# PROGLACIAL SUCCESSIONS OF SPRINGTAIL ASSEMBLAGES (COLLEMBOLA) ALONG RETREATING GLACIERS IN KABARDINO-BALKARIA, GREATER CAUCASUS, RUSSIA

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Since the end of the Little Ice Age, glacier retreat has been recorded globally, with its rates steadily increasing. Glacier forelands serve as convenient areas for studying the patterns of biotic community formation during primary succession. Collembola (hereinafter – springtails) typically play key roles in primary successions, being among the first colonists of territories newly freed from ice. The present study focuses on successional changes in springtail assemblages in the valleys of the Cherek-Khulamsky (Bezengi) and Adylsu along the Bezengi and Kashkatash glacier forelands, respectively (Kabardino-Balkaria, northern Caucasus). The Cherek-Khulamsky valley is located within the Kabardino-Balkarian High-Mountain State Nature Reserve, while the Adylsu valley is part of the Prielbrusye National Park. The objective of the present study is characterising the species composition and structure of springtail assemblages along the glacier chronosequences, as well as identifying the local features of the dynamics of these communities. Using standard soil zoological methods, we examined springtail communities across ten precisely dated plots (1–150 years since deglaciation) in both study valleys. On both locations, pioneer springtail complexes formed immediately after glacier retreat include specialised species, such as representatives of the *nivalis* group of the genus *Desoria*, which are replaced by widely distributed forms within 3–5 years. The dynamics of successional processes vary significantly between the Bezengi and Kashkatash glacier forelands. At Bezengi, the species richness has gradually increased, reaching a maximum after 135 years, whereas at Kashkatash, a sharp diversity increase is observed as early as 74 years since glacier retreat, at the shrub overgrowth stage. Springtail density also varies: at Bezengi it fluctuates from 36 individuals/dm$^2$ to 177 individuals/dm$^2$, reaching the maximum values just 14 years after deglaciation (grassland stage), while at Kashkatash the first noticeable population increase up to 632 individuals/dm$^2$ is recorded on 74-year old surfaces, with an absolute maximum (726 individuals/dm$^2$) achieved in 150-year old pine forests. The Kashkatash glacier foreland shows more pronounced differentiation between early (pioneer) and late (forest) successional stages than that of Bezengi, evident in both population abundance and species composition. At the same time, radical changes in springtail communities are observed in both valleys during transitions either from grasslands to shrublands or from shrublands to forests. Comparison with similar studies reveals a great role of the local features of a particular foreland. Regional differences could be accounted for by microclimatic, geomorphological and biotic factors. At Bezengi, where subalpine grasslands subject to anthropogenic influence predominate, succession seems to proceed more smoothly, while at Kashkatash the development of pine forests creates stable conditions favouring the formation of sustainable communities. Orographic features, such as slope steepness and the presence of rigels, also render a substantial impact, determining the environmental patchiness and the rate of successional changes. The data obtained contribute to understanding the patterns of biotic community formation in montane ecosystems under deglaciation and emphasise the need for further comparative studies to predict changes under global warming conditions.

**Key words:** arthropods, chronosequence, climate change, glacier forelands, montane ecosystem, pioneer species, primary succession

## Introduction

Degradation of the montane glacier cover is known to be global, documented since the end of one of the coldest periods of the latest millennia, i.e. the Little Ice Age (circa 1850) (Zemp et al., 2015; Solomina et al., 2016; Tielidze et al., 2025). The Caucasus is home to approximately 2200 glaciers (Tielidze et al., 2022) which, according to the recent forecasts, may lose 60% to 100% of their mass within 75 years, depending on temperature change scenarios (Tielidze & Wheate, 2018; Hock et al., 2019; Rounce et al., 2023). Against the background of such a rapid glacial retreat, the understanding of ecosystem formation processes on newly exposed surfaces becomes increasingly topical. Areas with precisely established deglaciation chronologies are of particular value, as data on the age of ice-free surfaces allow for step-by-

step tracking the succession in developing ecosystems. This is why glacial valleys are often regarded as ideal natural laboratories for studying the dynamics of biotic communities during primary succession (Walker et al., 2010; Hågvar et al., 2020; Ficetola et al., 2021).

Primary zoocoenotic successions in deglaciation environments have actively been studied in recent years (Hågvar et al., 2020; Ficetola et al., 2021; Antipova & Babenko, 2024; Makarova et al., 2024; Hågvar, 2025). Particular attention has been paid to the key role of arthropods in early colonisation processes, which occur even before the establishment of vascular plants (Hodkinson et al., 2002; Hågvar et al., 2020; Hågvar & Gobbi, 2022). Substantial datasets have been accumulated for various regions of Northern (Hodkinson et al., 2004; Seniczak et al., 2006; Hågvar et al., 2009; Hågvar, 2010, 2012, 2025) and Southern Europe (Janetschek, 1949, 1958; Kaufmann, 2001; Kaufmann et al., 2002; Gobbi et al., 2006a,b, 2007, 2011, 2017; Crosta et al., 2025). Among all arthropod groups, Collembola (also – springtails) are of particular interest as bioindicators of ecosystem status due to their high sensitivity to environmental change (Van Straalen, 1997, 1998; Ponge, 2003; Greenslade, 2007). Numerous studies confirm their crucial roles as a key component of pioneer communities in primary succession (e.g. Kaufmann et al., 2002; Hågvar, 2010, 2012; Hågvar et al., 2020; Antipova & Babenko, 2024). Springtails are not only among the first colonisers of ice-free terrain, but they also actively participate in initial soil formation processes. They accelerate organic matter accumulation and create a trophic foundation for subsequent invertebrate colonisations (König et al., 2011; Raso et al., 2014; Hågvar & Pedersen, 2015; Sint et al., 2019; Gravesen et al., 2024). Their activities promote microbial community development and substrate structure improvement, making them essential «ecosystem engineers» during early succession stages.

Owing to the long history of glaciological research in the Caucasus, precise reconstructions of glacial degradation processes have been established for many glaciers in the region (Bushueva, 2013; Tielidze et al., 2020; Solomina et al., 2016, 2024). These data have not only enabled tracking the glacial retreat dynamics, but they have also laid the foundation for targeted studies of invertebrate succession in post-glacial ecosystems (Antipova & Babenko, 2022, 2024; Babenko & Ponomarev, 2023; Makarova et al., 2024). Of particular interest seems to be a recent multi-taxon study of invertebrate communities in the Tsey Gorge, North Ossetia-Alania, spanning a chronological interval of 1 to 170 years, which revealed several important ecological patterns. First, pioneer taxa colonising ice-free terrain within the first year were identified, including testate amoebae, mites, spiders, harvestmen, beetles, true bugs, and springtails. Notably, endemic species, specifically those adapted to harsh alpine conditions, dominated in those early colonisers, highlighting the uniqueness and high-degree specialisations in the local fauna. Second, as surface age increased, substantial shifts were observed not only in species composition, but also in the dominance structure of multiple taxocoenes. Third, the most pronounced transformations appear to have occurred during transitions between plant formations (e.g. grasslands to shrubs and then to forests), particularly within the first 20–50 years, after which the rate of change markedly declined. In mature forest communities (100–170 years), invertebrate diversity stabilised, but remained lower than in undisturbed ecosystems (Makarova et al., 2024). All the patterns observed are fully applicable to Collembola, as confirmed by the results of their detailed study (Antipova & Babenko, 2024). The question remains open as to how universal these patterns are: whether they are specific only to the Tsey Gorge or reflect broader trends in post-glacial successions in the high mountains of the Caucasus, or even beyond. Answering this question requires further comparative studies on other glaciers in the region, as well as the integration of the data obtained from similar investigations in other montane areas.

The present study aims to contribute to the understanding of these processes through expanding the geographical scope of research on post-glacial successions of Collembola communities in the Caucasus. Its objective is characterising the species composition and community structure of springtails at various succession stages along Bezengi and Kashkatash, two glacier forelands of Kabardino-Balkaria. It is noteworthy that the Caucasus region, despite its significance as a major biogeographic hotspot with high levels of endemism (Myers et al., 2000), remains insufficiently studied in terms of its Collembola fauna. Thus, this research is also of interest from the perspective of documenting regional springtail diversity.

## Material and Methods

### *Fieldwork and study sites*

Springtails were sampled during fieldwork in the high-altitude zone of the northern macro-slope of the Central Caucasus, near the valley glaciers of Bezengi and Kashkatash (Fig. 1). The collection periods were 19.07–01.08.2022 and 12–13.09.2022 in Bezengi (25 days in total) and 14.07–07.08.2023 in Kashkatash (25 days in total). Selection of these glacial valleys was based not only on their distinct microclimatic and geomorphological features, but also on the availability of extensive data on glacier retreat chronology (Bushueva & Solomina, 2012; Bushueva, 2013).

### *Bezengi Glacier foreland*

The Bezengi Glacier, located in the eponymous gorge within the Kabardino-Balkarian High-Mountain State Nature Reserve, is the largest glacier in the Caucasus. Its tongue is northeastern in exposure, being clearly confined through pronounced morphological lateral spurs and showing a relatively low gradient in the lower section (Fig. S1A). The distal part of the glacier lies in a flattened valley, far away from the axial line of the Greater Caucasus Ridge. As of 2020, it covered 34.8 ± 0.8 km$^2$, with a length of 17.5 km, and the terminal section (below 5 km) is heavily mantled by moraine deposits (Tielidze et al., 2022). The maximum ice thickness reaches 420–450 m, and the glacier feeds the River Cherek-Khulamsky (Cherek-Bezengiysky). To the south, the glacier is shielded by the 13-km long Bezengi Wall that blocks warm air masses from the Arabian Peninsula, Black Sea, and Mediterranean. Consequently, the Bezengi valley experiences frequent fog. The mean annual precipitation ranges at 900–1400 mm, reaching 2373 mm in some years (Gazaev et al., 2018). Parent rocks include carbonates, sandstones, granites, and glacial deposits near the terminus (Kushnov et al., 2022). The glacier has been in retreat since the mid-XIX century, having since lost ca 2.5 km by 2020.

The study proglacial zone spans 2020–2153 m a.s.l. (Fig. 2A), with landscapes dominated by subalpine and alpine grasslands used as pastures and hayfields lower in the Bezengi valley (Uligova et al., 2019). The woody vegetation includes young stands of *Betula*, thickets of *Salix*, *Juniperus*, and *Rhododendron* (Bondarenko, 2011). The area lies at the boundary of the Tersky and Elbrus variants of the East-North Caucasian zonation type (Sokolov & Tembotov, 1989). The climate is continental (Gazaev et al., 2018), with mean annual temperatures of 4.7°C at 1700 m a.s.l. and 2.9°C near the glacier (2000 m a.s.l.) (Gazaev & Bozieva, 2020). Both glacier retreat chronology and phytocoenotic data are provided in Table 1 and Table S1.

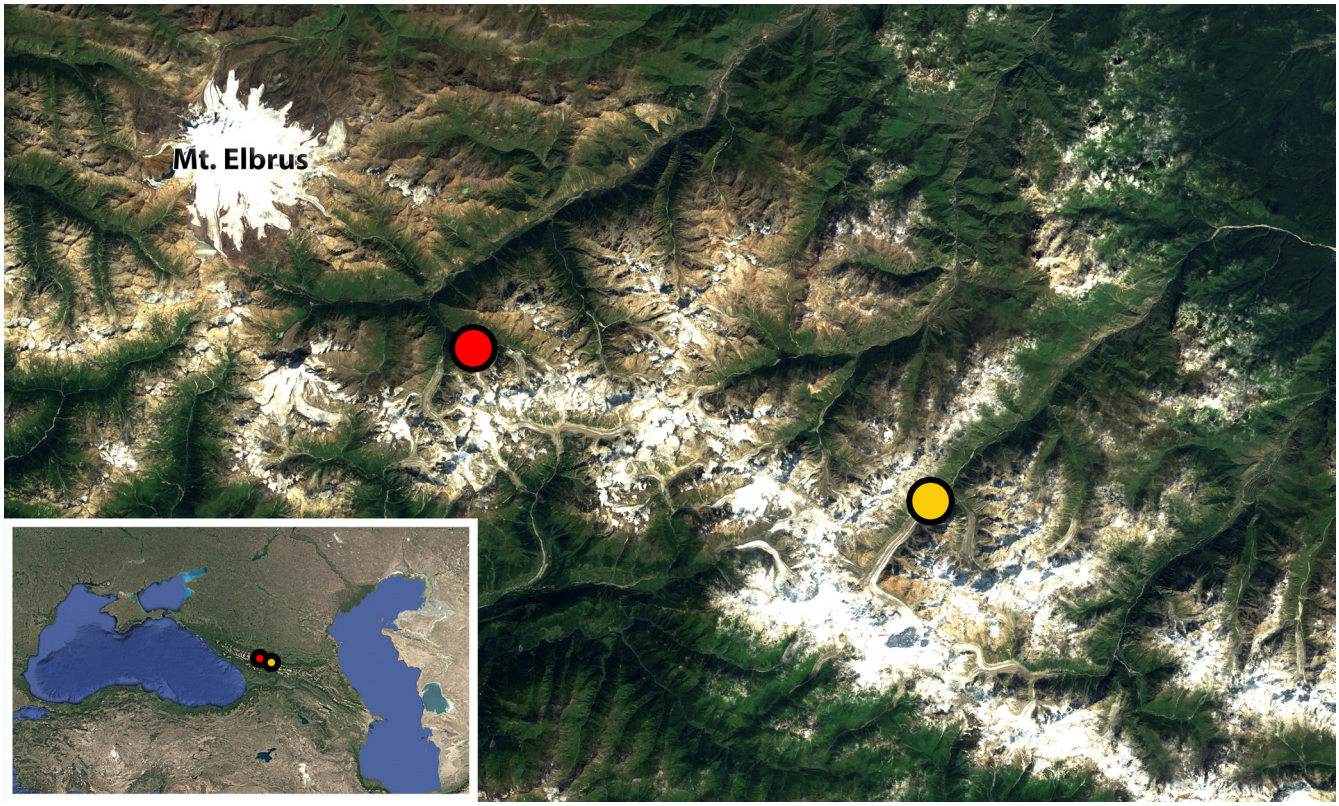


**Fig. 1.** Map showing the forelands of the Bezengi (yellow point) and Kashkatash (red point) glaciers, Greater Caucasus.

### *Kashkatash Glacier foreland*

The Kashkatash Glacier, situated on the steep slope of a lateral spur in the upper Adylsu Valley (a right tributary of the River Baksan), is part of the Prielbrusye National Park. This north-facing valley glacier covered 2.5 km$^2$ with a length of 4.6 km in 2012 (Bushueva & Solomina, 2012). Its proglacial zone is steeper and more varied in topography (Fig. S1B), extending from 2270 m a.s.l. to the glacier's terminus at 2615 m a.s.l. (Fig. 2B). Since the mid-XIX century, the Kashkatash Glacier has lost approximately 1 km of its length (as of 2023). The foreland floor and slopes feature well-defined moraine ridges covered by *Betula*-dominated forests and *Pinus*-dominated forests. The Kashkatash Glacier belongs to the Elbrus variant of the East-North Caucasian zonation (Sokolov & Tembotov, 1989), being characterised by a drier climate due to orographic effects. Both Mezhmassiv ridge and Skalisty ridge block Mediterranean-Black Sea moisture, while the Caspian Lowland supplies dry air currents. Both glacier retreat chronology and phytocoenotic data are given in Table 2 and Table S2.

### *Reconstructing the Glacier chronosequences*

To compile spatio-temporal reconstructions of glaciers, modern satellite images (XXI century), archival aerial photographs (from the mid-XX century to the late XX century), old maps, descriptions by travellers and explorers, and photographs (from the late XIX century to the early XX century) were used.

**Table 1.** Short description of study plots along the Bezengi Glacier foreland, Greater Caucasus

| Plot | Year of ice retreat | Age of surfaces | Altitude (m a.s.l.) | Habitat type and dominant vegetation | Visual plant cover estimation |
|---|---|---|---|---|---|
| I | 2020–2021 | 0–2 | 2153 | Sandy-gravel scree surface with few plantlets (near the left side slope of the gorge) | 0% |
| II | 2019 | 3 | 2165 | Sandy-gravel surface with sparse cushions of *Minuartia imbricata* (M.Bieb.) and *Chamaenerion colchicum* (Albov). | 3% |
| III | 2011 | 11 | 2155 | Sandy-gravel surface with clumps of *Myricaria germanica* (L.) and *Chamaenerion colchicum*, cushions of *Minuartia imbricata* and moss. | 20% |
| IV | 2008 | 14 | 2145 | Stony mound with thickets of *Vicia alpestris* Steven and *Chamaenerion colchicum*, isolated *Salix* shrubs | 40–50% |
| V | 1987 | 35 | 2136 | Shrub *Salix* association with mixed herbs and moss patches | 90% |
| VI | 1957 | 65 | 2101 | A young forest of *Betula litwinowii* with *Salix* spp. and forbs | 100% |
| VII | 1946 | 76 | 2066 | Forest successional stage formed by *Salix* spp., herbaceous cover (predominantly grasses and various *Fabacea*) | 100% |
| VIII | 1910s | ~112 | 2076 | A forb grassland with *Juniperus sabina* shrubs, scattered young *Betula litwinowii* along the moraine and with abundant moss-lichen hummocks. | 95% |
| IX | 1887 | 135 | 2044 | Mixed forest of *Betula litwinowii* Doluch. and *Salix* spp. with *Juniperus sabina* L., diverse herbaceous cover, and thick litter layer | 100% |
| X | 1870s | ~150 | 2021 | A forb grassland with patches of *Juniperus sabina* shrubs, scattered birch trees (*Betula litwinowii*) and *Rubus idaeus* L. thickets | 100% |

**Table 2.** Short description of study plots along the Kashkatash Glacier foreland, Greater Caucasus

| Plot | Year of ice retreat | Age of surfaces | Altitude (m a.s.l.) | Habitat type | Visual plant cover estimation |
|---|---|---|---|---|---|
| I | 2022 | 1 | 2615 | Sandy-gravel surface without evident vegetation | 0% |
| II | 2020 | 3 | 2600 | Rocky surface with single plantlet of *Salix kazbekensis* Skvortsov, *Salix* sp. and *Chamaenerion colchicum* (Albov) | 2% |
| III | 2018 | 5 | 2588 | Rocky surface with grass association with *Chamaenerion colchicum* and scattered small *Salix* sp. and *Betula litwinowii*, interspersed with stream-fed pools | 5% |
| IV | 1987 | 36 | 2545 | Rocky surface with grass association with young *Salix* spp. and *Betula litwinowii*. | 3% |
| V | 1949 | 74 | 2520 | Shrubland stage: *Salix-Betula* growth with young *Pinus sylvestris* L. on moraine slopes, featuring *Hedysarum caucasicum* M.Bieb., *Poa badensis* Willd., *P. glauca* Vahl, and *Agrostis balansae* (Boiss.) (above rocky outcrops) | 70–80% |
| VI | 1932 | 91 | 2385 | Young *Salix-Betula* forest with single *Pinus sylvestris*, regeneration with *Hedysarum caucasicum* in the ground layer (under rock step, close to glacier stream) | 90% |
| VII | 1927 | 96 | 2322 | Young mixed forest (*Salix-Betula-Pinus*) with herb layer dominated by *H. caucasicum*, *Poa nemoralis* L., *Chamaenerion colchicum*, *Calamagrostis arundinacea* (L.) | 100% |
| VIII | 1911 | 112 | 2308 | *Pinus sylvestris* forest with *Betula* and *Salix* admixture, featuring *Hedysarum caucasicum* as the herb layer dominant | 90% |
| IX | 1870 | 150 | 2277 | Mature dead-cover pine forest with *Hedysarum caucasicum* | 50% |

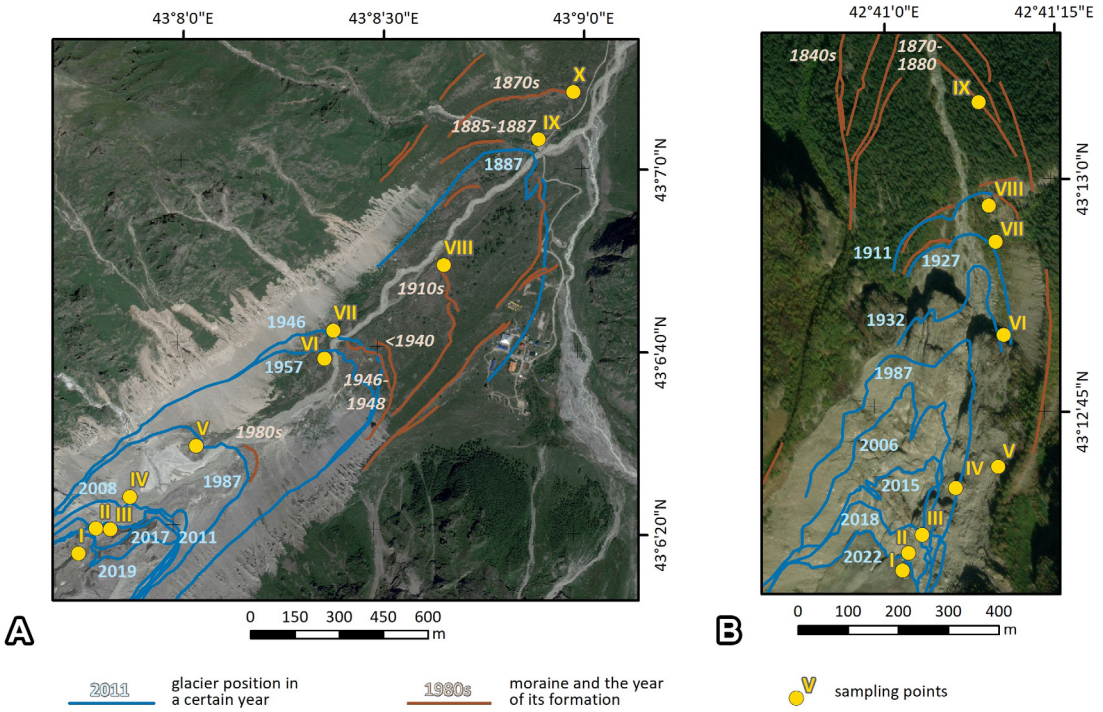


**Fig. 2.** Chronosequences of the Bezengi (A) and Kashkatash (B) glacier forelands, Greater Caucasus.

Remote sensing data were orthorectified (distortions associated with relief were removed) and co-registered using control points. The images were processed in the following sequence: one of the modern images was selected as a master and the other images were tied to it using control points (characteristic stable points in the terrain, such as a bridge, the corner of a house, a tree). The accuracy of image alignment using this method is within the first few pixels. In addition, modern medium-resolution satellite images were used to determine the speed and movement of the glacier in order to confirm the correctness of the glacier boundaries in the glaciated areas. A map by military topographers from the late XIX century was referenced using a co-ordinate grid, and then the reference was refined using control points of relief.

The terminal moraines were identified using remote sensing data, and their location and number were refined during field studies. The moraine complexes were dated using bioindication methods: dendrochronology and lichenometry, and these data were compared with historical descriptions. Samples of *Pinus sylvestris* L. trees were taken from moraine deposits for dendrochronological analysis (determination of tree age) and the diameters of a lichen (*Rhizocarpon geographicum* (L.) DC.) were measured. These data were then used to determine the age of the surface in accordance with the growth curve of lichens in the study area. Bioindication methods allow us to determine the minimum age of surfaces. Therefore old photographs and historical descriptions were also used for dating. The methods used are described in more detail in Bushueva (2013).

### *Study plots*

The selection of sampling plots was based on precise data regarding the minimum age of particular moraine deposits and the exposed postglacial surface in each glacial foreland. Accessibility, given the orographic constraints of the terrain, was also considered as a key factor. Consequently, in the Bezengi glacier foreland, all sampling plots were situated on the left bank of the glacial river, whereas at Kashkatash, they were located on the right bank (Fig. 2). Using georeferenced maps, we selected ten plots at Bezengi (I–X) and nine plots at Kashkatash (I–IX), covering the surface ages from 0 to 150 years. The dated period spans from the mid-XIX century to the year 2022 (Bezengi) or 2023 (Kashkatash).

In both forelands, the study postglacial zone encompassed the principal stages of primary vegetation succession: from bare soil near the glacier terminus, through grassland and shrubland phases, to forest communities. The Bezengi postglacial zone was distinguished by the complete absence of pine forests in late-successional stages; instead, it featured young *Betula litwinowii* stands interspersed with grassland communities (Fig. 3). In contrast, the Kashkatash foreland culminated in the establishment of mature pine forests (Fig. 4).

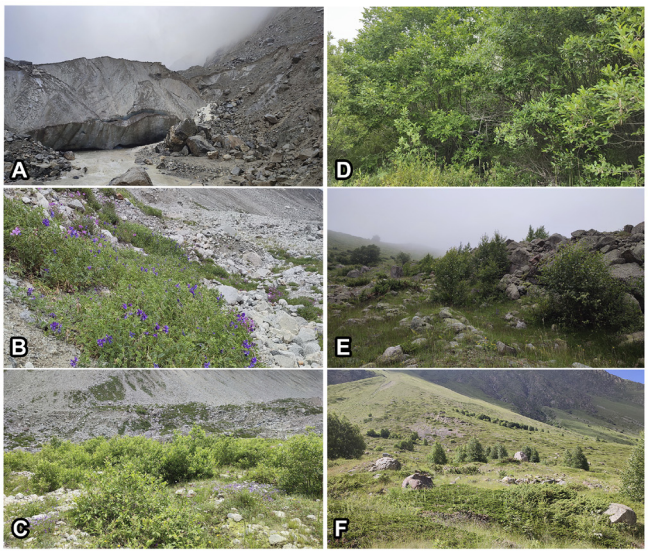


**Fig. 3.** Sampling plots along the Bezengi Glacier foreland, Greater Caucasus. Designations: A – plot I (bare ground, 0–2 years old since glacier retreat), B – plot IV (sparse *Vicia-Chamaenerion* herbaceous plant association, 14 years old), C – plot V (*Salix* shrub association, 35 years old), D – plot VII (*Salix* spp. thickets, 76 years old), E – plot VIII (subalpine forb grassland with scattered *Betula litwinowii* trees along the moraine, 112 years old), F – plot X (subalpine forb grassland with scattered *Betula litwinowii* and *Juniperus sabina*, ca 150 years old).

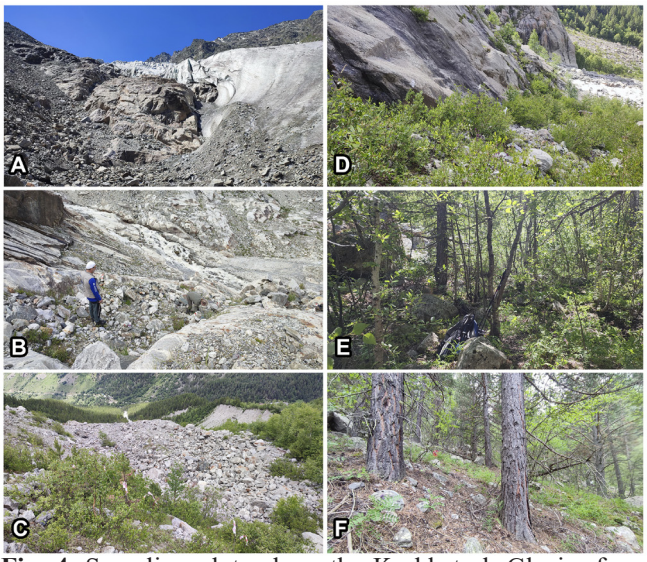


**Fig. 4.** Sampling plots along the Kashkatash Glacier foreland, Greater Caucasus. Designations: A – plot I (bare ground close to glacier, 1 years old since glacier retreat), B – plot IV (rare herbacious vegetation, 36 years old) , C – plot V (shrub associations of *Betula litwinowii* and *Pinus sylvestris*, 74 years old), D – plot VI with rock step (shrub associations dominated with *Salix* sp., 91 years old), E – plot VIII (*Pinus sylvestris* forest with *Salix* sp., 112 years old), F – plot IX (established *Pinus sylvestris* forest, ca 150 years old).

### *Collembola sampling methods*

The class Collembola is known for its high diversity of life forms (Stebaeva, 1970). This necessitates using a combination of collection methods for studying its fauna and populations (Babenko, 1985; Potapov & Kuznetsova, 2011). This is particularly relevant for postglacial landscapes where a wide range of natural habitat types has been developed (Ficetola et al., 2021; Antipova & Babenko, 2023; Valle et al., 2023). In both glacier forelands, material was collected following a unified protocol using standard soil-zoological methods. Larger litter-dwelling and atmobiotic forms were captured using aspirators and pitfall traps, these latter consisting of 200 ml plastic cups (6.5 cm diameter) buried in the ground. The cups were filled one-third with water from nearby glacial streams; no special preservatives were used due to the need to preserve fresh material for further molecular genetic analyses. Ten such traps were installed at each study plot and checked every 1–2 days when possible. Since some traps were lost due to natural causes (ice collapse, flooding) or anthropogenic factors (human interference), the total sampling effort amounted to 996 traps per day in the Bezengi foreland and 1688 traps per day at Kashkatash. Additionally, on pioneer sandy-pebble plots lacking visible vegetation, springtails were collected using substrate flotation, while sweep netting with an entomological net was employed in the plots with developed herbaceous vegetation.

To assess the abundance and composition of soil-dwelling springtails, we used extraction from soil samples with Tullgren funnels (e.g. Potapov & Kuznetsova, 2011). Samples were collected using a 5 × 5 × 5 cm steel frame with ten replicates per plot. To minimise animal loss during sample deformation during transport, each soil core was wrapped in newspaper and plastic bags before being placed in plastic containers. All samples were transported to Moscow for laboratory extraction, this being performed using cardboard funnels without heating for 7–10 days.

In the Bezengi foreland, soil samples were initially collected during summer (30–31 July), but preliminary examination after extraction revealed relatively low microarthropod abundance. It remains unclear whether this was due to local soil community characteristics or transport conditions. To obtain more representative data, an additional sampling trip was conducted 1.5 months following the initial collection (12–13 September).

Since no significant differences were found between the two seasonal surveys, the data were

combined into a single dataset for analysis. Consequently, species richness was evaluated using the combined data from both sampling periods, while the abundance values were averaged across all 20 replicates per plot. Thus, the total number of soil samples taken amounted to 200 at Bezengi and 90 at Kashkatash. Despite a two-fold larger sampling volume at Bezengi, the final material collected from the study plots was comparable, totaling approximately 7500 Collembola specimens from each valley.

***Comparative framework***

For comparison, we integrated the published data from the Tsey Glacier chronosequence in North Ossetia-Alania (Antipova & Babenko, 2024). The methodological consistency between the studies allows for inter-regional comparison of springtail succession dynamics across similar glacial chronosequences to be accomplished.

***Statistical analysis***

Alpha diversity at individual study plots was assessed using the Shannon index (H') and species richness. Species richness was defined as the total number of species recorded using all collection methods: Tullgren funnel extraction, pitfall traps, and manual sampling. Changes in species composition during succession (beta diversity) were evaluated using pairwise comparisons of samples based on Cody (1975) index. The index was calculated as follows:

$$\beta = \frac{g(H) + l(H)}{2},$$

where g(H) is the number of species gained, and l(H) is the number of species lost along the habitat gradient H (in this case, the successional chronosequence). The Cody index ranges from 0, indicating the complete faunal similarity, to a theoretical maximum of S/2 (where S is the total number of unique species across both sites), meaning the complete faunal dissimilarity. Higher index values signify a more pronounced species replacement and thus a lower community similarity between stages. Conversely, a stable index value over a series of succession stages indicates a stabilised community structure and a slowdown in the rate of species turnover.

The faunistic similarity between the communities was assessed using complete species lists obtained using all sampling methods. Hierarchical cluster analysis was performed applying the Dice-Sørensen coefficient (a similarity measure for binary data) in PAST 4.13 (Hammer et al., 2001). Clustering was conducted using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) algorithm with 1000 bootstrap replicates to assess cluster stability.

The community similarity was evaluated based on soil extraction data standardised per $dm^2$. Non-metric multidimensional scaling (NMDS) was applied using the Rho index (1–Is, where Is is Spearman rank correlation coefficient). The optimal 2D configuration was determined applying the metaMDS function with 100 random starts («trymax»). Ordination quality was assessed via stress values, and statistical significance of group separation was tested using ANOSIM. Analyses were performed in R 4.4.2 (R Core Team, 2024) using the packages vegan (Oksanen et al., 2025), tidyverse (Wickham et al., 2019), and ggplot2 (Wickham, 2016).

The relative species abundance was expressed as a percentage of total abundance per plot. Dominance classes followed the Engelmann (1978) scale: 0–1.3% – subrecedent (rare); 1.31–3.9% – recedent (low abundance); 3.9–12.4% – subdominant; 12.4–39.3% – dominant; 39.4–100% – eudominant.

## Results

***Fauna and successional dynamics along the Bezengi foreland***

A total of 69 springtail species from 41 genera and 17 families were recorded across the study plots at Bezengi (Table S3). The fauna was dominated by three major families: Isotomidae (17%), Entomobryidae (16%), and Tullbergiidae (16%). Considerable contributions were also observed due to Neanuridae (8%), Hypogastruridae (7%), Onychiuridae (6%), and Orchesellidae (6%), although the exact proportions for Orchesellidae remain uncertain due to unresolved taxonomy. The remaining ten families were represented by only 1–2 species each, with individual contributions not exceeding 3%.

In terms of biogeography, 40% species were trans-Holarctic or cosmopolitan, while Palearctic (16%) and European (16%) species were less prevalent. Only 7% were Caucasian endemics (including putative new species). Notably, 21% of the taxa could not be definitively identified to species, meaning their true distribution remains uncertain. Possibly, some of these unidentified forms may represent additional endemics, pending taxonomic revisions and descriptions of new species.

A comparison of Tullgren funnel data between the summer and autumn sampling periods revealed, but had minor differences: ten species were captured only in summer and only four species in autumn. Most of these were represented by single specimens, indicating high-degree randomness in their occurrence. Even the most abundant from among these unique species, *Mesaphorura krausbaueri* Börner, 1901, was uncommon, occurring at low densities ranging from 1.2 individuals per 1 $dm^2$ (hereinafter – ind./$dm^2$) to 6.4 ind./$dm^2$. The high overlap in core community composition between seasons and the low abundance of unique species demonstrate that variation in the sampling periods introduces minimal methodological noise, thereby supporting the decision to combine datasets for a more comprehensive analysis. The composition of dominant species in the Bezengi foreland varied across the chronosequence. On the pioneer plot (I), immediately after glacier retreat, a diverse assemblage of epigeic (surface-dwelling) species was recorded primarily through pitfall trapping. This community included representatives from multiple families and even different orders. In Tullgren funnel extractions, the surface-active species *Entomobrya* sp. 1 overwhelmingly dominated, being represented both by adults and numerous juveniles. Pitfall traps yielded relatively high abundances of *Ceratophysella dobrolyubovae* Babenko & Antipova, 2025 and *Desoria* sp. *nivalis*-group, with occasional records of Symphypleona (*Sminthurides* cf. *sexoculatus* Betsch & Massoud, 1970), *Orchesella* sp., and juvenile Tomoceridae (likely *Tomocerus vulgaris* (Tullberg, 1871)) (Table S5). However, substrate flotation of sandy pioneer soils proved ineffective, making it impossible to reliably estimate springtail density at this stage. A similar species composition, with only minor additions, persisted on sites II–III, characterised by outwash plain (sandur) landscapes.

On the 3-year old surface (plot II), the mean springtail abundance reached 79.6 ± 28.0 ind./$dm^2$ (Fig. 5B). A striking feature of this springtail community was the extreme dominance of *Anurophorus alpinus* Potapov & Stebaeva, 1990, accounting for 77% of the total abundance. This pattern was consistent across both pitfall traps and soil extractions. *Entomobrya* sp. 1 and *Ceratophysella dobrolyubovae* remained relatively abundant. The soil horizon already hosted several euedaphic (deep-soil dwelling) species, including at least three *Mesaphorura* species and the rare occurrence of *Friesea* cf. *albida* Stach, 1949. Thus, within just three years, species richness doubled, while faunal similarity (Sørensen-Dice index) between the first two sites did not exceed 65% (Fig. 6B, Fig. 7B).

By year 11 (plot III), where sparse *Epilobium* and *Myricaria* shrubs co-existed with extensive bare sand, the mean abundance declined to 36 ± 20 SE ind./$dm^2$, while the species richness increased to 14 compared with plot II. This diversity increase was driven by the addition of true soil-dwelling taxa, like the *Megalothorax* sp. *minimus*-group, *Protaphorura* sp. aff. *subarctica* (Martynova, 1976), and several *Mesaphorura* species (five recorded), which dominated both in abundance and species richness. Specifically, *Mesaphorura macrochaeta* Rusek, 1976 accounted for 56% of the total abundance, followed by *Ceratophysella dobrolyubovae* (20%), with *Protaphorura* sp. aff. *subarctica* (11%) and *Mesaphorura tenuisensillata* Rusek, 1974 (7%) as subdominants. Early pioneers (*Desoria* sp. *nivalis*-group, *Sminthurides* cf. *sexoculatus*) disappeared, while *Micranurida pygmaea* Börner, 1910, a forest-associated species, appeared and persisted throughout subsequent succession stages.

On the 14-year old surface (plot IV), where dense patches of legumes and fireweed grew among outwash plains, numerous new eurytopic species with broad distributions appeared, namely *Folsomides parvulus* Stach, 1922, *Isotoma caerulea* Bourlet, 1839, *Parisotoma notabilis* (Schäffer, 1896), *Proisotoma minima* Absolon, 1910, and *Pseudosinella octopunctata* (Börner, 1901). Among them, there were also some Caucasian endemics, namely *Orchesella caucasica* Stach, 1960 and *O. irregularilineata* Stach, 1960. This plot showed an exceptionally high activity of *Ceratophysella dobrolyubovae*, which was abundant in pitfall traps. Compared to the previous stage (plot III), the mean springtail density in the soil profile increased nearly five-fold (177 ± 31 SE ind./$dm^2$), largely due to the dominance of *Protaphorura unari* Rusek, 1995 (32%), a species recorded uniquely on this plot. The relative abundance of *Micranurida pygmaea* rose to 11%, while at least 25% of the springtail community was shared by five *Mesaphorura* species. This stage showed a peak diversity, with 20 species and a substantially increased Shannon index (2.3), among the highest in the successional series.

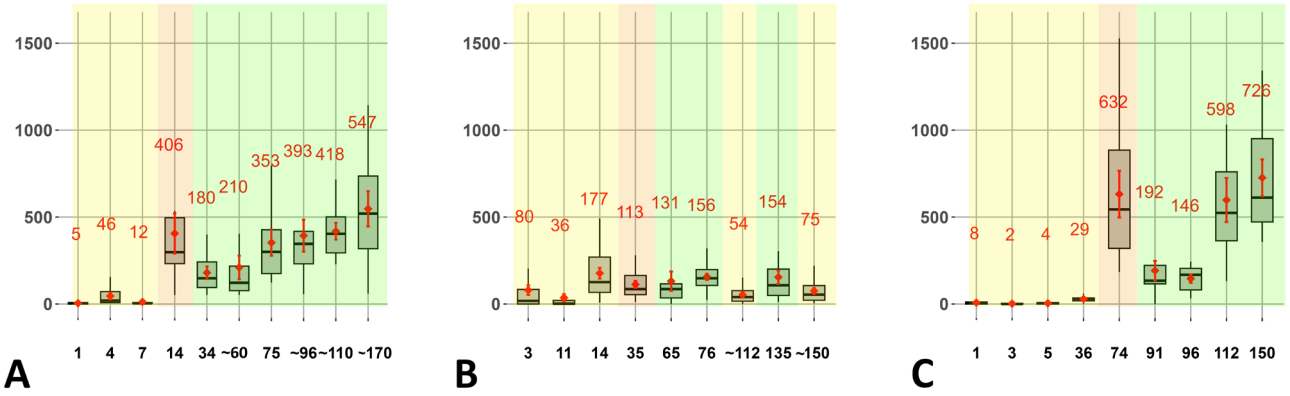


**Fig. 5.** Collembola community abundance dynamics along the chronosequence of glacier forelands, Greater Caucasus. Designations: A – Tsey glacier foreland, B – Bezengi glacier foreland, C – Kashkatash glacier foreland. The x-axis represents surface age (years old), and the y-axis shows abundance values (individuals per 1 $dm^2$). Boxplots show the median (central line), interquartile range (box), and data range (whiskers). Red diamonds indicate mean abundance (± SE) with numerical values shown above. The background colour indicates the type of plant association: yellow – grassland, orange – shrubland, green – forest.

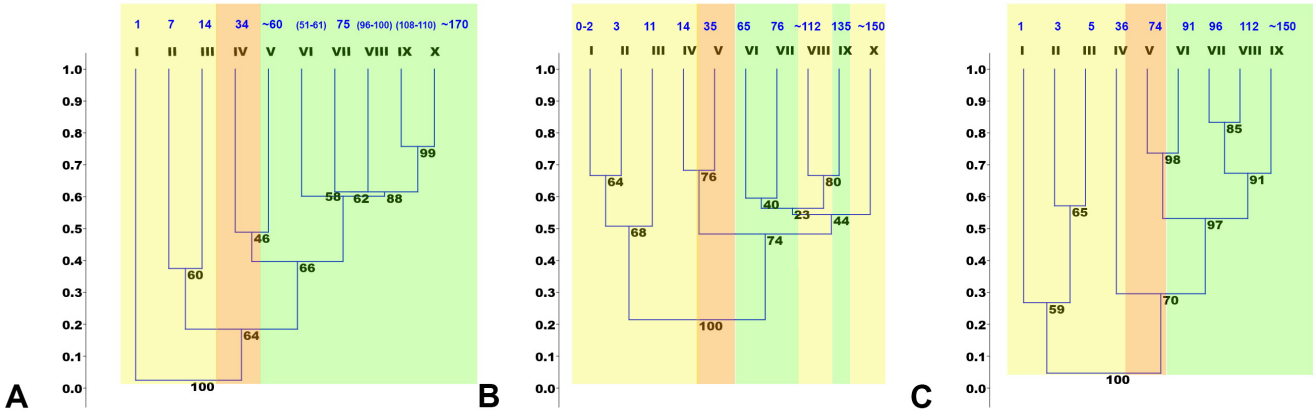


**Fig. 6.** Similarity of springtail assemblages in the glacier forelands, Greater Caucasus, based on Sørensen-Dice index. Designations: A – Tsey glacier foreland, B – Bezengi glacier foreland, C – Kashkatash glacier foreland. Study plots are marked with Roman numerals; surface ages (years old) are shown in blue Arabic numerals above each plot. The background colour indicates the type of plant association: yellow – grassland, orange – shrubland, green – forest.

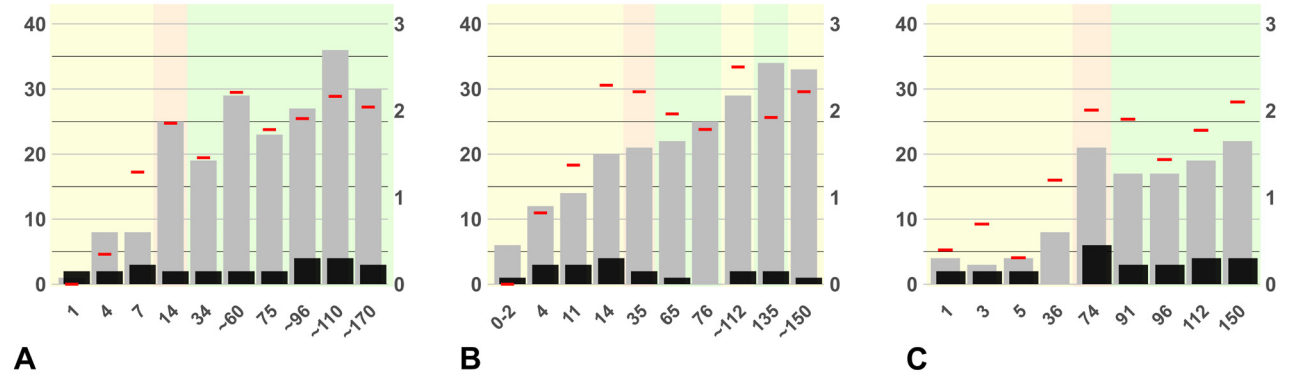


**Fig. 7.** Diversity measures across the chronosequences: total species richness (grey bars), number of Caucasian endemics (black bars), and Shannon index values (red lines) in the (A) Tsey glacier foreland, (B) Bezengi glacier foreland, and (C) Kashkatash glacier foreland. The x-axis represents surface age (years old); the y-axis shows number of species. The background colour indicates the type of plant association: yellow – grassland, orange – shrubland, green – forest.

At the shrub stage (plot V, 35 years old), with a nearly complete vegetation cover, the community structure remained similar to that in plot IV. Both species and generic richness were almost unchanged compared to plot IV, with faunal similarity between the plots V and VI amounting to 65% (Sørensen-Dice index; Fig. 6B). Key changes included the disappearance of *Anurophorus alpinus* and a sharp decline in the abundance of *Ceratophysella dobrolyubovae*, while the proportion of grassland-associated species increased (*Willemia intermedia* Mills, 1934, *Metaphorura orestia* Pomorski, Skarżyński & Kaprus', 1998, *Lepidocyrtus violaceus* (Geoffroy, 1762)). The mean density dropped to 112.6 ± 20.0 SE ind./dm$^2$, and the community became polydominant, with five widespread species being involved, namely *Mesaphorura macrochaeta* (21%), *M. hylophila* Rusek, 1982 and *Parisotoma notabilis* (16% each), *Metaphorura orestia* (13%), and *Micranurida pygmaea* (12%). The only subdominant was *Isotoma caerulea* (8%), primarily found in pitfall traps. The remaining 15 species were rare or low in abundance. Beyond plot V, the species turnover along the chronosequence involved gradual incorporation of new taxa and sporadic reappearances of older ones, maintaining the faunal similarity at 50–60% (Fig. 6B).

With further vegetation development and the formation of *Betula-Salix* thickets with developed litter (plots VI–VII, 65–76 years old), more mesophilic litter-dwelling species emerged, namely *Pseudachorutes vitalii* Kaprus' & Weiner, 2009, *Pseudisotoma sensibilis* s.l. (Tullberg, 1876), *Pygmarrhopalites principalis* (Stach, 1945), *P. secundarius* (Gisin, 1958), *Fasciosminthurus* cf. *sauteri* (Nayrolles & Lienhard, 1990), and *Folsomia dovrensis* Fjellberg, 1976. Pitfall trapping revealed a high activity of *Pseudachorutes vitalii* on both plots, with 60% faunal similarity between them. Species richness and mean density increased slightly: from 22 species (plot VI) to 25 species (plot VII), and from 131.4 ± 55 SE ind./dm$^2$ to 156.2 ± 18 SE ind./dm$^2$, respectively, while the Shannon index decreased to 1.8. The community structure shifted again: a nearly equal dominance by *Mesaphorura critica* Ellis, 1976 (31%) and *Parisotoma notabilis* (28%) gradually gave way to the eudominance of *Parisotoma notabilis*, joined by *Folsomia dovrensis*.

Plot VIII, separated by a 112-year old stony moraine with scattered low *Betula* trees and *Juniperus* shrubs, featured herbaceous layer dominated by grassland communities, including extensive moss-lichen clearings with underlying ant nests, while the litter layer remained poorly developed. Despite maintaining 55% faunal similarity with previous shrub stages, the springtail community exhibited distinct characteristics: a sharp decline in abundance and activity of litter-dwelling species from earlier plots contrasted with an increase in grassland-associated taxa such as *Willowsia buski* (Lubbock, 1870), *Entomobrya nicoleti* (Lubbock, 1868), *Sphaeridia pumilis* (Krausbauer, 1898), and *Sminthurus viridis* Latreille, 1840, alongside the ant-associated species *Cyphoderus albinus* Nicolet, 1842 and *Entomobryoides purpurascens* (Packard, 1873). The proliferation of mosses seems to account for the first appearance in the successional series of a slow-moving Neanurinae representative (*Endonura* cf. *alticola*), while the discovery of the ephemeral *Mackenziella psocoides* Hammer, 1953, a globally rare species despite its wide distribution (Schneider & D'Haese, 2023), is of particular interest. Notably, the taxonomic diversity increased to 29 species and the Shannon index reached its maximum value (2.5) for the entire successional series, yet the mean density remained surprisingly low: 53.6 ± 12 SE ind./dm$^2$. The community retained a polydominant structure, but with an altered species composition: pitfall traps revealed high activity of *Fasciosminthurus* cf. *sauteri*, *Orchesella caucasica*, and *Isotoma caerulea* (juveniles of *Isotoma caerulea* constituting 21% soil-dwelling individuals), while *Mesaphorura macrochaeta* emerged as a secondary dominant (18%), and *Parosotoma notabilis* moved to subdominance (7%), being accompanied by *Mesaphorura tenuisensillata* (6%) and *Micranurida pygmaea* (5%).

Plot IX (135 years old), characterised by a dense, stunted *Betula-Salix* forest with a thick herbaceous cover and well-developed litter, demonstrated peculiar springtail assemblages. While retaining some grassland species, the community now incorporated typical forest-dwellers. *Micranurida pygmaea* and *Willemia anophthalma* Börner, 1910 increased in abundance, while *Parisotoma notabilis* achieved eudominance (54% total abundance). The mean density rose to 154.4 ± 39 SE ind./dm$^2$, with *Pseudachorutes vitalii* being particularly abundant in pitfall traps, likely due to the thick and moist litter layer. This stage marked the peak of the number of species (34 species) along the chronosequence, but no peak of the Shannon index (Fig. 7B).

Further along the chronosequence, subalpine grasslands regain dominance. On the > 150-year old surface (plot X), the landscape featured a mosaic of *Juniperus* groves, scattered young *Betula*, and *Rubus* thickets, and diverse herbaceous flowering plants (Fig. 3F). While species diversity remained nearly unchanged from the previous stage (33 species), the species composition differed, although it mainly contained taxa already observed earlier in the succession. Notable exceptions included a few habitat-characteristic species, namely *Sminthurinus alpinus* Gisin, 1953, *S. aureus* Lubbock, 1836, *Tomocerina minuta* (Tullberg, 1877), *Entomobrya* spp., and the *Hypogastrura* sp. *viatica*-group, although most of them were recorded as single specimens. The total springtail abundance remained relatively low: 75.2 ± 12 SE ind./dm$^2$. The community core consisted of dominant *Parisotoma notabilis* (32%), with equally abundant *Protaphorura sakatoi* (19%) and *Mesaphorura macrochaeta* (16%), while *Isotoma caerulea* (10%) occurred in a lower number of individuals. The remaining soil-dwelling springtails were exceptionally scarce. However, the surface activity showed an increased presence of Symphypleona taxa (*Sphaeridia pumilis* and *Fasciosminthurus* cf. *sauteri*), along with *Isotoma caerulea* and *Orchesella* spp.

Comparison of the springtail communities across the differently aged plots in the Bezengi valley using the Spearman rank correlation coefficient (Rho index) revealed that all study postglacial habitats showed considerable similarity in their springtail assemblages (Fig. 8B). The sample points from plots of different ages formed a poorly structured general cluster. ANOSIM analysis demonstrated statistically significant differences between groups ($p < 0.0001$), but only a moderate separation strength ($R = 0.338$), indicating that the graph primarily reflects general trends while potential distortions cannot be excluded. The Cody index increased gradually with surface age, from 3 to 16, but remained well below its theoretical maximum throughout the chronosequence (Fig. 9B).

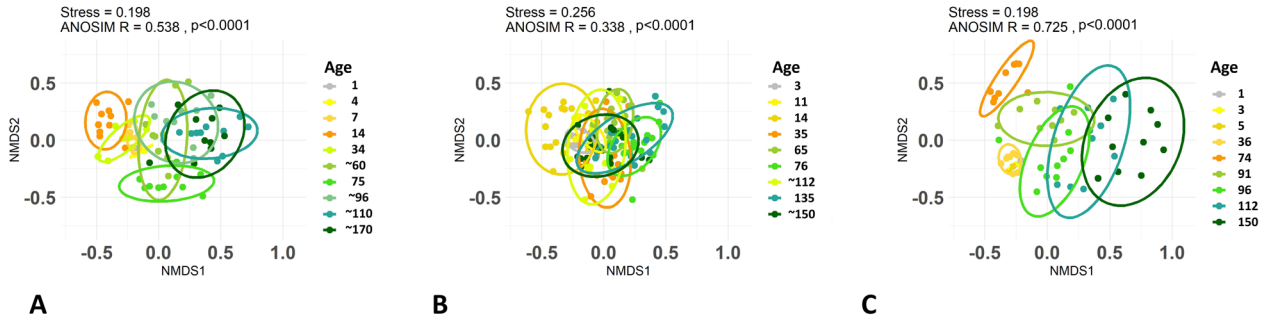


**Fig. 8.** Non-metric multidimensional scaling (NMDS) based on a distance matrix calculated using the Rho index (1–Spearman coefficient) for data obtained in the (A) Tsey glacier foreland, (B) Bezengi glacier foreland, and (C) Kashkatash glacier foreland (Greater Caucasus). Ellipses indicate 95% confidence intervals. Group means represent the number of plots.

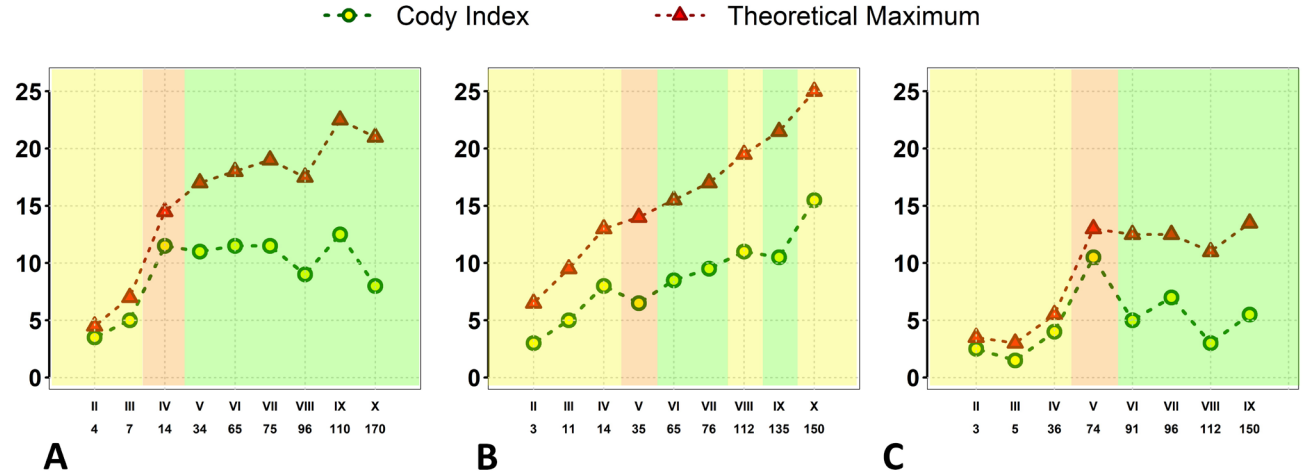


**Fig. 9.** Changes in Cody-index values across the chronosequences in Tsey glacier foreland (A), Bezengi glacier foreland (B), and Kashkatash glacier foreland (C) (Greater Caucasus). The x-axis represents surface age (years old), and the y-axis shows Cody-index values. Background colours indicate plant association types: yellow – grassland, orange – shrubland, green – forest.

In summary, the springtail community succession along the study transect in the Bezengi valley is characterised by frequent species turnovers, unstable dominance structures, fluctuating abundance (without distinct peaks), and a gradual increase in total species number (Fig. 5B, Fig. 7B, Table S4). The species composition of the first three youngest plots occupies clearly isolated positions. All of them show low similarity with other plots. Subsequent springtail communities of the shrubland plots IV and V are particularly similar, while assemblages from the older plots also show moderate similarity levels and consistently cluster together (Fig. 6B).

***Fauna and successional dynamics along the Kashkatash foreland***

The postglacial plots in the Kashkatash valley harboured 48 species from 31 genera and 11 families (Table S6). The most species-rich family was Isotomidae (29%), followed by Hypogastruridae (13%) and Neanuridae (12%). Entomobryidae and Tullbergiidae each accounted for 10% of the total species diversity, while Onychiuridae represented 8%, and Sminthuridae and Tomoceridae 6% each. The remaining three families (Dicyrtomidae, Neelidae, Orchesellidae) were represented by only a few species each.

Similar to the Bezengi foreland fauna, the chorological structure of Kashkatash springtail communities showed a high proportion of widely distributed species (cosmopolitan, Holarctic, and Palearctic), in total comprising 29% of the fauna. European species were relatively scarce (12%), while Caucasian endemics accounted for about 19%. The distribution ranges of 40% species remain unknown due to insufficient taxonomic knowledge of certain groups. The absolute dominant in abundance was *Parisotoma notabilis*, constituting 31% of all springtail populations across the study plots.

On open stony-sandy substrates near the glacier terminus (Plot I), the pioneer springtail complex included several species, mostly Isotomidae (*Folsomides* sp., *Proisotoma* sp., *Desoria* sp. *nivalis*-group), with a single specimen of *Supraphorura furcifera* (Börner, 1901) (Onychiuridae) recorded. Most species were represented by solitary juvenile specimens, suggesting possible accidental introduction from surrounding habitats. The only confirmed resident of Plot I was a *nivalis*-group species of *Desoria*, with a soil density of 8 ind./dm$^2$ and about 200 individuals (both adults and juveniles) captured in traps. This taxon appeared sporadically on younger plots (up to five years old), but disappeared completely further along the chronosequence. Notably, the *Desoria* sp. *nivalis*-group was also found living directly on the ice surface, morphologically similar to forms previously observed on pioneer plots at Bezengi.

In subsequent successional stages (3–5 years after deglaciation, plots II–III), where surfaces remained minimally affected by soil formation and consisted mainly of stony substrates with patchy vegetation, the springtail diversity remained low (3–4 species). The community structure differed markedly from the pioneer stage, dominated by the epigeic xerophilic species *Orchesella caucasica*, apparently well-adapted to low humidity and open habitats. The remaining fauna was extremely depauperate, consisting of occasional migrants or opportunistic species characteristic of early successional stages. The mean densities were remarkably low (2–4 ind./dm$^2$) on both plots.

The next surface studied (plot IV) was visually similar to previous stages (Fig. 4B), but substantially differed in age, because its formation began 36 years after deglaciation. The species richness of the springtail community doubled (reaching eight species), and the Shannon index increased four times (to 1.2), while the species complex characteristic of earlier successional stages disappeared completely. Although the cluster analysis of coenotic faunal similarity showed a rather isolated position of the springtail community on this plot (Fig. 6C), only two species could be considered unique inhabitants, namely *Entomobrya* sp. and *Sminthurus* cf. *multipunctatus* Schäffer, 1896, whereas exactly half of the species composition occurred almost continuously further along the chronosequence. These included *Micranurida pygmaea*, comprising 44% of the total community on this plot, *Lepidocyrtus* cf. *lignorum*, the most abundant in traps, *Parisotoma notabilis*, a ubiquitous species becoming dominant in more mature habitats; and *Tomocerus* sp., which also increased in abundance as vegetation developed. With an average density of 29 ind./dm$^2$ on the plot, the soil-dwelling community structure featured, besides *Micranurida pygmaea*, another dominant was *Folsomides parvulus* (38% of the total community), and the subdominants were *Tomocerus* sp. and *Parisotoma notabilis*, constituting 10% and 5% of the community, respectively.

Plot V (74 years old) is located on a relatively steep moraine slope and represents a shrub successional stage with young *Betula*, *Pinus* and *Salix* trees, where a litter layer is being actively formed and herbaceous vegetation is well-developed (Fig. 4C). This stage is characterised by peaks in both abundance and diversity indices of Collembola. Compared to the previous plot IV, the abundance increased 22 times, while species richness and the Shannon index rose 2.6-fold and 1.7-fold, respectively (Fig. 5C). Starting with plot V, the species diversity fluctuates between 17–22 species, with new species, genera and even families appearing (Fig. 7C). The faunal composition of this plot includes at least five unique species recorded only there, namely *Spatulosminthurus* sp., *Sminthurus caucasicus* Karsch, 1893, *Folsomia alpina* Kseneman, 1936, *Plutomurus* sp., and *Friesea* cf. *laszloi* Palacios-Vargas & Traser, 1996. For the first time, true soil-dwelling life forms from such genera as *Willemia*, *Protaphorura*, *Mesaphorura*, and *Oligaphorura* appear. Notably, *Oligaphorura absoloni* becomes eudominant in the soil community, accounting for 28% of the total abundance on plot V. Against this background of peak abundance and diversity, at least four species stand out with abundance ranging at 12–14%, including *Ceratophysella dobrolyubovae*, which is most abundant in soil traps.

Cluster analysis revealed 75% of the faunal similarity between plot V (74 years old) and plot VI (91 years old), despite the steep bedrock step separating both (Fig. 4D, Fig S1B). From this point onward, a clear slowdown in succession becomes apparent: the fauna includes only two unique species, each represented by few specimens. The community restructuring manifested in both an overall decrease in the mean density to 192 ind./dm$^2$ and a shift in dominance patterns. In the soil, the eurytopic species *Parisotoma notabilis*, characterised by a high genetic diversity in the Caucasus (Striuchkova et al., 2024), starts dominating completely. This species maintains its dominance through all subsequent successional stages. Among the subdominants, soil-dwelling life forms start prevailing.

Plots VII (96 years old) and VIII (112 years old), represented by young mixed forests, demonstrate 80% faunal similarity in their springtail communities (Fig. 6C). Both communities show a clear dominance structure: exactly half of the total abundance on both plots consists of *Parisotoma notabilis*, with *Vertagopus* sp. appearing as a secondary dominant (27% and 16% abundance, respectively). However, there are redistributions in the ratios of individual subdominants accounts for the observed change in the Shannon index. Of particular interest is a sharp increase in the abundance of *Pseudachorutes vitalii* and the overall increase in springtail density from 146 ind./dm$^2$ to 598 ind./dm$^2$. This may have been caused by the formation of a stable litter horizon.

The transition to a mature *Pinus sylvestris* forest with a ground cover (plot IX, 150 years old) is accompanied by a decrease in faunal similarity with previous stages to 60%. The community faces the reappearance of some xerophilic species from earlier successional stages, namely *Folsomides parvulus* and *Pseudoanurophorus binoculatus* Kseneman, 1934. The group's specificity is determined by such species as *Mesaphorura jirii* Rusek, 1982, *Micranurida pongei* Rusek, 1982, and *Folsomia dovrensis*. Nevertheless, *Parisotoma notabilis* maintains its eudominant status, while *Protaphorura* sp. aff. *subarctica* occupies the position of a secondary dominant, with *Pseudachorutes vitalii* remaining predominant in traps. The population density continues increasing and reaches 726 ind./dm$^2$.

According to multivariate ordination analysis, the springtail communities across the differently aged postglacial plots at Kashkatash seem to show a better structured organisation than at Bezengi (Fig. 8C). A significant separation between the springtail communities was revealed (ANOSIM: $R = 0.725$, $p < 0.001$), indicating substantial differences in community structure. The distribution of points corresponding to the springtail communities aligns well with both surface age and vegetation development. Pioneer complexes (I–IV) on sparsely vegetated plots are clearly distinct from more mature stages, which variation ranges substantially overlap. The intermediate successional stage (plot V) serves as a connecting link between these two extreme groups, reflecting the ongoing community restructuring in this phase. The Cody index rose sharply during the first 74 years of succession, approaching its theoretical maximum. Following the peak on the 74-year-old surface, a decreasing trend was observed in the older stages (Fig. 9C). A similar phenomenon was observed in the springtail communities of the Tsey foreland, where the turnover peaked much earlier, at 14-year-old surface only (Fig. 9A).

Thus, the Kashkatash glacier foreland demonstrates relatively clear dynamics of springtail communities across postglacial plots, mirroring ecosystem recovery stages and following the retreat of the Kashkatash Glacier. Early stages (0–5 years old) feature an extremely impoverished fauna (3–4 species), being represented by specialised pioneer taxa adapted to extreme conditions of open rocky substrates. With vegetation development and soil formation (36–74 years old), there is a sharp increase in species richness (up to 20 species) and abundance (up to 632 ind./dm$^2$), accompanied by a growing diversity of soil-dwelling life forms. During forest stages (96–112 years old), the abundance continues increasing while the community turnover slows down, with core dominants (*Parisotoma notabilis*) persisting though (Table S7).

***Comparing the efficiency of Tullgren funnels and pitfall trapping in the study forelands***

A comparative analysis revealed complementary efficiencies of the two methods in both forelands. At Bezengi, only 14 species (20% of the total number) were recorded using both techniques, albeit in various abundances. Pitfall trapping alone yielded at least 12 species (17%), and the identification of a further four species from soil samples was only possible due to adult specimens captured in the traps. When these four species are added to the trap-exclusive count, the effectiveness of pitfall trapping is increased accordingly. Thus, approximately 23% of the fauna would have been missed without pitfall trapping. Conversely, Tullgren funnels were more effective for assessing the abundance and for capturing soil-dwelling life forms, with 51% of the total fauna found by using this method alone.

A similar pattern was observed at Kashkatash. Here, 17 species (35%) were shared using both methods. Pitfall trapping alone yielded at least ten species (21%), enabling the identification of eight additional species from funnel samples and bringing the total fraction undetected by funnels to approximately 35%. Meanwhile, Tullgren funnels alone accounted for 44% of species.

The most pronounced disparity between the methods applied was observed at the earliest pioneer stages, prior to soil horizon formation and vegetation development. At Bezengi, Tullgren funnels recovered only a single *Entomobrya* specimen from the pioneer plot, whereas pitfall trapping yielded at least six species in substantial numbers (totalling 134 individuals). At the Kashkatash pioneer plot, funnel efficiency was slightly higher but still inferior to pitfall trapping, as they collected only juveniles, while traps primarily captured adults. However, as the soil profile developed, the effectiveness of Tullgren funnels for species detection increased sharply in both valleys.

## Discussion

To discuss our results on a broader regional scale, we incorporated the published data from the Tsey Glacier chronosequence in North Ossetia-Alania (Antipova & Babenko, 2024) into a comparative analysis of two glacial forelands in Kabardino-Balkaria. This integrated approach revealed distinct patterns of springtail succession at both regional and local scales and provided new insights into the group's faunal composition across the Caucasus. In total, 124 springtail species were recorded across the three study forelands. Despite the similar climatic conditions and geographic proximity of the Bezengi and Kashkatash glacial forelands, the structure of the springtail communities differs markedly even at the level of macrotaxon dominance. At Bezengi, the dominant and most species-rich families are Isotomidae, Entomobryidae, and Tullbergiidae, vs. Isotomidae, Hypogastruridae, and Neanuridae at Kashkatash. These differences may reflect habitat specifics and historical faunal developments. Both valleys share the predominance of Isotomidae, a pattern typical of European forest ecosystems (Kuznetsova, 1985, 2005; Taskaeva, 2005; Chernov et al., 2010; Shveenkova, 2022). However, all observed taxa represent the most diverse Collembola families, which are typical for a temperate climate (Kaprus', 2010).

The origin, stability, and specificity of pioneer species complexes are crucial in studying proglacial succession (Hågvar & Gobbi, 2022; Hågvar et al., 2024). Numerous explorations confirm that springtails are among the first colonisers of ice-free terrain, forming the basis for more complex trophic networks (Janetschek, 1949; Hodkinson et al., 2004; Hågvar, 2010; König et al., 2011; Raso et al., 2014; Hågvar & Pedersen, 2015; Sint et al., 2019; Hågvar & Gobbi, 2022; Antipova & Babenko, 2024; Makarova et al., 2024). European pioneer springtail assemblages are dominated by specialised Isotomidae species (Hågvar, 2010; Gwiazdowicz et al., 2020; Hågvar et al., 2020; Valle et al., 2022), some of which survive

directly on glacier surfaces (Buda et al., 2020; Valle et al., 2025). Their ecological requirements appear to be linked to the ice marginal zone, limiting dispersal beyond glacial influence (Hågvar & Gobbi, 2022). Proglacial springtail communities show substantial regional variations (Hågvar et al., 2020), a pattern corroborated by our data. Both forelands under study hosted springtails from the earliest succession stages, including sites adjacent to glacier fronts, this being consistent with observations in North Ossetia-Alania (Antipova & Babenko, 2024). However, the pioneer assemblages differed significantly: Bezengi's early succession (0–3 years old) supported a diversity several times higher than Kashkatash. Notably, some putative pioneer species occurred in a few specimens, possibly representing random colonists from adjacent slopes rather than true pioneers (Hågvar et al., 2024). Of particular interest seems to be the alpine *nivalis*-group (*Desoria* spp.), consistently recorded during initial succession in both valleys, but disappearing within three years after deglaciation. The dominance of this group near glacier fronts, with multiple age cohorts present, suggests a genuine pioneer status. This interpretation is reinforced by a morphologically similar taxon found at the Tsey Glacier (North Ossetia-Alania), namely *Desoria* sp. aff. *duodecimoculata* Denis 1927 (Antipova & Babenko, 2024). This taxon, belonging to the *nivalis*-group, has originally been described from European high altitudes (Potapov, 2001; Valle et al., 2025). Shared ecological specialisations imply a unique cryophilic pioneer complex adapted to ice-margin ecosystems, although integrative taxonomic studies are needed to confirm species identities (Valle et al., 2025).

The dynamics of succession processes also show local differences. Although the Cody index values increased with surface age in all forelands, indicating a continuous species turnover, the trajectories of these changes were fundamentally distinct. These differences likely reflect varying succession mechanisms. At the Tsey foreland, the community formed and stabilised rapidly within 14–34 years. In contrast, the succession at Bezengi was more extended, with community composition continuing to change even at the most mature stages. At Kashkatash, a sharp turning point in community dynamics was observed after 74 years, probably triggered off by a radical shift in environmental conditions that could have led to a massive species replacement and followed by a slowdown in succession. A comparison of the Cody index with its theoretical maximum shows the regional species pool as being sufficiently rich everywhere; however, this potential is realised differently depending on local conditions. The dynamics of the Shannon index further underscore the distinct successional pathways in various forelands. While peak index values occurred on surfaces of varying ages, all forelands showed nonlinear shifts in diversity following the shrub stage. This pattern seems to indicate a reorganisation of the community's dominant structure, characterised by a decrease in the evenness of abundance distribution.

At Bezengi, species richness rose gradually, peaking at later stages, whereas Kashkatash reached mature-community diversity within 74 years, this coinciding with shrub establishment (Fig. 7). A parallel acceleration occurred in the Tsey valley, where shrub-associated diversity peaks emerged on considerably younger surfaces (at 14 years old), being also accompanied by species richness spikes (Antipova & Babenko, 2024). Notably, elevated richness at this stage was observed not only for Collembola but also for many other invertebrates (see Babenko & Ponomarev, 2023; Makarova et al., 2024). At Bezengi, Tullgren funnels did not reveal significant fluctuations in springtail abundance throughout the succession (Fig. 5B). This pattern was observed both in individual seasonal sampling periods and in the combined dataset (Fig. S3). Moreover, the overall springtail abundance there was substantially lower than in other studied valleys, despite greater sampling effort. This may indicate fundamental differences in springtail population dynamics across the respective glacial forelands. Nevertheless, pitfall trapping recorded a mass emergence of *Ceratophysella dobrolyubovae* on the 14-year old surface (grassland stage), revealing a sharp increase in springtail abundance at this stage (Table S5). Thus, one might hypothesise that springtail community composition is linked to surface age rather than the type of developing plant community. In contrast, at Kashkatash, both taxonomic diversity and abundance increased sharply only after 74 years, coinciding with the shrubland phase, like in the Tsey foreland. This discrepancy suggests that springtail dynamics depend not just on surface age but also on valley-specific conditions.

Multivariate scaling (Fig. 8B,C) revealed more predictable successional transitions at

Kashkatash than at Bezengi, where the communities formed poorly differentiated clusters. Importantly, this weak clustering pattern at Bezengi was consistent with the analyses of both individual seasonal datasets and their combination (Fig. S2). This consistency strongly suggests that the observed low differentiation is a genuine characteristic of the springtail community in the Bezengi valley, rather than a methodological artifact arising from data pooling. At first glance, weak successional structuring of springtail communities across succession stages at Bezengi could be attributed to the complex influence of anthropogenic factors. Such impact might lead to simplified community structure, increased proportion of eurytopic species, reduced abundance of specialised taxa, and enhanced spatial heterogeneity of their distribution. The gentle slopes in the Bezengi valley are dominated by subalpine meadows historically used for agriculture (haymaking and grazing; Tsepkova, 2011; Uligova et al., 2019). However, major human impacts were limited to the lower gorge, avoiding our study area. The nearby mountaineering camp (2000 m a.s.l., operational since the 1960s) could theoretically contribute to recreational pressure. However, the long-term lacking river crossings to the left river bank as well as restriction of mass tourists suggest minimal actual impact. Therefore, anthropogenic impact seems an unlikely explanation for the observed changes in springtail community structure at Bezengi, although, in the Kashkatash valley, postglacial communities indeed recover with minimal human interference.

However, the key factor shaping the community structure may be the more complex orographic pattern of the Kashkatash valley, characterised by pronounced altitude gradients and the presence of rock steps (riegels). This creates a mosaic of microclimatic conditions that could promote sharp community differentiation. Of particular importance is the development of the mature pine forests in the Kashkatash valley that stabilises microclimatic parameters. These conditions likely determine the formation of a stable core of dominant species and facilitate the appearance of forest-dwelling springtails in the late succession stages.

Ecological studies on Collembola in the North Caucasus that would allow an assessment of how closely late-stage proglacial communities approach the complexes of low-mountain forests are extremely scarce. Intense research has been conducted in the late 1980s in coniferous forests of the Teberda State Nature Reserve (Karachay-Cherkessia, Russia) at 1300–2350 m a.s.l. (Dobrolyubova, 1984a,b, 1987, 1988, 1995). These data allow us to estimate only the level of species diversity and general population density of springtails, while comparison of species similarity is complicated by subsequent changes in the taxonomy of Collembola.

At Bezengi, the species diversity in late successional stages, despite the virtual absence of developed forests, reaches the levels recorded from the pine forests in the Teberda State Nature Reserve during single surveys (approximately 30 species). However, the mean population density of springtails is substantially lower there. At Kashkatash, the opposite pattern is observed: the diversity in the final proglacial pine forest fails to reach that in mature pine forests, while the abundance even exceeds the regional average of 580 ind./dm$^2$. The abundance may be related not so much to the peculiarities of proglacial territories as to the difference in absolute altitudes of the communities compared (Dobrolyubova, 1995).

More recent data on the Collembola communities in old-growth Caucasian forests are presented in Kuznetsova et al. (2019) for the North-Ossetian State Nature Reserve and Teberda State Nature Reserve (1600–1800 m a.s.l.), located 70–140 km from the glaciers we studied here. Importantly, part of this research was conducted in the Tsey Gorge, enabling local-scale comparisons with the data from the Tsey Glacier (Antipova & Babenko, 2024). Even after 170 years old of deglaciation, the springtail community of the Tsey foreland has still not reached the diversity level of lower-altitude forests, although the population density slightly exceeds the average values for regional pine forests. Comparisons of proglacial pine forests at Kashkatash with the results obtained by Kuznetsova et al. (2019) revealed a similar pattern.

Despite the relatively short geographical distance between the locations compared, an analysis of the species lists of Collembola from both valleys in Kabardino-Balkaria demonstrated a low faunal similarity with the communities recorded in the North-Ossetian State Nature Reserve and Teberda State Nature Reserve. This confirms the high environmental heterogeneity characteristic of mountain systems. Given the high local specificity of the Caucasian Collembola fauna, we believe that comparing proglacial sites with native

communities is to be conducted at a finer scale, for example, within a single gorge.

It should be emphasised that the differences observed in the diversity and, to some extent, the abundance of springtail assemblages were revealed primarily through combining the two most widely used methods in soil zoological research, i.e. Tullgren funnels and pitfall trapping. Numerous studies have been dedicated to the application and comparative effectiveness of these techniques for surveying the springtails (e.g. Babenko, 1985; Missa et al., 2008; Querner & Bruckner, 2010; Antipova & Babenko, 2023; Valle et al., 2023). Tullgren funnels have been well established to primarily detect soil-dwelling life forms, while the pitfall trapping mostly yield surface-active species, i.e. each method have its own limitations. Their effectiveness largely depends on the ratio of life forms in the community and the substrate type (Joosse, 1965; Potapov & Kuznetsova, 2011; Kawaue et al., 2016). For instance, in habitats with a developed soil profile, the extraction method is superior to pitfall trapping and often allows the detection of up to 70% of the fauna (Potapov & Kuznetsova, 2011). Overall, our data confirm that at Bezengi and Kashkatash, funnel extractions revealed 71% and 79% of the total fauna, respectively. However, when an adjustment is made for juvenile specimens, which could only be identified due to adults captured in the traps, these values drop to 65% for both valleys, which nevertheless remains a relatively high value.

It seems also important to note that pitfall trapping does not allow estimating the absolute abundance but rather records animal activity density. Therefore, data from using this method are difficult to interpret quantitatively and cannot be directly compared with extraction results (Joosse, 1965; Potapov & Kuznetsova, 2011). Consequently, all analyses of abundance in this study are based only on soil extraction samples and thus largely disregard surface-active springtails, which proportion can be substantial, especially on pioneer substrates. This represents a significant limitation. Since pioneer substrates are of particular interest for studying the early succession stages and colonisation processes, we consider it critical to supplement the traditional funnel techniques with pitfall trapping or other qualitative capture methods that are more effective for sandy-pebbly substrates (Mertens et al., 2007; Kawaue et al., 2016; Valle et al., 2023). This is particularly relevant for the initial stages of proglacial succession, prior to the formation of a closed vegetation cover.

## Conclusions

The differences observed in the patterns and rates of successional processes may be attributed to a complex of interrelated local factors, including microclimatic conditions, soil formation characteristics, and the orographic features of the valleys. Assessing these factors proves challenging due to their high spatial and temporal variability, coupled with insufficient long-term monitoring data. Furthermore, the intricate interplay between biotic and abiotic components in mountain ecosystems complicates the identification of key drivers governing succession.

Nevertheless, several consistent patterns emerge in postglacial springtail succession, notably the formation of highly specialised pioneer communities and gradual increases in diversity. The initial successional stages proceed in a relatively uniform way; the first colonisers are representatives of the *Desoria nivalis*-group adapted to life on recently deglaciated terrain. This pioneer community is rapidly replaced predominantly by widespread species that quickly attain substantial abundance in the developing ecosystem.

Despite valley-specific successional trajectories, a general trend of increasing species richness over time is evident. Fundamental questions remain unresolved; what represents the potential maximum diversity in high-altitude ecosystems and which are the terminal successional stages convergent across valleys, or do local conditions permanently render distinctive characteristics on the springtail communities? These questions demand further investigation, as understanding the regional succession dynamics proves crucial for predicting the responses of high-mountain ecosystems to climate changes.

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## Supporting Information

Additional data for the paper by Antipova et al. (2026) may be found in the **Supporting Information**.

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# ПРОГЛЯЦИАЛЬНЫЕ СУКЦЕССИИ ГРУППИРОВОК КОЛЛЕМБОЛ (COLLEMBOLA) ВДОЛЬ ОТСТУПАЮЩИХ ЛЕДНИКОВ КАБАРДИНО-БАЛКАРИИ, БОЛЬШОЙ КАВКАЗ, РОССИЯ

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С конца Малого ледникового периода отмечается глобальное сокращение ледников, темпы которого неуклонно возрастают. Ледниковые долины представляют собой удобные площадки для изучения закономерностей формирования биотических сообществ в ходе первичных сукцессий. Collembola (далее – коллемболы) играют, как правило, ключевую роль в первичных сукцессиях, являясь одними из первых колонизаторов освобождающихся ото льда территорий. Исследование посвящено изучению сукцессионных изменений в группировках коллембол (Collembola) в долинах рек Черека-Хуламского (Безенгийского) и Адылсу в условиях отступания ледников Безенги и Кашкаташ (Центральный Кавказ, Кабардино-Балкария, Россия). Черек-Хуламская долина расположена в пределах Кабардино-Балкарского высокогорного заповедника, а долина Адылсу входит в состав национального парка «Приэльбрусье». Цель работы – охарактеризовать видовой состав и структуру сообществ коллембол на разных стадиях сукцессии, а также выявить локальные особенности в динамике этих сообществ. Исследование проводилось на постгляциальных территориях с точно установленной хронологией дегляциации в пределах десяти участков возрастом от 1 до 150 лет, что позволило проследить поэтапное формирование группировок коллембол. Сбор материала осуществлялся комплексом методов, традиционных в почвенно-зоологической практике. В обеих долинах пионерные комплексы коллембол формируются сразу после отступления ледника и включают специализированные виды, такие как представители группы *nivalis* из рода *Desoria*, которые через 3–5 лет сменяются широко распространенными формами. Динамика сукцессионных процессов в долинах Безенги и Кашкаташ имеет существенные различия. В Безенги видовое богатство увеличивается постепенно, достигая максимума через 135 лет, тогда как в Кашкаташе резкий рост разнообразия отмечается уже через 74 года, на кустарниковой стадии зарастания. Плотность коллембол также варьирует неоднозначно: в Безенги она колеблется от 36 экземпляров на 1 экз./дм$^2$ (экз./дм$^2$) до 177 экз./дм$^2$, достигая максимального значения уже спустя 14 лет после дегляциации (на луговой стадии), тогда как в Кашкаташе первый заметный подъем численности до 632 экз./дм$^2$ наблюдается на 74-летней поверхности, а абсолютный максимум (726 экз./дм$^2$) достигается в 150-летних сосновых лесах. В долине Кашкаташа отмечается более выраженная дифференциация населения между ранними (пионерными) и поздними (лесными) стадиями сукцессии по сравнению с Безенги. При этом кардинальные изменения в сообществах наблюдаются при смене луговых биотопов кустарниковыми либо при переходе от кустарников к лесу. Сравнение с данными аналогичных исследований свидетельствует о немаловажной роли региональных особенностей конкретных горных ущелий. Региональные различия объясняются микроклиматическими, геоморфологическими и биотическими факторами. В Безенги, где преобладают субальпийские луга, подверженные антропогенному воздействию, сукцессия протекает более плавно, в то время как в Кашкаташе развитие сосновых лесов создает стабильные условия, способствующие формированию устойчивых сообществ. Существенное влияние оказывают орографические особенности – крутизна склонов и наличие ригелей определяют мозаичность условий и скорость сукцессионных изменений. Полученные сведения вносят вклад в понимание закономерностей формирования биотических сообществ горных экосистем в условиях дегляциации и подчеркивают необходимость дальнейших сравнительных исследований для прогнозирования изменений в условиях глобального потепления.

**Ключевые слова:** виды-пионеры, горные экосистемы, изменение климата, ледниковые предгорья, первичная сукцессия, хронопоследовательность, членистоногие