

Habitat and humidity preferences of ground beetle communities (Coleoptera, Carabidae) on the Belasitsa Mts. (North Macedonia). Ecological traits of ground beetles

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Abstract



This paper presents functional traits – habitat and humidity preferences, of ground beetles along the altitudinal gradient on Belasitsa Mts., thus contributing to the knowledge of the ground beetles' responses to environmental changes.

The research was carried in the period April – November 2010, by using pitfall traps.

Four ecological categories of ground beetles were recorded according to their habitat preferences: forest generalists, forest specialists, eurytopic species and open-area species, as well as five categories according to the humidity preferences: xerophiles, mesoxerophiles, mesophiles, mesohygrophiles and hygrophiles.

Forest generalists as well as mesohygrophiles dominated throughout the entire gradient. Higher abundance of forest generalists and specialists, relatively low share of eurytopic forms and the absence of open space individuals indicated the existence of well-preserved oak forest habitats in the lower altitudinal belt of Belasitsa. In contrast, the absence of forest specialists in beech forests from the higher elevations is a clear indicator of forest degradation.

Keywords: ecological traits, ground beetle responses, mountain

Introduction

The family of ground beetles (Coleoptera: Carabidae) abounds in species that are characterized by certain preferences to specific microclimatic and soil conditions and high bioindicative significance and representativeness. By studying their ecology and distribution, a clear insight of the habitat conditions and the ecosystem in general is obtained (Rainio & Niemelä 2003, Shibuya et al. 2011, Ludwiczak et al. 2020).

According to Butterfield (1997), ground beetles respond to climate changes by altering their place of residence rather than modifying physiological adaptations, thus emphasizing their usefulness as bioindicators of environmental changes, which can

be seen through the long history of their use as bioindicators (e.g. Lindroth 1949, Thiele 1977, Niemelä et al. 1994, Niemelä 1996, Lövei & Sunderland 1996, Rainio & Niemelä 2003, Ludwiczak et al. 2020). The importance of such studies using bioindicators is even greater if we take into account that in forest ecosystems, as a result of altitudinal gradients, there are differences in the composition and structure of the communities that inhabit different altitudinal belts and habitats.

Due to the southern position and the influence of the Mediterranean climate, Belasitsa is among the first mountains in Republic of North Macedonia to be influenced by the climate changes, altering species ecology and distributional ranges and triggering their movement to the higher parts of the mountains

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(MoePP 2014, Peñuelas et al. 2017). So far, few ecological studies on ground beetle communities of the Belasitsa Mountain were published (Kostova 2015; Cvetkovska-Gjorgjievska et al. 2017, 2020, 2022, 2024).

Therefore, the aim of this paper was to present functional traits – habitat and humidity preferences of ground beetles, along the altitudinal gradient on Belasitsa, as baseline study contributing to the knowledge of the ground beetle responses to environmental changes.

Material and methods

Study site

Belasitsa is a high mountain with an area of 198.21 km², situated at the south-eastern part of North Macedonia, bounded between Bulgaria and Greece (Fig. 1) (Melovski et al. 2013). The northern part of Belasitsa is covered with beech and chestnut forests, while pastures and areas of thermophilic oak forests dominate at the southern side.

The study was conducted on the northern side of Belasitsa Mountain near the village of Koleshino. Lower parts of the mountain are with cinnamomic forest soils, and the brown forest and mountain meadow soils are most common at the higher parts (Filipovski et al. 1996). The climate at lower elevations (300-1000 m a.s.l.) is sub-Mediterranean (with low precipitation rate and high temperature), while the mountain belt over 1000 m is influenced by the typical mountainous climate, characterized with higher precipitation and lower temperatures (Filipovski et al. 1996).

Sampling design

Fourteen localities (L1-L14) at different altitudes (from 240 to 1450 m a.s.l.) along an altitudinal gradient were chosen (Fig. 1) covering major vegetation types represented by several climazonal forests on the northern slopes of the Belasitsa Mts. First five localities (L1-L5) were in forests of White oak and Oriental hornbeam; sites L6-L9 were in Sessile oak forest; L10 was set within Sub-mountain beech forest; L10-L13 were allocated within a Mountain beech forest, and L14 represents a clear-cut area in a European beech (*Fagus sylvatica*) forest. Data about the localities, altitudes and dominant forest types are presented in Tab. 1.

Beetle sampling

Ground beetles were collected by pitfall traps (plastic cups with volume of 0.5 L, diameter of 8.5 cm and height of 11.5 cm) placed along a transect line following an isohypse. At each locality 10 pitfall traps were placed 10 m apart and in line with the soil surface, thus covering the different altitudinal zones on the Belasitsa Mountain. In total, 140 traps were placed in 14 different localities (L1-L14). Formaldehyde-vinegar solution (1:7; 200 ml) was used as a preservative. The material was collected monthly, at the end of the month, in the period April – November 2010.

Data analyses

Ground beetles were classified in four ecological groups regarding habitat preference: forest specialists (typical forest dwellers), forest generalists (mainly forest

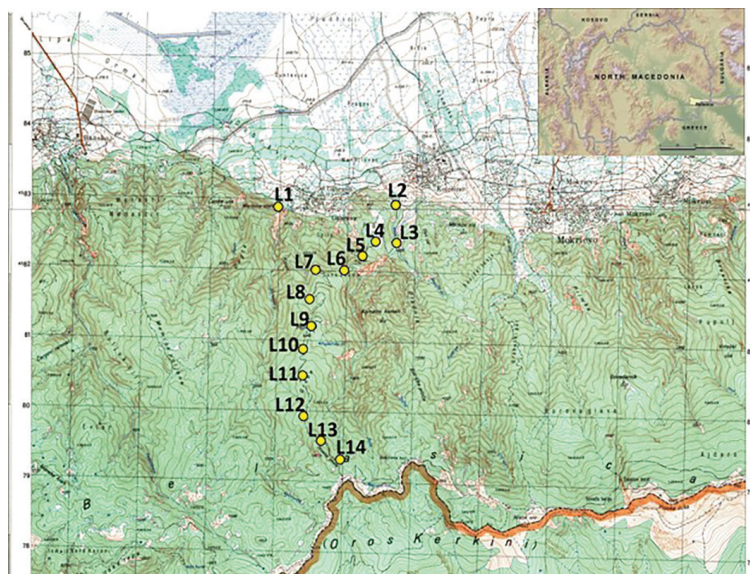


Figure 1. Topographic map and location of the investigated area on the Belasitsa Mountain

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	Slope (%)	Vegetation cover (%)
L1	250 a.s.l.	Near the locality of Markova Skala; ass. <i>Quercus pubescentis</i> - <i>Carpinetum orientalis</i> Horvatić 1939	41.382297; 22.771482	70	80
L2	327 a.s.l.	Under the viewing point near the Koleshino Waterfall; ass. <i>Quercus pubescentis</i> - <i>Carpinetum orientalis</i> Horvatić 1939	41.377504; 22.812616	70	85
L3	415 a.s.l.	Near the Koleshino Waterfall; ass. <i>Quercus pubescentis</i> - <i>Carpinetum orientalis</i> Horvatić 1939	41.372145; 22.807476	15	90
L4	500 a.s.l.	Near the locality of Pod; ass. <i>Quercus pubescentis</i> - <i>Carpinetum orientalis</i> Horvatić 1939	41.371468; 22.804530	70	50
L5	587 a.s.l.	Between the localities of Pod and Suva Cheshma ass. <i>Quercus pubescentis</i> - <i>Carpinetum orientalis</i> Horvatić 1939	41.370699; 22.800324	10	60
L6	693 a.s.l.	Near the locality of Suva Cheshma; ass. <i>Fraxino orni</i> - <i>Quercetum petraeae</i> Em 1968	41.368247; 22.799759	40	90
L7	767 a.s.l.	Near the locality of Popadija; ass. <i>Fraxino orni</i> - <i>Quercetum petraeae</i> Em 1968	41.369374; 22.795384	25	70
L8	847 a.s.l.	Near the locality of Popadija; ass. <i>Fraxino orni</i> - <i>Quercetum petraeae</i> Em 1968	41.366565; 22.794000	15	90
L9	1038 a.s.l.	Near the locality of Popadija; ass. <i>Fraxino orni</i> - <i>Quercetum petraeae</i> Em 1968	41.359571; 22.794153	20	95
L10	1100 a.s.l.	Near the locality of Popadija; ass. <i>Festuco heterophyllae</i> - <i>Fagetum</i> (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.358462; 22.790140	25	85
L11	1200 a.s.l.	Near the locality of Popadija; ass. <i>Calamintho grandiflorae</i> - <i>Fagetum</i> (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.352880; 22.791669	60	90
L12	1300 a.s.l.	Near the locality of Groba; ass. <i>Calamintho grandiflorae</i> - <i>Fagetum</i> (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.347933; 22.792675	60	90
L13	1385 a.s.l.	Near the locality of Pisana Skala; ass. <i>Calamintho grandiflorae</i> - <i>Fagetum</i> (Em 1965) Rizovski & Džekov ex Matevski et al. 2011	41.344122; 22.793764	45	60
L14	1442 a.s.l.	Near the locality of Pisana Skala; clear-cut area	41.341242; 22.798297	25	60

dwellers), open-area species and eurytopic species (habitat generalists), and five groups considering humidity preferences: xerophiles, mesoxerophiles, mesophiles, mesohygrophiles and hygrophiles. The species were arranged in these groups according Lindroth (1992).

Average abundance of the ground beetles was presented as number of individuals per trap (ind. trap⁻¹). Statistical analysis was performed for the data of collected 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. Data were log(x+1) transformed in order to obtain normal distribution.

Nonparametric tests, Kruskal-Wallis, followed by Mann-Whitney U tests, were applied to check for the differences in average beetle abundance within and between the localities. These results are presented with box plots.

Spearman rank correlation (R) was used to analyze the relationship between the altitude and average abundance of species with different preferences for habitat and humidity.

The similarity between communities of all localities, regarding the abundance of different ecological groups was compared with Bray-Curtis paired group (clusters were joined based on the average distance between all members in the two groups) (Sommerfeld, 2008, Hammer et al., 2013).

All statistical data analyses were performed with the statistical programmes STATISTICA 7 (StatSoft, Inc. 2004) and PAST (Hammer et al. 2013). Significant values were those with $p < 0.05$.

Results

In total 8680 individuals belonging to 38 species were collected. The list of collected species has

been already published in Cvetkovska-Gjorgjievska et al. (2018), while species distributional range and abundance (ind-trap⁻¹) along altitudinal gradient has

been published in Cvetkovska-Gjorgjievska et al. (2022). Species belonging to the given ecological group is presented in Tab. 2.

Table 2. Categorization of ground beetles in relation to their habitat and humidity preferences

Habitat preference		Humidity preference	
forest generalists	<i>Abax (Abacopercus) carrinatus</i> (Duftschmid 1812)	xerophiles	<i>Amara (Amara) aenea</i> (De Geer 1774)
	<i>Amara (Amara) convexior</i> Stephens 1828		<i>Harpalus (Harpalus) tardus</i> (Panzer 1797)
	<i>Amara (Amara) similata</i> (Gyllenhal 1810)	mesoxerophiles	<i>Amara (Amara) convexior</i> Stephens 1828
	<i>Asaphidion flavipes</i> (Linne 1761)		<i>Amara (Amara) curta</i> Dejean 1828
	<i>Carabus (Archicarabus) montivagus montivagus</i> Palliardi 1825		<i>Calathus (Calathus) fuscipes fuscipes</i> (Goeze 1777)
	<i>Carabus (Chaetocarabus) intricatus intricatus</i> Linne 1761		<i>Calthus (Neocalathus) erratus erratus</i> (C. R. Sahlberg 1827)
	<i>Carabus (Megodontus) violaceus azurescens</i> Dejean 1826		<i>Carabus (Archicarabus) montivagus montivagus</i> Palliardi 1825
	<i>Carabus (Oreocarabus) hortensis</i> Linne 1758		<i>Carabus (Procrustes) coriaceus cerisyi</i> Dejean 1826
	<i>Carabus (Tomocarabus) convexus dilatatus</i> Dejean 1826		<i>Harpalus (Harpalus) distinguendus distinguendus</i> (Duftschmid 1812)
	<i>Cychrus semigranosus balcanicus</i> Hopffgarten 1881		<i>Harpalus (Harpalus) smaragdinus</i> (Duftschmid 1812)
	<i>Harpalus (Harpalus) atratus</i> Latreille 1804		<i>Harpalus (Harpalus) tenebrosus</i> Dejean 1829
	<i>Harpalus (Harpalus) honestus honestus</i> (Duftschmid 1812)		<i>Harpalus rufipes</i> (Degeer, 1774)
	<i>Harpalus (Harpalus) rubripes</i> (Duftschmid 1812)	<i>Trechus (Trechus) quadristriatus</i> (Schrank 1781)	
	<i>Harpalus (Harpalus) tenebrosus</i> Dejean 1829	mesophiles	<i>Abax (Abacopercus) carrinatus</i> (Duftschmid 1812)
	<i>Molops rufipes belasicensis</i> Mlynar 1977		<i>Amara (Amara) eurynota</i> (Panzer 1796)
<i>Myas (Myas) chalybaeus</i> (Palliardi 1825)	<i>Calosoma (Calosoma) inquisitor</i> Linne 1758		
<i>Notiophilus substriatus</i> G. R. Watterhouse 1833	<i>Harpalus (Harpalus) atratus</i> Latreille 1804		
<i>Synuchus vivalis</i> (Illiger 1798)	<i>Harpalus (Harpalus) honestus honestus</i> (Duftschmid 1812)		
<i>Tapinopterus (Tapinopterus) balcanicus belasicensis</i> Mařan 1933	<i>Harpalus (Harpalus) rubripes</i> (Duftschmid 1812)		
<i>Trechus (Trechus) subnotatus</i> Dejean 1831	<i>Notiophilus substriatus</i> G. R. Watterhouse 1833		
forest specialists	<i>Calosoma (Calosoma) inquisitor</i> Linne 1758	<i>Trechus (Trechus) subnotatus</i> Dejean 1831	
eurytopic species	<i>Amara (Amara) aenea</i> (De Geer 1774)	mesohygrophiles	<i>Trechus nigrinus</i> Putzeys, 1847
	<i>Amara (Amara) curta</i> Dejean 1828		<i>Amara (Amara) similata</i> (Gyllenhal 1810)
	<i>Amara (Amara) eurynota</i> (Panzer 1796)		<i>Carabus (Chaetocarabus) intricatus intricatus</i> Linne 1761
	<i>Calthus (Neocalathus) erratus erratus</i> (C. R. Sahlberg 1827)		<i>Carabus (Megodontus) violaceus azurescens</i> Dejean 1826
	<i>Carabus (Procrustes) coriaceus cerisyi</i> Dejean 1826		<i>Carabus (Oreocarabus) hortensis</i> Linne 1758
	<i>Harpalus (Harpalus) rufipalpis rufipalpis</i> Sturm 1818		<i>Carabus (Tomocarabus) convexus dilatatus</i> Dejean 1826
	<i>Harpalus (Harpalus) tardus</i> (Panzer 1797)		<i>Cychrus semigranosus balcanicus</i> Hopffgarten 1881
	<i>Harpalus rufipes</i> (Degeer, 1774)		<i>Harpalus (Harpalus) rufipalpis rufipalpis</i> Sturm 1818
	<i>Nebria (Nebria) brevicollis</i> (Fabricius 1792)		<i>Molops rufipes belasicensis</i> Mlynar 1977
	<i>Philorhizus notatus</i> (Stephens 1827)		<i>Myas (Myas) chalybaeus</i> (Palliardi 1825)
	<i>Pterostichus (Platysma) niger niger</i> (Schaller 1783)		<i>Pterostichus (Pseudomaseus) anthracinus</i> (Illiger 1798)
	<i>Pterostichus (Pseudomaseus) anthracinus</i> (Illiger 1798)		<i>Synuchus vivalis</i> (Illiger 1798)
	<i>Trechus (Trechus) quadristriatus</i> (Schrank 1781)		<i>Tapinopterus (Tapinopterus) balcanicus belasicensis</i> Mařan 1933
<i>Trechus nigrinus</i> Putzeys, 1847	hygrophiles	<i>Asaphidion flavipes</i> (Linne 1761)	
open-area species		<i>Calathus (Calathus) fuscipes fuscipes</i> (Goeze 1777)	<i>Nebria (Nebria) brevicollis</i> (Fabricius 1792)
		<i>Harpalus (Harpalus) distinguendus distinguendus</i> (Duftschmid 1812)	<i>Pterostichus (Platysma) niger niger</i> (Schaller 1783)
<i>Harpalus (Harpalus) smaragdinus</i> (Duftschmid 1812)	undefined preference	<i>Philorhizus notatus</i> (Stephens 1827)	

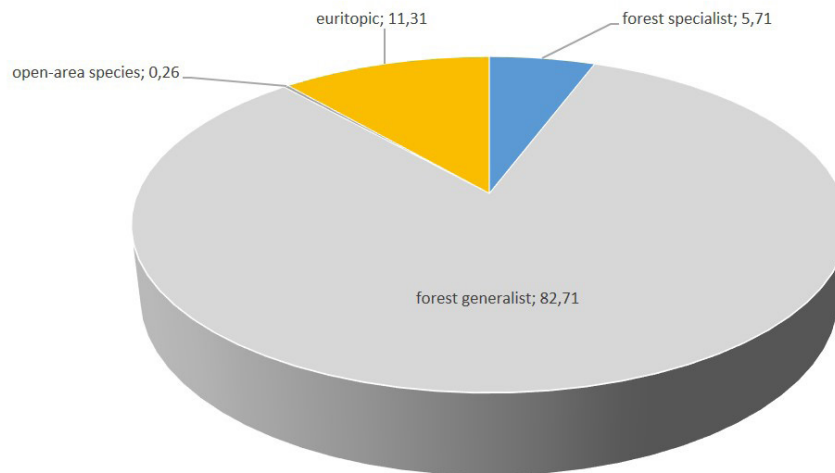


Figure 2. Relative participation (%) of the ground beetles regarding their habitat preferences

Habitat preference

Twenty species were forest generalists: *Trechus subnotatus*, *Amara similata*, *Abax carinatus*, *Harpalus atratus*, *H. tenebrosus*, *H. honestus*, *H. rubripes*, *Myas chalybaeus*, *Notiophilus substriatus*, *Carabus montivagus*, *C. convexus*, *C. coriaceus*, *C. hortensis*, *C. violaceus*, *C. intricatus*, *Cychrus semigranosus*, *Amara convexior*, *Molops rufipes*, *Tapinopterus balcanicus* and *Synuchus vivalis*. Only one species, *Calosoma inquisitor*, was considered as a typical forest specialist.

Thirteen species were considered as eurytopic species: *Carabus coriaceus*, *Calathus erratus*, *Pterostichus niger*, *Pterostichus anthracinus*, *Nebria brevicollis*, *Philorhizus notatus*, *Harpalus rufipes*, *H. rufipalpis*, *H. tardus*, *Trechus quadristriatus*, *T. nigrinus*, *Amara convexior* and *A. similata*, while *Calathus fuscipes fuscipes*, *Harpalus distinguendus* and *Harpalus smaragdinus* preferred open-areas.

The largest share of the total community had forest generalists, followed by eurytopic species. Forest specialists occurred subdominantly, while the open space dwellers were represented with an extremely low percentage (Fig. 2).

Forest generalists also stand out with the highest values (from 0.51 ind.trap⁻¹ in L14 to 29.50 ind.trap⁻¹ in

L10) of the mean annual abundance, followed by the eurytopic species (0.03 ind.trap⁻¹ in L8 to 4.88 ind.trap⁻¹ in L14) (Tab. 3).

The abundance of **forest specialists** decreased with increasing altitude ($R = -0.309$; $p < 0.05$) (Fig. 3a). Their presence was registered in the localities of the lower altitudinal belt up to an altitude of 847 m (L8). Most **forest generalists** occurred in high abundance along the entire altitudinal gradient, with significantly ($p < 0.05$) highest abundance in L10, and lowest in L5 and L14 (Fig. 3b). Although in low abundance, the presence of **eurytopic species** (habitat generalists), was registered throughout the entire altitudinal gradient, with highest value ($p < 0.05$) in L14 (the clear-cut area) (Fig. 3c). The presence of **open-area species** was evidenced only in the localities L6-L8, L10, L11 and L14 (Fig. 3d).

Humidity preference

Eleven species were considered as mesoxerophiles according to the humidity preferences: *Amara convexior*, *A. curta*, *Calathus fuscipes*, *C. erratus*, *Carabus montivagus*, *C. coriaceus*, *Harpalus distinguendus*, *H. smaragdinus*, *H. tenebrosus*, *H. rufipes* and *Trechus quadristriatus*. Only two species

Table 3. Mean annual abundance of the ground beetles regarding their habitat preference along the altitudinal gradient of the Belasitsa Mts.

Habitat preference	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14
Forest specialists	0.41	0.00	0.26	0.74	0.03	0.65	4.04	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Forest generalists	2.38	2.35	2.90	3.11	0.64	2.46	7.56	6.15	6.30	29.50	14.84	7.31	3.73	0.51
Open-area species	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.14	0.00	0.01	0.05	0.00	0.00	0.03
Eurytopic species	1.05	1.23	0.98	0.26	0.56	0.45	0.05	0.03	0.10	0.19	1.41	0.26	0.84	4.88

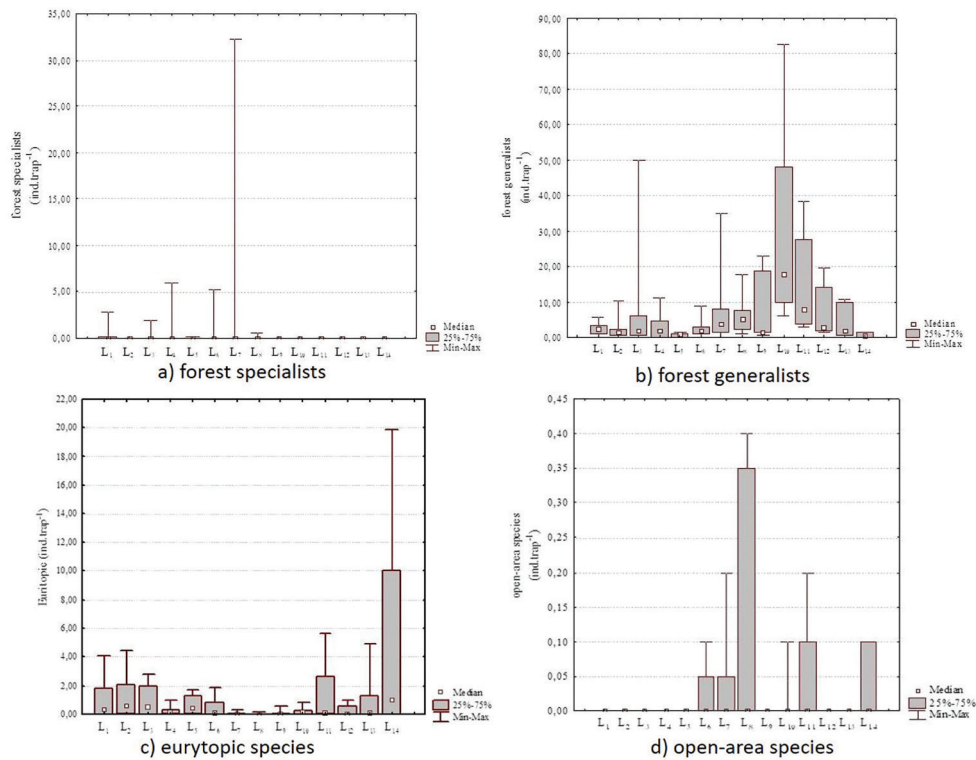


Figure 3. Average abundance of forest specialists (a), forest generalists (b), eurytopic species (c), open-area species (d), along the altitudinal gradient of the Belasitsa Mts.

(*Amara aenea* and *Harpalus tardus*) were xerophiles. Most of the species (12): *Amara similata*, *Carabus intricatus*, *C. violaceus*, *C. hortensis*, *C. convexus*, *Cychnus semigranosus*, *Harpalus rufipalpis*, *Molops rufipes*, *Myas chalybaeus*, *Pterostichus anthracinus*, *Synuchus vivalis* and *Tapinopterus balcanicus*, were categorized as mesohygrophiles. Nine species (*Abax carinatus*, *Amara eurynota*, *Calosoma inquisitor*, *Harpalus atratus*, *H. honestus*, *Harpalus rubripes*, *Notiophilus substriatus*, *Trechus subnotatus* and *Trechus nigrinus*) were

mesophiles, while *Asaphidion flavipes*, *Nebria brevicollis* and *Pterostichus niger* were considered as hygrophiles.

It is obvious that the research area on Belasitsa Mountain was mainly inhabited by mesohygrophiles in comparison to mesoxerophiles, mesophiles, hygrophiles and xerophiles (Fig. 4).

The mean annual abundance of the mesohygrophiles varied between 0.55 ind.trap⁻¹ in L5 to 29.43 ind.trap⁻¹ in L10, in comparison to hygrophiles registered in very low

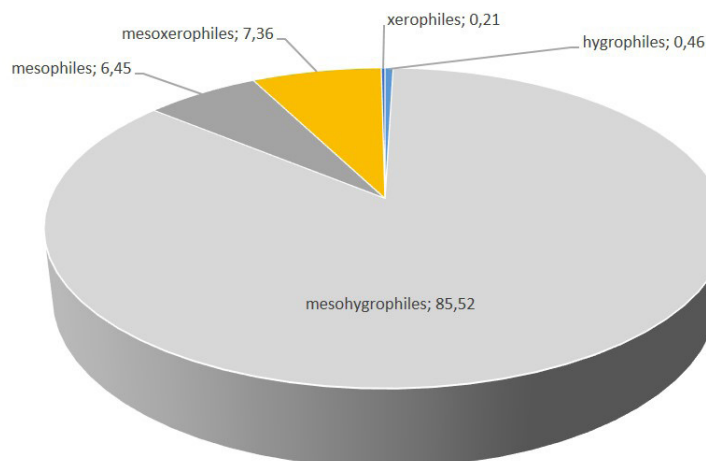


Figure 4. Relative participation (%) of the ground beetles regarding their humidity preferences

Table 4. Mean annual abundance of ground beetles regarding humidity preference, along the altitudinal gradient of the Belasitsa Mts.

Humidity preference	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14
xerophiles	0.04	0.06	0.00	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.03	0.00	0.01	0.05
mesoxerophiles	1.21	1.50	1.09	0.31	0.50	0.43	0.10	0.15	0.10	0.15	1.26	0.25	0.79	0.20
mesophiles	0.85	0.03	0.26	0.74	0.18	0.78	4.08	0.09	0.00	0.05	0.00	0.00	0.00	0.40
mesohygrophiles	2.23	1.99	2.79	3.05	0.55	2.36	7.50	6.14	6.30	29.43	14.69	7.30	3.71	4.75
hygrophiles	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.08	0.31	0.03	0.05	0.01

abundance (0.01 ind.trap⁻¹ – 0.08 ind.trap⁻¹) throughout the researched period (Tab. 4).

With the increasing altitude, the abundance of mesohygrophiles ($R = 0.316$; $p < 0.05$) and hygrophiles ($R = 0.311$; $p < 0.05$) increased, while the abundance of mesoxerophiles decreased ($R = -0.309$; $p < 0.05$). The abundance of xerophiles and mesophiles did not change significantly along the gradient (Fig. 5).

Discussion

Habitat preferences: Spearman’s correlation analysis enabled the separation of taxa that are sensitive to altitudinal changes and consequently to changes of vegetation type. It was noticed that *Carabus convexus*, *C. coriaceus*, *C. montivagus*, *C. intricatus*, *Calosoma inquisitor*, *Myas chalybaeus*, and *Harpalus tardus* prefer

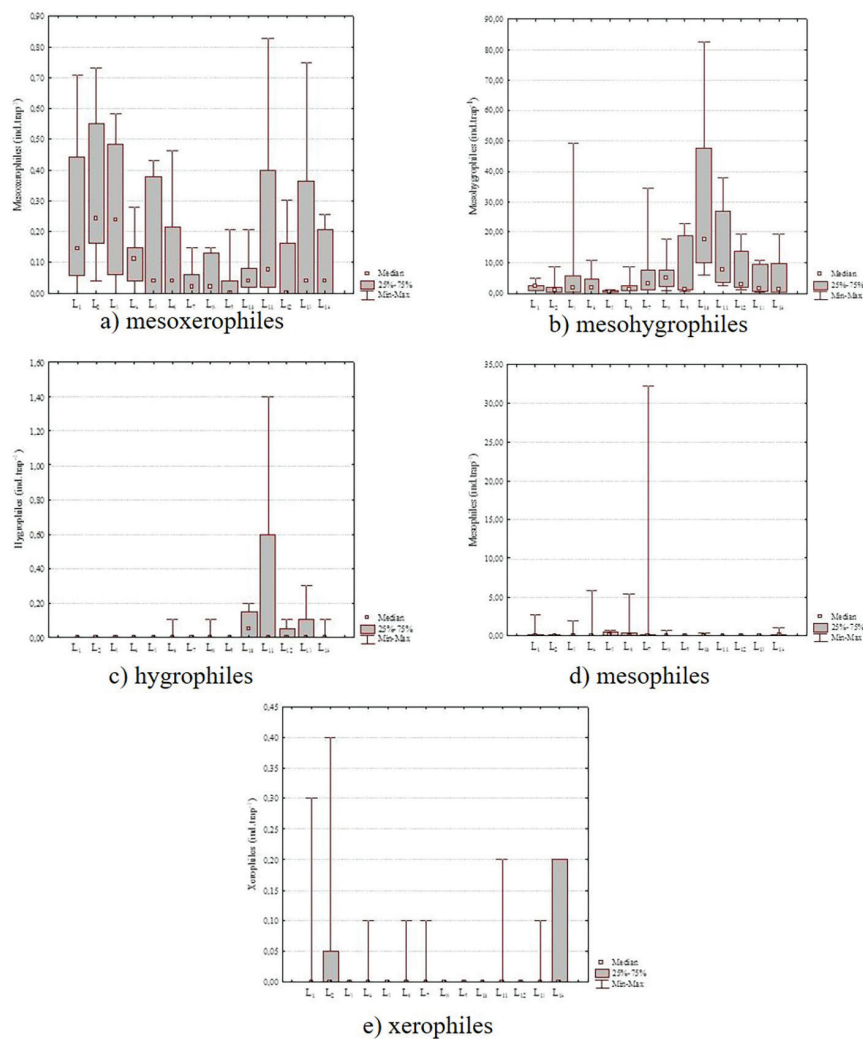


Figure 5. Average abundance of mesoxerophiles (a), mesohygrophiles (b), hygrophiles (c), mesophiles (d) and xerophiles (e), along the altitudinal gradient of the Belasitsa Mts.

oak forests, which was confirmed with significant decrease of their abundance with the increasing altitude and changes of vegetation type from oak to beech forest and clear-cut area.

In contrast, the abundance of *Trechus quadristriatus*, *Cychrus semigranosus*, *Tapinopterus balcanicus*, *Molops rufipes*, *Nebria brevicollis*, *Amara eurynota*, *A. aenea*, *A. convexior* and *Synuchus vivalis* was significantly higher in localities under beech forest.

In addition to these results, cluster analysis of ground beetle abundance showed two groups of localities inhabited by species with similar habitat preferences: L1-L6 and L7-L13, joined at almost identical levels of similarity (47% and 46%, respectively), as well as the marked separation of the last locality L14 (Fig. 6a).

Despite the presence and higher abundance of forest generalists and specialists, oak forests from the lower part of the gradient (L1-L6), were also distinguished by a relatively low participation of eurytopic forms and the absence of species that prefer open space (in L1-L4). This situation is actually an indicator of well-preserved forest habitats. According de Warnaffe & Lebrun (2004) and Nietupski et al. (2023) a relatively low abundance of eurytopic and ground beetle species that prefer open spaces serves as an indicator of well-preserved forest habitats. In unmanaged forests, the dominance of typical forest species suggests a healthy ecosystem, whereas an increase in open-area species often correlates with habitat disturbance and degradation.

Significantly lower abundance of forest generalists in L5 contributes to the separation of this locality, while the presence of open area species and moderate increase of forest generalists caused separation of the carabidocoenosis of L6 from the others. The highest abundance of open-area dwellers was registered in L8, due to favourable micro-habitats, with rich shrub and

grass vegetation. The communities of L8 and L9 (about 96% similarity level) were composed mainly by forest generalists, while eurytopic forms and forest specialists were presented with significantly low abundance.

The reduced abundance, as well as the absence of forest specialists in the beech belt (L10-L13), including the clear-cut area (L14), is a reliable indicator of a certain degree of degradation of the beech forest. According to Martinez et al. (2009), this situation points up to the lack of suitable habitats for forest specialists. Actually, only one species (5.71%), *Calosoma inquisitor*, was considered as a typical forest specialist showing significantly high abundance in oak forests at the interval of 250-850 m a.s.l. (L1-L8), with highest values at the altitude of 750 m a.s.l. (L7).

The studied beech belt (L11-L14) on the northern slope of Belasitsa was characterized by a certain degree of degradation as a result of logging, which leads to greater insolation, higher temperature, lower percentage of humidity creating suitable conditions for settlement of forest generalists and eurytopic forms. That is why beech forests were inhabited by eurytopic forms as opposed to oak forests, which were inhabited by forest specialists.

The clear-cut area (L14) was characterized by the highest percentage of open space and eurytopic species (Fig. 6a), which is an expected phenomenon characteristic of logged habitats (de Warnaffe & Lebrun 2004).

Humidity preference: With the increase in altitude and consequent change along the gradient of oak forests – beech forests – clearing, there is a significant decrease in the abundance of mesoxerophiles, and a significant increase in the number of mesohygrophiles, especially at the altitude between 1050-1100 m, which is actually the transition zone between the oak and beech forests.

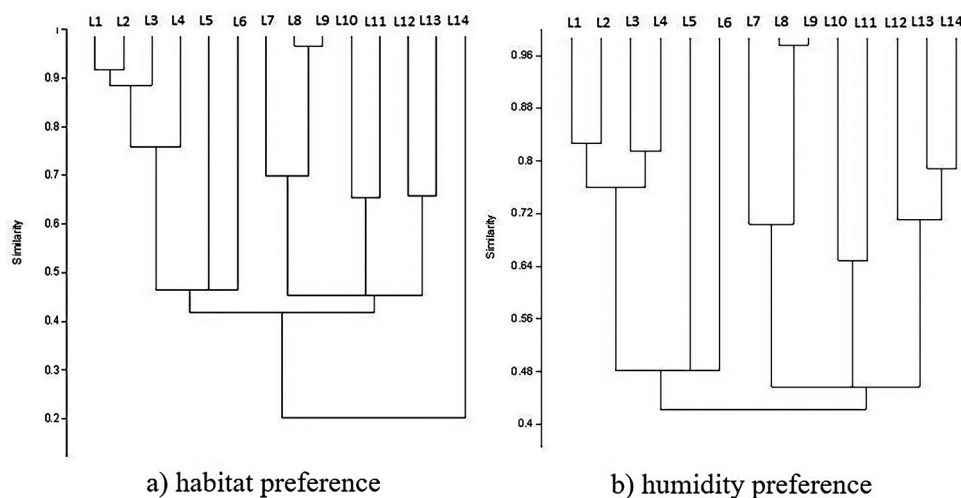


Figure 6 UPGMA (unweighted pair-group average) Bray-Curtis (constrained) coefficient of similarity of ground beetle communities along the altitudinal gradient of the Belasitsa Mts., according to their habitat (a) and humidity preference (b)

When analysing the results, the abundance of mesoxerophiles was higher ($p < 0.05$) in the localities up to an altitude of 693 m (L6), dominated by ass. Orno-Quercetum petraeae. In montane beech forest, at an altitude of 1200 m (L11), the overall abundance of mesoxerophiles increased again, mainly because of the increased abundance of *Trechus quadristriatus*.

The abundance of the hygrophilous species was positively correlated with the altitude and consequently with change of the oak to beech forests. The highest abundance was registered in L11 (1200 m), due to the abundance of *Asaphidion flavipes*, *Nebria brevicollis* and *Pterostichus niger*. With the exception of *Calosoma inquisitor*, other mesophilic species were registered in low abundance throughout the gradient. The relative participation of xerophilic species was very low, mainly due to the low abundance of *Harpalus tardus* and *Amara aenea*.

Therefore, clear separation of two groups of carabidocoenoses (those of L1-L6 with about 49% similarity level and L7-L14 with about 46% similarity level) was due to the absence of hygrophiles and the extremely low number of mesophilic species in L1-L6, in contrast to L7-L14 group where mesophiles were absent and mesohygrophilic and hygrophilic species were registered in higher abundances (Fig. 6b).

Similarly, the research of Wetherbee et al. (2021) showed that the beetles found in beech habitats often have functional traits that are adapted to higher moisture levels, such as preferences for decaying wood and litter that retains humidity. In contrast, oak forest beetles are more adapted to drier conditions and may exhibit different foraging behaviors and reproductive strategies.

Kirichenko-Babko et al. (2020) as well, analyzed how climate variations influence the structure of ground beetle communities in forests and wetlands. The study identified three main groups of ground beetles based on their humidity preferences: xerophilous, mesohygrophilous and hygrophilous species. This study demonstrates that ground beetle communities differ between oak and beech forests due to the contrasting humidity conditions, with oak forests supporting more xerophilous species due to drier conditions, and beech forests which tend to retain more moisture harboring hygrophilous ground beetles. This differentiation is crucial for understanding the ecological roles that ground beetles demonstrate in their environments.

Conclusion

Forest generalists, as well as mesohygrophiles dominated throughout the entire gradient. The higher abundance of forest generalists and specialists in oak forests at lower altitudes (250 – 700 m), relatively low share of eurytopic forms and the absence of open space

individuals indicate the existence of well-preserved oak forest habitats in the lower altitudinal belt.

In contrast, lower abundance of forest specialists in beech forests is a reliable indicator of a certain degree of degradation of forest habitats of the upper altitudinal belt, while highest percentage of eurytopic and open-space individuals in the clear-cut area is an expected situation for such habitats.

In view of the above, these findings illustrate the ecological significance of habitat and humidity preferences in determining the distribution and diversity of ground beetle species between oak and beech forests. This study also highlights that forest management practices altering microclimate can impact the diversity and composition of these ecologically important insect communities. Therefore, when predicting the degree and rate of decline in the stability of forest ecosystems, ground beetles can be a useful indicator.

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