paris.

Christman MC, DC Culver. 2001. The relationship between cave biodiversity and available habitat. J. Biogeogr. **28:** 367-380.

Colwell RK. 2004. EstimateS vers. 7. Available at http://viceroy.eeb.uconn.edu/estimates Accessed 1 Feb. 2010.

Colwell RK, JA Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R. Soc. Lond. B **345:** 101-118.

Coope GR, AS Wilkins. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. Phil. Trans. R. Soc. Lond. B **344:** 19-26.

Culver DC, L Deharveng, A Bedos, JL Lewis, M Madden, JR Reddell et al. 2006. The mid-latitude biodiversity ridge in terrestrial cave fauna. Ecography **29:** 120-128.

Dole-Olivier MJ, F Castellarini, N Coineau, DBP Galassi, P Martin, N Mori et al. 2009. Towards an optimal sampling strategy to assess groundwater biodiversity: comparison across six European regions. Freshwater Biol. **54:** 777-796.

Everitt BS, S Landau, M Leese. 2001. Cluster analysis, 4th ed. New York: Oxford Univ. Press.

Field R, BA Hawkins, HV Cornell, DJ Currie, JAF Diniz-Filho, JF Guégan et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. J. Biogeogr. **36:** 132-147.

Gobbi M, M Isaia, F De Bernardi. 2011. Arthropod colonisation of a debris-covered glacier. Holocene. **21:** 225-236.

Gotelli NJ, AM Ellison. 2004. A primer of ecological statistics. Sunderland, MA: Sinauer Associates.

Habel JC, T Assmann. 2009. Relict species: phylogeography and conservation biology. Berlin and Heidelberg: Springer-Verlag, 468 pp.

Hammer Ø, DAT Harper, PD Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol. Electron. **4:** 9.

Hampe A, AS Jump. 2011. Climate relicts: past, present, future. Annu. Rev. Ecol. Evol. Syst. **42:** 313-333.

Hewitt GM. 1999. Post-glacial re-colonization of European biota. Biol. J. Linn. Soc. **8:** 87-112.

Holsinger JR. 2000. Ecological derivation, colonization, and speciation. *In* H Wilkens, DC Culver, WF Humphreys, eds. Ecosystems of the world, vol. 30, Subterranean ecosystems. Amsterdam: Elsevier, pp. 399-415.

Hortal J, PAV Borges, C Gaspar. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. J. Anim. Ecol. **75:** 274-287.

Hughes PD. 2006. Quaternary glacial history of the Mediterranean mountains. Progr. Phys. Geogr. **30:** 334-364.

Humphreys WF. 2000. Relict fauna and their derivation. *In* H Wilkens, DC Culver, WF Humphreys, eds. Ecosystems of the world, Vol. 30, Subterranean ecosystems. Amsterdam: Elsevier, pp. 417-432.

Juan C, BC Emerson. 2010. Evolution underground: shedding light on the diversification of subterranean insects. J. Biol. **9:** 17.

Latella L. 2005. Il contributo del Museo Civico di Storia Naturale di Verona allo sviluppo della biospeleologia. Studi Trentini Sci. Nat. Acta Biol. **81:** 15-22.

Latella L, U Sauro. 2007. Aspects of evolution of an important geoecosystem in the Lessinian Mountain (Venetian Prealps). Acta Carsol. **36:** 69-75.

Latella L, U Sauro. 2011. Note di Storia Naturale del sottosuolo dei Monti Lessini e del suo popolamento. Quaderno Cult.-Lessinia ieri oggi domani. **34:** 57-64.

Marazzi S. 2005. Atlante orografico delle Alpi - SOIUSA Priuli and Verlucca, Italy.

Parmesan C. 1996. Climate and species range. Nature **382:** 765-766.

Pasa A. 1954. Carsismo e idrografia carsica nel gruppo del M. Baldo e nei Lessini veronesi. C.N.R., Centro Studi Geografia Fisica, Ricerche sulla morfologia e idrografia carsica, 5. Bologna, Italy: Tipografia Mareggiani, 150 pp.

Rahbek C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. **8:** 224-239.

Ruffo S. 1938. Studio sulla fauna cavernicola della regione veronese. Boll. Istit. Entomol. R. Univ. degli Studi Bologna **10:** 70-116.

Sauro U. 1973. Il Paesaggio degli alti Lessinia. Studio geomorfologico. Mus. Civico Storia Nat. Verona Mem. fuori serie **6:** 161 pp.

Sbordoni V. 1982. Advances in speciation of cave animals. *In* Barigozzi, C, ed. Mechanisms of speciation. New York: Liss, pp. 219-240.

Schuldt A, T Assmann. 2009. Environmental and historical effects on richness and endemism patterns of carabid beetles in the western Palaearctic. Ecography **32:** 705-714.

Zorzin R, L Agostini, MC Montecchi, P Torri, CA Accorsi. 2011. Tanella cave (Monte Baldo - Verona, Italy): a record of environmental data on the last glacial period. Acta Carsol. **40:** 189-205.