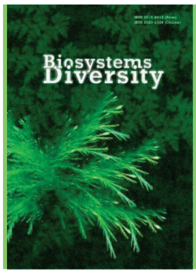

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The rapid response of the ground beetle communities to the meadow steppe habitat loss in West Podillia (Ukraine)

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Ground beetles (Coleoptera: Carabidae) stand out as one of the most diverse families not just among insects but also among all living organisms on Earth. They have emerged as essential bioindicators of environmental disturbance, reflecting changes in ecosystems due to agricultural, forestry, and urbanization practices. The presence, abundance, and species composition of carabid communities serve as reliable indicators of habitat quality and ecosystem health. We conducted a comprehensive study of the meadow-steppe habitats, utilizing ground beetles as sensitive ecological indicators. We delineated four distinct groups of species based on ecological preferences and habitat affinities: I) steppe xerothermophilic stenobionts; II) steppe and ruderal xero- and mesophilic eurybionts; III) meadow and ruderal meso- and hygrophilous eurybionts; and IV) forest meso- and hygrophilous steno- and eurybionts. Our findings elucidate a distinct response of ground beetle species groups to transformation processes occurring within meadow steppes. Species belonging to group I (*Brachinus crepitans*, *Ophonus rupicola*, *O. puncticollis*, *Leistus ferrugineus*) expanded notably in distribution under conditions characterized by xerophilization and elevated temperatures. Conversely, species within group II (*Harpalus atratus*, *H. caspius*, *H. hospes*, *H. solitaris*, *Ophonus azureus*) and group III (*Amara aenea*, *A. familiaris*, *Calathus fuscipes*, *Carabus cancellatus*, *C. convexus*, *Cylindera germanica*, *Harpalus affinis*, *H. latus*, *H. rubripes*, *H. xanthopus*, *Pterostichus atrorufus*, *P. cupreus*, *P. strenuus*) showed a comparable response to the habitat, with a preference for higher soil moisture. Species within group IV (*Abax carinatus*, *A. parallelepipedus*, *A. parallelus*, *Carabus arvensis*, *C. glabratus*, *C. linnei*, *C. nemoralis*, *C. ulrichii*, *C. variolosus*, *Cychrus caraboides*, *C. semigranosus*, *Leistus piceus*, *Limodromus assimilis*, *Molops piceus*, *Pterostichus melanarius*, *P. niger*, *P. oblongopunctatus*) demonstrated an association with markedly different environmental conditions, characterized by significant moisture levels and relatively lower soil temperatures conducive to their existence. Steppe species (group I) were observed in only 12 out of 27 sample plots of meadow steppes, while a significant presence of species from groups II and III was evident in most cases, indicating mesophilization due to shrub and tree vegetation expansion. Forest species of ground beetles (group IV) were prevalent in the majority of meadow steppe sample plots, reflecting disruption of plagioclimax likely resulting from the cessation of traditional economic practices. Despite the presence of the meadow-steppe vegetation, steppe species of ground beetles were entirely absent, suggesting their potential as early indicators of ongoing changes in the meadow-steppe habitats.

Keywords: biodiversity; soil fauna; Carabidae; anthropogenic pressure; afforestation; plagioclimax; climatic climax; ecological succession; edge effect; bioindication.

Introduction

Ground beetles (Coleoptera, Carabidae) are one of the most diverse families not only of insects but also of living things in general on Earth, with more than 40,000 known species worldwide (Bouchard, 2017; Lorenz, 2021). Over 2,700 species of ground beetles are known in Europe (Wachmann et al., 1995), and in Ukraine there are about 750 species from 117 genera (Rizun, 2003; Puchkov, 2011). In the region of our study, Western Podillya, about 360 species of ground beetles are known so far (Rizun & Kapelyukh 2003).

Ground beetles represent a diverse and widely distributed group of insects, inhabiting a variety of ecosystems worldwide except for the extreme deserts and polar regions (Rainio & Niemelä, 2003). Their ecological importance stems from their role as predators, feeding on a wide range of invertebrates, playing a crucial role in shaping of functional diversity within ecosystems (Brygadyrenko, 2015c, 2015d). However, the dietary habits of ground beetles are not limited to predation, as many species exhibit herbivorous and omnivorous behaviors (Rizun, 2003; Korolev & Brygadyrenko, 2014). This versatility in feeding habits contributes to their ecological adaptability and habitat differentiation (Sumarokov & Zamoroka, 2020). Their distribution reflects a balance between ecological preferences and habitat availability, with certain species showing adaptations to specific environmental conditions (Eyre & Luff 2004; Brygadyrenko & Reshetniak, 2014; Putchkov et al., 2019, 2020). The Carabidae communities comprise both eurytopic and stenotopic species, with different sensitivity to habitat alteration (Rainio & Niemelä, 2003). Thus, ground beetles have emerged as valuable bioindicators of environmental disturbance, reflecting both natural and human-induced changes in ecosystems due to agricultural and forestry practices and urbanization (Kotze & O'Hara, 2003; Rainio & Niemelä, 2003; Putchkov et al., 2019). The presence, abundance, and species composition of carabid communities can serve as indicators of habitat quality and ecosystem health (Rainio & Niemelä, 2003; Kotze et al., 2011; Diedus & Rizun, 2018).

Steppe and forest-steppe landscapes dominate Ukraine, encompassing approximately 75% of its territory (Zamoroka et al., 2018). However, these landscapes have undergone significant anthropogenic transformation, primarily into croplands. Natural steppe ecosystems persist in highly fragmented forms, primarily in landscape features unsuitable for agricultural cultivation, such as gullies, ravines, steep river slopes, and rock outcrops (Lysenko et al., 2010). The extent of steppes decreases sharply from south to north and from east to west. At the northern and western distribution limits, steppes serve as extrazonal ecosystems, intermingling with forests to create a mosaic landscape characteristic of the forest-steppe transition zone between steppe and forest biomes (Habel et al., 2013; Zamoroka et al., 2018; Campbell et al., 2021; Chytrý et al., 2022). In these transition zones, steppes are typically represented by semi-natural meadow steppes and steppe meadows growing on rendzinas or strong, alkaline chernozem soils, primarily formed on limestone substrates (Bielova et al., 2022; Kuzemko, 2022).

In the west of the Podillia Highland, meadow steppes are dispersed in small fragments, with an average area of 0.13 km² (Zamoroka et al., 2018). These meadow steppes thrive under the influence of a relatively humid continental climate, characterized by precipitation ranging between 650–700 mm annually (Lysenko et al., 2010; Botti, 2018; Zamoroka et al., 2024). The moist climatic conditions in the western meadow steppes distinguish them significantly from their eastern ones, evident in the prevalence of broad-leaved grasses and forbs in the vegetation cover (Kuzemko, 2022). Specifically, the composition of plant species in Western Podillia exhibits a balanced ratio of steppe and meadow species at 1:1 (Shumska & Dmytrash-Vatseba, 2018), contrasting with the ratio of 5:1 observed in the meadow steppes of the Kyiv Plateau in the east (Hrytsenko, 2007). This disparity is reflected in the vegetation of the West Podillian meadow steppes, characterized by dominant plant communities such as *Brachypodieta pinnati*, *Elytrigieta intermediae*, *Cariceta humilis*, *Festuceta valesiacae*, *Teucrieta chamaedrytis*, *Stipeta capillatae*, *Stipeta pennatae*. The others, such as *Stipeta pulcherrimae*, *Stipeta tirsae*, *Helictotrichoneta desertori*, *Seslerieta heufleranae*, and *Festuceta pallentis* are rare (Lysenko et al., 2010; Shumska, 2018). The vegetation of meadow steppes exhibits resilience and stability over time, maintaining its structure for extended periods, a phenomenon known as plagioclimax. This stability is primarily attributed to anthropogenic pressures that inhibit the establishment of tree and shrub vegetation (Campbell et al., 2021).

The origin and evolution of meadow steppes remain incompletely understood, with two prevailing hypotheses proposed to elucidate their emergence. The first hypothesis posits that meadow steppes represent relict ecosystems from past geological epochs (Feurdean et al., 2015; Horsák et al., 2015; Chytrý et al., 2019, 2022; Novák et al., 2019). Shumilovskikh et al. (2018) demonstrated that during Atlantic time of the Holocene, 7.0–4.5 kiloannum (ka), the forest-steppe subbiome in Eastern Europe extended northward by 50–70 km. Conversely, the second hypothesis suggests that meadow steppes have anthropogenic origins resulting from deforestation (Hejcman et al., 2013; Chytrý et al., 2022). However, paleopalynological data indicate that significant deforestation in the forest-steppe region has occurred only within the last 400 years (Shumilovskikh et al., 2018). Kajtoch et al. (2016) phylogenetically link the modern forest-steppe, particularly its fauna, with the Pleistocene steppe-tundra. Zamoroka et al. (2018) proposed a hybrid hypothesis, suggesting that meadow steppes originated from periglacial steppe-tundra and were sustained by the migratory movements of large herbivore herds during the Pleistocene and early Holocene. This is supported by the presence of geographically isolated populations of steppe species and the distribution of numerous subendemic taxa (Dmytrash-Vatseba, 2018; Zamoroka, 2019; Zamoroka et al., 2024). Subsequent evolution and maintenance of meadow steppes were facilitated by human agricultural practices, including cattle husbandry and hay harvesting. Deforestation and anthropogenic disturbances also played significant roles in sustaining meadow steppes (Shumilovskikh et al., 2018; Zamoroka et al., 2018). A similar hypothesis was later proposed by Chytrý et al. (2022).

In the past two decades, significant changes have occurred in the economic utilization of meadow steppes in the West Podillia region, marked notably by the abandonment of traditional practices such as cattle grazing and hay harvesting (Zamoroka et al., 2018; Kuzemko, 2022). These changes have resulted in the loss of meadow-steppe habitats due to spontaneous vegetation successions (Dmytrash-Vatseba, 2018; Yashchenko et al., 2021). However, the extent of changes and the response of the ground beetle communities to the transformation of the meadow steppes into shrub and forest habitats remain poorly understood. This emerging environmental issue has received very little attention in the scientific literature. Notably, Kanarsky (2021) documented a decline in the diversity of the ground beetle communities in Holohory and Voroniaky ecoregions within West Podillia (see regional subdivision details in Zamoroka et al. (2012)). He attributed this decline to the fragmentation and afforestation of meadow steppes, likely exacerbated by contemporary climate changes. Tsaryk & Yavornytskyi (2020) also highlighted the transformative impact of spontaneous vegetation succession in meadow steppes on soil mesofauna communities in the same region. Zamoroka & Dmytrash-Vatseba (2018) observed a decline in Carabidae diversity in Burshtyn Opillia, linking it to habitat size and isolation as primary factors driving local extinctions. They proposed a general framework for understanding the transformation of soil arthropod communities in isolated steppe habitats (Zamoroka & Dmytrash-Vatseba, 2018).

Materials and methods

Our study was conducted in three clusters located in the western part of the Podillia Highland (Fig. 1a, 1b). These clusters encompass three designated nature conservation areas, namely: I – Kremenetski Hory National Park (KHNP), II – Medobory Nature Reserve (MPZ), and III – Halych National Park (HNPP). Comprehensive climatic characteristics of the studied areas are provided in Table 1.

Table 1

Climatic characteristics of the studied clusters due to climatic norm of 1950–2000

Climatic index	Cluster I	Cluster II	Cluster III
Mean annual temperature, °C	+7.3	+7.3	+7.2
Sum of the average daily temperature above +10°C	+2600	+2600	+2600
Mean monthly temperature (January), °C	-4.8	-5.1	-5.6
Mean monthly temperature (July), °C	+18.6	+18.8	+18.2
Sum of days/year with temperatures above +25°C, days	40	45	40
Sum of days/year with temperatures below -10°C, days	30	30	25
Mean annual precipitations, mm	610	630	650
Mean monthly precipitation (January), mm	34	34	29
Mean monthly precipitation (July), mm	85	92	104
Mean air humidity, %	79	78	79
Mean annual evaporation, mm	280	320	320
Annual solar radiation, MJ/m^2	3600	3600	3600
Annual radiation balance, MJ/m^2	1300	1400	1400
Annual photosynthetically active radiation, MJ/m^2	1700	1750	1700
Annual duration of sunshine, hours	1975	2000	1980
Number of cloudy days	90	80	80
Mean annual surface albedo, %	19	20	20
Ground freezing depth, cm	60	62	59
Snow depth, cm	16	19	21
Snow Cover Duration, days	71	75	76
Growing Season Length, days	206	210	210

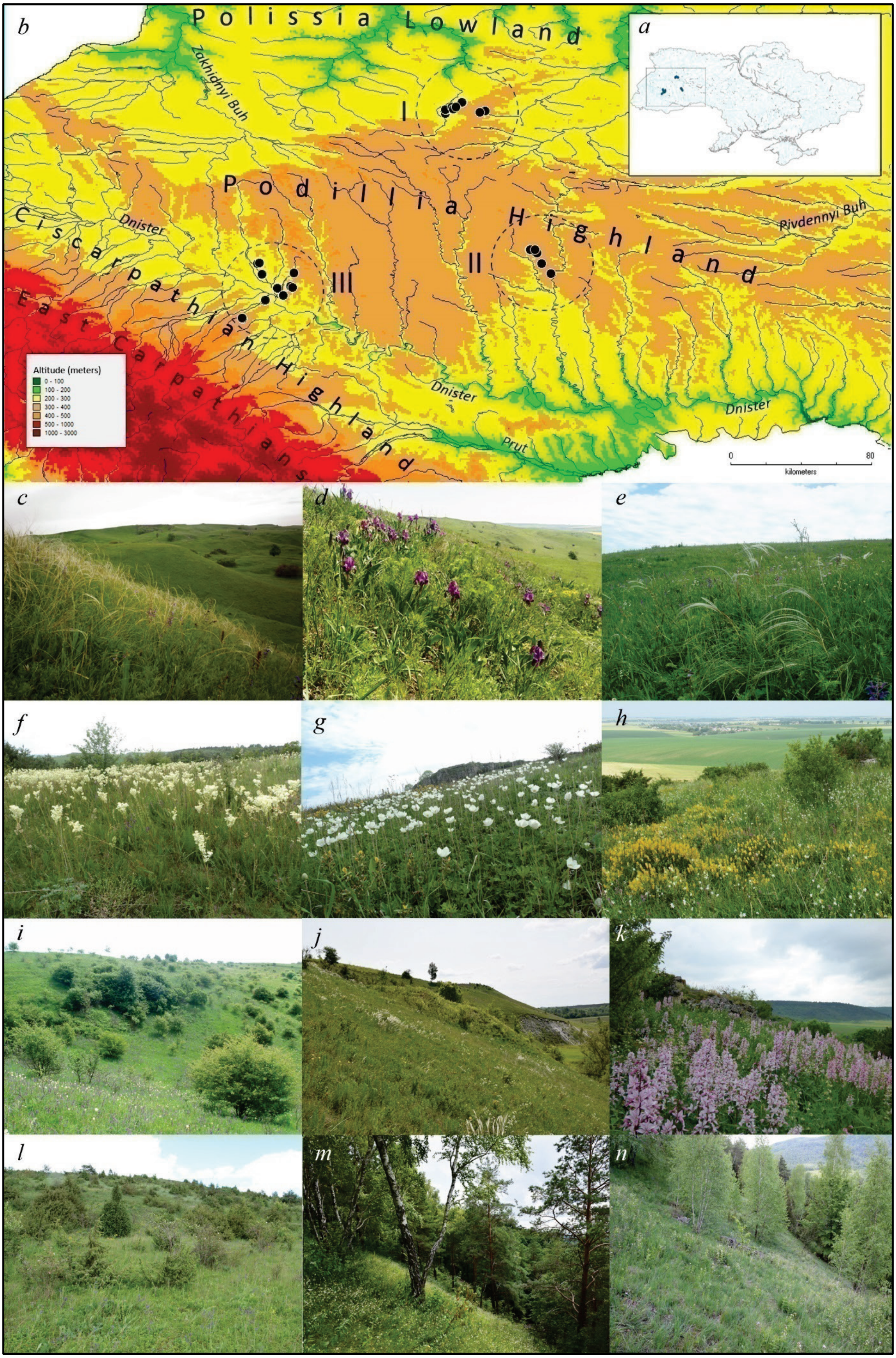

Fig. 1. Location of the studied clusters (I–III) within Ukraine (*a*) and Western Podillia (*b*) and examples of meadow steppes in plagioclimax (*c*–*h*) and at different succession stages due to shrub and forest expansion (*i*-*n*)

A total of 51 sample plots were established across three clusters, comprising 27 target plots within meadow steppes, 4 plots within pine plantations replacing steppes, and 20 control plots (Table 2). The target habitat, meadow steppes, was distributed among the clusters as follows: 7 plots in the Cluster I (KHNP), 6 plots in the Cluster II (MPZ), and 14 plots in the Cluster III (HNP). The selected sample plots were representative of the meadow-steppe habitats in terms of their size, vegetation, local relief heterogeneity, and degree of transformation. A multi-level control approach was employed in this study, involving comparisons between the meadow steppe target habitats and natural forest habitats, post-forest meadow habitats, fallow habitats. This methodological approach allowed us to discern the trends in meadow-steppe habitats transformation and the response of the ground beetles communities to these changes.

The size of the standard sample plot was 100 m^2 (10 × 10 m), within which five soil pit traps were deployed. These traps were arranged in an envelope configuration, with four placed along the edges and one positioned at the center. Each trap consisted of a plastic container with a 1-liter volume, featuring an entrance hole with a diameter of 120 mm. The traps were filled with a concentrated fixative solution composed of disodium tetraborate (50%) and sodium chloride (50%), designed to extend the exposure period. Material collection occurred every 4 weeks from April to October. Subsequently, the collected specimens were transported to the laboratory and preserved in 96% ethanol for long-term storage.

Table 2
The brief characteristic of the studied sample plots in Clustes I–III within the West Podillia Highland

Cluster	Sample plot code	Coordinates	Habitat type	Habitat area, km^2	Type of transformation
I	KHNP1	50.061110, 25.635834	meadow steppe	0.02	overgrowth with shrubs
I	KHNP2	50.060829, 25.637227	pine plantation	0.02	artificial afforestation
I	KHNP3	50.059999, 25.637778	hornbeam forest	0.15	secondary forest
I	KHNP4	50.079549, 25.644804	meadow steppe	0.01	overgrowth with shrubs
I	KHNP5	50.079999, 25.643889	pine plantation	0.05	artificial afforestation
I	KHNP6	50.080833, 25.641111	hornbeam-oak forest	0.07	secondary forest
I	KHNP7	50.091387, 25.673057	meadow steppe	0.01	overgrowth with shrubs
I	KHNP8	50.091665, 25.673611	hornbeam forest	0.80	secondary forest
I	KHNP9	50.091944, 25.673889	hornbeam-oak forest	0.80	secondary forest
I	KHNP10	50.083674, 25.682078	meadow steppe	0.001	overgrowth with shrubs
I	KHNP11	50.083889, 25.681665	hornbeam-oak forest	1.01	secondary forest
I	KHNP12	50.084165, 25.681945	hornbeam-oak forest	1.01	secondary forest
I	KHNP13	50.071008, 25.844956	meadow steppe	0.10	overgrowth with shrubs
I	KHNP14	50.071429, 25.845701	pine plantation	0.03	artificial afforestation
I	KHNP15	50.066111, 25.816940	meadow steppe	0.18	overgrowth with shrubs
I	KHNP16	50.118126, 25.727898	meadow steppe	0.01	overgrowth with shrubs
I	KHNP17	50.118053, 25.726389	pine plantation	0.08	artificial afforestation
I	KHNP18*	49.871836, 25.561997	meadow steppe	1.06	overgrowth with shrubs
I	KHNP19*	50.100121, 25.722149	meadow steppe	0.04	overgrowth with shrubs
I	KHNP20	50.093332, 25.695832	beech forest	0.09	old aged forest
II	MPZ1	49.348609, 26.102457	meadow steppe	0.17	overgrowth with shrubs
II	MPZ2	49.343338, 26.105461	meadow steppe	0.17	overgrowth with shrubs
II	MPZ3	49.340221, 26.110868	meadow steppe	0.17	overgrowth with shrubs
II	MPZ4	49.285566, 26.136002	meadow steppe	0.01	overgrowth with shrubs
II	MPZ5	49.356319, 26.074656	meadow steppe	0.01	overgrowth with shrubs
II	MPZ6	49.356676, 26.076704	meadow steppe	0.01	overgrowth with shrubs
II	MPZ7	49.357387, 26.100400	ash-oak forest	1.21	secondary forest
II	MPZ8	49.233167, 26.185830	hornbeam forest	61.23	secondary forest
III	HNP1	49.159896, 24.771636	meadow steppe	0.11	wildfire
III	HNP2	49.159930, 24.772167	meadow steppe	0.11	wildfire
III	HNP3	49.119030, 24.804644	meadow steppe	0.11	wildfire
III	HNP4	49.168141, 24.839962	meadow steppe	0.06	overgrowth with shrubs
III	HNP5	49.225260, 24.693234	meadow steppe	1.38	wildfire
III	HNP6	49.225499, 24.693257	meadow steppe	1.38	wildfire
III	HNP7	49.225894, 24.693805	meadow steppe	1.38	wildfire
III	HNP8	49.228546, 24.695269	meadow steppe	1.38	wildfire
III	HNP9	49.285690, 24.669182	meadow steppe	0.09	overgrowth with shrubs
III	HNP10	49.285455, 24.670034	meadow steppe	0.09	overgrowth with shrubs
III	HNP11	49.121286, 24.801953	meadow steppe	0.11	wildfire
III	HNP12	49.120226, 24.802900	meadow steppe	0.11	wildfire
III	HNP13	49.235483, 24.857606	meadow steppe	0.01	overgrowth with shrubs
III	HNP14	49.235001, 24.857370	meadow steppe	0.01	overgrowth with shrubs
III	HNP15	48.998447, 24.593881	post-forest fallow	0.10	wildfire
III	HNP16	48.998650, 24.593741	post-forest fallow	0.10	wildfire
III	HNP17	49.002443, 24.590420	post-forest meadow	0.001	overgrowth with shrubs
III	HNP18	49.002233, 24.590981	post-forest meadow	0.001	overgrowth with shrubs
III	HNP19	49.158694, 24.770303	post-steppe fallow	0.16	wildfire
III	HNP20	49.158997, 24.771361	post-steppe fallow	0.16	wildfire
III	HNP21	49.093013, 24.707165	post-forest meadow	0.03	overgrowth with shrubs
III	HNP22	49.161169, 24.850816	oak forest	0.77	secondary forest
III	HNP23	49.161747, 24.850926	oak forest	0.77	secondary forest
III	HNP24	49.287657, 24.681247	oak forest	0.29	old aged forest
III	HNP25	49.096810, 24.709978	beech forest	1.00	secondary forest

Note: * – no ground beetles were detected in the plots KHNP18 and KHNP19, which were excluded from further analysis.

We recorded a total of 14 environmental indicators across both localities and sample plots. Specifically, the following ecological indicators were assessed in localities (with each locality potentially containing more than one sample plots):

1) area (Patc.siz): the area of the habitat patch;

2) marginal effect (Margin.e): the ratio of the perimeter length to the area of the locality;

3) degree of degradation (Degrad.): the cumulative impact of anthropogenic factors, invasive alien species, and natural successions;

4) shrub overgrowth (Bush.inv): the proportional coverage of the site area by shrubs;

5) tree dominance (Trees): the proportional cover of the site area by trees;

6) wildfire frequency (Fire): the occurrence rate of wildfires;

Information regarding the following ecological indicators was gathered at each sample plot:

1) soil pH (pH): the hydrogen ion concentration in the soil solution;

2) nitrogen content (N): the concentration of dissolved nitrogen in the soil;

3) soil humidity (Humid.): the level of soil moisture in the field;

4) soil temperature (Soi.temp): the temperature of the soil at a depth of 10 cm;

5) light intensity (Light): the illumination level of the soil surface;

6) plant projective cover (Pla.proj): the extent of soil cover by plants;

7) grass stand height (Pla.heig): the average height of the grass stand;

8) plants biomass (Pla.biom.): the air-dry aboveground plant biomass per square meter.

The processing of collected materials involved several stages, including initial preparation and sorting of samples, species identification, and mounting of samples to create control collections. The specimens were then stored in collections located at various institutions, including Kremenetski Hory National Park (Kremenets), Medobory Nature Reserve (Husyatyn), Halych National Park (Halych), the State Museum of Natural History (Lviv), and Vasyl Stefanyk Precarpathian National University (Ivano-Frankivsk).

We organized the raw data collected in the field studies, including the species composition and relative abundance of the ground beetles, along with 14 environmental variables, into two distinct logical matrices within the spreadsheet application MS Excel 2016. The first matrix illustrated the relationships between the abundance of each of the ground beetle species and the sample plots, while the second matrix depicted the ecological variables associated with each sample plot. The primary data underwent transformation into a relative measurement scale suitable for subsequent machine analysis. This scale ranged from 0 points to 3 points, where a score of 0 indicated a complete absence of connection between the analyzed parameters, while a score of 3 signified the maximum connection. Additionally, a score of 1 represented a low level of connection, while a score of 2 indicated an average level of connection. Further statistical analysis involved computing classification statistics using Canonical Correspondence Analysis (CCA) (ter Braak, 1986) with the Monte Carlo probability test (1000 permutations), employing Canoco 4.56 software (1997–2009 Biometris – Plant Research International, Wageningen, The Netherlands, Cajo J. F. ter Braak & Peter Smilauer). Visualization of the CCA results was conducted using CanoDraw 4.14 software (1999–2009 Peter Smilauer).

Results

Through the course of our research, the investigation yielded a total of 124 species of ground beetles across all sample plots. Of these species, 74 were observed within the study target habitats of meadow steppes. Detailed listings and catch rate of these species are represented in Tables 3–5.

Table 3
The species composition and the catch rate (specimens per 100 traps/days) of the ground beetles on the meadow steppe sample plots of Cluster I – Kremenetski Hory National Park

Species	Sample plots						
	KHNP1	KHNP4	KHNP7	KHNP10	KHNP13	KHNP15	KHNP16
Cicindela campestris Linnaeus, 1758	2.1	–	–	–	2.1	–	–
Leistus ferrugineus (Linnaeus, 1758)	–	–	–	–	–	–	2.1
Carabus arvensis Herbst, 1784	2.1	6.3	–	6.3	6.3	8.4	–
C. cancellatus Illiger, 1798	2.1	–	–	–	–	–	–
C. convexus Fabricius, 1775	10.8	–	–	10.8	–	–	2.1
C. coriaceus Linnaeus, 1758	2.1	4.2	2.1	18.4	–	2.1	–
C. glabratus Paykull, 1790	2.1	–	12.0	–	–	–	–
Poecilus versicolor (Sturm, 1824)	–	4.2	–	6.3	–	–	–
Pterostichus melanarius (Illiger, 1798)	–	–	2.1	–	–	–	–
P. niger (Schaller, 1783)	–	–	–	2.1	–	–	–
Abax carinatus (Duftschmid, 1812)	–	–	–	2.1	–	4.2	–
A. parallelepipedus (Piller & Mitterpacher, 1783)	8.4	2.1	2.1	4.2	–	–	–
Dolichus halensis (Schaller, 1783)	–	–	–	2.1	–	–	–
Amara aenea (DeGeer, 1774)	–	–	–	4.2	–	–	–
Harpalus modestus Dejean, 1829	–	–	–	2.1	–	–	–
Number of species	7	4	4	10	2	3	2

Table 4
The species composition and the catch rate (specimens per 100 traps/days) of the ground beetles on the meadow steppe sample plots of Cluster II – Medobory Nature Reserve

Spesies	Sample plots					
	MPZ1	MPZ2	MPZ3	MPZ4	MPZ5	MPZ6
Leistus ferrugineus (Linnaeus, 1758)	2.1	–	2.1	4.2	2.1	2.1
Carabus besseri Waldheim, 1822	–	–	–	–	2.1	–
C. cancellatus Illiger, 1798	2.1	16.3	302.4	–	–	–
C. scabriusculus Olivier, 1795	–	–	–	4.2	–	–
Notiophilus laticollis Chaudoir, 1850	4.2	2.1	–	–	–	–
Broscus cephalotes (Linnaeus, 1758)	4.2	–	–	–	2.1	–
Trechus quadristriatus (Schrank, 1781)	–	–	2.1	–	–	–
Poecilus cupreus (Linnaeus, 1758)	6.3	54.2	32.1	–	–	–
Poecilus sericeus Waldheim, 1824	2.1	2.1	2.1	–	–	–
Pterostichus melanarius (Illiger, 1798)	4.2	4.2	16.3	–	6.3	4.2
P. melas (Creutzer, 1799)	6.3	–	2.1	–	–	–
P. niger (Schaller, 1783)	–	–	2.1	–	6.3	2.1
P. ovoideus (Sturm, 1824)	–	–	2.1	–	–	–
Abax carinatus (Duftschmid, 1812)	–	–	–	–	2.1	4.2
A. parallelepipedus (Piller & Mitterpacher, 1783)	–	–	2.1	–	–	–
A. parallelus (Duftschmid, 1812)	–	–	–	–	22.0	2.1
Calathus erratus (Sahlberg, 1827)	–	–	–	–	–	2.1
C. fuscipes (Goeze, 1777)	2.1	2.1	22.0	–	–	–
C. melanocephalus (Linnaeus, 1758)	–	–	4.2	–	8.4	2.1
Anchomenus dorsalis (Pontoppidan, 1763)	–	–	–	–	10.8	–
Synuchus vivalis (Illiger, 1798)	–	–	2.1	–	–	–
Amara aenea (DeGeer, 1774)	2.1	2.1	2.1	–	–	–
A. consularis (Duftschmid, 1812)	2.1	–	2.1	–	–	–

Spesies	Sample plots					
	MPZ1	MPZ2	MPZ3	MPZ4	MPZ5	MPZ6
A. eurynota (Panzer, 1796)	–	2.1	–	–	–	–
A. familiaris (Duftschmid, 1812)	–	2.1	–	–	–	–
A. littorea Thomson, 1857	–	–	2.1	–	–	–
Zabrus spinipes (Fabricius, 1798)	–	6.3	6.3	–	–	–
Harpalus affinis (Schrank, 1781)	4.2	–	–	–	–	–
H. caspius (Steven, 1806)	4.2	8.4	2.1	–	–	–
H. distinguendus (Duftschmid, 1812)	2.1	–	–	–	–	–
H. griseus (Panzer, 1796)	2.1	–	–	–	–	–
H. politus Dejean, 1829	2.1	–	–	–	–	–
H. rubripes (Duftschmid, 1812)	–	–	12.0	–	–	–
H. tardus (Panzer, 1797)	–	2.1	2.1	–	–	–
Pseudoophonus calceatus (Duftschmid, 1812)	2.1	–	–	–	–	–
P. rufipes (DeGeer, 1774)	4.2	10.8	58.4	–	66.3	4.2
Ophonus azureus (Fabricius, 1775)	4.2	–	4.2	–	–	–
O. puncticollis (Paykull, 1798)	8.4	–	16.3	–	–	–
Anisodactylus signatus (Panzer, 1796)	–	–	2.1	–	–	–
Syntomus truncatellus (Linnaeus, 1761)	–	4.2	–	–	–	–
Microlestes maurus (Sturm, 1827)	–	2.1	2.1	–	–	–
Number of species	20	15	25	2	10	8

Table 5
The species composition and the catch rate (specimens per 100 traps/days) of the ground beetles on the meadow steppe sample plots of Cluster III – Halych National Park

Spesies	Sample plots													
	HNP1	HNP2	HNP3	HNP4	HNP5	HNP6	HNP7	HNP8	HNP9	HNP10	HNP11	HNP12	HNP13	HNP14
Cicindela campestris Linnaeus, 1758	–	2.1	–	–	–	–	–	–	–	4.2	–	2.1	–	–
Leistus ferrugineus (Linnaeus, 1758)	–	4.2	74.2	–	2.1	14.2	30.8	12.0	–	–	–	2.1	–	-
Carabus cancellatus Illiger, 1798	28.4	12.0	10.8	–	4.2	2.1	–	–	2.1	–	–	–	–	–
C. convexus Fabricius, 1775	–	–	2.1	2.1	2.1	2.1	–	–	–	–	–	2.1	–	–
C. coriaceus Linnaeus, 1758	–	–	–	–	–	–	–	–	–	–	2.1	–	6.3	8.4
C. excellens Fabricius, 1798	–	–	–	–	10.8	2.1	10.8	6.3	–	–	–	–	–	–
C. scabriusculus	–	–	2.1	–	16.3	63.1	63.1	–	–	–	–	–	–	–
C. ulrichii Germar, 1824	–	–	–	2.1	–	–	–	–	–	–	–	–	42.1	–
C. violaceus Linnaeus, 1758	2.1	2.1	–	–	2.1	–	–	–	–	–	–	–	–	–
Notiophilus laticollis Chaudoir, 1850	–	–	4.2	–	–	–	–	–	–	–	–	–	–	–
N. palustris (Duftschmid, 1812)	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
T. quadristriatus (Schrank, 1781)	–	–	–	–	–	–	–	6.3	–	–	–	–	–	–
Asaphidion flavipes (Linnaeus, 1761)	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
Poecilus cupreus (Linnaeus, 1758)	5.2	8.4	–	2.1	2.1	–	–	–	–	–	-	–	–	–
Pterostichus melanarius (Illiger, 1798)	–	–	54.2	–	–	–	–	–	–	–	–	–	–	–
P. nigrita (Paykull, 1790)	–	–	16.3	–	–	–	–	–	–	–	–	–	–	–
P. strenuus (Panzer, 1796)	–	–	–	–	2.1	–	–	–	–	–	–	–	–	4.2
P. vernalis (Panzer, 1796)	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–
Abax carinatus (Duftschmid, 1812)	–	–	8.4	–	–	–	–	–	–	–	–	–	–	–
A. parallelepipedus (Piller & Mitterpacher, 1783)	–	–	2.1	–	–	–	–	–	–	–	–	–	–	12.0
A. parallelus (Duftschmid, 1812)	–	–	–	–	–	–	–	–	–	–	2.1	–	–	12.0
Calathus fuscipes (Sahlberg, 1827)	–	–	108.4	–	–	–	–	–	–	–	–	–	–	–
Anchomenus dorsalis (Pontoppidan, 1763)	–	–	–	–	4.2	–	–	–	–	–	–	–	–	–
Amara aenea (DeGeer, 1774)	–	–	–	–	–	–	–	–	–	–	2.1	–	2.1	-
A. aulica (Panzer, 1796)	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
A. fusca Dejean, 1828	–	–	4.2	–	–	–	–	–	–	–	–	–	–	–
A. ovata (Fabricius, 1792)	2.1	–	6.3	2.1	–	–	–	–	–	–	–	–	–	–
Harpalus affinis (Schrank, 1781)	–	–	–	4.2	2.1	2.1	2.1	–	–	–	–	–	–	–
H. atratus Latreille, 1804	–	–	14.2	–	–	–	–	–	–	–	–	–	–	–
H. griseus (Panzer, 1796)	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–
H. hospes Sturm, 1818	–	–	–	4.2	2.1	2.1	-	–	–	–	–	–	–	–
H. latus (Linnaeus, 1758)	–	–	26.3	4.2	2.1	4.2	4.2	–	–	–	–	6.3	–	4.2
H. politus Dejean, 1829	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–
H. pumilus Sturm, 1818	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
H. rubripes (Duftschmid, 1812)	–	8.4	14.2	2.1	–	12.0	2.1	–	–	–	–	2.1	–	–
H. solitaris Dejean, 1829	–	2.1	4.2	–	–	–	2.1	–	–	–	–	–	–	–
H. tardus (Panzer, 1797)	–	–	–	–	–	2.1	-	–	–	–	–	–	–	–
Pseudoophonus calceatus (Duftschmid, 1812)	4.2	2.1	–	–	–	–	2.1	–	–	–	22.1	–	–	–
P. rufipes (DeGeer, 1774)	42.1	14.2	2.1	2.1	–	–	2.1	–	–	–	6.3	–	–	–
Ophonus puncticollis (Paykull, 1798)	–	–	184.2	–	10.8	42.0	48.4	2.1	–	–	2.1	–	–	–
O. rupicola (Sturm, 1818)	–	–	20.0	–	6.3	2.1	16.3	–	–	–	–	–	–	–
Panagaeus bipustulatus (Fabricius, 1775)	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–
Badister bullatus (Schrank, 1798)	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–
Microlestes maurus (Sturm, 1827)	–	–	–	–	20.0	–	–	–	–	–	–	–	–	–
Microlestes minutulus (Goeze, 1777)	–	4.2	–	–	–	–	–	–	–	–	–	–	–	–
Cymindis humeralis (Geoffroy, 1785)	–	–	2.1	–	2.1	–	–	–	–	–	–	–	–	–
Drypta dentata (Rossi, 1790)	–	–	2.1	–	–	–	–	4.2	–	–	–	–	–	–
Brachinus crepitans (Linnaeus, 1758)	–	–	–	–	40.3	23.2	156.3	52.1	–	–	–	–	–	–
Number of species	6	10	25	12	18	13	13	6	1	1	6	5	3	5

Our working hypothesis posited that ground beetle communities exhibit responses to alterations in the vegetation cover of meadow steppes. We hypothesized that insects serve as more sensitive indicators of ecosystem changes compared to plants. Specifically, transformational processes such as the reduction in the area of meadow steppes, spontaneous afforestation, invasion by alien plant species, and anthropogenic pressures are anticipated to prompt the changings of the ground beetles communities at a faster rate than the eventual loss of the meadow steppe habitat itself.

For testing of our hypothesis, we used CCA to classify the ground beetles within a multidimensional space defined by a multitude of environmental factors, thereby uncovering their sensitivity to the variables influencing sample plots, encompassing both meadow steppes and control habitats. Furthermore, through the examination of species distribution within the canonical space, we identified a cluster of species closely associated with the meadow-steppe habitats, indicating their dependency on these specific ecological conditions for survival. These species were subsequently utilized as key indicators for assessing the degree of degradation within the meadow-steppe habitats.

The outcomes of our CCA underscored the responsiveness of the ground beetles to environmental parameters. Consequently, we delineated four distinct groups of species based on their ecological preferences and habitat affinities (Fig. 2; Table 6). These groups include: I) steppe xero-thermophilic stenobionts; II) steppe and ruderal xero- and mesophilic eurybionts; III) meadow and ruderal meso- and hygrophilous eurybionts; IV) forest meso- and hygrophilous steno- and eurybionts.

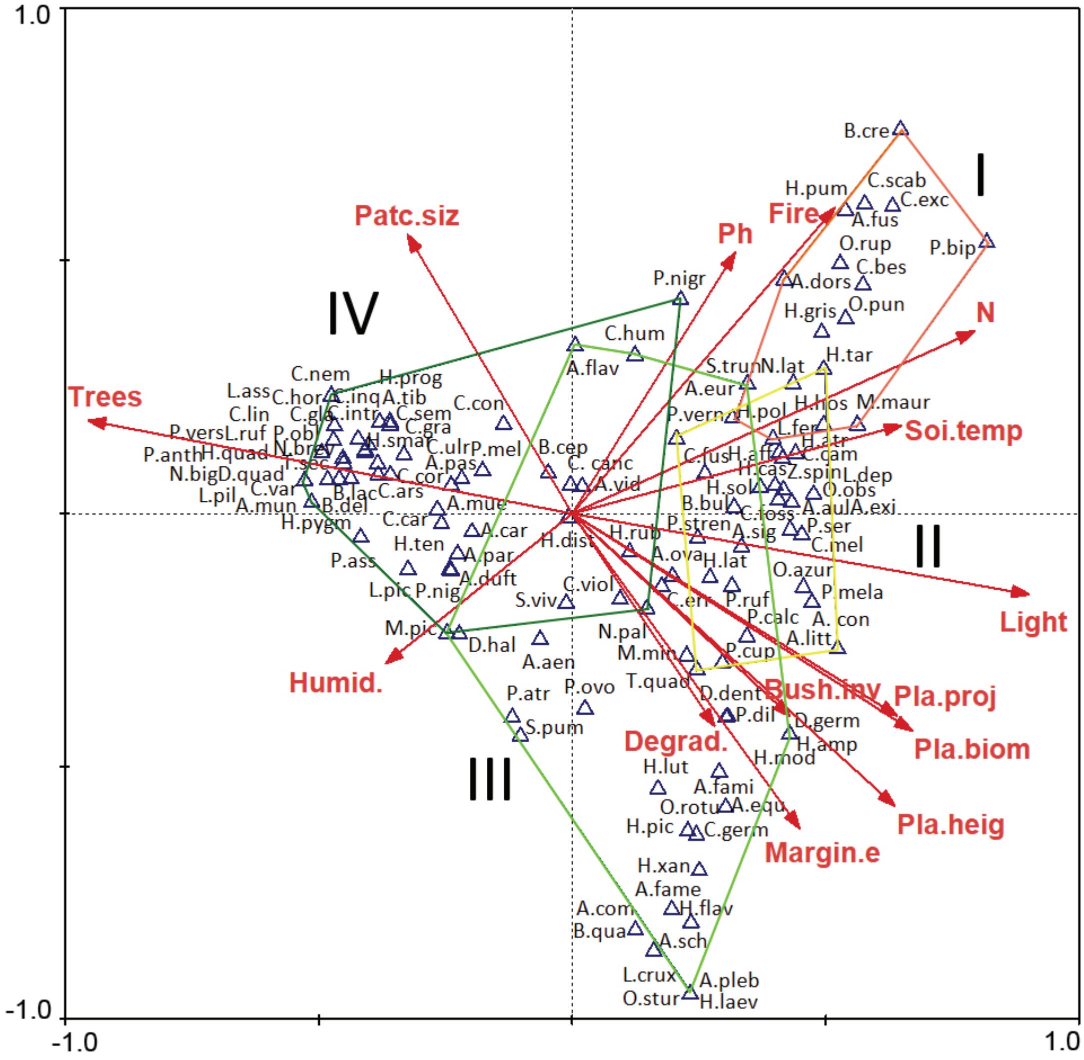

Fig. 2. Distribution of the ground beetles species in the canonical space with 14 additional ecological dimensions: I – steppe xero-thermophilic stenobionts; II – steppe and ruderal xero- and mesophilic eurybionts; III – meadow and ruderal meso- and hygrophilous eurybionts; IV – forest meso- and hygrophilous steno- and eurybionts; see methods for abbreviations of environmental variables and Table 6 for species names

Group I, comprising steppe xerothermophilic stenobionts, holds pivotal significance in our study. Species within this group inhabit the driest habitats, rendering them valuable indicators of steppe conditions. While many species in Group I are rare, notable examples such as *B. crepitans*, *O. rupicola*, *O. puncticollis*, and *L. ferrugineus* are abundantly present in the most pristine meadow steppe patches, often occupying dominant positions. Additionally, species like *C. scabriusculus*, *C. excellens*, and *C. besseri* are prevalent in large meadow steppe patches, typically exceeding 10 hectares in area – a critical threshold for many of these species (Zamoroka et al., 2018). Maintenance of the plagioclimax within meadow steppe patches is crucial for the persistence of group I species. Particularly, the removal of excess aboveground plant biomass through periodic dry grass burning plays a vital role. Our Canonical Correspondence Analysis (CCA) results indicate that Group I species thrive under conditions of intermittent dry grass burning, which effectively suppresses shrub encroachment onto meadow steppes, thereby inhibiting the establishment of mesophilic meadow and the forest ground beetles species. Associated environmental factors determining the viability of group I species include alkaline soil pH, elevated nitrogen levels, considerable warming of the soil, and low soil moisture levels. Under conditions conducive to mesophilization within the meadow-steppe habitats and the subsequent influx of moisture-loving the ground beetles, group I species face intense competition and may either locally extinct or become exceedingly rare.

Group II, comprising steppe and ruderal xero- and mesophilic eurybionts, encompasses a significant array of species crucial for comprehending degradation and successional processes within disturbed meadow-steppe habitats. The majority of species in group II exhibit broad ecological niches and are distributed across both xero- and mesophilic habitats. Moreover, we commonly found them in fallow lands and agricultural environments. Key and abundant species within group II include *H. atratus*, *H. caspius*, *H. hospes*, *H. solitaris*, and *O. azureus*. Additionally, species such as *P. rufipes*, *P. calceatus*, and *Z. spinipes* thrive in highly disturbed habitats, including fallow lands and arable areas.

Group III, consisting of meadow and ruderal meso- and hygrophilous eurybionts, represents the most diverse assemblage among all groups. Species within Group III are notably characterized by their affinity for ecotones, indicating their adaptation to forest edges. However, these species also demonstrate versatility in their habitat preferences, being capable of inhabiting meadow habitats, meadow-shrub transitional zones, shrub habitats, and sparse forests. Key ecological factors influencing their distribution include sufficient insolation (in comparing with forest species) of the soil surface, large above-ground biomass of herbaceous plants, and moisture content. Species within group III serve as valuable indicators of ecosystem changes, offering insights into the degree of margin effects and successional transformations associated with the transition of meadow steppes from the plagioclimax to climate climax. Typical of mesophilic meadows and often abundant, species within this group include *A. aenea*, *A. familiaris*, *C. fuscipes*, *C. cancellatus*, *C. convexus*, *C. germanica*, *H. affinis*, *H. latus*, *H. rubripes*, *H. xanthopus*, *P. atrorufus*, *P. cupreus*, and *P. strenuus*. In habitats with significant increased soil moisture, species belonging to the genera *Agonum*, *Asaphidion*, *Bembidion*, and *Notiophilus* often dominate the communities.

Table 6
Subdivision of the ground beetles into ecological groups according to CCA

Group	Group-specific species	Multigroup species
I	*Amara fusca* (A.fus), *Anchomenus dorsalis* (A.dors), *Brachynus crepitans* (B.cre), *Carabus besseri*, (C.bes), *Carabus excellens* (C.exc), *Carabus scabriusculus* (C.scab), *Harpalus griseus* (H.gris), *Harpalus pumilus* (H.pum), *Microlestes maurus* (M.maur), *Ophonus puncticollis* (O.pun), *Ophonus rupicola* (O.rup), *Panagaeus bipustulatus* (P.bip)	Overlap with Group II: *Harpalus atratus* (H.atr), *Harpalus hospes* (H.hos), *Harpalus politus* (H.pol), *Harpalus tardus* (H.tar), *Leistus ferrugineus* (L.fer) Overlap with Group III: *Amara eurynota* (A.eur), *Harpalus politus* (H.pol), *Notiophilus laticollis* (N.lat), *Syntomus truncatellus* (S.trun)
II	*Acupalpus exiguus* (A.exi), *Amara aulica* (A.aul), *Amara consularis* (A.con), *Amara littorea* (A.litt), *Calathus melanocefalus* (C.mel), *Cicindela campestris* (C.cam), *Harpalus affinis* (H.aff), *Harpalus caspius* (H.cas), *Licinus depressus* (L.dep), *Ophonus azureus* (O.azur), *Oxypselaphus obscurus* (O.obs), *Poecilus cupreus* (P.cup), *Poecilus sericeus* (P.ser), *Pterostichus melas* (P.mela), *Zabrus spinipes* (Z.spin)	Overlap with Group I: *Harpalus atratus* (H.atr), *Harpalus hospes* (H.hos), *Harpalus politus* (H.pol), *Harpalus tardus* (H.tar), *Leistus ferrugineus* (L.fer) Overlap with Group III: *Anisodactylus signatus* (A.sig), *Badister bullatus* (B.bul), *Calathus fuscipes* (C.fus), *Clivina fossor* (C.foss), *Harpalus laevipes* (H.laev), *Harpalus politus* (H.pol), *Harpalus solitaris* (H.sol), *Notiophilus laticollis* (N.lat), *Pseudoophonus calceatus* (P.calc), *Pseudoophonus rufipes* (P.ruf), *Trechus quadristriatus* (T.quad)
III	*Amara communis* (A.com), *Amara equestris* (A.equ), *Amara famelica* (A.fame), *Amara familiaris* (A.fami), *Amara ovata* (A.ova), *Amara plebeja* (A.pleb), *Bembidion quadrimaculatum* (B.qua), *Calathus erratus* (C.err), *Cylindera germanica* (C.germ), *Daichromus germanus* (D.germ), *Drypta dentata* (D.dent), *Harpalus amplicollis* (H.amp), *Harpalus flavescens* (H.flav), *Harpalus latus* (H.lat), *Harpalus luteicornis* (H.lut), *Harpalus picipennis* (H.pic), *Harpalus modestus* (H.mod), *Harpalus xanthopus* (H.xan), *Lebia cruxminor* (L.crux), *Microlestes minutulus* (M.min), *Olisthopus rotundatus* (L.rotu), *Olisthopus sturmii* (O.stur), *Patrobus atrorufus* (P.atr), *Pterostichus diligens* (P.dil), *Pterostichus ovoideus* (P.ovo), *Pterostichus strenuus* (P.sten), *Stomis pumicatus* (S.pum)	Overlap with Group I: *Amara eurynota* (A.eur), *Harpalus politus* (H.pol), *Notiophilus laticollis* (N.lat), *Syntomus truncatellus* (S.trun) Overlap with Group II: *Anisodactylus signatus* (A.sig), *Badister bullatus* (B.bul), *Calathus fuscipes* (C.fus), *Clivina fossor* (C.foss), *Harpalus laevipes* (H.laev), *Harpalus solitaris* (H.sol), *Leistus ferrugineus* (L.fer), *Pseudoophonus calceatus* (P.calc), *Pseudoophonus rufipes* (P.ruf), *Trechus quadristristus* (T.quad) Overlap with Group IV: *Agonum duftschmidi* (A.duft), *Agonum viduum* (A.vid), *Amara aenea* (A.aen), *Asaphidion flavipes* (A.flav), *Carabus cancellatus* (C.canc), *Carabus violaceus* (C.viol), *Cymindis humeralis* (C.hum), *Dolichus halensis* (D.hal), *Harpalus distinguendus* (H.dist), *Harpalus rubripes* (H.rub), *Nothiophilus palustris* (N.pal), *Pterostichus vernalis* (P.vern), *Synuchus vivalis* (S.viv)
IV	*Abax carinatus* (A.car), *Abax parallelepipedus* (A.par), *Abax paralellus* (A.pas), *Abax schueppeli* (A.sch), *Agonum muelleri* (A.mue), *Amara municipalis* (A.mun), *Amara tibialis* (A.tib), *Badister lacertosus* (B.lac), *Bembidion deletum* (B.del), *Broscus cephalotes* (B.cep), *Calosoma inquisitor* (C.inq), *Carabus arsensis* (C.ars), *Carabus coriaceus* (C.cor), *Carabus convexus* (C.con), *Carabus glabratus* (C.gla), *Carabus granulatus* (C.gra), *Carabus hortensis* (C.hor), *Carabus intricatus* (C.intr), *Carabus linnaei* (C.lin), *Carabus nemoralis* (C.nem), *Carabus ulrichii* (C.ulr), *Carabus variolosus* (C.var), *Cychrus caraboides* (C.car), *Cychrus semigranosus* (C.sem), *Dromius quadraticollis* (D.quad), *Harpalus progrediens* (H.prog), *Harpalus pygmaeus* (H.pygm), *Harpalus quadripunctatus* (H.quad), *Harpalus smaragdinus* (H.smar), *Harpalus tenebrosus* (H.ten), *Leistus piceus* (L.pic), *Leistus rufomarginatus* (L.ruf), *Limodromus assimilis* (L.ass), *Loricera pilicornis* (L.pil), *Molops piceus* (M.pic), *Nebria brevicollis* (N.brev), *Notiophilus biguttatus* (N.big), *Pterostichus anthracinus* (P.atr), *Pterostichus melanarius* (P.mel), *Pterostichus niger* (P.nig), *Pterostichus nigrita* (P.nigr), *Pterostichus oblongopunctatus* (P.obl), *Poecilus versicolor* (P.vers), *Trechus secalis* (T.sec)	Overlap with Group III: *Agonum duftschmidi* (A.duft), *Agonum viduum* (A.vid), *Amara aenea* (A.aen), *Asaphidion flavipes* (A.flav), *Carabus cancellatus* (C.canc), *Carabus violaceus* (C.viol), *Cymindis humeralis* (C.hum), *Dolichus halensis* (D.hal), *Harpalus distinguendus* (H.dist), *Harpalus rubripes* (H.rub), *Nothiophilus palustris* (N.pul), *Pterostichus vernalis* (P.vern), *Synuchus vivalis* (S.viv)

Group IV, consisting of forest meso- and hygrophilous steno- and eurybionts, exhibits a distinct preference for closed forest habitats. These species infrequently venture into open meadow habitats, including steppe areas. However, they display a notable response to successional stages following the transition of meadow steppes from the plagioclimax towards climate climax, particularly encroachment by shrub and subsequent forest vegetation. A significant portion of the forest ground beetles species within group IV spreads into remnants of meadow steppes adjacent to forested areas, which typically occupy areas of less than 1 hectare. The presence of group IV species in meadow and the meadow-steppe habitats signifies the shift from plagioclimax to climatic climax. Prominent species within group IV in the research region include: *A. carinatus*, *A. parallelepipedus*, *A. parallelus*, *C. arvensis*, *C. glabratus*, *C. linnei*, *C. nemoralis*, *C. ulrichii*, *C. variolosus*, *C. caraboides*, *C. semigranosus*, *L. piceus*, *L. assimilis*, *M. piceus*, *P. melanarius*, *P. niger*, *P. oblongopunctatus* etc.

Furthermore, CCA was conducted to identify the primary ecological factors characterizing the habitats within the sample plots (Fig. 3). Our findings distinctly reveal that the plagioclimactic meadow steppe ecosystem in the West Podillia region persists solely under conditions of human-mediated removal of aboveground plant biomass. With the cessation of hay harvesting and livestock grazing in the past two decades, wildfire emerges as the sole factor influencing the maintenance of meadow steppes. This assertion is unequivocally supported by our results for the sample plots in group I (Fig. 3). Upon the cessation of anthropogenic pressures, meadow steppes rapidly become unstable and undergo ecological successions, ultimately becoming overgrown with shrub and tree vegetation (as observed in sample plots in group II). Artificially afforested meadow-steppe habitats (sample plots in group IV) exhibit ecological similarities to natural forests (sample plots in group V). Additionally, it is essential to highlight the sample plots in group III, which encompass fallow habitats and are distinct from others. Our findings elucidate a distinct response of the ground beetles species groups (I–IV) to transformation processes occurring within fragments of meadow steppes. The response of various ground beetle species groups to alterations in xerothermal environmental conditions can vary significantly. In conditions characterized by xerophilization and elevated environmental temperatures, species belonging to Group I exhibit a notable expansion in distribution. Conversely, species within groups II and III display a comparable response to the habitat, although with a preference for higher soil moisture. In contrast, species within group IV demonstrate an association with markedly different environmental conditions, characterized by significant moisture levels and relatively lower soil temperatures conducive to their existence.

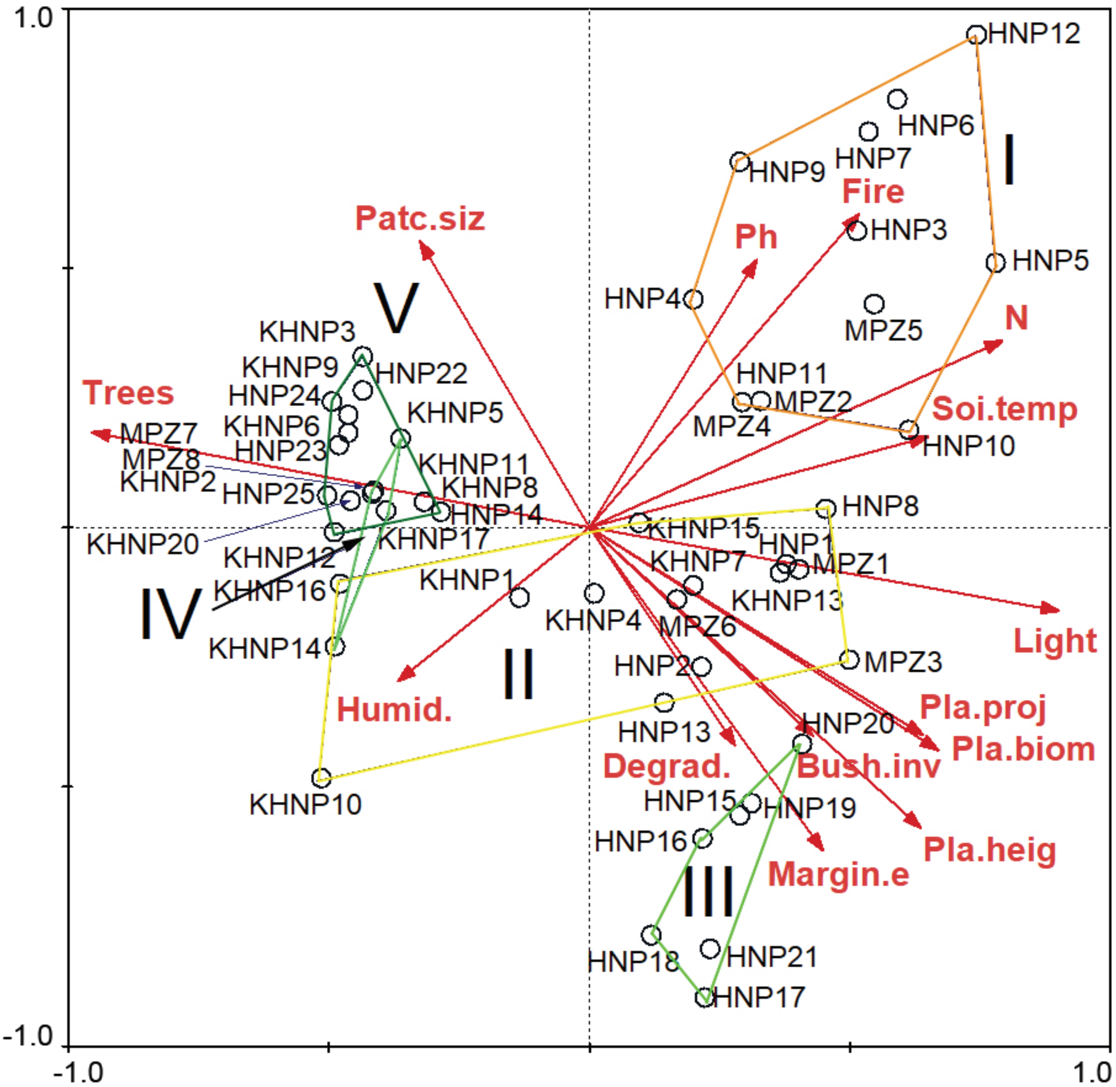

Fig. 3. Distribution of sample plots in the canonical space with additional ecological dimensions: I – well-preserved meadow steppes; II – transformed meadow steppes; III – fallows and post-forest meadows; IV – pine plantations on the meadow steppes; V – forests; for abbreviation see methods

The assessment of the ground beetle groups' participation in the meadow steppe fauna reveals that suitable conditions for the persistence of steppe species have largely been compromised across most of the studied fragments. Steppe species (group I) are observed in only 12 out of 27 sample plots of meadow steppes (Fig. 4). Among these, their representation exceeds 10% of the total fauna composition in 8 sample plots. Notably, in only 2 of these plots do group I species constitute 50% of the fauna. Conversely, a significant presence of species from groups II and III is evident in most cases, indicating the mesophilization of meadow steppe conditions due to shrub and tree vegetation expansion. Forest species of ground beetles (group IV) are prevalent in the majority of meadow steppe sample plots, reflecting the disruption of the plagioclimax and plant successions. Notably, forest species of ground beetles are absent only in the sample plots (HNP7 and HNP8) within the largest area (1.38 km^2) of the "Kasova Gora" locality in the Halych National Park (cluster III). Conversely, a substantial proportion (up to 60%) of forest species is observed in the remaining sample plots of meadow steppes. Among the three nature conservation areas, the meadow steppes within the Kremenetski Hory National Park (cluster I) exhibit the most pronounced transformation, with no species from group I recorded. Additionally, all plots (excluding KHNP1, KHNP10, and KHNP13) lack species from groups II and III, being instead inhabited by forest (group IV) species of the ground beetles. These results likely stem from the cessation of traditional economic practices in meadow steppe fragments, leading to the accumulation of dead plant biomass and subsequent overgrowth by shrub and tree vegetation. It is noteworthy that despite the presence of meadow steppe vegetation in the aforementioned research areas, the steppe species of the ground beetles are completely absent. This suggests that the ground beetles may serve as very early and precise indicators of the ongoing changes in the meadow-steppe habitats.

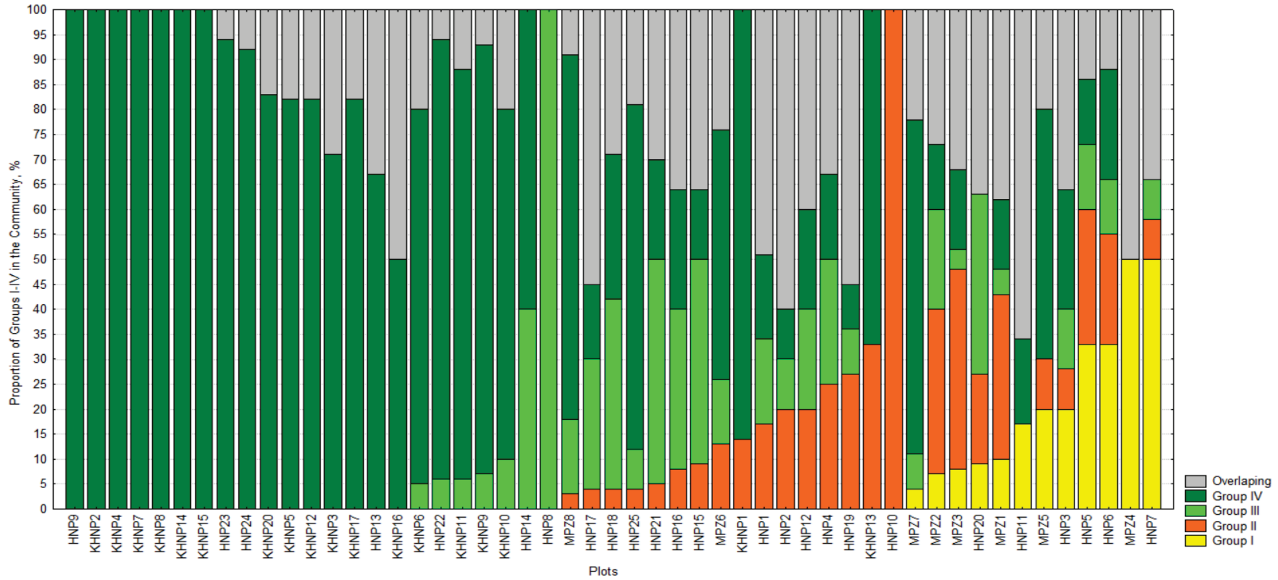

Fig. 4. The percentage representation of the focal groups in the ground beetle communities among the sample plots: group I – steppe xerothermophilic stenobionts; group II – steppe and ruderal xero- and mesophilic eurybionts; group III – meadow and ruderal meso- and hygrophilous eurybionts; group IV – forest meso- and hygrophilous steno- and eurybionts

Discussion

The contemporary challenge of the meadow-steppe habitats loss is intricately linked to the discontinuation of their traditional economic utilization, notably livestock grazing and hay harvesting. This phenomenon is deeply rooted in the profound social, economic, and political transformations within Ukrainian society, which are embedded within global dynamics in the post-soviet and post-socialist space (Hölzel et al., 2002). The dwindling of the meadow-steppe habitats consequent to the cessation of anthropogenic pressures represents a novel ecological concern. While analogous processes have been observed in certain steppe reserves following the imposition of absolute reserve regulations (Rusin, 2006; Ustymenko et al., 2019; Larionov, 2022), their occurrence in exploited lands remained largely uncharted. This underscores the prolonged state of plagioclimax experienced by preserved fragments of meadow steppes, largely influenced by human intervention (Zamoroka & Dmytrash-Vatseba 2018). The discontinuation of economic activities in these meadow steppe fragments caused their plagioclimax interruption, triggering further succession toward climatic climax characterized by their replacement by shrub and forest vegetation.

The ground beetles are widely recognized as reliable indicators of ecosystem changes due to their stringent habitat requirements, which encompass factors such as temperature, moisture levels, soil composition, food availability, and vegetation structure (Brygadyrenko, 2015c, 2015d; Dedus & Rizun, 2018; Wei et al., 2020; Putchkov & Brygadyrenko, 2022). Variations in the abundance of individual the ground beetles species reflect their response to environmental shifts (Eyre & Luff, 2004; Putchkov et al., 2019; Avtaeva et al., 2019, 2021), often serving as proxies for transformative processes within ecosystems. Such fluctuations in the ground beetle species populations are frequently linked to habitat fragmentation, degradation, alterations in vegetation cover, and changes in land use practices (Putchkov et al., 2019, 2020; Wei et al., 2020; Langraf et al., 2024a, 2024b). It is widely acknowledged that the responsiveness of the ground beetles to ecosystem changes is species-specific (Wei et al., 2020). While certain species exhibit strong associations with specific habitats and are highly sensitive to even minor alterations (Rizun, 2004), others demonstrate a greater tolerance for significant environmental perturbations and may even thrive in disturbed habitats (Eyre & Luff, 2004; Brygadyrenko, 2016; Faly et al., 2017, 2023; Putchkov et al., 2019). Thus, both species that are sensitive to habitat loss and those that proliferate in disturbed environments can serve as valuable indicators of ecosystem transformations, aiding in the assessment of habitat alteration extents.

Our study highlights the effectiveness of ground beetles as indicators of meadow steppes plagioclimax interruption. The meadow steppe vegetation was observed to varying degrees across all 27 samples plots; however, the steppe ground beetles were only present on 12 (45%) of these sites. This finding corroborates earlier research indicating that larger fragments of meadow steppes tend to support the persistence of the steppe ground beetles (Zamoroka & Dmytrash-Vatseba, 2018). Notably, the steppe species of Coleoptera comprise only a small fraction (7%) of the regional fauna, with nemoral accounting for 81%, boreo-montane species for 5%, and ubiquists for 7% (Sumarokov & Zamoroka, 2020).

There has been a longstanding debate in the scientific community regarding the persistence of incumbent species versus the influx of new species amidst landscape alterations (Eyre & Luff, 2004). Our research reveals that the changing of the ground beetle fauna within meadow steppes occurs well in advance of landscape transformations. Such fluctuations in the ground beetle fauna composition stem from functional shifts within the ecosystem, particularly influenced by the margin effect. Notably, smaller meadow steppe fragments exhibit a more pronounced displaying of the margin effect (Bieringer et al., 2013; Lacasella et al., 2014; Zamoroka & Dmytrash-Vatseba 2018; Aleksanov et al., 2023). Lacasella et al. (2014) propose that the forest ground beetles display a greater propensity for encroaching upon open meadow habitats, infiltrating them to a considerable extent. Their analysis suggests that a minimum width of 600 m is required for meadow habitats to sustain a balanced and self-sufficient community of the meadow ground beetles. Our results are almost completely consistent with their conclusions. We demonstrated a full conversion of ground beetle communities within all meadow-steppe habitats in cluster I, wherein they have been supplanted by forest species (group IV). Conversely, in cluster II and cluster III, such transformation is observed in 17% and 21% of the meadow-steppe habitats, respectively. This disparity is attributed to both landscape structure and historical land-use practices within these clusters. Specifically, in cluster I, extensive afforestation of meadow steppes occurred through pine plantations in the 1970s, while clusters II and III were predominantly utilized as hayfields and pastures. Presently, all three clusters are under conservation status, and the ongoing loss of meadow-steppe habitats reflects the consequences of reservatogenic successions.

Our research elucidates that, beyond mere area, the periodic removal of aboveground plant biomass is a critical determinant for the persistence of steppe species of the ground beetles. Our CCA (Fig. 2) revealed that steppe species of ground beetles are exclusively found within meadow-steppe habitats subjected to periodic, often seasonal, fires of dry grass. As an alternative means of biomass removal, hay harvesting has significantly declined and even ceased over the past two decades. Consequently, the primary method to sustain the plagioclimax within fragments of meadow steppes is through controlled burning.

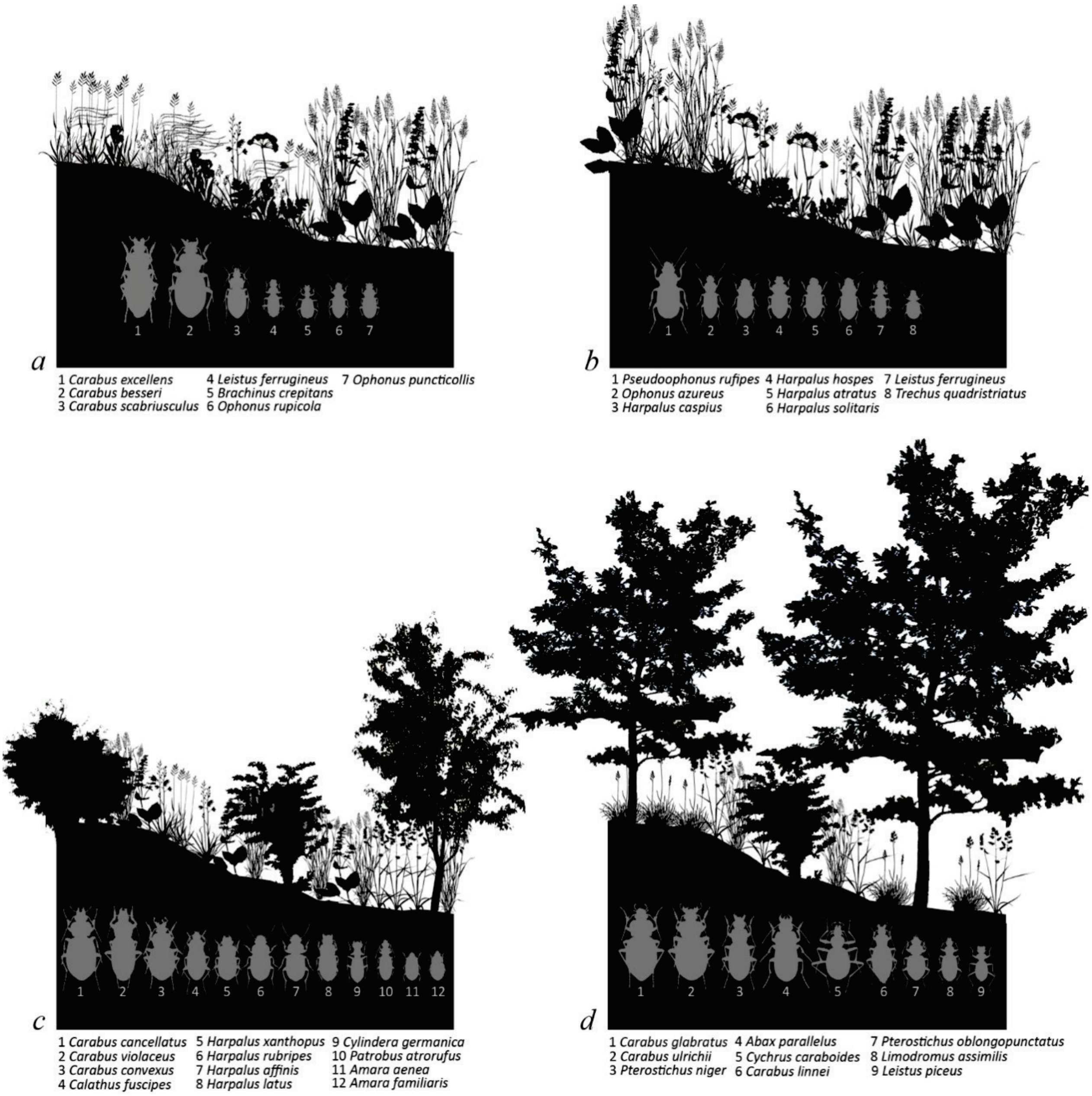

Fig. 5. The main stages of ground beetle community transformations associated with meadow steppe habitat loss: *a* – meadow steppe intermediated by plant biomass removal (plagioclimax); *b* – meadow steppe with plant biomass accumulation; *c* – bush expansion in meadow steppe habitats; *d* – emergence of forests and the closing of the forest canopy (climatic climax); the most abundant species of Carabidae are shown

We found that the increase in aboveground plant biomass, grass stand height, and soil cover by plants (Figs. 2 and 3) contributes to the mesophilization of habitats, facilitating the active colonization of meadow steppes by mesophilic and hygrophilic species of the ground beetles of groups II and III (Fig. 5b, 5c). The accumulation of litter and moisture retention in the soil create favorable conditions for the existence of the mesophilic ground beetles (Brygadyrenko, 2005). The encroachment of these species into the meadow-steppe habitats is also linked to shrub expansion (Figs. 2 and 3), resulting in a mosaic landscape where various vegetation types coexist in close proximity. While this mosaic initially promotes a high level of the ground beetles diversity (Lacasella et al., 2014), long-term ecological successions lead to the local extinction of the steppe (group I) and meadow (groups II and III) species. Our research indicates that the original meadow-steppe ground beetles fauna (plagioclimax stage) is eventually supplanted by meadow species (intermediate succession stage) and ultimately by forest species (climatic climax stage) (Fig. 5). Notably, large epigean biomorphs such as *Carabus* are among the first to disappear during the transformation of the meadow-steppe ground beetle communities. We observed large *Carabus* species (e.g., C. *excellens*, *C. besseri*, *C. scabriusculus*) exclusively in fragments of meadow steppes spanning 0.1 km^2 or more. This phenomenon mirrors the anthropogenic transformation of the ground beetle communities in urban forests (Brygadyrenko, 2006; Putchkov et al., 2019, 2020), a pattern also observed in the meadow steppes of Pivnichne Podillia National Park (Kanarsky, 2021). These processes exhibit a regular nature (Lacasella et al., 2014).

The progressive expansion of shrub and forest vegetation upon remnants of meadow steppes results in the complete loss of these habitats. Concurrently, the forest-dwelling fauna of the ground beetles assumes dominance, persisting even in the presence of long-standing "windows" of varying sizes and configurations within the forest canopy. The phenomenon of forest ground beetles exerting significant dominance over meadows is well-documented in the literature (Lacasella et al., 2014) and holds implications for the conservation of these ecosystems. Notably, the ground beetle communities within meadow steppes artificially afforested with pine plantations in cluster I (Fig. 3) do not exhibit significant distinctions from adjacent deciduous or mixed forests. The impact of canopy closure, density of herbs layer and depth of litter in both pine and deciduous forests, as described in existing literature (Brygadyrenko, 2015a, 2015b, 2016; Faly & Brygadyrenko, 2018), appears to be compensated for in the studied pine plantation habitats by the development of a dense understory.

Conclusion

In summary, our findings underscore the pronounced sensitivity of the ground beetle communities to the ongoing transformation processes within the meadow steppes of West Podillia. We observed a noticeable absence of steppe species (group I) of the ground beetles in approximately 65% of the meadow-steppe sample plots. This pattern is particularly evident in fragments of meadow steppe characterized by limited spatial extent or encroachment of shrub vegetation. These areas, formerly utilized as hayfields or temporary pastures, now lie abandoned, undergoing ecological successions marked by litter accumulation and heightened soil moisture levels. Consequently, these conditions have facilitated the colonization of these areas by mesophilic and hygrophilic meadow species (groups II and III) of the ground beetles. Additionally, a notable proportion of the communities comprises forest species of ground beetles (group IV), which have begun to colonize meadow steppes concomitant with their contemporary overgrowth by shrub and forest vegetation.

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The authors affirm that the research was carried out without any commercial or other affiliations that could be perceived as a possible conflict of interest.

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