Macedonian Journal of Ecology and Environment
Vol. 26, issue 1
pp. 53 - 60
Skopje (2024)
ISSN 1857 - 8330 (on-line)
ISSN 0354-2491 (print)
Original scientific paper
Available online at www.mjee.org.mk
DOI: https://doi.org/10.59194/MJEE24261053cgj

Reproduction and hibernation strategy of ground-beetles (Coleoptera, Carabidae) along altitudinal gradient

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Abstract

Reproduction and hibernation strategies of ground-beetle community along altitudinal gradient on Belasica Mt. were studied. Ground-beetles were systematically collected at 14 different localities by pitfall traps, with monthly dynamics in the period April-November 2010. Four types of reproduction were registered: spring, autumn, spring-autumn and plastic reproduction and both types of hibernation: larva and imago. Dissimilarities in ground beetles' assemblages between localities were analyzed with cluster analysis. Two groups of localities were registered. First group includes communities inhabiting lower parts, i.e. L1-L4 which were joined on approximately 0.78 % and 0.66% level of similarity (respectively), and the second one groups ground-beetles inhabiting upper altitudinal belt i.e. L7-L14, at 0.54% similarity level of reproduction and hibernation (respectively). Spring breeders as well as ground beetles with plastic reproduction dominated in the localities from upper altitudinal belt. Their abundance as well as the abundance of ground-beetles with adult hibernation was positively correlated with the increasing altitude. These two functional groups of the ground-beetle community are closely interconnected, as confirmed by almost identical dendrographs of the similarity of the carabidocenoses along the gradient.

Keywords: functional traits, ground-beetles, climate change, mountain

Introduction

Ground beetles (Carabidae) are often regarded as ecological indicators, reflecting subtle shifts in environmental conditions due to their sensitivity to various ecological factors (McGeoch 1998). Among these, climatic mechanisms play an important role in shaping ground beetle communities, particularly along altitudinal gradients. Understanding the interaction between climatic variables and beetle assemblages offers valuable insights into their potential sensitivity to environmental changes.

Altitudinal gradients provide natural laboratories for studying the impacts of climatic variations on functional characteristics of ground-beetle communities. As elevation increases, temperature, precipitation, and other climatic factors undergo predictable shifts, creating distinct ecological zones and ground beetles with their functional traits such as reproduction and hibernation exhibit remarkable adaptations to these gradients.

According to Butterfield (1997) ground-beetles respond to changes by changing their habitat rather than changing their physiological adaptations, thus emphasizing their usefulness as favorable bioindicators of environmental changes. Furthermore, altitudinal gradients serve as natural corridors for species migration and dispersal in response to climatic changes.

Submitted: 20.05.2024;
Accepted: 04.06.2024

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Ground beetles, with their diverse ecological niches and mobility, may track shifting climatic zones by colonizing new habitats or retreating to higher elevations.

The Macedonian mountains and surrounding regions boast a rich variety of ecosystems, ranging from temperate forests to alpine meadows. This ecological diversity provides a broad spectrum of habitats and species, making it an ideal setting for assessing the impacts of climate change on ecological traits.

The topography of North Macedonia encompasses significant altitudinal gradients, with peaks reaching heights up to or over 2,000 meters. These gradients create diverse microclimates, allowing researchers to study the effects of elevation on climate variability and functional traits of species. By examining changes of species behavior along elevation gradients, insights of how organisms respond to shifting climatic conditions can be obtained.

Belasica Mt. is situated at the southeastern part of North Macedonia, and represents the upper limit where the Mediterranean climate is present. Therefore, it is one of the first mountains in Republic of North Macedonia to be influenced by climate change (MoePP 2014), considering that these types of changes are particularly expected in the Mediterranean regions (Cvetkovska-Gjorgjievska et al. 2017, 2020, 2022; Peñuelas et al. 2017; Matevski et al. 2020).

In the absence of ecological researches focused on the functional characteristics of animal communities inhabiting mountain ecosystems, the aim of this study was to determine whether the altitude gradient affects reproduction and hibernation as ecological traits of ground-beetles on Belasica Mt.

This study is among the first ones to provide basic data for the future impacts of climate change on reproduction and hibernation strategy of carabid communities not only on Belasica Mt., but in general for the territory of North Macedonia.

Material and methods

Study area

The research was carried out on the northern slopes of Belasica Mountain near North Macedonia's southeast border with Greece and Bulgaria (Fig. 1).

It is a high mountain of 198.2 square kilometers (Melovski et al. 2013). The soil types at higher parts of the mountain are primarily mountain-meadow and brown-forest, whereas cinnamon-forest soils are found at lower parts of the mountain (Filipovski et al. 1996). The mountain belt above 1000 m alt. is influenced by a typical mountainous climate, which is defined by increased precipitation and lower temperatures. The climate at lower elevations (300-1000 m a.s.l.) is sub-Mediterranean (low precipitation rate and high temperature) (Filipovski et al. 1996).

Sampling design

Fourteen localities (L1–L14) and four climazonal forests representing the main vegetation types were selected at various elevations (240–1450 m a.s.l.) along an altitudinal gradient (Fig. 1b). The first five localities (L1-L5) are under forests of White oak and Oriental hornbeam; L6-L9 are under Sessile oak forest; L10 is located within a submontane beech forest; L11-L13 are assigned within a montane beech forest; L14 is a clear-cut region within a montane beech forest.

Ground beetles were collected by pitfall traps placed along a transect line that followed an isohypse. Pitfall traps were made of plastic cups with a volume of 0.5 L, a diameter of 8.5 cm, and a height of 11.5 cm. Ten pitfall traps were positioned ten meters apart along a transect line that spanned 100 meters at each locality, so covering every altitudinal zone. Throughout the 14 distinct localities (L1-L14), 140 traps were positioned

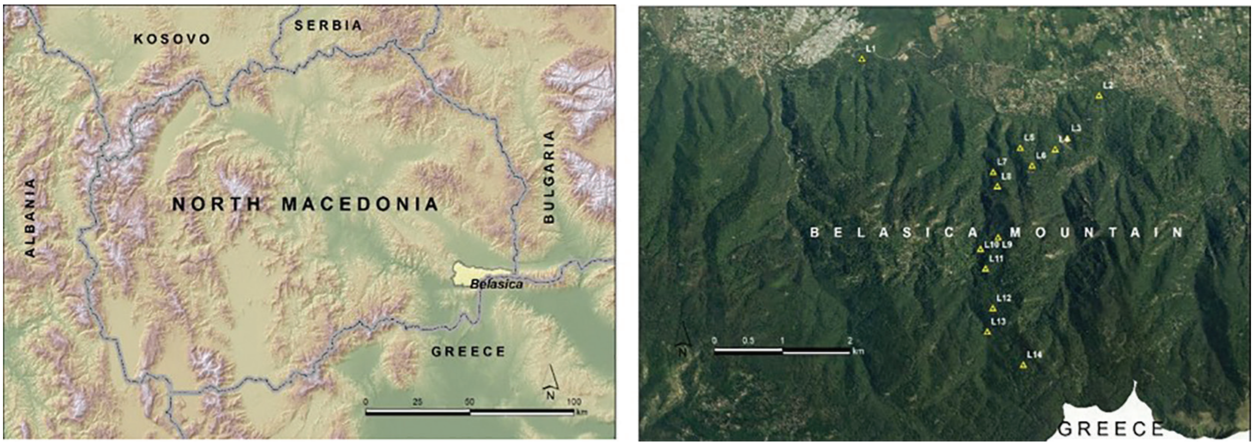

Figure 1. Topographic map of the investigated area on Belasica Mountain

Table 1. List of the investigated localities with the data about the altitudes, GPS coordinates slope and dominant vegetation type

Code	Altitude (m)	Locality	GPS coordinates
L1	250 a.s.l.	Near the locality of Markova Skala; ass. *Querco pubescentis-Carpinetum orientalis* Horvatić 1939	41.382297 22.771482
L2	327 a.s.l.	Under the viewing point near the Koleshino Waterfall; ass. *Querco pubescentis-Carpinetum orientalis* Horvatić 1939	41.377504 22.812616
L3	415 a.s.l.	Near the Koleshino Waterfall; ass. *Querco pubescentis-Carpinetum orientalis* Horvatić 1939	41.372145 22.807476
L4	500 a.s.l.	Near the locality of Pod; ass. *Querco pubescentis-Carpinetum orientalis* Horvatić 1939	41.371468 22.804530
L5	587 a.s.l.	Between the localities of Pod and Suva Cheshma ass. *Querco pubescentis-Carpinetum orientalis* Horvatić 1939	41.370699 22.800324
L6	693 a.s.l.	Near the locality of Suva Cheshma; ass. *Fraxino orni-Quercetum petraeae* Em 1968	41.368247 22.799759
L7	767 a.s.l.	Near the locality of Popadija; ass. *Fraxino orni-Quercetum petraeae* Em 1968	41.369374 22.795384
L8	847 a.s.l.	Near the locality of Popadija; ass. *Fraxino orni-Quercetum petraeae* Em 1968	41.366565 22.794000
L9	1038 a.s.l.	Near the locality of Popadija; ass. *Fraxino orni-Quercetum petraeae* Em 1968	41.359571 22.794153
L10	1100 a.s.l.	Near the locality of Popadija; ass. *Festuco heterophyllae-Fagetum* (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.358462 22.790140
L11	1200 a.s.l.	Near the locality of Popadija; ass. *Calamintho grandiflorae-Fagetum* (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.352880 22.791669
L12	1300 a.s.l.	Near the locality of Groba; ass. *Calamintho grandiflorae-Fagetum* (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.347933 22.792675
L13	1385 a.s.l.	Near the locality of Pisana Skala; ass. *Calamintho grandiflorae-Fagetum* (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.344122 22.793764
L14	1442 a.s.l.	near the locality of Pisana Skala; clear-cut area	41.341242 22.798297

at vertical intervals of 100 meters, signifying varying heights on the northern slopes of Belasica Mountain. To avoid floods, metal roofs were placed above each trap and the traps were positioned parallel to the soil's surface.

A 1:7 solution of formaldehyde and vinegar (200 ml) was used as a preservative. The study was conducted every month in the period April - November of 2010.

Data analyses

The list of species is already published in Cvetkovska-Gjorgjievska et al. (2018). Species were categorized and analyzed according their reproduction and hibernation types (Lindroth 1992). The abundance of species with different reproduction and hibernation type was analyzed for each altitude along the altitudinal gradient. The abundance of ground-beetles was represented as number of individuals per trap ($ind \cdot trap^{-1}$).

Statistical analysis was performed for the data of collected ground beetles at each altitude. Species abundance data were tested for normal distribution and variance of homogeneity by using Shapiro-Wilks and Levene's tests, respectively. To obtain normal distribution, data were log(x+1) transformed.

Nonparametric tests, Kruskal-Wallis, followed by post-hoc Mann-Whitney U tests (which follows when significant differences are recorded with the Kruskal Wallis ANOVA test) were applied to check for the differences in average abundance of species, within and between localities. These results are presented with box plots, which allow visual comparisons of centers and spread through the five-number summary (minimum, lower quartile, median, upper quartile, maximum), dividing the data into four equally sized sections (Pfannkuch 2006).

Spearman rank correlation (r_s) was used to analyze the relationship between the altitude and average abundance of species with different reproduction and hibernation strategies.

The similarity of reproduction and hibernation strategies of ground-beetles between different localities was compared with Bray-Curtis paired group cluster analysis (clusters were joined based on the average distance between all members in the two groups) (Somerfield 2008, Hammer et al. 2013).

All statistical data analyses were done with statistical software STATISTICA 7 and PAST. Significant values were those with p<0.05.

Results and discussion

During the research, four categories of breeders (spring, spring-autumn, autumn and plastic breeders) and three hibernation types (imago hibernators, larval hibernators and species with irregular hibernation) were registered.

Out of all 38 species and 8680 specimens, 17 species (*Abax carinatus carinatus, Amara curta, Amara similata, Calosoma inqisitor, Carabus montivagus montivagus, Carabus intricatus intricatus, Carabus convexus dilatatus, Harpalus atratus, Harpalus honestus honestus, Harpalus rufipalpis rufipalpis, Harpalus tardus, Harpalus tenebrosus, Molops rufipes belasicensis, Myas chalybaeus, Notiophilus substriatus, Pterostichus anthracinus* and *Tapinopterus balcanicus belasicensis)* were spring breeders representing 90.82% of the total community (Fig. 2a). These species reproduce at the very beginning of the vegetation period (Larsson 1939), mainly during May, June, the pupal stages transform into imago during the autumn period and always hibernate in the adult stage (Lindroth 1949). In fact, the predominance of spring breeders in mountain ecosystems is an expected phenomenon, because overwintering in the imago stage is one of the ways to protect against the unfavorable conditions at high-altitudes. Ten species (*Carabus coriaceus cerisyi, Calathus erratus erratus, Calathus fuscipes fuscipes, Nebria brevicollis, Harpalus rubripes, Harpalus rufipes, Harpalus smaragdinus, Trechus subnotatus, Trechus tristis* and *Trechus quadristriatus*) constituting 7,01% of the total community were autumn breeders, with reproduction in late summer (mainly July and August) and early autumn (Larsson 1939) and is usually followed by hibernation in the larval stage (Lindroth 1949).

Five species *(Carabus violaceus azurescens, Carabus hortensis, Cychrus semigranosus balcanicus* and *Pterostichus niger)* demonstrated plastic reproduction (2.14%), while *Harpalus distinguendus distinguendus* with only 0.02% participation, was the only registered species known to be spring-autumn breeder, which breeds in the middle or end of spring until the beginning of the autumn period (Fig. 2a).

Regarding the hibernation strategy, 18 species were imago hibernators (*Abax carinatus carinatus, Amara aenea, Amara curta, Amara eurynota, Amara similata, Asaphidion flavipes, Calosoma inguisitor, Carabus montivagus montivagus, Carabus intricatus intricatus, Carabus convexus dilatatus, Harpalus atratus, Harpalus distinguendus distinguendus, Harpalus honestus, Harpalus tardus, Harpalus tenebrosus, Molops rufipes belasicensis, Pterostichus anthracinus* and *Tapinopterus balcanicus belasicensis*), 9 were larval hibernators (*Calathus fuscipes fuscipes, Calathus erratus, Carabus violaceus azurescens, Carabus coriaceus cerisyi, Harpalus smaragdinus, Harpalus rufipes, Nebria brevicollis,*

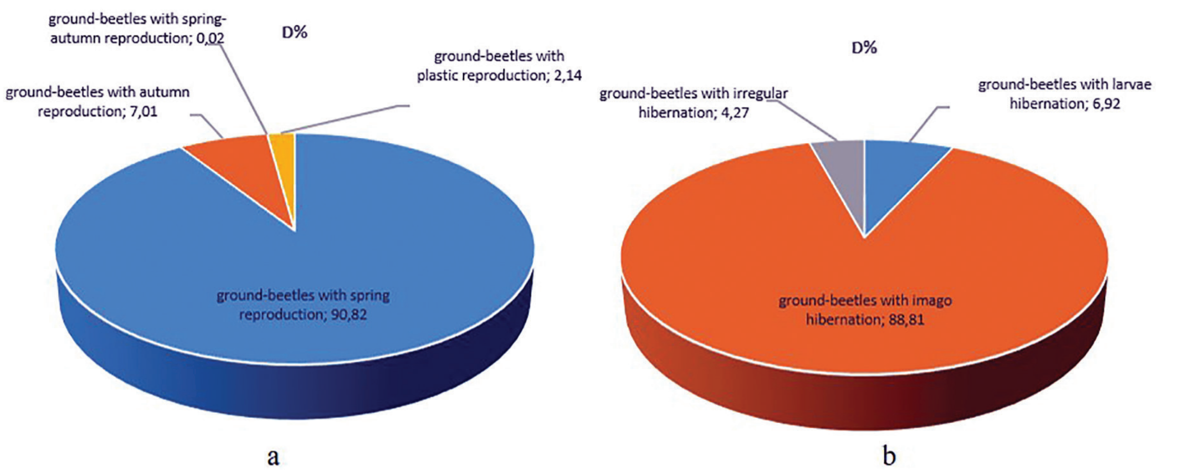

Figure 2. Relative participation of ground-beetles on Belasica Mt. regarding their reproduction (a) and hibernation (b) strategy

Pterostichus niger and *Trechus quadristriatus*) and 3 species (*Cychrus semigranosus balcanicus, Harpalus rufipes* and *Myas chalybaeus*) had irregular hibernation.

The largest share (88.81%) in the community had species overwintering in the adult stage, while larval over-winterers made up 6.92% of the community, and species with irregular hibernation appeared with 4.27% of the total community (Fig. 2b).

The overall pattern of species reproduction and hibernation also showed differences between localities mainly because of significant differences of the abundance of dominant and subdominant species.

According to the results (Fig. 3a), spring-breeders showed high abundance and dominance throughout the entire gradient, with highest values in L9, L10 and L11, and significantly ($p<0.05$) lowest values in L5. Autumn breeders showed more homogenous distribution along the gradient, with the exception of L4, L6-L10, L12 were lowest values were registered (Fig. 2b). The presence of the species *Harpalus distinguendus distinguendus,* the only species with mixed spring-autumn reproduction at L7 is insignificant (Fig. 2d), while species with plastic reproduction were registered only in localities from upper altitudinal belt, demonstrating positive correlation with increasing altitude ($R=0.536$, $p<0.05$), with significantly ($p<0.05$) higher abundance in L10 compared to their abundance in L6-L8 (Fig. 2c).

Considering the shorter reproductive period, reproduction at higher altitude is a challenge for ectotherms, which is actually compensated by special reproductive strategies. Closely associated with the reproduction are the duration of the development period and hibernation, which also changed along the gradient (Fig. 4). In this case, only the abundance of adult hibernators was positively correlated ($R= 0.237$; $p<0.05$) with the increasing altitude, and consequently with changes of oak to beech forests (Fig. 4a). Namely, low temperature at higher parts of the gradient prolongs the development of insects and increases the mortality rate in the pre-reproductive period (Hu et al. 2011), and to prevent this phenomenon, hibernation takes place in the imago stage, which is more resistant to lower temperatures than the larva.

Furthermore, we found that the hibernation stage was a strong predictor of the likelihood that carabids would occur. However, there was a strong connection between the species' hibernation stage and reproduction time.

This is confirmed by the almost identical dendrograms shown on Fig. 5a and 5b. Namely, when analyzing similarity of reproduction and hibernation strategies of ground-beetle's between different localities and vegetation types, two groups of localities were registered. First group includes communities inhabiting lower parts, i.e. L1-L4 which

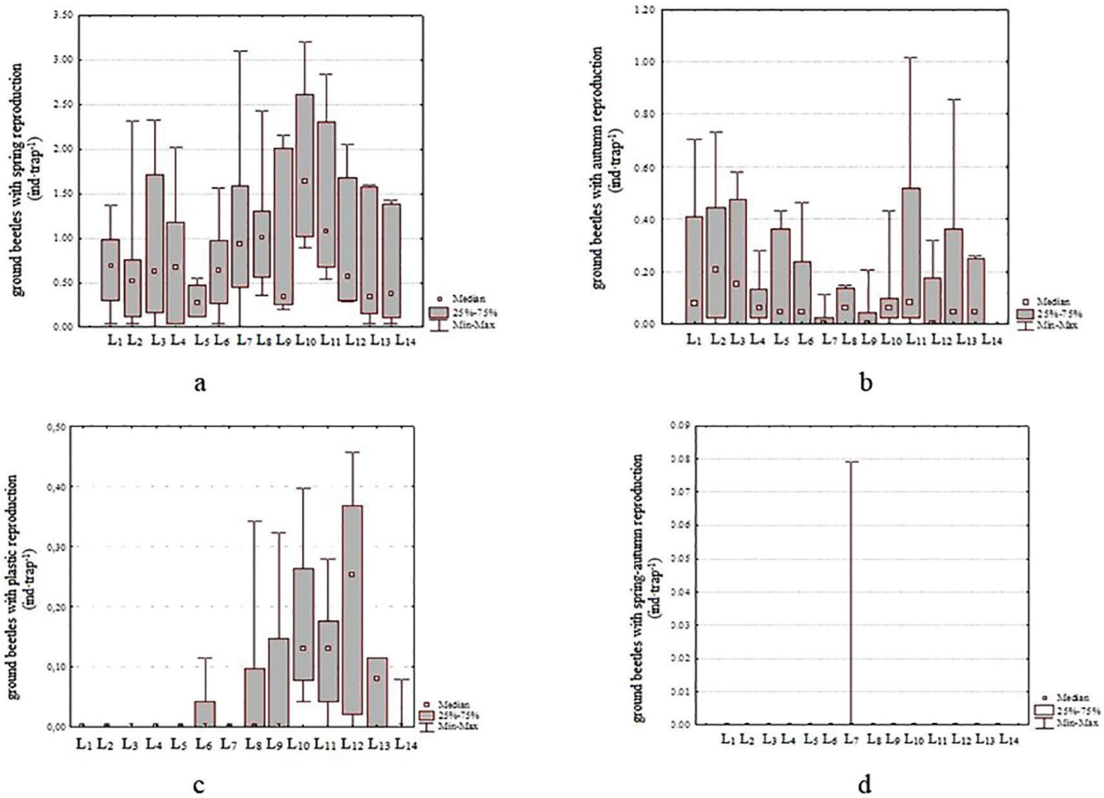

Figure 3. Average abundance (ind·trap^{-1}) of ground-beetles along altitudinal gradient on Belasica Mt., with a) spring reproduction, b) autumn reproduction, c) plastic reproduction, d) mixed (spring-autumn) reproduction

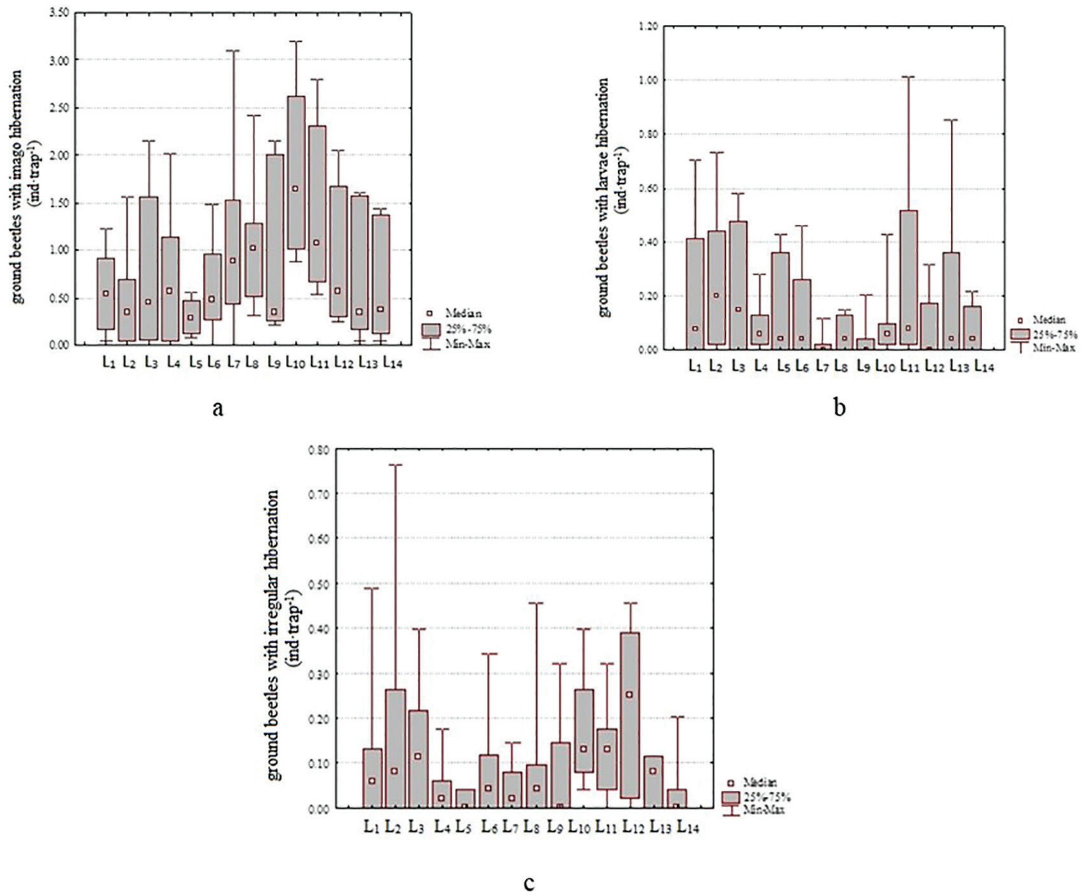

Figure 4. Average abundance (ind·trap^{-1}) of ground-beetles along altitudinal gradient on Belasica Mt., with a) imago hibernation, b) larvae hibernation, c) irregular hibernation

were joined on approximately 0.78 % and 0.66% level of similarity (respectively), and the second one groups ground-beetles inhabiting upper altitudinal belt i.e. L7-L14, at 0.54% similarity level of reproduction and hibernation (respectively).

Spring breeders and imago hibernators dominated the entire altitudinal gradient, however there were species with different reproduction and hibernation strategy appearing in one or another locality. Therefore the subgrouping among communities at different altitudes//localities is expressed.

Regarding the **reproduction strategy**, the feature that unites the first four localities (L1-L4) is the relatively higher abundance of spring and low abundance of autumn breeders, as well as the absence of individuals with plastic and spring-autumn reproduction. Localities from the L7-L14 group are distinguished by the appearance of species with plastic reproduction, whose abundance significantly increases with the increasing altitude. At the same time the abundance of spring breeders is higher with significantly highest values in L10-L11 (mainly due to high abundance of the dominant *Tapinopterus balcanicus belasicensis* and *Molops rufipes belasicensis*), and lower values towards L12, L13 and L14.

Therefore, the gonads of females at higher altitudes mature at the beginning of spring and the reason why spring-breeding larvae mainly live in these areas is that this way the larva has favorable conditions to develop throughout the summer before it turns into an imago and enters the overwintering stage (Thiele & Weber 1968, Refseth 1988, Ottesen 1995). The activity of the spring breeding forms is short-lived, and towards the end of the summer, another slightly weaker activity follows, and it is probably the result of ground-beetles looking for favorable places for wintering in that period, or the recorded activity is actually the activity of another new generation towards the end of the season (De Zordo 1979).

A high degree of association was observed between the increasing altitude and the abundance of individuals with plastic reproduction. Namely, the number of plastic breeders in the interval L8-L13 (847-1385 m a.s.l.) is mainly due to the higher abundance of *Cychrus semigranosus balcanicus*, whose abundance increases with the increasing altitude, especially in the localities under beech forest.

The ground-beetles of L5 and L6 are singled out because in L5 the number of spring breeders decreased, while in L6 increased. In L6 the presence of plastic breeders was also recorded.

Spring reproduction of ground beetles is correlated with imago hibernation. Hence, according to the **hibernation type**, the adult over-winterers dominated throughout the entire altitudinal gradient and their abundance was positively correlated with the increasing altitude as well as with changes of vegetation structure (oaks-beech forests). Regarding the hibernation strategy, the cluster analysis showed separation of two groups of hibernators, inhabiting localities L1-L4 and L7-L14. First group unites communities from the interval L1-L4 however within the group, a subgrouping of the first three localities at about 79% level of similarity is recorded, which is due to overwintering larvae, mainly of *Carabus coriaceus cerisyi*.

In the second group of localities (L7-L14), three subgroups were recorded, between the carabidocoenoses of L8-L9, L10-L11 (with the highest values of both adult and larval overwintering) and L13-L14, which are connected with lower similarity. The mountain forest belt (L7 – L11) is characterized with high abundance of adult winterers. Namely, in these localities, the abundance of *Tapinopterus balcanicus belasicensis* and *Molops rufipes belasicensis* begins to increase, and *Carabus convexus dilatatus* and *Calosoma inquisitor* reach their maximum abundance. In the following localities, its abundance decreases intensively until it is completely absent. Hence, the abundance of larval hibernators is lower in the interval L7 - L10, in contrast to the localities under mountain beech forest (L11-L13) where the species *Nebria brevicollis* and *Trechus quadristriatus* are also represented.

In the following localities (L12-L13), the number of adult winterers gradually decreases, but is still higher than the abundance of larval winterers (*Nebria brevicollis, Trechus quadristriatus* and *Carabus violaceus azurescens*). Against the high abundance of larval overwinterers in L13, in the community from L12 there is an increase in the abundance of species with irregular hibernation. The clear-cut area (L14) is also dominated by adult winterers, because of the high abundance of *Harpalus rufipalpis rufipalpis*, but also of other *Amara* and *Harpalus* species.

Conclusion

The relationship between altitude, vegetation types, microclimate changes, and the reproductive and hibernation strategies of ground beetles highlights their role as reliable bioindicators of climate change in mountainous regions. Altitude influences the distribution of ground beetles by shaping microclimatic conditions, which in turn affects their reproductive cycles and hibernation behaviors.

Ground beetles, with their sensitivity to environmental changes and close association with specific microhabitats, provide valuable insights into the ecological impacts of climate change in mountain ecosystems. By monitoring ground beetle populations along altitudinal gradients, researchers can gain valuable insights into the ecological impacts of climate change, including shifts in species distributions, phenological changes, and community composition. Monitoring ground beetle populations along altitudinal

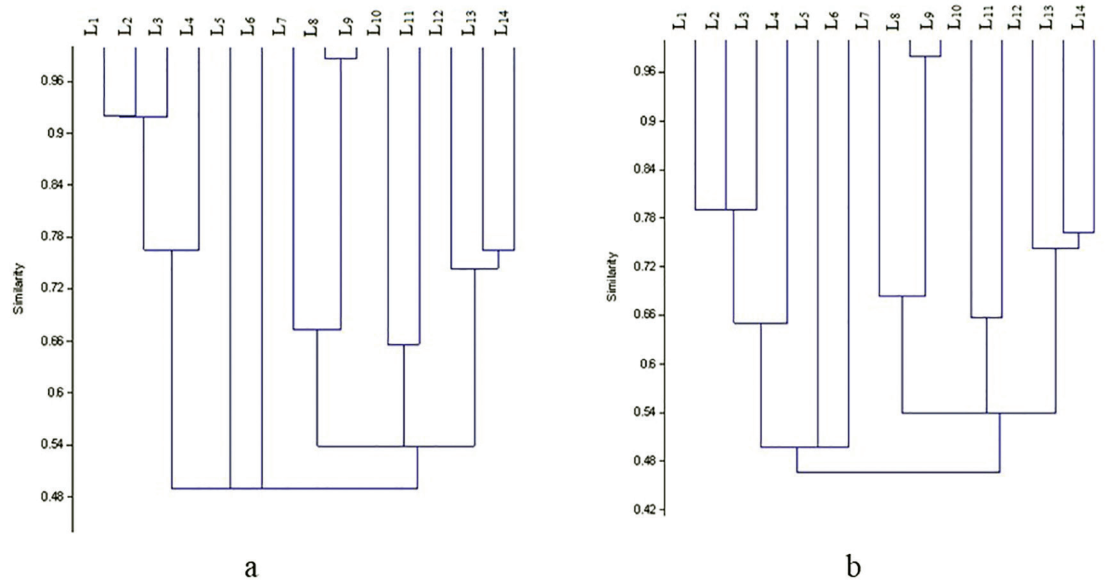

Fig. 5 UPGMA (unweighted pair-group average) Bray-Curtis (constrained) coefficient of similarity of ground-beetle along the altitudinal gradient of pl. Belasica Mt., according their reproduction (a) and hibernation strategies (b)

gradients can thus serve as an effective tool for detecting early signs of climatic disturbances and informing conservation efforts. By recognizing ground beetles as bioindicators of climate change, we can leverage their ecological significance to better understand and mitigate the consequences of global warming on mountain biodiversity and ecosystem functioning.

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