Small mammals in a mountain ecosystem: the effect of topographic, micrometeorological, and biological correlates on their community structure

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Abstract
An increasing number of studies have investigated spatial and temporal patterns in species richness and assemblage composition in mountain ecosystems along altitudinal gradients. Small mammals have been successfully used as indicators of environmental health and as proxies of biodiversity. However, information about the composition and distribution of species assemblages in the mosaic of habitat and rocky landform types at a high altitude is still lacking for most of the mountain regions. Through the use of live traps and camera trapping, we described the small mammal community living above the treeline of the Western Dolomites (Italian Alps), investigating the species richness, abundance of individuals and community composition in relation to topographic, micrometeorological, mesohabitat, and biological correlates. A total of five species and 50 individuals were sampled, analysed, and released. At the extremes of the analysed altitudinal range (i.e. 1900 vs 2900 m a.s.l.), community composition was completely different and species richness was related to elevation, steepness, and vegetation cover. At the same time, the taxonomic distinctness of ground-dwelling arthropods (namely carabid beetles and spiders), a proxy of habitat complexity, showed higher values in areas with a greater small mammal species richness. We found a positive effect of steepness and rocky landform type “carsism” on the number of captured individuals, showing the importance of the availability of shelters and underground burrows for the sampled species. As a confirmation of the altitudinal shift for these species in relation to the ongoing climate change, we detected a negative impact of sub-surface ground temperature on small mammal abundance during the monitoring period. In conclusion, small mammals represent an excellent model for understanding the evolutionary processes of ecosystems, population dynamics under changing environmental conditions, and habitat vulnerabilities.

Keywords Altitudinal gradients · Species richness · Eulipotyphla · Species assemblages · Rodentia

Introduction

Evidence about the biotic responses to ongoing climate change is continuously growing (Chen et al., 2011; Feeley et al., 2020; Lenoir & Svenning, 2015; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2002; Zhu et al., 2022), and we also realized species vulnerability to future change world-wide (Moritz & Agudo, 2013; Rowe et al., 2015). There is a general trend towards upward and poleward shifts of elevational and latitudinal boundaries of species’ ranges (Chen et al., 2011; Lenoir et al., 2008; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Thomas & Lennon, 1999; Walther et al., 2002), with “leading edge” expansions, where populations shift at northern or upper range margins following climate changes, detected more often than “lagging
edge” contractions, where populations reduce their ranges (Angert et al., 2011; Hill et al., 2011; Morelli et al., 2012). A number of recent studies have investigated spatial and temporal patterns in species richness and life history traits along altitudinal gradients (e.g. Billman et al., 2021; Gobbi et al., 2021; Ross et al., 2021; Shoo et al., 2006; Viterbi et al., 2013). Mountain ecosystems are sensitive and reliable indicators of climate change, encompassing steep environmental gradients in small geographic areas and thus being outstanding natural laboratories for biodiversity studies (Sun et al., 2020). In these areas, many environmental factors correlate with elevation, including temperature (e.g. Wu et al., 2013) and productivity (e.g. Ramirez-Bautista & Williams, 2019).

However, information about the composition and distribution of species assemblages in the mosaic of habitat and rocky landform types available at a high altitude is still lacking for most of the mountain regions and most taxonomic groups. This is probably due to the difficulties in reaching high-altitude areas and collecting quantitative data under harsh environmental conditions, specifically on alpine fellfields. Small mammals, Rodentia and Eulipotyphla, are the most diverse group of mammalian species, showing a wide range of sizes, behaviours, and niche uses (Nowak & Walker, 1999), also in the Italian peninsula (Loy et al., 2019). They play key roles in food webs, including important ecological roles in mountain ecosystems such as ground-dwelling arthropod predators and seed predators and dispersers (Martin-Regalado et al., 2019; Mortelliti et al., 2019), as ecosystem engineers in soil aeration and nutrient mixing through their burrowing habit (Zhang et al., 2003), and as a prey for mammalian and avian predators (Love et al., 2000; Moore et al., 2003). These taxa are particularly suitable for examining elevation patterns because they are commonly found along mountain slopes, have higher speciation rates and species turnover among habitats than larger mammals (Lopez et al., 2016; Sun et al., 2020).

In this context, small mammals are useful indicators of environmental health and biodiversity (Flowerdew et al., 2004; McCain & Colwell, 2011). Due to the ongoing climate change, low-elevation species expanded their ranges and high-elevation species contracted theirs, leading to changed community composition at mid and high elevations, also with possible species competition and replacement (Moritz et al., 2008). Indeed, during elevational migrations, abiotic factors can affect species composition by limiting the species to those who have specific functional traits necessary to live under these abiotic conditions (Graham et al., 2009; Webb, 2000). These abiotic conditions may act as a filter that prevents the establishment of species that have disfavored traits (Weiher et al., 1998).

The aim of this study was (1) to describe the small mammal community and the species distribution above the tree line of the Western Dolomites (Italian Alps) from 1900 to 2900 m a.s.l., (2) to investigate the species richness and the small mammal abundance in relation to topographic elevation, steepness, micrometeorological (temperature and relative humidity), biological (abundance of ground-dwelling arthropod acting as potential prey and/or proxy of habitat complexity), and mesohabitat (habitat and landform types) correlates and iii) to evaluate the activity rhythms during day-night time slots (and related temperature and humidity conditions). We expected lower species richness and abundance at higher elevation and in extreme temperature and relative humidity conditions.

Materials and methods

Study area

The fieldwork was carried out on the Brenta Dolomites (46°12'N, 10°53'E), in the Adamello Brenta Nature Park (Trento Province, Central-Eastern Alps, Northern Italy; Fig. 1). Round sample areas (n = 6; radius = 100 m) were set up every 200 m from 1900 to 2900 m a.s.l. with a general western aspect (Fig. 1). Sample areas spatial arrangement provided the independence and representativeness of the data collected for each type of environment (see ESM 1 for major details on environmental and micrometeorological description of each sample area). The environments include the uppermost larch forest (Larix decidua) at lower altitudes, alpine prairie with outcropping rock alternating with limestone floors and Grostè peak characterized by alpine calcareous grassland (PAT Geoportal: http://www.territorio.provincia.tn.it, accessed on 12 February 2022; Geomorphologic database of BioMiti Project, Zanoner et al., 2019).

Potential predators are represented by diurnal birds of prey (e.g. Aquila chrysaetos, Falco tinnunculus), opportunistic birds in finding sources of nutrition (e.g. Corvus corax) and night-active raptors (Strix aluco, Asio otus, Aegolius funereus, Glaucidium passerinum, Bubo bubo). Terrestrial predators were mammals (Volpes vulpes, Mustela nivalis, Mustela erminea, Martes foina, Martes martes) and reptiles (Hierophis viridiflavus; Zamenis longissimus, Vipera aspis, Viperus berus) (Adamello Brenta Nature Park – official monitoring data).

Data collection

Small mammals were monitored by setting up in each sampling area a catch grid of 16 Sherman LFA live traps (size = 7.6 × 8.9 × 22.9 cm; mass = 227 g; 4 × 4 grid; step = 5 m) with 10 g of food bait (i.e. a mixture of sunflower
seed, corn, dried fruit, apple, pork cubes and water) and dry grass, to attract animals and allow them to build a temporary shelter (Gagliardi & Tosi, 2012; Gurnell & Flowerdew, 1982; Hoffmann et al., 2010). To ensure safe monitoring, 1, 2 or 3 replicas were made, depending on the thickness of the snow cover and the accessibility to the high-altitude monitoring areas. Trapping was conducted between June and August 2020. After a prebaiting night, traps were set out for 3 consecutive 24 h periods with collection occurring at 8.00–9.00 AM and PM of each day. For each sampled individual, species identity, sex, reproductive status (Hoffmann et al., 2010), body mass and body measurements (Gagliardi & Tosi, 2012; Hoffmann et al., 2010) were recorded. Biometrical measures were used as a confirmation of species identification (i.e. length of head-body, tail, hind foot, and ear) and, together with reproductive status, to assess the age class (young, sub-adult, adult) according to available literature and technical reports in Trento Province (Northern Italy, e.g. Caldonazzi et al., 2018a, 2018b; Ferrari, 2016; Locatelli & Paolucci, 1996, 1998). Before release, animals were marked by shaving their hair in specific areas of the skin, a method that makes the animals temporarily recognizable in accordance with the timing of the monitoring sessions (Gagliardi & Tosi, 2012; Hoffmann et al., 2010).

In four sample areas (ID = 2, 3, 4 and 6; see Fig. 1), 8 camera-traps (SG2060-Xe) were placed alternatively in each catch grid 1-m in front of the live traps during prebaiting and capture periods to analyse the rhythms of daily activity (e.g. Viviano et al., 2022). Cameras were placed at a height of ~10–30 cm from the ground and were kept active 24 h, to take one video (10 s) at each animal passage (trigger time = 1 s; see ESM2 for major details).

Elevation (m a.s.l.), steepness (degree), vegetation cover (%), large rock slide deposit (%) and carsism (%) were derived from the Digital Elevation Model (DEM) raster at a 1 m spatial resolution (PAT Geoportal: http://www.territorio.provincia.tn.it, accessed on 12 February 2022), the Habitat Nature 2000 code vector map (PAT Geoportal: http://www.territorio.provincia.tn.it, accessed on 12 February 2022) and the landform type vector map (Geomorphologic database of BioMiti Project; Zanoner et al., 2019) in QGIS 3.16 (QGIS Development Team, 2021) (see Table 1 for a complete list of variables describing the ecological context).

In addition, data logger (Tinytag Plus 2 TGP-4500) was installed in each sampling area to record micrometeorological parameters (i.e. the hourly temperature and hourly percentage of relative humidity) at 5–10 cm depth in the ground and at the height of 150 cm from the ground on a wooden
Table 1 Potential predictors of species richness and aspecific abundance of small mammals throughout the Brenta Dolomites (46°12′N, 10°53′E), within the Adamello Brenta Nature Park (Trento Province, Central-Eastern Alps, Northern Italy)

| Independent variable | Description | Source |
|----------------------|-------------|--------|
| Topographic characteristics | Elevation | Mean elevation in m a.s.l. of the traps-grid | Digital Elevation Model—1 m resolution—Trento Province official data |
| | Slope | Mean slope in degree of the traps-grid | Digital Elevation Model—1 m resolution—Trento Province official data |
| Mesohabitat features | Large rock slide deposit | Percentage of large rock slide deposit of the traps-grid | Geomorphologic database of BioMiti Project—Adamello Brenta Nature Park official data |
| | Carsism | Percentage of carsism of the traps-grid | Geomorphologic database of BioMiti Project—Adamello Brenta Nature Park official data |
| | Vegetation cover | Percentage of the traps-grid covered by vegetation | Ortophoto maps 2014–2016—Trento Province official data |
| Micrometeorological conditions | Sub-surface ground Temperature\(^{a}\) | Mean temperature (°C) at 5–10 cm depth in the ground during each trap-session (12 h) | Data logger (Tinytag Plus 2 TGP-4500) |
| | Sub-surface relative humidity\(^{b}\) | Percentage of humidity at 5–10 cm depth in the ground during each trap-session (12 h) | Data logger (Tinytag Plus 2 TGP-4500) |
| | Air Temperature \(^{a}\) | Mean temperature (°C) at the height of 150 cm from the ground during each trap-session (12 h) | Data logger (Tinytag Plus 2 TGP-4500) |
| | Relative Humidity air\(^{b}\) | Percentage of humidity at the height of 150 cm from the ground during each trap-session (12 h) | Data logger (Tinytag Plus 2 TGP-4500) |
| Biological correlates | Species richness\(^{c}\) | Values obtained for Coleoptera Carabidae, Arachnida Araneae | Pitfall trap monitoring in BioMiti Project—Adamello Brenta Nature Park official data (Gobbi et al., 2021) |
| | Abundance\(^{c}\) | | Pitfall trap monitoring in BioMiti Project—Adamello Brenta Nature Park official data (Gobbi et al., 2021) |
| | Taxonomic distinctness\(^{c}\) | | Pitfall trap monitoring in BioMiti Project—Adamello Brenta Nature Park official data (Gobbi et al., 2021) |
| | Average body length | | Pitfall trap monitoring in BioMiti Project—Adamello Brenta Nature Park official data (Gobbi et al., 2021) |

\(^{a,b,c}\): The same upper letters indicate the presence of collinearity among independent variables (\(|r_p| \geq 0.7\))
support covered by a white coating to prevent direct sunlight that can lead to the overheating.

We associated with each monitoring session and area data on species richness (i.e. the total number of species collected), abundance (i.e. the total number of individuals sampled), taxonomic distinctness (i.e. a measure that emphasizes the average taxonomic relatedness between species within a community; Clarke & Warwick, 1998; Paschetta et al., 2013) and average body length (mm; i.e. a proxy of available biomass, Moretti et al. 2017) of carabid beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae). As reported by Clarke and Warwick (1998), we calculated the taxonomic distinctness as the average path length between any two randomly chosen individuals, conditional on them being from different species (i.e. the ratio between taxonomic diversity and the value it would take were there to be no taxonomic hierarchy). We selected these two taxonomic groups because (1) they are potential ground-dwelling prey for some of the captured small mammals (i.e. Soricidae; Klenovšek et al., 2013), (2) they are among the most common and most studied ground-dwelling and top-predator arthropods living at high altitudes, and (3) previous data were already available for the investigated sampling areas (see Gobbi et al., 2021; Petri et al., 2021 for major details about data collection, species identification and measurements).

Data analysis

After evaluating the trapping success and mortality rate, for each sampling area we reported the list of sampled species, the species richness (i.e. the number of detected species), the number of individuals trapped for each species, and the dominance index (i.e. the probability that two individuals randomly selected from the sample belong to the same species: Simpson, 1949). Data were considered according to day-night trapping sessions.

We fitted linear models testing the effect of the topographic (elevation, steepness), micrometeorological (temperature and relative humidity), biological (abundance of ground-dwelling arthropod acting as potential prey) and mesohabitat variables on species richness and abundance of small mammals in the study areas (see Table 1). We tested for collinearity among independent variables using a correlation matrix (Pearson correlation coefficient, $r_p$) and did not include correlated variables in the same model if $|r_p| \geq 0.7$ (Sokal & Rohlf, 1995).

We z-transformed continuous independent variables to compare the relative effects of predictors on species richness and aspecific abundance (i.e. the total number of captured individuals, without considering the species) of small mammals. We used Akaike's Information Criterion for small sample size (AICc; Burnham & Anderson, 2002) to select the best-fitting sets of models. We selected all models within 2 AICc units of the best fitting model (i.e. $\Delta$AICc $\leq$ 2, indicating substantial evidence to support the candidate model; Burnham & Anderson, 2002). We checked assumptions of normality, homoscedasticity, and independence by inspecting standardized residual plots (Zuur et al., 2010). We obtained the effect of each variable (i.e. parameter estimation) included in the confidence set of models via model averaging (model.avg function in MuMin package for R; Burnham & Anderson, 2002; Symonds & Moussalli, 2011). We assessed model goodness of fit using the adjusted $R^2$.

Daily activity rhythms were evaluated considering “activity” as the cumulated period animals spend outside their shelter sites, regardless of their behaviour (Lashley et al., 2018). For all videos, we recorded the date and the time of capture and number of individuals. In order to limit bias and lack of reliability in our analyses, we classified all the captured animals into two groups: Sorex sp. and Arvicolinae.

The close morphological resemblance makes the discrimination inside the Sorex genus and the Arvicolinae subfamily not always possible from camera-trap records. Number of small mammal video-captures (N/h) in each 1 h time slot inside the sample area during 24 h/day period was evaluated and considered in relation to mean temperature (°C) at 5–10 cm depth in the ground.

Statistical analyses were performed in R version 4.1.2 (www.r-project.org, R Core Team, 2021).

Results

Live trapping results and small mammal community structure

Trapping success for small mammals was 8.0% representing 97 captures from 1216 trap-sessions (day trapping success: 4.4% representing 21 captures from 480 trap-days; night trapping success: 10.3% representing 76 captures from 736 trap-nights). During the study, the 97 capture-events led to the identification of 50 individuals of small mammals of 5 species, including one insectivore and four rodents (Fig. 2 and Table 2). We identified the snow vole (Chionomys nivalis; $n = 21$), the bank vole (Myodes glareolus; $n = 13$), the common vole (Microtus arvalis; $n = 3$), the genus Microtus subgenus Terricola (Microtus (Terricola) spp.; $n = 3$ represented by Microtus multiplex and/or Microtus subterraneus), and the Valais shrew (Sorex antinorii; $n = 10$). At the extremes of the altitudinal range (i.e. ~1900 vs 2900 m a.s.l.), community compositions were completely different: we trapped only Chionomys nivalis ($n = 4$) at 2892 m a.s.l., while we detected Myodes glareolus ($n = 12$), Microtus (Terricola) spp. ($n = 3$) and Sorex antinorii ($n = 9$) at 1867 m a.s.l. However, it should be considered that only one session was performed in the highest sample area, instead of three
sampling sessions, due to the persistence of snow cover. Mortality rate was 13.4% (69.2% Sorex antinorii, 23.1% Chionomys nivalis and 7.7% Myodes glareolus).

Environmental correlates

Among potential predictors of small mammal species richness, we revealed the importance of three variables: elevation, steepness, and vegetation cover. While an increase in altitudinal range had a negative effect on species richness, greater steepness and a higher percentage of vegetation cover allowed an increase in the number of species (Table 3a). The taxonomic distinctness of Carabidae and Araneae showed higher values in areas with a greater small mammal species richness (Table 3a).

Throughout the Brenta Dolomites, steepness and rocky landform type “carsism” had a positive effect on the number of captured individuals. A negative impact on small mammal abundance was related to higher value of sub-surface ground temperature during the monitoring period, detecting fewer individuals in areas with the highest temperature values (Table 3b). Also, in this case the taxonomic distinctness of Carabidae and Araneae showed higher values in areas with a greater density of small mammals (Table 3b).
Camera trapping results

In total, 898 h of video-trapping (51% during daytime and 49% during nighttime) collected 295 videos of small mammals, of these 251 were considered as independent events (i.e. recognized a different individual or registration made after at least 15 min). Forty-three events (17.13%) were recorded during daylight, while 208 events (82.87%) during nighttime. Other 63 videos were discarded as it was not possible to identify the species with enough confidence (21.4% of total, in accordance with Viviano et al., 2022).

The daily activity of small mammals showed an important peak after the sunset, while a further increase was recorded before the sub-superficial ground temperatures reached the highest daily values (2–4 PM; Fig. 3). This peak was mostly due to the activity of the Sorex sp. recorded in the lowest altitude sample area (see supplementary material ESM3 for more details). The relative humidity was always ≥ 95% for the whole video-trapping period in each sample area, so the variance of this factor was negligible.

Discussion

The data collected gave the possibility to highlight the variables affecting the species richness and abundance of small mammal community above the treeline.

In Italy, the snow vole is distributed in the continental area (Alps and Northern-Central Apennines; Toschi, 1965; Amori et al., 1986; Nappi & Aloise, 2015; Loy et al. 2019). It is very common in high mountain land, and it is the only European mammal found at 4700 m on the French slope of the Monte Bianco massif (Saint Girons, 1973). Nappi (2002), analysing 157 bibliographical, museum and unpublished data described the altitudinal range in Italy from 170 to 3700 m a.s.l.. In the Alps, the upper altitudinal limit is determined by the height of the peaks (e.g. 1820–2959 m in the Western Italian Alps; Patriarca & Debernardi, 1997); however, in Italy the snow vole predominantly occurs between 1500 and 2000 m of altitude, as it is mainly influenced by the ecological niche rather than by temperatures (Nappi, 2002). In the Dolomites, it had previously been reported at 2700 m a.s.l. (Locatelli & Paolucci, 1996) and this study updates the presence of this species up to 2829 m a.s.l. at Grostè peak. The optimal habitat is represented by open areas with a rocky substrate consisting of large boulders that occupy 90% of the surface, with a maximum of 10% of vegetation cover (Janeau, 1980). In our study, these characteristics were recorded over the 2700 m a.s.l., where the greatest abundance of individuals was found (see Fig. 1).

At the lowest investigated altitude (1900 m a.s.l.), we revealed the presence of the bank vole, the Valais shrew, and the genus Microtus subgenus Terricola. Among the fossozial rodents, we confirmed the presence of M. multiplex and M. subterraneus, distinguishable only with genetic investigation or analysing the dental and cranial morphology. All these species are linked to wooded areas from the hills to the mountains (up to over 2000 m of altitude; Patriarca & Debernardi, 1997). In some cases, it is also present in open or rocky areas, as long as they are covered with shrubs.
The areas located at higher altitudes and with a lower degree of vegetation cover showed, as expected, a lower small mammal species richness. However, it should be considered that the climatic and environmental changes underway, and which occur more rapidly in extreme environments, are causing an upward shift of species (Rowe et al., 2010). It is interesting to note that the steepness contributes positively to describe the species richness, highlighting the choice of safer and more protected areas (i.e. areas with greater abundance of shelters to prevent predation). Indeed, the presence of shelters plays a fundamental role for these species, in all the different environments but above all in areas with limiting climatic-environmental characteristics (Dickman et al., 2011; Ecke et al., 2001; Sabino-Marquès & Mira, 2011; Torre et al., 2022).

At the same time, the taxonomic distinctness of carabid beetles and spiders, as well as a habitat complexity index (Clarke & Warwick, 1999; Warwick & Clarke, 1998), showed higher values in areas with more small mammal species. Since taxonomic diversity is a proxy of environmental maturity/stability (Paschetta et al., 2013), high values should be related to a high availability of trophic niches (i.e. areas with lower competition, greater availability of trophic resources, shelter areas, and suitable environmental conditions).

Considering small mammal abundance, our results confirmed the importance of shelter areas and habitat complexity. Indeed, a greater abundance of small mammals was revealed in areas with more underground burrows.

We detected a negative impact of sub-surface ground temperature on small mammal abundance during the monitoring period, detecting fewer individuals in areas with the highest temperature values. This relationship might suggest a possible altitudinal shift for these species in relation to the ongoing climate changes. Also the daily activity showed the lowest values when the sub-surface ground temperatures...
reached the highest daily values. These high temperatures are also avoided by the genus *Sorex* which shows a bimodal activity, with the need to feed even during the daytime hours. Despite the presence of a high vegetation cover (in fact the genus *Sorex* was detected only in the sample area at a lower altitude), the hottest hours are in any case avoided. It is important to note that the activity of Arvicolinae in this high-altitude environment differs greatly from the activity found in wooded areas (Viviano et al., 2022). However, this can be due not only to the environmental and climatic characteristics but also to an anti-predatory strategy (e.g. O’Brien et al., 2018).

As small mammals play a crucial ecological role in food chains, as well as for bioindication, there is an urgent need to continuously monitor their status, population trends, and altitudinal shift. They represent excellent models for understanding the evolutionary processes in ecosystems, population dynamics under changing environmental conditions, and habitat vulnerabilities.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflict of interest** The authors have declared that no competing interests exist.

**Ethical approval** The study complies with all relevant national, regional and provincial Italian laws and with the ethical standards of scholarly research.

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