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–paleosol sequences from northeast Armenia (Southern Caucasus) 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-steppe, 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 Caucasus 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–paleosol sequences (Pecsi and Richter, 1996; Antoine et al., 2009; Meszner et al., 2011; Markovic et al., 2015; Vlaminck et al., 2018; Schaeftl 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; Obreht 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-steps 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–paleosol 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. Łożek, 1990; Moine et al., 2005, 2008; Penkman et al., 2011; Limondin-Lozonet and Pourre, 2014; Jurčíková 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
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 terrestrial gastropods in the Caucasus region.

**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 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 thus a protected retreat during glacial periods, whereby hygrothermophilic tertiary relict flora are still preserved in the large-scale refuges of the Hyrkan and Colchic lowland areas (Zazanashvili et al. 2000, 2004). According to Gobejishvili (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 Likhi 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-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
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

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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.
The depicted ecological information is discussed below (see Fig. 4). The composition and abundance of species are depicted in Figs 2 and 3, while a 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.

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 biosтратigraphy 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 palaeosol formations (calcareous pseudomycelia), bioturbation, root channels and numerous krotovinas. Moreover, some taxa are represented by very few specimens, 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.

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

| Lithofacies types | Interpretation |
|-------------------|----------------|
| S                 | Palaeosol      |
| WS                | Weak palaeosol formation |
| L                 | Loess          |
| V                 | Tephras        |
| C                 | Relocated colluvial material |
| F                 | Strongly weathered loess |

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 biosтратigraphy 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 = 0.01716), 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.
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; Zazanashvili 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.

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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 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 anthropogenenic 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 orobiomes 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 orobiomes 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.
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]

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

Loess layers and interstitial 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 phases 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 Karabagha 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 C. eichwaldi armeniaca, which occurs in dry open steppe habitat with cereals and wormwoods (Artemisia absinthium), or cereals and herbs. Sometimes consumes insects and other invertebrates. Often has burrows within colonies of Microtus arvalis and Microtusoussulis.’ (Kryštul et al., 2008)

BL 58 Microtus arvalis
Common 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 et al., 2016).

BL 59 sp. Microtus indet.
comp. Microtus arvalis
BL 81 Insectivor (Erinaceomorpha, Soricomorpha or Chiroptera)
Insectivorous (e.g. hedgehog, mole or bat)

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. Microtus indet. | comp. Microtus arvalis (comp. Steiner, 1972) |
| BL 9   | sp. Microtus indet. | comp. Microtus arvalis |
| BL 19  | sp. Mesocricetus brandti | Common name Brandt’s Hamster. The species occurs in dry open steppe habitat with cereals and wormwoods (Artemisia absinthium), or cereals and herbs. Sometimes consumes insects and other invertebrates. Often has burrows within colonies of Microtus arvalis and Microtussocialis.’ (Kryštul et al., 2008) |
| BL 58  | Microtus arvalis | 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 et al., 2016). |
| BL 59  | sp. Microtus indet. | comp. Microtus arvalis |
| BL 81  | Insectivor (Erinaceomorpha, Soricomorpha or Chiroptera) | Insectivorous (e.g. hedgehog, mole or bat) |

Differences between palaeosol complexes
To identify environmental conditions related to the different pedocomplexes, we compared all associated gastropod...
Vegetation zone
Gastropod lives in sheltered mountain meadows/valley positions or hide under stones or shrub.

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 7. Categorisation of (orographic) vegetation zones after Akramovski (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]
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...
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 malacozones 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 (malacozones 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 successions 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 calcified 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 (Alexandro-wicz et al., 2014). Thus, a detailed statement about the ecosystems for these periods is complicated for now.

Fig. 9 Gastropod results (Mollusc spectrum and malacozone – sedimentological parameters (lithofacies, carbonate content and organic carbon content) for section BL correlated with n-alkane ratios of this study site (Trgui 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 shrubsteppe. 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; Obreht 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 Obreht (2016, 2019) the continual uplift of the Alpine–Himalayan orogenic belt (see Mosar et al., 2010; Rohlf 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 Obreht 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 Milankovcic cycles (see Zech et al., 2011; Obreht 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 nC₂₉ 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 Markovčić et al. (2015) at loessies 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 nC₂₉ 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 phylology, 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 glacial. 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 steppe 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 ecostatigraphy and assigned corresponding malacozones to certain ecotypes. Accordingly, we assume more humid conditions during the palaeoecological conditions, we elaborated an ecostratigraphy 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 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 (Coef., left column) and the level of significance (p, right column) is indicated. Significant correlations are marked with * for weakly correlated, ** for moderately correlated and *** 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 Sekvar.

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

Table S6 Checklist of the shell 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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