

New insights into Southern Caucasian glacial–interglacial climate conditions inferred from Quaternary gastropod fauna

CHRISTIANE RICHTER,^{1*} DANIEL WOLF,¹ FRANK WALTHER,² STEFAN MENG,³ LILIT SAHAKYAN,⁴ HAYK HOVAKIMYAN,⁴ TILMANN WOLPERT,⁵ MARKUS FUCHS⁵ and DOMINIK FAUST¹

¹Dresden University of Technology, Department of Physical Geography, Dresden, Germany

²University Hamburg, Centre of Natural History, Hamburg, Germany

³Ernst-Moritz-Arndt-University Greifswald, Department of Geology, Greifswald, Germany

⁴National Academy of Sciences of the Republic of Armenia, Department of Geology, Yerevan, Armenia

⁵Justus-Liebig-University Giessen, Gießen, Germany

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ABSTRACT: In the present study, we performed gastropod analyses on loess–palaeosol sequences from northeast Armenia (Southern Caucasia) covering at least three glacial–interglacial cycles. The elaborated ecostratigraphy shows significant patterns of species composition related to the succession of pedocomplexes and loess, respectively. Pedocomplexes included species that can be associated with high-grass to forest-steppe biomes, indicating increased humidity for these sections compared to the loess layers. In contrast, loess layers that relate to glacial periods are associated with gastropod species of semidesert environments with shrub- and shortgrass-steppes, indicating semiarid to arid conditions. Furthermore, the loess deposits do not show any evidence for cold-adapted gastropod species. Therefore, we suggest that average July temperatures in the study area were above 10 °C, even during periods of loess deposition. Consequently, we propose that the limiting factor for tree growth during glacial periods was aridity, rather than temperature. In addition, we observe environmental differences between the various glacial times, with our results indicating a trend towards steadily increasing aridity in Southern Caucasia across the Middle to Late Pleistocene. © 2020 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Armenia; land snails; molluscs; palaeosol; stratigraphy

Introduction

Loess deposits are important archives for the reconstruction of Quaternary environmental and climatic conditions. As a multitude of marine and terrestrial archives show, the Quaternary climate was characterised by strong fluctuations. Within loess deposits, these fluctuations led to the development of loess–palaeosol sequences (Pecsi and Richter, 1996; Antoine *et al.*, 2009; Meszner *et al.*, 2011; Marković *et al.*, 2015; Vlaminck *et al.*, 2018; Schaetzl *et al.*, 2018). There have been extensive studies on loess in recent decades, but global climate relations and their impact on local environmental conditions, especially on terrestrial ecosystems, leave fundamental questions unanswered (Zeeden *et al.*, 2018; Obrecht *et al.*, 2019). Recently, Wolf *et al.* (2016) described and investigated loess deposits in the Southern Caucasian region, thus closing a spatial gap in global loess research (see e.g. Jefferson *et al.*, 2003; Muhs and Bettis, 2003; Wolf *et al.*, 2016). These loess deposits from the northeastern foreland of the Lesser Caucasus provide excellent archives for investigation of the causal network between climatic conditions, sediment supply and soil formation processes. Pedogenesis for Middle to Late Pleistocene deposits in western and central Asia is usually associated with higher palaeotemperatures and elevated humidity (Dodonov and Baiguzina, 1995; Joannin *et al.*, 2010), which is consistent with the central

European loess belt. Palynological studies provided detailed information on environmental conditions and palaeovegetation in the wider study region. For the interglacial phases, there are indications of extensive occurrences of forests to forest-steppes for areas north of the Greater Caucasus (Bolikhovskaya and Molodkov, 2006) and at Lake Van (Litt *et al.*, 2014; Kwiecien *et al.*, 2014; Pickarski and Litt, 2017). However, since pollen can be transported over long distances and therefore may also be biased by fractionation, the information about glacial palaeovegetation is still uncertain. In addition, recent *n*-alkane studies conducted on loess–palaeosol sequences (LPS) in northeast Armenia show ambivalent results with regard to sedimentological proxies and bioproxy signals (Trigui *et al.*, 2019). Therefore, it is important to investigate several biological markers in order to compare environmental information and to approach a reliable reconstruction of palaeoecological conditions. Due to their frequent occurrence and good conservation in Pleistocene deposits, the analysis of (sub)fossil gastropods is a central part of Quaternary science (e.g. Ložek, 1990; Moine *et al.*, 2005, 2008; Penkman *et al.*, 2011; Limondin-Lozouet and Preece, 2014; Juříčková *et al.*, 2014; Rousseau *et al.*, 2007; Horsák *et al.*, 2019). Gastropods are very sensitive to environmental changes and are therefore particularly suitable for displaying palaeoecological conditions. However, research on palaeo-records for the study area has been very sparse so far. For Armenia, there were extensive investigations by Steklov (1966) on the occurrence of neogenic molluscs, but detailed studies on Quaternary

*Correspondence: Christiane Richter, as above.
E-mail: christiane_richter@tu-dresden.de

terrestrial gastropods in the Caucasus region are still pending. As ecosystems in this study area are unique and characterised by high endemism, our results will serve as an important bridge to establish the connection to gastropod records in neighbouring loess regions, such as the Carpathian Basin (e.g. Alexandrowicz *et al.*, 2002, 2014; Stoica *et al.*, 2007; Sümegi *et al.*, 2018; Obreht *et al.*, 2019) or Eastern Siberia (Danukalova *et al.*, 2007; Osipova and Danukalova, 2011; Danukalova *et al.*, 2015). One of the central questions of this study was whether it is possible to distinguish different biozones within the deposits. We also wanted to find out to what extent environmental and climate conditions can be derived from gastropod communities and biozones, respectively. Based on extensive gastropod studies, which were strongly focused on the succession of stratigraphic units according to Wolf *et al.* (2016), our results provide new insights into Pleistocene conditions associated with at least three glacial–interglacial cycles.

Study area

The study area is situated in the northeastern foothills of the Lesser Caucasus close to the Armenian village of Sevkar (Fig. 1 and Fig. A.1). The investigated outcrops, section Sevkar (680 m a.s.l.; 41°00′23″ N, 45°10′22″ E) and section BL (680 m a.s.l.; 41°01′32.9″ N, 45°10′00.7″ E), are located in the catchment of the river Aghstev. This river drains into the Azerbaijani Kura Basin, which is part of the tectonic depression between the Lesser Caucasus and the Greater Caucasus. The bedrock below the Quaternary deposits within the study area mainly consists of Mesozoic sediment and volcanic rock. Today, the study area is characterised by a humid, temperate climate with hot summers and an average annual precipitation of 507 mm, with a maximum of 85 mm in May and a minimum of 20 mm in December and January. The mean annual temperature is 11.1 °C, with the highest monthly average of 22.3 °C in summer and the lowest of –0.1 °C in winter.

Since the Pleistocene, the Caucasus mountain chain climatically separated Southern Caucasia from cold winds from the north. The tectonic depression between the Greater and Lesser Caucasus was thus a protected retreat during glacial periods, whereby hygrothermophilic tertiary relict flora are still preserved in the large-scale refuges of the Hyrcan and Colchic lowland areas (Zazanashvili *et al.* 2000, 2004). According to



Figure 1. Topographic map of the study region, with the red rectangle marking the study area (modified from maps-for-free.com). [Color figure can be viewed at wileyonlinelibrary.com]

Gobejshvili (2004), the low altitude and high drought of the Lesser Caucasus limited the maximum ice advance for the last glaciation to 1700 m a.s.l. Today, the mountain ridge of the Likh range (see Fig. 1) separates the study area from humid air masses from the Black Sea (Lydolph, 1977), leading to higher aridity in the Kura Basin.

Methods

Fieldwork

Based on detailed lithostratigraphic and geochemical investigations by Wolf *et al.* (2016), the two sections Sevkar and BL (see Wolf *et al.*, 2016) were selected for the mollusc analyses in order to have sequences as complete and undisturbed as possible. Mollusc samples were taken with a volume of 10 L sediment each, with the sample positions selected according to lithological units as shown in Figs 2 and 3. We collected 81 samples from the BL site over a height of 28 m and 18 samples from the Sevkar site over a height of 10 m. A detailed stratigraphic description of the Sevkar and BL sections was published by Wolf *et al.* (2016). A brief description of the lithofacies types (see Fig. 2 and 3) is given in Table 1.

Laboratory analysis

Extraction of gastropod shells

All samples were wet-sieved to the fraction > 500 µm to extract the shells. Since the sediment was highly aggregated by clay content of up to 60%, the samples had to be additionally prepared with a laboratory shaker for 3 to 10 h before sieving, depending on the material. Heavily soiled shells were cleaned with an ultrasonic bath. Extracted shells were determined and quantified using a stereomicroscope with 20- to 40-fold magnification. Pictures were processed with an Axiocam ICc1 microscope camera with z-stack capable software. Complete shells and diagnostic shell fragments were counted and offset against each other as described, for example, by Ložek (1990) and Richter *et al.* (2019).

Optically stimulated luminescence dating

First luminescence age estimates were performed for the section of BL, using the polymineral fine grain fraction (4–11 µm). To minimise age underestimation as a result of anomalous fading, a modified post-IR IRSL225 protocol was applied (Buylaert *et al.*, 2009) and no fading correction procedure was performed. Therefore, the two luminescence ages represent preliminary minimum age estimates and should be interpreted with caution. Further experimental details are given in the supporting information (Table A.1).

Generation of malacozones

The subdivision of the sections into malacozones was based on both absolute occurrence and abundance of certain taxa. The defined malacozones are presumed to correspond to ecostratigraphic zones and are named after the dominant members of the respective assemblages.

Statistical analyses

Cluster analysis

To determine the similarity between assemblages, a cluster analysis based on the Morisita similarity index (Morisita, 1959) was applied. Therefore, we considered both qualitative

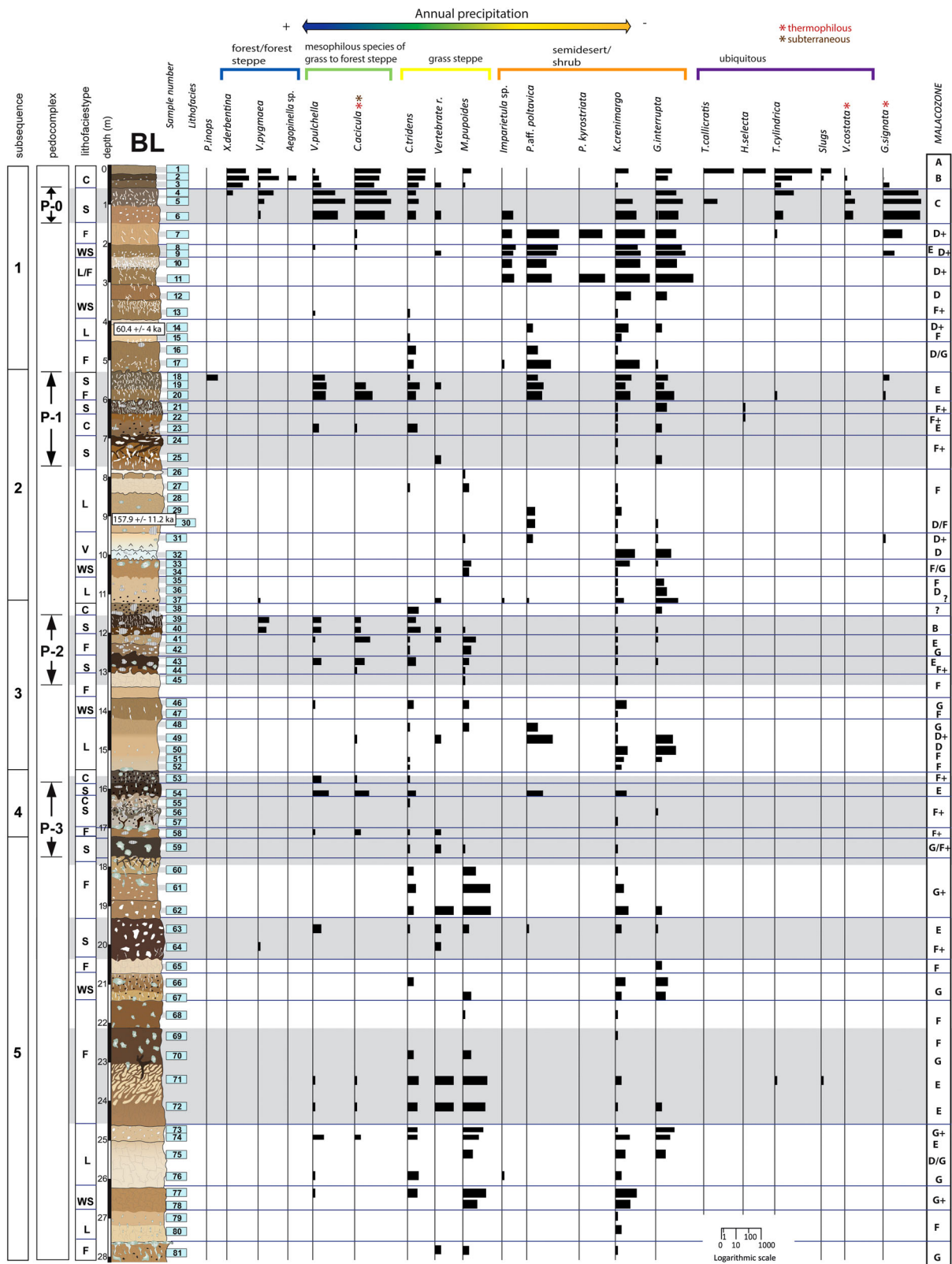


Figure 2. Mollusc diagram illustrating the species composition and abundances for gastropods of the BL section. The legend can be taken from Fig. 3. Malacozones are depicted according to the text (on the right). Coloured brackets at the top show the allocation of each taxon to ecological categorisations; the arrow bar visualises the implication on the associated moisture regime. We refer to the digital version for coloured figures. [Color figure can be viewed at wileyonlinelibrary.com]

presence–absence data and quantitative abundance data. The index was calculated for all sample pairs using the palaeontological statistics software PAST (published by Hammer, Harper and Ryan, 2001), and varies from 0 (no similarity) to 1 (full similarity). The results are presented as a dendrogram in which the most similar samples are combined into clusters.

Test of significance

We used the *t* test as the significance test. The statistical test procedure was used to quantify the relevance (significance) of gastropod species dependencies on environmental parameters (magnetic susceptibility, organic carbon content, granulometric

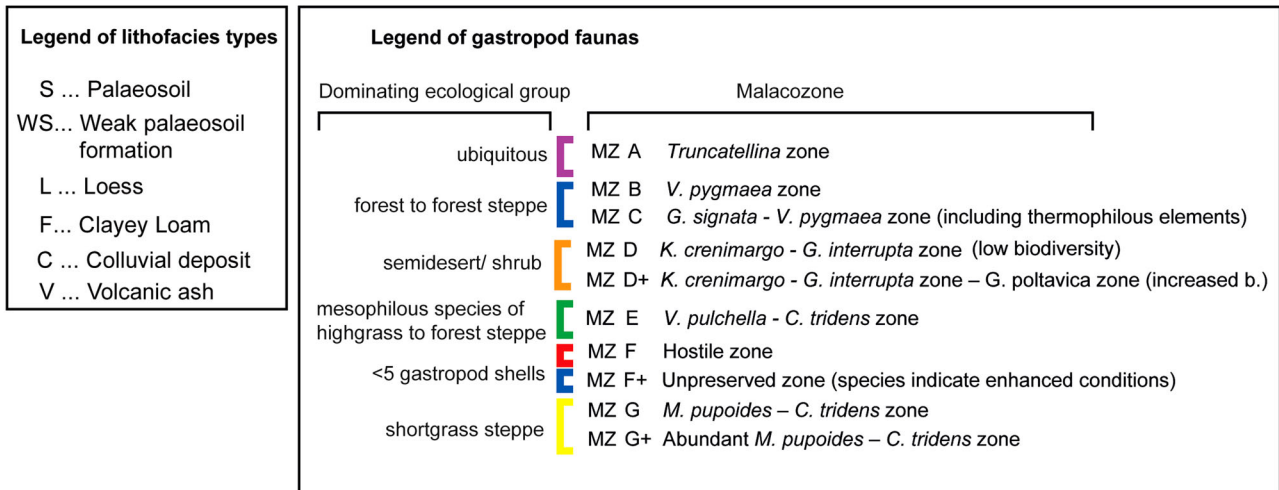
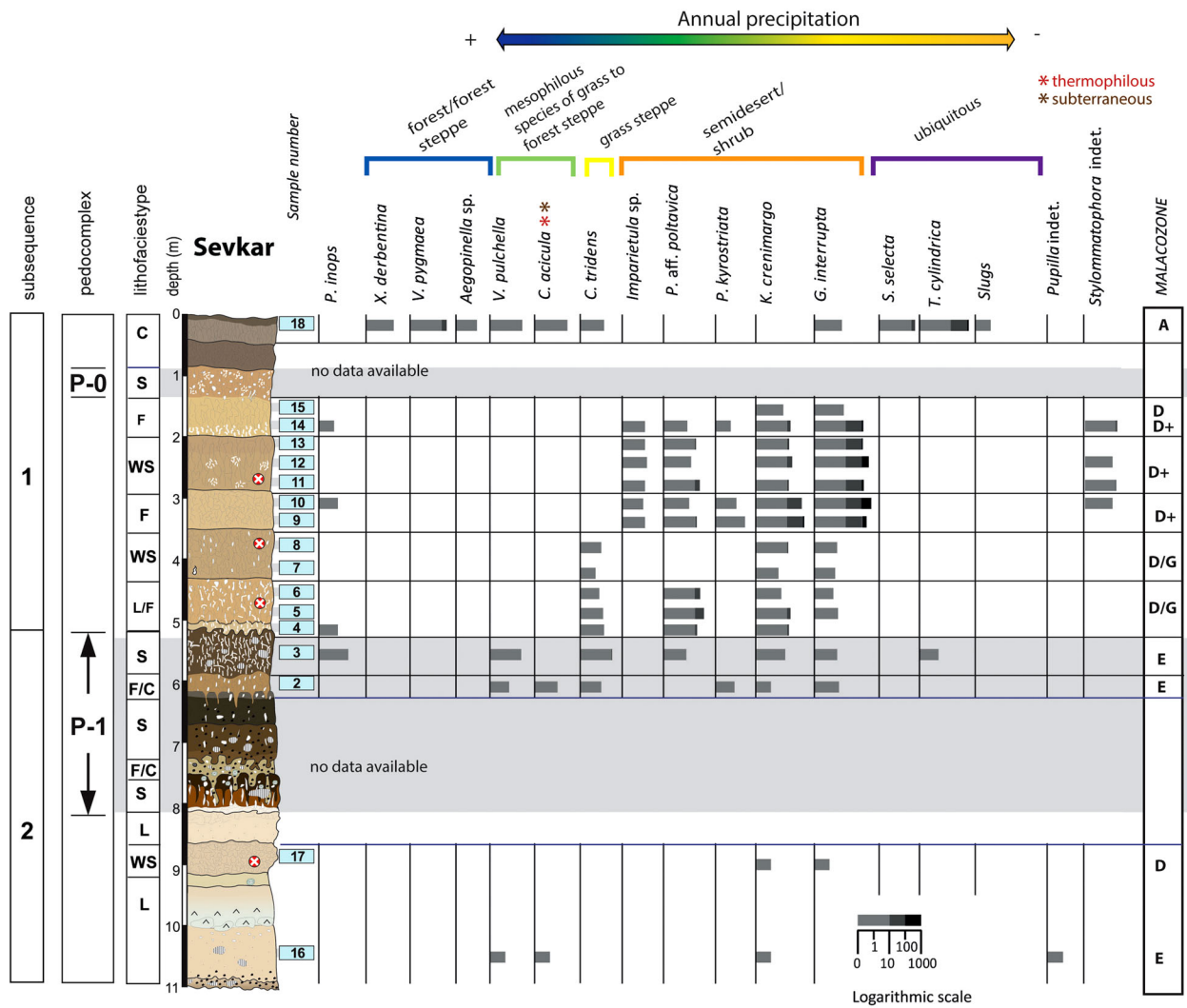


Figure 3. Mollusc diagram illustrating the species composition and abundances for gastropods of the Sevkar section. Malacozones are depicted according to the text (on the right). Coloured brackets at the top show the allocation of each taxon to ecological categorisations; the arrow bar visualises the implication on the associated moisture regime. [Color figure can be viewed at wileyonlinelibrary.com]

data, carbonate content, conductivity) extracted from Wolf *et al.* (2016). The modelling of the regression model and the determination of the relevant variables was performed using the palaeontological statistics software PAST (published by Hammer, Harper & Ryan, 2001). In Table A.2, significantly related pairs (level of significance $p < 0.05$) were marked with asterisks (***) strong correlation, ** moderate correlation, * weak correlation).

Results

Composition of investigated gastropod assemblages

The gastropod fauna of the investigated profile sites BL and Sevkar comprises at least 20 terrestrial species. In total, (sub) fossil shells and shell fragments of 10 296 individuals were found, belonging to the following taxa: *Aegopinella* indet.

Table 1. Description of lithofacies types in sections Sevkar and BL.

Lithofacies types		
Abbreviation	Description.	Interpretation
S	Dark-brown to blackish coloured loam to clay with clay content predominantly between 35 and 58% and 0.2 to 1.2% organic matter (Corg); partly containing reworked clay pebbles as well as in situ pedogenic features such as crumbly to prismatic aggregates, pedogenetic carbonate enrichments (calcareous pseudomycelia), bioturbation, root channels and numerous krotovinas	Palaeosol
WS	Weakly weathered, brownish coloured loamy silt to loam, in situ pedogenesis is indicated by gradually increasing loam content to the top	Weak palaeosol formation
L	Silt, containing carbonate and volcanic glass	Loess
V	Light bluish coloured material, predominantly volcanic glass	Tephra
C	Loam with incorporated dark rounded clay pebbles	Relocated colluvial material
F	Homogeneous clayey loam with sharp boundaries to the adjacent layers	Strongly weathered loess

(Lindholm, 1927), *Cecilioides acicula* (Müller, 1774), *Chondrula tridens* (Müller, 1774), *Gibbulinopsis interrupta* (Reinhardt in Martens, 1876), *Gibbulinopsis signata* (Mousson, 1873), *Imparietula* indet. (Lindholm, 1925), *Kalitinaia crenimargo* (Pfeiffer, 1848), *Multidentula pupoides* (Krynicky, 1833), *Pupilla bipapulata* (Akramowski, 1943), *Pupilla kyros-triata* (Walther & Hausdorf, 2014), *Pupilla inops* (Reinhardt, 1877), *Pupilla* aff. *poltavica* (Boettger, 1889), *Pupilla triplicata* (Studer, 1820), *Stenomphalia selecta* (Klika, 1894), *Truncatellina callicratis* (Scacchi, 1833), *Truncatellina cylindrica* (Férussac, 1807), *Vallonia costata* (Müller, 1774), *Vallonia pulchella* (Müller, 1774), *Vitrea pygmaea* (Boettger, 1880), *Xeropicta derbentina* (Krynicky, 1836) (see Fig. 4). The composition and abundance of species are depicted in Figs 2 and 3, while a detailed record is given in the supplementary material Tables A.3 and A.4. The depicted ecological information is discussed below (see 'Discussion').

Malacozonation

In order to detect significant changes in gastropod assemblages, we compared all samples of the same localities with respect to species composition, biodiversity, abundance and peak phases of certain taxa. In the following, eight different malacozones are defined and described. These correspond to an ecozonal biostratigraphy and usually reappear within the period investigated. Assemblages in colluvial layers must be treated with caution, as related taphocoenoses may contain both in situ and displaced shells. Likewise, the occurrence of *C. acicula* should be treated with caution, as this taxon is a subterranean species that can burrow 40 to 70 cm deep into the ground (e.g. Bonham, 2005). If one considers the expected shifts of the actual occurrence into overlying units, it seems that *C. acicula* occurs mainly at transitions from interglacial to glacial phases. Another possible scenario could be that the topsoils have been eroded and only the lower-lying subsoils are preserved. However, the shells of this species occur predominantly in connection with palaeosols, but within glacial deposits they hardly occur at all. Therefore, we assume that their presence is related to pedogenesis, or possibly to post-pedogenic transition phases towards drier conditions that provide enough organic matter as food source. Although *C. acicula* has not been used to define malacozones, significant occurrences of the species are similarly described below. The malacozones are composed as shown in Table 2.

Cluster analysis

The dendrogram (Fig. 5) shows the results of the cluster analysis (see above, 'Statistical analyses'). Typically associated species in terms of presence-absence data, frequencies and

peak phases are clustered and probably shared common habitats. We used the results to compare which ecological requirements overlap for the clustered species in order to determine the smallest common tolerance range. From this tolerance range, the palaeoenvironments were derived as discussed below (see 'Discussion').

Test of significance

In order to figure out dependencies between certain gastropod species and palaeoenvironmental parameters, we conducted a *t* test. The results show a significant relationship between *V. pygmaea* and increased carbon content ($p=0.00042027$), as well as between *M. pupoides* and increased clay content ($p=0.0038586$). In addition, there is a moderate dependence for *V. pulchella* ($p=0.027681$), *T. cylindrica* ($p=0.01176$), *X. derbentina* ($p=0.010833$), *G. signata* ($p=0.025623$) and *C. acicula* ($p=0.020867$) on elevated organic carbon content; and for *G. signata* ($p=0.012271$), *C. acicula* ($p=0.021892$) and *Imparietula* sp. ($p=0.029607$) on electrical conductivity in the lithological units. A detailed regression table is given in the supplementary material (Table A.2).

Subsequently, we plotted all samples together with their respective clay and organic carbon content in Fig. 6, as these parameters are most significantly related to the gastropod distributions. The ecological implications of the gastropod samples are indicated by differing signatures in Fig. 6.

Fig. 6 Diagram showing clay contents and organic carbon contents for all gastropod samples. The ecological implications of the gastropod samples were identified in the sample name labelling and by different signatures as shown in the legend. Different soil colours are distinguished and labelled as shown in the legend. We refer to the digital version for coloured figures.

Remains of non-mollusc organisms

Vertebrates

We found several tooth fragments, complete teeth and bones of small mammals. Remains that allowed a determination of taxa are listed in Table 3.

Arthropoda

Numerous arthropod remains have been found in the deposits, which could not be specified. However, the mandible of a beetle was found in sample 3 of the site BL, which can be assigned to the genus *Lucanus*. All eligible species of the genus live in warm, open, and relatively humid forests with *Quercus*, *Fagus* and *Carpinus*.



Figure 4. (1–2) *Harmozica selecta*⁽¹⁾ (a: apical view, b: apertural view, c: umbilical view), (3) *Xeropicta derbentina*⁽¹⁾, (4) *Chondrula tridens*⁽¹⁾, (5) *Vallonia costata*⁽²⁾, (6) *Vitrea pygmaea*⁽²⁾, (7) Inner plate of a slug, (8) *Microtus arvalis* (chewing surface of a molar tooth), (9) *Lucanus*⁽²⁾ indet. (mandible), (10–12) *Pupilla kyrostriata*⁽³⁾, (13–15) *Pupilla* aff. *poltavica*⁽³⁾, (16) *Truncatellina cylindrica*⁽¹⁾, (17–18) *Gibbulinopsis interrupta*⁽³⁾, (19–20) *Pupilla inops*⁽³⁾, (21) *Cecilioides acicula*⁽²⁾–⁽¹⁾ From colluvial layers BL1 and BL2; ⁽²⁾ From Holocene layers BL4 and BL5; ⁽³⁾ From last glacial deposits of BL. [Color figure can be viewed at wileyonlinelibrary.com]

Discussion

Derivation of palaeoecosystems based on the distribution of modern gastropods

Modern gastropod fauna of the study area

The Caucasus region supports a very rich and highly endemic snail fauna, in which evolution has taken place in situ over millions of years (Sysoev and Schileyko, 2009; Pokryszko

et al., 2011; Tarkhnishvili *et al.*, 2012). In addition, the Caucasus region is one of the biologically richest, but at the same time most threatened, regions on Earth and, according to Conservation International, one of the four Eurasian biodiversity hotspots (Myers *et al.*, 2000; Zazanashvil *et al.*, 2004). There are currently 318 land snail species listed, of which 66% are endemic (Walther *et al.*, 2014). This high number of endemics contributes to a low level of knowledge about the specific ecological requirements of the Caucasian gastropod fauna.

Table 2. Description of the malacozones in sections Sevkar and BL.**MZ A *Truncatellina* zone**

This is characterised by the highest biodiversity for the period under study. The dominant species are ubiquitous species such as *T. callicratis*, *S. selecta* and *T. cylindrica*. This zone shows a parallel occurrence of elements of different ecological groups such as *V. pygmaea* and *X. derbentina* representative of forest ecosystems, *V. pulchella* (and *C. acicula*) as mesophilous steppe elements, and *G. interrupta* and *K. crenimargo* as xerophilous steppe to semidesert species. The corresponding assemblages also include *M. pupoides*, slug remains and *C. tridens*.

MZ B *V. pygmaea* zone

This zone is characterised by the presence of the mesophilous species *V. pulchella* and *V. pygmaea*, the latter living in humid steppes to forest biotopes. Respective assemblages furthermore include *C. tridens* (*C. acicula*) and partially forest-steppe species such as *X. derbentina* and *Aegopinella* indet. This zone is characterised by a comparatively high biodiversity.

MZ C *G. signata* – *V. pygmaea* zone

Similar to malacozone B, but dominated by thermophilous elements such as *G. signata* (also high abundances of *C. acicula*). Respective assemblages furthermore include *G. interrupta* and *V. costata*.

MZ D *K. crenimargo* – *G. interrupta* zone

The malacofauna of this zone are limited to the occurrence of *K. crenimargo* and *G. interrupta*.

MZ D+K *K. crenimargo* – *G. interrupta* – *P. aff. poltavica* zone

This zone is characterised by a dominance of *K. crenimargo* and *G. interrupta* predominantly accompanied by *P. aff. poltavica*, with occasional presence of *P. kyrostriata*.

MZ E *V. pulchella* – *C. tridens* zone

This zone is characterised by the occurrence of the mesophilous species *V. pulchella* and the subterranean species *C. acicula*, which live in moist open ground to forest steppe biotopes, as well as the grassland species *C. tridens*, *M. pupoides* and *G. signata* sporadically appear. Respective assemblages furthermore include *K. crenimargo*, *G. interrupta* and occasionally *P. aff. poltavica*.

MZ F *Hostile* zone

Corresponding assemblages contain fewer than five individuals, suggesting hostile conditions.

MZ F+ *Unpreserved* zone

Corresponding assemblages contain fewer than five individuals, but contain species which indicate favourable conditions, including demanding species such as *V. pygmaea*, *V. pulchella* and *C. tridens*.

MZ G *M. pupoides* – *C. tridens* zone

This zone is characterised by the presence of *M. pupoides*, *K. crenimargo* and *C. tridens*. Occasionally *P. aff. poltavica* appears. These species are supposed to live on short-grass steppes with scattered shrub vegetation. Vertebrate remains are common.

MZ G+ *Abundant M. pupoides* – *C. tridens* zone

Similar to malacozone G, but additionally including *G. interrupta* and sporadically *V. pulchella*. This zone furthermore is differentiated from zone G by a generally higher biodiversity.

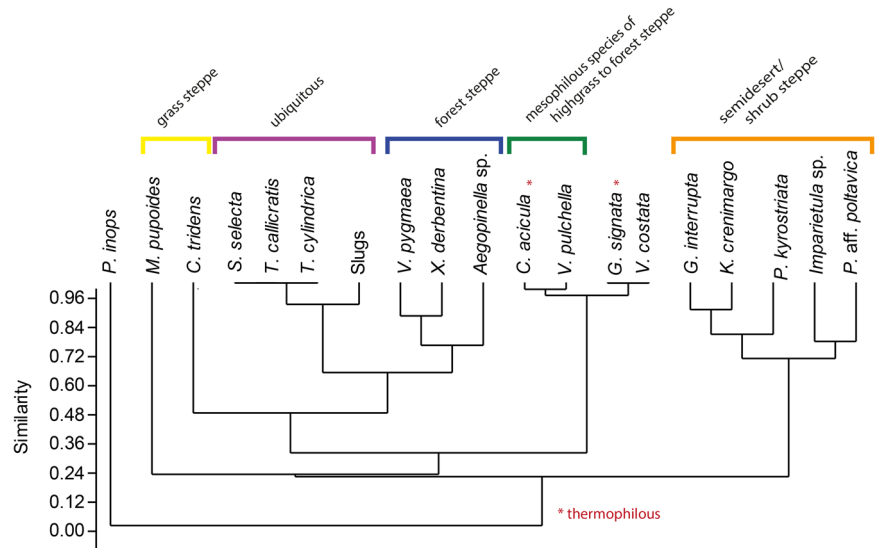
evolutionary conditions (dispersal ability, competition, topographic barriers and distance to refuges) influence the distribution of specific species. There is probably no environment today that corresponds to that of the Pleistocene, which was assumedly characterised by only weakly developed calcareous soils, strongly alternating climatic conditions and a hydrologic cycle that is different from the recent one. The comparison with current conditions must therefore always be viewed with some reservation. In order to detect palaeo-specific distribution anomalies and to identify typically associated species in the past, we conducted a cluster analysis. This analysis is able to identify peculiarities in the distribution of species that may occur due to local specifics or palaeoclimatic conditions, and to distinguish between natural and anthropogenic triggers. Based on this cluster analysis and the ecological categorisations by Akramovski (1949 and 1976), we have assigned the (sub-)fossil gastropod species to the modern Southern Caucasian vegetation types as shown in Fig. 7. These vegetation types correspond to orbiomes and partly include anthropogenic vegetation.

Climatic conditions derived from gastropod habitats

Based on the orographic ecological zones of Akramovski (1976) (Fig. 7), we have defined four ecological groups and three subgroups, which also find equivalents in the lateral geographic vegetation zones, corresponding to different climatic conditions. In the next step, we assigned these climate-induced zonobiomes to the climate classification by Troll and Paffen (Troll–Paffen annual seasonality categories, see Landsberg *et al.*, 1963) and suggest that palaeoclimatic conditions can be derived, as shown in Fig. 7. These climate conditions reflect a gradient in annual precipitation amounts as well as in average summer and winter temperatures. However, there are some problems in assigning current vegetation types to prehistoric environments. For example, it seems problematic to classify gastropod species, which live in the phryganoid vegetation today, as this vegetation type was probably created by degradation under pasture pressure and anthropogenic influences. Even these anthropogenic influences can hardly be quantified and vary locally. The pressure on the orbiomes in the continental central part of Southern Caucasia is particularly high for Armenia, since the largest part of the population settles there, which differs, for example, from Georgia and Azerbaijan, where people live more in the foothills and valleys (Dzhaoshvili, 1988). It has not been sufficiently investigated whether gastropod species living today in the young phryganoid vegetation should, under purely natural vegetation conditions, be allocated to semidesert shrub vegetation or whether phryganoid vegetation replaces more humid vegetation such as high-grass steppes or even forests. In addition, the forest-steppe ecosystems in the study region were extensively displaced by deforestation and the spread of pastures. In contrast, it can be assumed that forest steppes were possibly widespread in the study area during the Pleistocene interglacial periods. The distribution of gastropods in the sediments in combination with their ecological assignment is shown in the mollusc diagrams Figs 2 and 3. In addition, the mollusc spectrum in Fig. 8 shows the proportion of the ecological groups represented for each assemblage. Deviations in the assigned ecology between stratigraphic malacozones and the contained individual taxa are based on the concept of ecotones, in which the species common to the neighbouring assemblages can coexist (see Van der Maarel, 1990). Such overlaps are further reinforced by the fact that each stratum corresponds to a time period and not to a single time recording.

The most relevant literature in this context is the work of Akramovski (1949, 1976). The distribution of taxa is biased by a complex intersection of several factors. It is not yet fully understood which factors are best suited to explain the distribution of species within the Caucasus region; nevertheless, we listed the known ecological demands of each species in the appendix (Table A.5). In order to interpret the palaeo-record, we have assigned all relevant species to the vegetation zones as described by Akramovski (1976). The allocation therefore applies to the specific local conditions in Southern Caucasia and partly deviates from the distribution patterns of the respective species in other distribution areas. The distribution of species may differ due to local climatic differences such as continentality, i.e. in drier regions compared with more humid regions, etc. (see Horsák *et al.*, 2010). Additionally, different

Figure 5. Dendrogram showing typically associated gastropod species in the palaeo-record of the studied sections. Assumed ecological categorisations as discussed in the text are marked with brackets. [Color figure can be viewed at wileyonlinelibrary.com]



Gastropod assemblages in context with sedimentological parameters

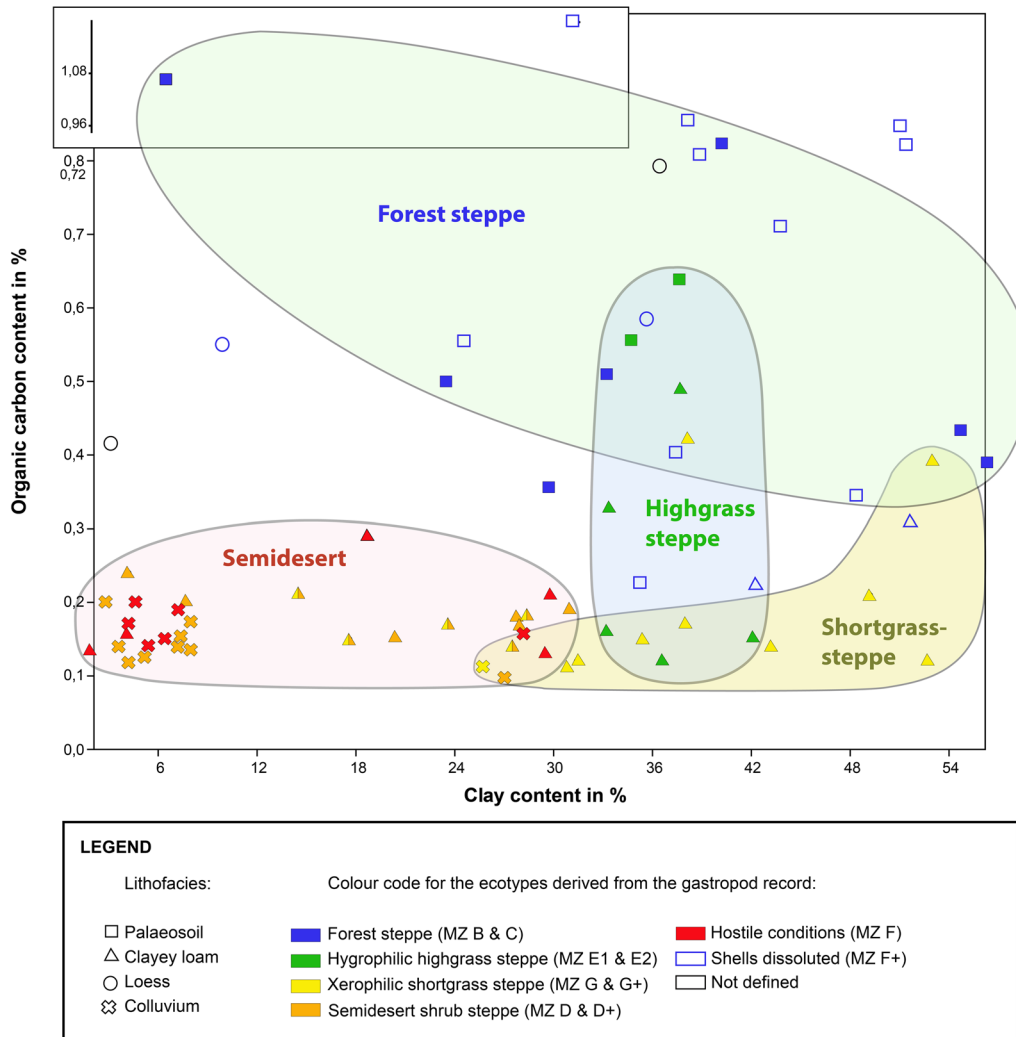


Figure 6. Diagram showing clay content and organic carbon content for all gastropod samples. The ecological implications of the gastropod samples were identified in the sample name labelling and by different signatures as shown in the legend. Different soil colours are distinguished and labelled as shown in the legend. We refer to the digital version for coloured figures. [Color figure can be viewed at wileyonlinelibrary.com]

Table 3. Vertebrate taxa of the palaeo-record represented by micro remains (teeth and bones) sorted by gastropod sample IDs of the profile site BL.

Sample	Taxon	Ecology
BL 6	sp. <i>Microtus</i> indet.	comp. <i>Microtus arvalis</i> (comp. Steiner, 1972)
BL 9	sp. <i>Microtus</i> indet.	comp. <i>Microtus arvalis</i>
BL 19	sp. <i>Mesocricetus brandti</i>	Common name Brandt's Hamster. 'The species occurs in dry open steppe habitat with cereals and wormwoods (<i>Artemisia absinthium</i>), or cereals and herbs. Sometimes consumes insects and other invertebrates. Often has burrows within colonies of <i>Microtus arvalis</i> and <i>Microtus socialis</i> .' (Kryštufek <i>et al.</i> , 2008)
BL 58	<i>Microtus arvalis</i>	Common name field vole, which apparently prefers open vegetation with a higher degree of grass cover and low values of tree cover, with a preference for open meadows (Miklos and Ziak, 2002) in Southern Caucasia. It lives in the alpine zone up to 3800 m near streams. It is found in a wide variety of open habitats including moist meadows, pastures, forest steppe and moist forest (Yigit <i>et al.</i> , 2016).
BL 59	sp. <i>Microtus</i> indet.	comp. <i>Microtus arvalis</i>
BL 81	Insectivor (<i>Erinaceomorpha</i> , <i>Soricomorpha</i> or <i>Chiroptera</i>)	Insectivorous (e.g. hedgehog, mole or bat)

What restricted tree growth during glacial phases – drought or cold?

Loess layers and interstadial palaeosols are characterised by the absence of gastropod species that live in forests and forest steppes. This indicates that there was apparently no tree growth during glacial times. Basically we consider two different types of treelines for the study area: a cold-induced alpine treeline and a drought-induced desert treeline (see Fig. 9). The desert treeline marks the area in which prolonged drought prevents tree growth. This is particularly the case in continental dry areas, where the vegetation period is typically interrupted by two periods of drought: once in summer by strong evaporation and once again in winter by the persistently solid state of the groundwater. In comparison, the alpine treeline occurs when mean summer temperatures are below 6–8 °C, biased by local specifics such as the prevalent bioclimate and occurring taxa (Körner and Paulsen, 2004; comp. D'Odorico *et al.*, 2013). This cold-induced treeline of the alpine and arctic regions approximates the 10 °C isotherm of average July temperatures (see *inter alia* Smithson *et al.*, 2013). In order to determine whether tree growth during glacial periods has been prevented by the advancement of the alpine treeline or the desert treeline towards the study sites, we compared prevalent gastropod species for the different glacial phases. We looked for species which currently typically inhabit the alpine zone of northeast Armenia such as *Anatolya brevior*, *Caucasigena eichwaldi armeniaca* and *Karabaghia bituberosa*, as these species should indicate an overall colder climate. However, the studied LPS did not contain these cold-adapted species. All the more, deposits and palaeosols linked to glacial times were represented by species such as *K. crenimargo*, *G. interrupta*, *P. kyrostriata*, *P. aff. Poltavica* and *Imparietula* indet., which today typically live in habitats of summer-warm semideserts (e.g. shrub steppes) and phryganoid vegetation. Nevertheless, it should be noted that gastropods are not primarily dependent on temperature, but rather on humidity conditions (see e.g. Obreht *et al.*, 2019). Therefore, in comparison with recent ranges of species, it is still problematic to find equivalent ecosystems that could correspond to those of the Pleistocene. Nevertheless, since the gastropod species of glacial times do not contain cold-adapted species but correspond to xerophilic communities occurring in high continental (cool temperate) semideserts and shrub steppes, we assume for these sites that tree growth during glacial times was not limited by the descent of the alpine treeline under cold conditions, but that the desert treeline

ascended from the Kura Basin and prevented tree growth due to aridity. Therefore, we suggest that the average July temperatures during glacial times in the study area were above 10 °C (see Fig. 7). The limiting factor for tree growth at the BL and Sevkar sites (630 m a.s.l.) was therefore most probably drought, rather than low annual temperatures. This is in good agreement with the lithostratigraphic record, which shows no indications of permafrost.

In addition, it is striking that also in the pedocomplexes and even the interglacial periods included therein, the palaeo-record does not contain typical forest species as they occur in forest ecosystems of the modern study region such as *Pomatias rivularis*, *Sphyradium doliolum* or *Acanthinula aculeata* (see Table A.6; see e.g. Cameron *et al.*, 2013). Instead, taxa in the palaeo-pedocomplexes rather contain species which can be allocated to forest steppes with scattered trees and barren xerophilic forests at the most. This raises the question of whether dense forest ecosystems did not occur or whether the related gastropod shells were not preserved. It is well known that snail shells are easier to dissolve under humid conditions and are mostly absent from interglacial palaeosols (see Ložek, 1990). The carbonate contents (Fig. 8) show that strong decalcification processes have taken place within the most intense palaeosols (linked to the mollusc samples BL 4 and BL 5 of pedocomplex P-0; BL 18, BL 19, BL 24 and BL 25 of pedocomplex P-1; BL 39, BL 40, BL 43 and BL 44 of pedocomplex P-2; and samples BL 54, BL 55, BL 58 and BL 59 of pedocomplex P-3) and related gastropod assemblages are characterised by a very small number of preserved shells (Malacozone F+). However, these shells are not restricted to the ecologically most robust species, but include more hygrophilous taxa such as *V. pulchella* or *V. pygmaea*. Given the small number of preserved shells, it is difficult to draw detailed conclusions about the palaeoecosystem. For example, the original assemblage could also have been dominated by forest species. This assumption may be reinforced by the fact that decalcification processes are distinct in forest ecosystems, which produce more aggressive fulvic and humic acids. Evidence for forest ecosystems is given by the remains of a stag beetle in sample BL 3 (Holocene age), which usually lives in oak forests (see above, 'Arthropoda'). However, the gastropod results do not yet allow a reliable interpretation of palaeoconditions for the pedocomplexes.

Differences between palaeosol complexes

To identify environmental conditions related to the different pedocomplexes, we compared all associated gastropod

<p>Vegetation zone after Akramowski (1976) corresponding to orobionomes/ orographic zonation</p>	<p>Subalpine and alpine zone Gastropods live in sheltered mountain meadows/ valley positions or hide under stones or shrub.</p>	<p>Forest zone Taxa represent a diverse gastropod fauna. Species live in shady to open forest biotopes such as leaf litter, clearings, rotten trees, stones or moss.</p>	<p>Meadow-steppe in other literature kept as part of the forest steppes, characterised by meadows with perennial forbs and solitary groups of trees predominantly <i>Quercus</i> and <i>Pinus</i></p>	<p>Steppe Gastropods hide in grasses which keep humidity also during summers, but also under stones and underground. Taxa include species that are also typical for semideserts with <i>Artemisia</i> shrub</p>	<p>Frigans and xerophilous forest (bush forest) Vegetation is not predominated by herbs but shrub with thorns and different species. Xerophilous forests manifest in scattered trees with xerophilous base vegetation but with no typical forest species among the grass</p>	<p>Semidesert Typically dominated by dry shrub vegetation. <i>Artemisia</i> shrub or stones serve as shelter. In more humid/cooler microhabitats, taxa can intersect with species generally found in</p>	
<p>Allocation of gastropod species from the palaeorecord</p>							
<p>Corresponding vegetation zone based on Troll-Paffen climate classification</p>	<p>Type I Tundra climates with cool summers (warmest month 6 to 10°C) and great winter cold (coldest month below 8°C);</p>	<p>Type III 5 Continental climates with cold winters (annual fluctuation 30-40°C, coldest month -10 to -20°C and moderately warm and moderately humid summers (warmest month 15 to 20°C); continental deciduous and broad-leaved and mixed forest as well as forest steppe</p>	<p>Type III 9 Wintercold humid steppe with minimum 6 humid month; vegetation period in spring and early summer; highgrass steppe with perennial forbs and xerophilous fauna elements; steppes with fertile</p>	<p>Type III 10 Semiarid wintercold steppe climate with lower annual precipitation than III 9. In Russia corresponds to zone of castanozems and short grass to dwarf shrub steppes</p>	<p>(??) Degraded, anthropogenic vegetation-corresponds to either 1) Semidesert shrub (pro: gastropods feed on plants) or 2) degraded grass to forest steppe (pro: gastropods sensitive to higher aridity linked to semidesert) 3)</p>	<p>Type III 12 wintercold desert steppes and deserts predominated by shrub-steppe (<i>Artemisia</i> steppe)</p>	
<p>Derived ecotype/ palaeo vegetation</p>	<p>(1) alpine meadow</p>	<p>(2) Forest - not represented</p>	<p>(3a) Forest steppe Ecotone of (2) and (3b)</p>	<p>(3b) Highgrass steppe</p>	<p>(3c) Shortgrass steppe</p>	<p>??</p>	<p>(4) Shrubsteppe</p>
<p>Climatic parameters</p>							

Figure 7. Categorisation of (orographic) vegetation zones after Akramowski (1976) with modern distributions of the gastropod taxa recorded for sequences Sevkar and BL. The chart shows the equivalent ecotypes with assumed palaeovegetation and related environmental conditions as derived from Troll-Paffen categories. The arrow-bars show mean annual temperatures and precipitation related to particular vegetation types (after Walter and Breckle, 1994). [Color figure can be viewed at wileyonlinelibrary.com]

assemblages. In addition, we investigated whether there is a relationship between malacologically derived ecotypes and palaeosol features. Potential dependencies were tested by a significance test (see ‘Test of significance’, above). Regarding this, species of relatively more humid ecosystems such as *X. derbentina*, *V. pulchella* and *V. pygmaea* significantly correlate with increased organic carbon content, while the grassland species *M. pupoides* and the presence of small mammal remains (see ‘Vertebrates’, above) significantly correlated with increased clay content. Based on these results we plotted clay together with organic carbon content for gastropod samples in combination with the malacozones and ecotypes that they are assumed to represent. The assemblages with the highest proportion of forest (steppe) species in parallel

show the highest content in organic carbon, suggesting a higher net primary productivity, biased by degradation and accumulation of the biomass. However, erosion of the uppermost soil layers should be considered. Since the loess deposits and palaeosols of the BL and Sevkar sections contain certain amounts of tephric material, the high organic content may also be caused by andosolisation. In andosols, the coupling of allophanes and organic matter forms bonds that are relatively stable, leading to (modern) soils that commonly show >6% of organic carbon in both A and B horizons, and the typical dark colour. Although the palaeosols in the studied LPS cannot generally be classified as andosols according to the World Reference Base for Soil Resources (FAO [Food and Agriculture Organization of the United Nations], 1998), it is assumed that

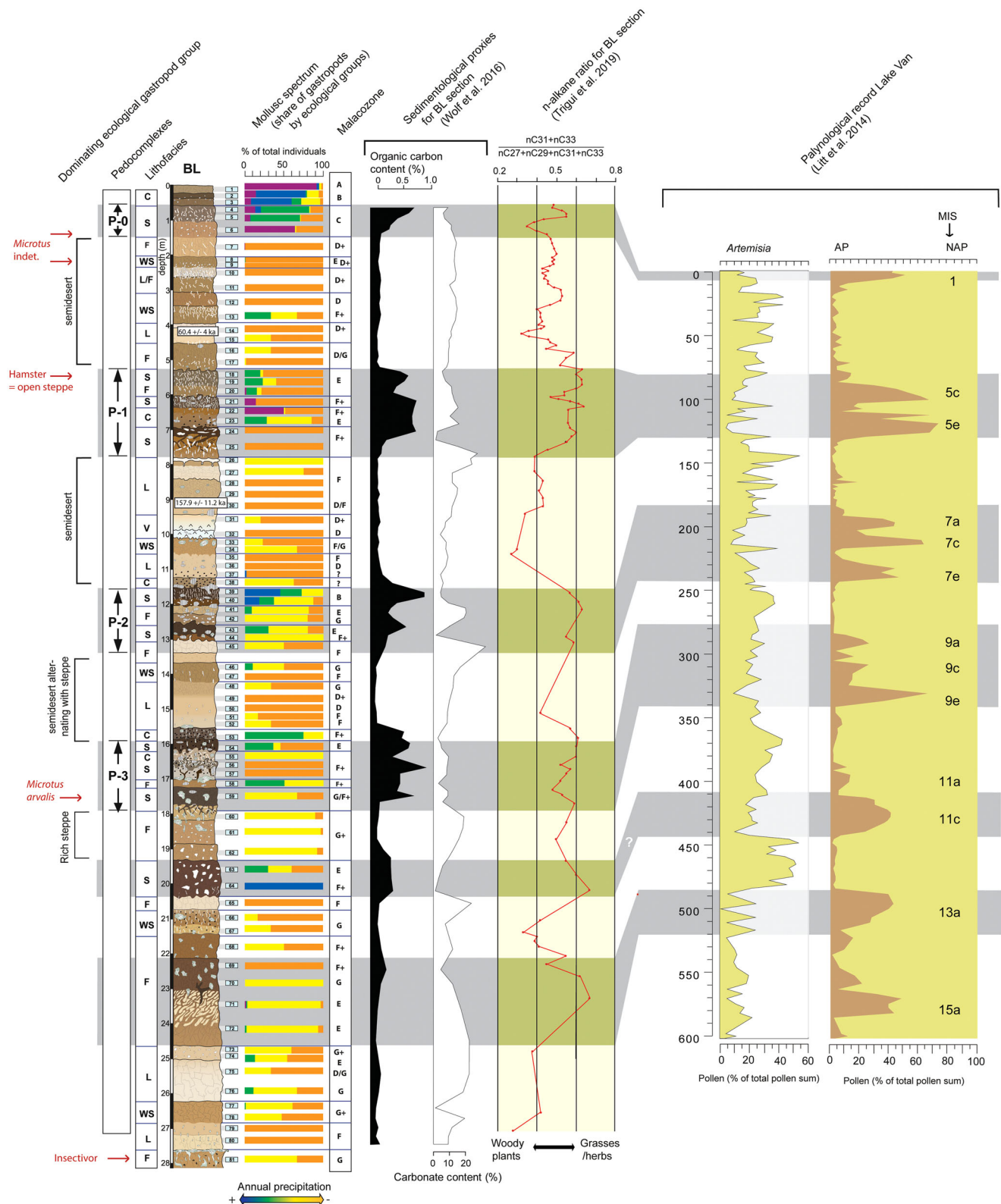


Figure 8. Gastropod results (Mollusc spectrum and malacozonation) and sedimentological parameters (lithofacies types, carbonate content and organic carbon content) for section BL correlated with *n*-alkane ratios of this study site (Trigui *et al.*, 2019) and palynological record of Litt *et al.* (2014) for Lake Van. The legend can be taken from the legend to Fig. 3. A more detailed description of the lithofacies types is given in the supplementary material Table A.5). We refer to the digital version for coloured figures. [Color figure can be viewed at wileyonlinelibrary.com]

they might be partly based on similar soil formation processes. Andosolic processes might also explain the unusually high clay content of the majority of the palaeosols, with values of up to 60%. Therefore, andosolic processes, under humid edaphic conditions, can lead to rapid weathering of amorphous volcanic material to allophanes. Even if the clay content

additionally varies depending on the initial composition of the source substrate (including content of tephric material; degree of reworking/relocation), it may also be an indicator for the intensity of weathering related to increased edaphic humidity. With respect to the compilation in Fig. 6, it appears that a general transition from arid semi-desert conditions to moister

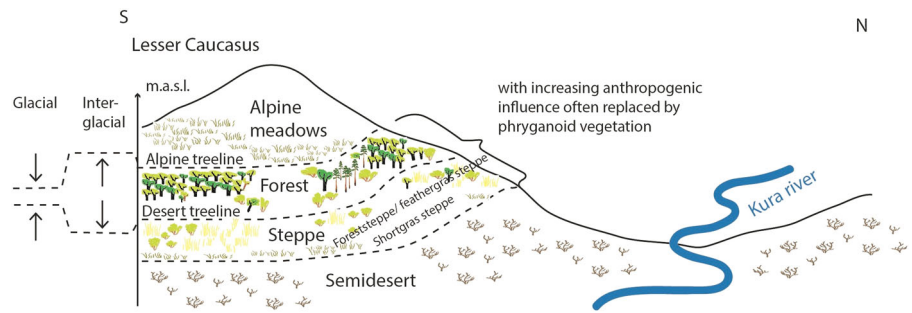


Figure 9 Proposed changes of treelines related to glacial-interglacial cycles in the study area. [Color figure can be viewed at wileyonlinelibrary.com]

steppe conditions coincides with palaeosol samples showing a clay content of more or less 30%. Palaeosols with clay content higher than 30% are related to short-grass steppe, high-grass steppe or forest steppe. The fact that soils linked to short-grass steppe have similarly high clay content to soils linked to forest steppe (Fig. 6) shows that the intensity of clay formation does not follow the trend of continual increase of edaphic humidity that is usually associated with the transition of the different vegetation types. We thus assume that as soon as slightly higher edaphic moisture becomes available, processes of mineral weathering and secondary clay formation accelerated rapidly as a result of the transformation of volcanic glass into amorphous clay minerals.

Comparison between sections Sevkar and BL

Comparing the mollusc data of the Sevkar and BL sections, the loess layers below P-1 for both sites are dominated by *K. crenimargo* and *G. interrupta*. The thanatocoenosis of the subsequent pedocomplex P-1, (Sevkar samples 2 and 3) can be assigned to malacozone E, characterised by high biodiversity and mesophilous species and coincides with BL samples 20 to 18. Between Sevkar samples 3 and 4 there is a strong decrease in biodiversity and species composition towards drier conditions, represented by semidesert and short-grass steppe species, which can equally be observed in BL samples 18 to 14. At both sites, these deposits are interrupted with a temporary absence of *P. aff. Poltavica* (Sevkar samples 7 and 8, BL 12 and BL 13), while the younger sediments (Sevkar samples 9 and 10) are characterised by a biodiverse semidesert shrub community and recurrence of *P. aff. poltavica*. The upper colluvial layer in both sections shows a similar taphocoenosis of ubiquitous species. Unlike BL, the Sevkar sequence does not contain shells of *G. signata*. However, the stratigraphic units of BL representing the peak phases of *G. signata* (malacozone B and C) have not been sampled at the Sevkar site. Nevertheless, solitary shells of *G. signata* in the lower part of BL might indicate that the latter, due to its south-southwesterly exposure, receives more solar radiation than the northeast-easterly exposed site of Sevkar, thus favouring the spread of the thermophilous *G. signata*. Altogether, the close match of associations in related stratigraphic units across both sections indicates that the succession and composition of malacozones seem to be consistent over the study area.

Reconstruction of palaeoecosystems and humidity conditions

The investigated LPS archive at least the last three glacial-interglacial cycles, although the temporal classification should be considered with caution, since luminescence dating is still in progress. With regard to a chronological assignment, it should also be noted that the temporal connection between marine isotope stages and the formation of loess deposits and

palaeosols, respectively, is still problematic, since the ongoing coupling processes and potential reaction shifts are not yet fully understood (Bolikhovskaya and Molodkov, 2006, Zeeden *et al.*, 2018). However, based on biostratigraphic patterns of the gastropod records and the first preliminary luminescence age estimates (see Figs 2 and 8), we assume that within the LPS, parts of the pedocomplexes (presumably the lowermost palaeosols of the pedocomplexes) refer to interglacial periods (i.e. MIS 5e, MIS 7, MIS 9). Based on their contained gastropod fauna, we furthermore assume these interglacial phases to be assigned to generally more humid conditions (see Fig. 8). The corresponding assemblages are represented by species, e.g. of the *V. pulchella* – *C. tridens* zone (MZ E) or *V. pygmaea* zone (MZ B), containing taxa that occur in high-grass and forest steppes (see Fig. 2). The parallel prevalence of vertebrate remains (e.g. in BL 6, BL 9, BL 13, BL 58 and 59) assigned to open grassland to forest-steppe ecosystems (see ‘Vertebrates’, above) supports these results. These ecosystems typically correspond to an average annual precipitation of above 300 mm. The increased humidity is consistent with the findings of Djamali *et al.* (2008), who investigated pollen records and concluded warmer and moister conditions for interglacials, indicated for Lake Urmia by forest-steppe species with *Quercus*, *Juniperus* and *Pistacia*. While mollusc shells are usually well preserved in pure (calcareous) loess, they are quickly corroded and dissolved in (fossil) soils and aeolian loams (see Ložek, 1990; Říhová *et al.*, 2018; ‘What restricted tree growth during glacial phases – drought or cold?’, above). For example, any data on stratigraphic features and soil analytical measurements indicate that the lowest palaeosol of pedocomplex P-1 at BL (depth 7–8 m, Fig. 2) represents a distinct interglacial soil. However, gastropod analyses revealed a poor preservation status of mollusc shells due to intense dissolution processes within the decalcified soil horizons. These preservation problems of gastropod shells in intensely developed palaeosols have also been observed in adjacent study areas such as the Ukrainian loess archives (Alexandrowicz *et al.*, 2014). Thus, a detailed statement about the ecosystems for these periods is complicated for now.

Fig. 9 Gastropod results (Mollusc spectrum and malacozonation) and sedimentological parameters (lithofaciess types, carbonate content and organic carbon content) for section BL correlated with n-alkane ratios of this study site (Trigui *et al.*, 2019) and palynological record of Litt *et al.* (2014) for Lake Van. A more detailed description of the lithofacies types is given in the supplementary material Tab. A.5). We refer to the digital version for coloured figures.

We furthermore assume, as discussed above, that glacial times related to loess deposition are generally characterised by drier conditions than the interglacial and interstadial periods linked to pedogenesis. In these dry phases, semidesert species such as *K. crenimargo*, *G. interrupta* and *Imparietula* indet. occur. However, we observed significant differences between different glacial-interglacial cycles. Deposits directly below pedocomplex P-3 that were tentatively assigned to MIS 10 (see

chronological allocation in Fig. 8) contain rich gastropod associations of the abundant *M. pupoides* – *C. tridens* zone (MZ G+) typical of dry harsh grassland ecosystems. They can probably be assigned to the xerophilous short-grass steppes. Mollusc associations presumably linked to the subsequent glacial period contemporaneous with MIS 8 (between pedocomplexes P-3 and P-2) are related to a mixture of *M. pupoides* – *C. tridens* fauna (MZ G) and *K. crenimargo* – *G. interrupta* – *P. aff. poltavica* zone (MZ D+). They indicate comparably more arid conditions including both species of short-grass steppe and shrub-steppe ecosystems. We assume that these communities lived in a transitional zone between both vegetation types, possibly characterised by dry grasslands with scattered *Artemisia* shrub. Within the last two glacials (MIS 2–4 and MIS 6), an increase in gastropod species typical of semidesert habitats can be observed. They are represented by the *K. crenimargo* – *G. interrupta* – *P. aff. poltavica* zone (MZ D+) and *K. crenimargo* – *G. interrupta* zone (MZ D). We suppose that these communities lived in dry shrubsteppes. We therefore assume an increase in drought towards semiarid to fully arid climatic conditions. Based on the absence of typical cold-resistant species (as discussed above), it is assumed that temperatures in July were above 10 °C (see ‘Comparison between sections Sevkar and BL’, above). A comparison of the two periods reveals a difference in the biodiversity of gastropods. Lower species richness in semidesert assemblages during MIS 6 compared with the last glacial period may have been caused by higher geomorphological instability and activity during MIS 6. The deposits which are assumedly linked to MIS 6 reveal increased fine sand content (see Wolf *et al.*, 2016). These may indicate higher wind strengths in dry phases on one hand, but on the other hand also an increased tephra input, since the fine sand grains consist predominantly of volcanic glass. An increased volcanic influence would also affect the gastropods, since, for example, in the tephra layer (sample BL 32) only the most adaptable and robust species, *G. interrupta* and *K. crenimargo*, survived (see Fig. 2). This species poverty, as in sample BL 32, in combination with a comparatively high abundance of the individual species is typical for stressed ecosystems. For the last glacial, in contrast, richer semidesert environments interlocked with occurrences of more hygrophilous species such as *V. pulchella* (samples BL 8 and BL 13) might point to sections that were not only characterised by stability but also by increased humidity. These fluctuations within the last glacial period have also been observed by Pickarski *et al.* (2015) for the Lake Van area and may indicate the succession of several stadial and interstadial periods. Overall, with respect to the different glacial periods characterised by loess deposition, we found clear indications for a steady increase in aridity from the bottom to the top of the LPS (see Fig. 8).

A similar situation has been reported for LPS in the southeast–central European lowlands of the Carpathian and Lower Danube Basins (Buggle *et al.*, 2013; Obrecht *et al.*, 2016, 2018). Our results reinforce an aridisation trend for the last three glacial cycles. Supplementary to these studies, we found the strongest evidence for aridisation among the different glacial phases. A possible explanation for this aridisation could be, as proposed *inter alia* by Buggle *et al.* (2013) and Obrecht (2016, 2019) the continual uplift of the Alpine–Himalayan orogenic belt (see Mosar *et al.*, 2010; Robl *et al.*, 2015), leading to increased rain shadows of the Eurasian mountain chains. The uplift of the Caucasus region is very heterogeneous. Assuming a mean uplift rate of about 1 mm a⁻¹ (see Mosar *et al.*, 2010), the total uplift across our sequence would be about 300 m, which might have biased peri-mountainous atmospheric patterns. Although we do not yet have a clear

explanation for the causes of this aridisation trend, our results, similar to those of Liang *et al.* (2016) for the Sea of Azov region, indicate a supra-regional trend (see Obrecht *et al.*, 2019). In this context, Eurasian archives should be further explored, including those outside the influence of orogens, in order to consolidate the data. This would help to find possible explanations for the fluctuations in atmospheric circulation, which may be related, for example, to variations in atmospheric composition or Milankovic cycles (see Zech *et al.*, 2011; Obrecht *et al.*, 2019).

In order to make a comparison with other bioproxies, we compared the results of this gastropod analysis with *n*-alkane ratios measured at the BL profile (Trigui *et al.*, 2019) and pollen records from Lake Van (Litt *et al.*, 2014) (see Fig. 8). In general, the results of the gastropod analysis match with the results shown by Litt *et al.* (2014) for Lake Van. Interglacial periods at Lake Van (situated 1600 m a.s.l.) show a significant presence of arboreal pollen indicating an oak steppe-forest with pistachio and juniper, while glacial periods were dominated by non-arboreal pollen implying dwarf-shrub steppe and desert-steppe ecosystems.

The results of the *n*-alkane analyses by Trigui *et al.* (2019) show a dominance of the alkane chain length *n*C₂₉ for periods characterised by loess deposition. Related *n*-alkane ratios are generally interpreted as an indication of dominating woody plant taxa. However, tree growth during glacial periods contradicts the absence of equivalent gastropod species. One explanation for these alkane signals could be that the alkane record is not dominated by the type of vegetation but by changing chemotaxic processes as has been observed by Marković *et al.* (2015) at loesses of the Carpathian Basin. This is contradicted, however, by the fact that the Serbian loess was constantly dominated by grass, whereas in BL (this study) we observed a significant decrease in grasses and herbs to as low as 0% in the glacial phases (BL sample 36, see Trigui *et al.*, 2019), indicating a significant change in vegetation type. Trigui *et al.* (2019) discuss several possible influences on the alkane signals and show their high level of complexity. However, since the gastropod species of the glacial deposits in BL today feed mainly on the xerophilous *Artemisia* shrub, we suspect that the glacial *n*-alkane signals might represent this shrub signal, too. As many shrub taxa have similar alkane chain lengths to trees, so *Artemisia* species show a dominance of *n*C₂₉ alkanes (Wang *et al.*, 2018). Furthermore, Wang *et al.* (2018) report that leaf wax *n*-alkane productions were similar for all species within the same genus and thus dominated by their phylogeny, independent of their plant functional types (Wang *et al.*, 2018) (also see Rao *et al.*, 2011). As a consequence, there would be no difference between *Artemisia* species which grow in a mesophilous forest and desert shrub species of *Artemisia*. The assumption of shrub domination during colder and drier phases would also be consistent with the palynological record of Litt *et al.* (2014), which shows a high proportion of *Artemisia* pollen during glacials. If we consider the recent vegetation of the driest locations of the Caucasus region and central Asian semideserts, it is similarly characterised by a high abundance of xerophilic *Artemisia* shrub species. In summary, based on the data available to date, we assume that the glacial periods in our study area were dominated by an *Artemisia* shrub steppe (e.g. with *Artemisia fragrans*).

Furthermore, the interglacial dominance of grass-derived *n*-alkanes within the pedocomplexes of the studied LPS (Trigui *et al.*, 2019) could confirm the presence of grass-dominated forest steppes rather than dense forest ecosystems. These initial results show that it is possible to derive more detailed information by examining and comparing several biological

proxies and thus to obtain an increasingly uniform picture of the palaeo-landscape.

Conclusion

In this study, we performed gastropod analyses on LPS in northeast Armenia (Southern Caucasus), covering at least three glacial–interglacial cycles. In order to derive information about palaeoecological conditions, we elaborated an ecostratigraphy and assigned corresponding malacozones to certain ecotypes. Accordingly, we assume more humid conditions during the formation of pedocomplexes that might be related to interglacial and subsequent interstadial phases. According to our results, the corresponding ecosystems were characterised by high-grass and forest steppe. In addition, we found no evidence of dense forest cover. However, it should be noted that the preservation of shells in intensively developed palaeosols can be poor, as decalcification processes, particularly under forest ecosystems, are likely. In contrast, loess and loess-like deposits that we relate to glacial (stadial) periods contain species communities that occur primarily in semidesert ecosystems today. For these deposits, we additionally found a trend towards steadily increasing drought from the bottom to the top of the profiles indicating progressive aridification throughout the Middle to Upper Pleistocene period. While the lower part of the LPS was dominated by rich short-grass steppe ecosystems, the middle part indicates ecosystems with both shrub steppe and short-grass steppe. Subsequently, deposits formed during MIS 6 seem to be related to species-poor shrub steppe and high geomorphologic activity, while deposits linked to the last glacial period indicate a species-rich shrub steppe intercalated with sections of stability and improved conditions for gastropods (series of stadials and interstadials). The results also suggest that ecosystems during glacial periods were more stressed by drought than by cold, and that average temperatures in July were presumably above 10°C all the time. We therefore propose for the studied sites that environmental changes at the transition from interglacial to glacial periods were not characterised by the descent of a cold-induced treeline from the alpine zone, but rather that a drought-induced treeline spread from the Kura Basin to the higher altitudes of our investigated sections. In this study, Quaternary gastropods were used as palaeo-proxies in the Caucasus region for the first time. Based on gastropod analyses, we were able to extract detailed information for this little-known loess distribution area, enabling the knowledge of European and Asian sediment archives to be merged. In the past, biological proxies and geochemical parameters often showed contradictory results, particularly in adjacent study areas. We therefore recommend that archives should always be interpreted with a multi-proxy approach, as especially biological proxies such as gastropods can help to obtain a coherent picture of the palaeo-landscape.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 Supporting information on the luminescence dating procedure.

Table S2 Regression table showing all gastropod species and their relation to environmental parameters of the palaeorecord. For all environmental parameters, the Pearson correlation coefficient (Coeff., left column) and the level of significance (p, right column) is indicated. Significant correlations are marked with *for weakly correlated, ** for moderately correlated *** strongly correlated.

Table S3 Palaeo-record of the gastropod species for the section BL.

Table S4 Palaeo-record of the gastropod species for the section Sevkar.

Table S5 Gastropod taxa included in the palaeo-record and related ecological information.

Table S6 Checklist of the shelled terrestrial molluscs of Tavush based on a literature survey, own collections and museum material.

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Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

Conflicts of interest. We have no conflicts of interest to declare.

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