



Radiocarbon dated malacological records of two Late Pleistocene loess-paleosol sequences from SW-Hungary: Paleoecological inferences



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ABSTRACT

The two loess-paleosol sequences of Villánykövesd and Máza preserved specific paleoecological information of the Late Pleistocene environmental conditions in SW-Hungary. For malacological examinations, sampling of 12 cm intervals were used; homogenous amounts of sediment (ca. 5 kg) were collected. During the malacological examinations, more than 27,000 specimens were identified. Interpreting their environmental and climatic demands the paleoclimate and paleoenvironment of the last 80,000 years could be reconstructed. The results of the malacological investigations of Villánykövesd sequence indicated 5 malacological zones (MZs) by the snail species' dominant occurrence. All of the 5 MZs indicate mild climatic conditions with only one cooling phase. The mild climatic conditions were reconstructed by the high dominance of thermophilous species, especially *Pupilla triplicata*. This warmth loving, xerophilous and open vegetation preferring species is present in the entire sequence, which indicates a refuge area of *P. triplicata* around Villánykövesd. At the Máza sequence, 9 MZs could be allocated with mainly dominance of cold resistant species, indicating cooler climatic conditions than at Villánykövesd. The reason of the high ratio of cold resistant species and the high number of MZs could be the geographic exposition of the Máza sequence. The Máza sequence is located in a bench between higher and lower reliefs on the northern pediment area of Mecsek Mountains. This indicates the presence of a fluctuation zone for the snail species in the area of Máza sequence. The Late Pleistocene sequences possess different climatic and environmental conditions during same timeframe, therefore we highlight that the previously reconstructed mosaic-like environmental patters in the Carpathian Basin are real properties in the region.

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1. Introduction

Loessy sediments are widespread in the Carpathian Basin, covering ~10–15% of its area (Sümegi, 2001, 2005, 2007). For paleoecological reconstructions, these sediments are the most eligible from the Quaternary because these can provide various data from a relatively short timeframe. This is why loessy sediments of the Carpathian Basin are well investigated. The main investigation areas from Hungary are the Bácska loess plateau (Sümegi, 2005; Hupuczi and Sümegi, 2010; Sümegi et al., 2014), the high bank of the Danube River (Horváth, 1954; Hum, 1998; Hum and Sümegi, 2001; Újvári

et al., 2010, 2014, 2016; Bösken et al., 2017, in press), even the high bank of the Danube River in Croatia (Galović et al., 2009; Molnár and Sümegi, 2016; Molnár et al., 2010, 2011, 2014) and the Vojvodina loess plateau in Serbia (Marković et al., 2004, 2005, 2006, 2007, 2008). This paper represents mollusc-based paleoecological reconstructions from a less investigated area of Hungary, two loess-paleosol sequences of Villánykövesd and Máza from the SE part of the Transdanubia region (Fig. 1). Local and global climatic and paleoenvironmental effects are investigated in both sequences to obtain detailed results from the Late Pleistocene period.

2. Material and methods

It can be said that malacological examinations may produce the

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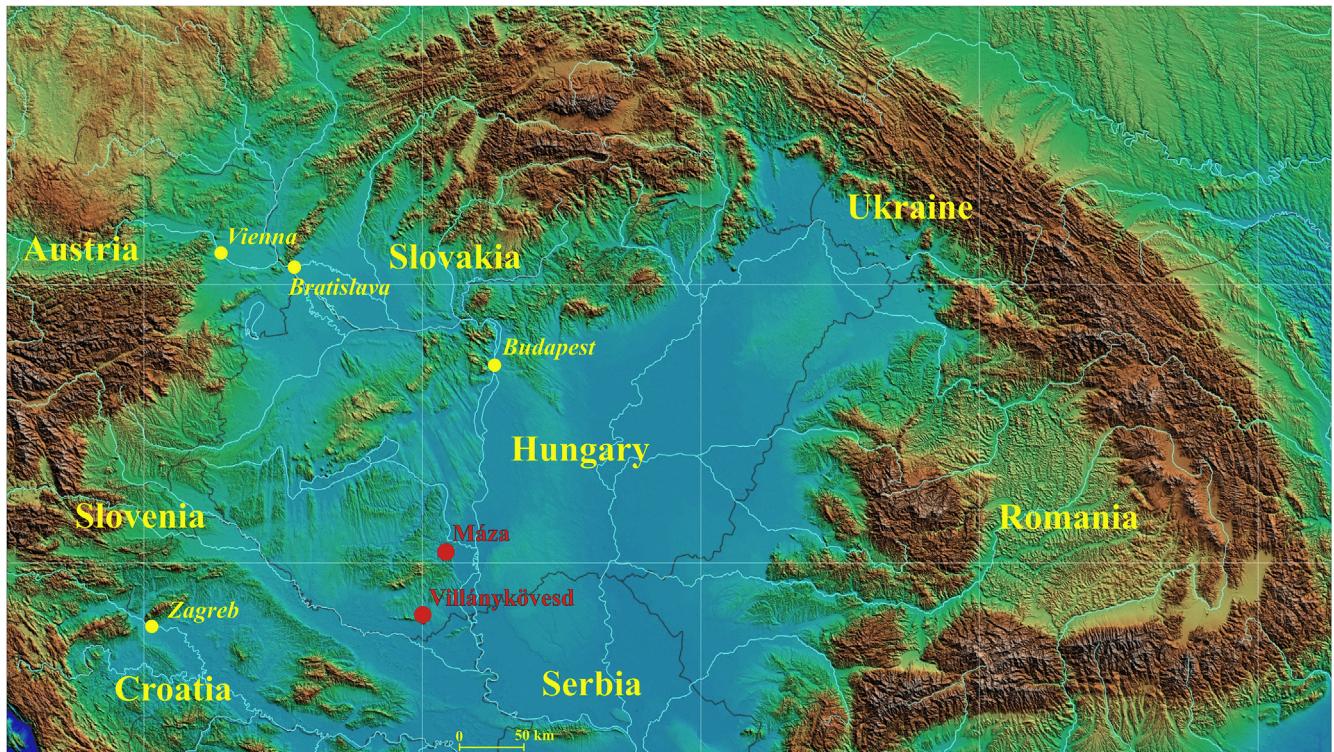


Fig. 1. Location of the investigated loess-paleosol profiles in Hungary and in the Carpathian Basin.

most comprehensive data about the climatic and environmental changes of a given area as reconstructed from loess. Certainly, high resolution (2–4 cm) examinations produce more accurate results from a shorter timeframe (Sümegi, 1996, 2003, 2004, 2007; Hupuczi and Sümegi, 2010; Persaitis and Sümegi, 2011; Böskén et al., 2017, *in press*). The employed sampling resolution for the examined sequences was 12 cm, because this resolution is used for the non-examined sequences.

The malacological examination contains 3 steps: sampling, wet-screening and shell identifying. After the sequence is cleaned, the sampling starts, ca. 5 kg (Sümegi, 1996) of sediment is collected from every 12 cm of the wall. Then every sample is wet-sieved through a 0.8 mm sieve. Before this procedure, the dry sediment is prepared with 10% concentrated H_2O_2 to clear the surface of the snail shells (Kroopp, 1983; Hum, 1998; Sümegi, 2001). Thereafter, the shells are assorted for identification. For this step, various identification books (Boycott, 1934; Soós L., 1943; Ant, 1963; Ložek, 1964; Kerney et al., 1983; Sysoev and Schileyko, 2009; Welter-Schultes, 2012) were used. Identification, and even the knowledge of each species' climatic and environmental demands, can aid creating paleoecological reconstruction datasets with rather simple mathematical calculations (Kroopp, 1983; Sümegi, 1989; Kroopp and Sümegi, 1992, 1995; Sümegi and Kroopp, 1995), such as the species' abundance and dominance relations per sample. By using these datasets, the snail species can be clustered into paleoecological groups such as climatic, humidity and vegetation cover demands (Sümegi and Kroopp, 1995; Sümegi, 1996, 2001). All three factors depend upon each other, and even the changes in other (less important) conditions.

Absolute ages are vital to place the examined sequences in geologic time (e.g. Sümegi, 2005). Therefore, radiocarbon dating was used to fulfil this requirement by the help of the DirectAMS Lab, Seattle, USA. Calibrating the raw age was done using the Calib 7.0.4 software by using intcal13.14c calibration curve with two

sigma ranges (Stuiver and Reimer, 1993). For the on-site lithologic description the Munsell Color Chart (Munsell, 1905) was employed. For making the figures, the Psimpoll software suite (Bennett, 1992) was used.

3. Geographical setting and lithology

Both loess-paleosol sequences are positioned west of the Danube River (right bank) in the south-eastern part of Transdanubia region in Hungary (Fig. 1). The loess-paleosol sequence of Villánykövesd is located between the villages of Villány and Villánykövesd, at the northernmost part of Villánykövesd brickyard ($45^{\circ}52'52.77''N$, $18^{\circ}26'23.40''E$). The elevation of the sequence is 127 m a.s.l., the height of the sequence was 805 cm. The Máza sequence is situated between the villages of Máza and Nagymányok, at the northern part of the mineyard of an old brick factory ($46^{\circ}17'09.58''N$, $18^{\circ}24'21.15''E$) at an altitude of 164 m a.s.l., the profile height is 864 cm.

For lithologic description the sediment layers were named using the Chinese loess-paleosol sequences' abbreviation terminology ("L" as loess and "S" as soil) (An et al., 1990; Ding et al., 2005; Gibbard and Cohen, 2008; Marković et al., 2008, 2015), further defined with the first letters of the sites: "V" for Villánykövesd, and "M" for Máza (Fig. 2).

4. Results

During the malacological examinations more than 27,000 snail shells were identified and clustered into three paleoecological groups by climatic- (thermophilous, mesophilous, cold-resistant and cryophilous), humidity- (xerophilous, mesophilous, sub-hygrophilous and hygrophilous) and vegetation cover demand (forest, ecotone and grassland dweller; Sümegi and Kroopp, 1995; Sümegi, 1996, 2001). By using these parameters, both sequences

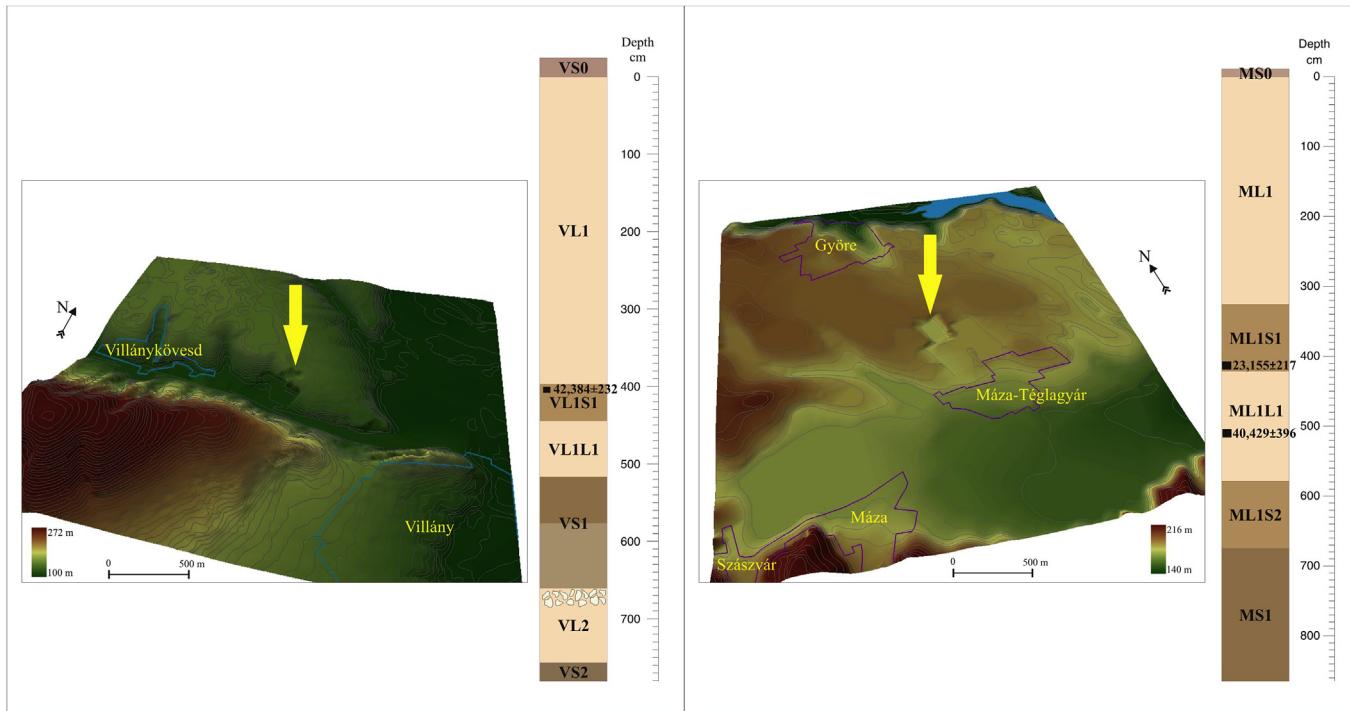


Fig. 2. 3D DTM of the sampled loess-paleosol sequences and their field lithology (yellow arrow shows the exact locations of the sequences; left: Villánykövesd, right: Máza). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

were divided into malacological zones (MZs), characterizing the climatic and environmental conditions in several depth/time frames.

4.1. Villánykövesd

The 65 samples of the Villánykövesd loess-paleosol sequence contained 11,657 identifiable snail shells of 26 terrestrial taxa. The average abundance distribution per sample was 179, but it was not uniformly distributed (Fig. 3). Observing the dominance relations of the species, it is clear that the dominance values of 2 snail species (the warmth loving and xerophilous *Pupilla triplicata* and the mesophilous *Vallonia costata*) are prevalent. A similar increased dominance of these two species are noticeable at the Petrovaradin loess-paleosol sequence, in Serbia (Marković et al., 2005). At Villánykövesd, 5 malacological zones (MZs) could be identified (Figs. 3 and 4).

MZ-1 spans the lowermost part of the sequence (780–680 cm). At this zone, the dominance of thermophilous and open vegetation preferring species (*P. triplicata*, *Helicopsis striata*, *Chondrula tridens*, *Granaria frumentum*) is clear. Besides these, *V. costata* also appeared with rather high dominance values. Summarizing, this MZ indicates steppe vegetation with smaller forested areas supported by the presence of forest-dweller species, such as *Vitrea subrimata* and *Limax* sp.

MZ-2 corresponds to the VS1 paleosol layer (680–515 cm), with continuous domination of *P. triplicata* and *H. striata*, and the disappearance of *V. costata*. In addition, mesophilous and moisture preferring species were present (*Vallonia pulchella*, *Nesovitrea hammonis*). This indicates increased humidity, possibly owing to more extended forest areas or the appearance of long-grass steppe areas.

MZ-3 spans from 515 to 385 cm, framing the VL1S1 and VL1L2 layers. It can be divided into 3 sub-zones according to the dominance changes of *V. costata* and *V. pulchella*. In the middle part of the

zone most of warmth-loving species disappear, and clear dominance of *V. pulchella* and *Limax* species arise (Fig. 3). This means lower temperatures, higher humidity and probably a forestation period at this division of MZ-3. This level may correspond to GS 13 interstadial, around 46,000–48,000 years ago (Björck et al., 1998).

At the uppermost part of the zone, a radiocarbon age of $42,384 \pm 232$ cal BP years is established, which means that the VL1S1 paleosol layer may correlate with the GI 12 interstadial period (Björck et al., 1998; Tzedakis et al., 2006). Following the line, the VS1 paleosol layer, compared with Chinese results (Ding et al., 2005), could estimate to MIS 3 interstadial, between 47,000 and 52,000 years (Björck et al., 1998; Gibbard and Cohen, 2008).

In MZ-4 (385–275 cm) a slight cold period is indicated by warmth-loving species abundance reduction to around 40–50% (Fig. 4). In addition, several cold-resistant and cryophilous species (*Trocholus hispidus* and *Vertigo pygmaea*) occurred. Among the mesophilous species besides *V. costata* forest and ecotone species (*Cochlicopa lubrica*, *Nesovitrea hammonis*, *Pucntum pygmaeum* and *Limax* species) occurred. Although the number of sub- and hygrophilous and forest-dwelling species increased, their aggregated abundance is still lower than for the open vegetation dwelling species. During this weak cold period, the open environment prevailed, but the area of forests and even the ecotone area increased.

MZ-5 is located between 275 cm and the Holocene soil with clear dominance of warmth-loving species (besides *H. striata* and *C. tridens* the *P. triplicata* is outstanding). The mesophilous species *V. costata* appeared with significant abundance values, and even some forest species (*Clausilia pumila*, *Vallonia enniensis*, *N. hammonis* and *Limax* species) are present, proving that the steppe-forest mosaic environment persisted until the Holocene.

Two interesting dominance changes could be observed in MZ-5: a decrease of *P. triplicata* (from 75% to 20%) and increase of *V. costata* (from 15% to 60%) in two levels around 250 cm (ca. 25–26,000 years ago) and 110 cm (ca. 15–16,000 years ago). The presence of *T. hispidus* and *Aegopinella ressmanni* species in these levels refer to

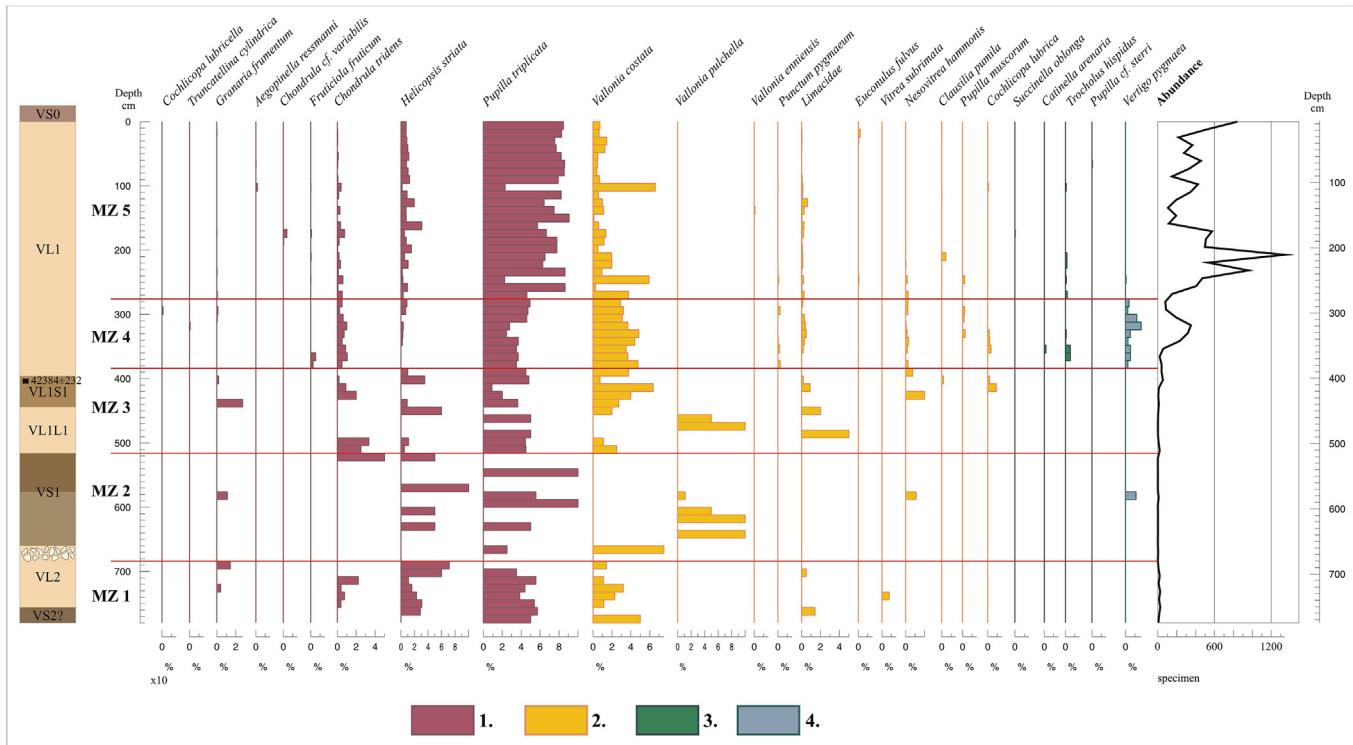


Fig. 3. Results of the malacological examinations in Villánykövesd sequence 1. – dominance relations of the various snail species (1. thermophilous, 2. mesophilous, 3. cold-resistant, 4. cryophilous species).

extended forest area. According to the ages these levels may coincide with Heinrich events H1 (GS 2) and H2 (GS 3) (Bond et al., 1993; Björck et al., 1998; Hemming, 2004; Gibbard and Cohen, 2008).

4.2. Máza

15,570 shells were identified of 24 terrestrial snail species from the 72 samples of the Máza sequence. The average abundance per sample was 216, but it was not equal (Fig. 5). Exploring the dominance relations at the Máza loess-paleosol sequence, 9 malacological zones (MZs) could be separated (Figs. 5 and 6).

The lowermost MZ-1 is spanning from 864 cm to 840 cm, covering the bottom part of the MS1 paleosol layer. The collective presence of the cold-resistant, hygrophilous, open vegetation preferring *Succinella oblonga*, the cold-resistant, sub-hygrophilous forest preferring *Trocholus hispidus* and the forest dwelling *Limax* species indicate a cool and partly forested paleoenvironment in this zone.

In the MZ-2 (840–708 cm), significant changes in the species composition occur, several warmth-loving, mainly open vegetation preferring (*Helicopsis striata*, *Chondrula tridens*, *Granaria frumentum*, *Pupilla triplicata*) and mesophilous (*Pupilla muscorum*, *Vallonia costata*) species occur in this zone. The open vegetation preferring and cold-resistant *Quickella arenaria* also occurred. Besides, the forest dwelling species (*Limax* sp., *T. hispidus*) disappear, indicating a warmer and less forested period in this zone. The warming should not have been strong because the dominance of cold-resistant species remained (Fig. 6).

MZ-3 extends between 708 and 492 cm, containing the upper part of the MS1 paleosol, the ML1S2 paleosol and the ML1L1 loess layers. In this zone, high abundance values of *P. muscorum*, *P. triplicata* and *V. costata* occurred. Forest dwelling species (*Limax* species, *T. hispidus* and the mesophilous *Vallonia pulchella* and

Nesovitrea hammonis) re-appear, besides other open vegetation preferring species (warmth-loving *Cochlicopa lubricella* and cold-resistant *Pupilla sterri*) occur. Some cryophilous species are also present (forest dwelling *Vallonia tenuilabris* and ecotone *Columella columella*), indicating slightly colder temperatures in this MZ. In this period, the forested area could have extended, but the open environment remained dominant.

Around 500 cm, a radiocarbon age of $40,429 \pm 396$ cal BP years was obtained, so MZ-3 can be parallel with the GI 11 interstadial period (Björck et al., 1998; Gibbard and Cohen, 2008). Moreover, the increased abundance of *C. tridens* and *P. triplicata* may refer to this period (GI 11).

From 492 cm to 420 cm, MZ-4 can be defined with significant changes in dominance relations. The cryophilous *C. columella* shows highest values in this zone indicating a tough and cold period. From the thermophilous species, only *P. triplicata* occurs; from the mesophilous only *Limax* species is present. Besides these changes, the cold-resistant *S. oblonga* and *T. hispidus* species appeared, indicating a cold period where the area of open environment increased, the forested areas shrunk, which may have been a refuge for some forest species during this cold period.

The uppermost part of MZ-4 is dated to $23,155 \pm 217$ cal BP years, which indicates that the MZ-4 cold period corresponds to the H2 Heinrich event (GS 3 stadial; Bond et al., 1993; Björck et al., 1998; Hemming, 2004; Gibbard and Cohen, 2008).

MZ-5 spans from 420 to 360 cm, and the VL1S1 paleosol layer. All cryophilous species disappeared and the dominance values of warmth-loving species slightly increased (Fig. 6). Besides, *P. triplicata* and *C. tridens* re-appeared with some mesophilous (*P. muscorum*, *V. costata*, *Euconulus fulvus*) and cold-resistant (*P. sterri*) species. These changes in dominance values indicate a generally milder climatic setting during this zone, and the area of forests could increase during this period.

In MZ-6 (360–258 cm), warmth-loving species disappear, the

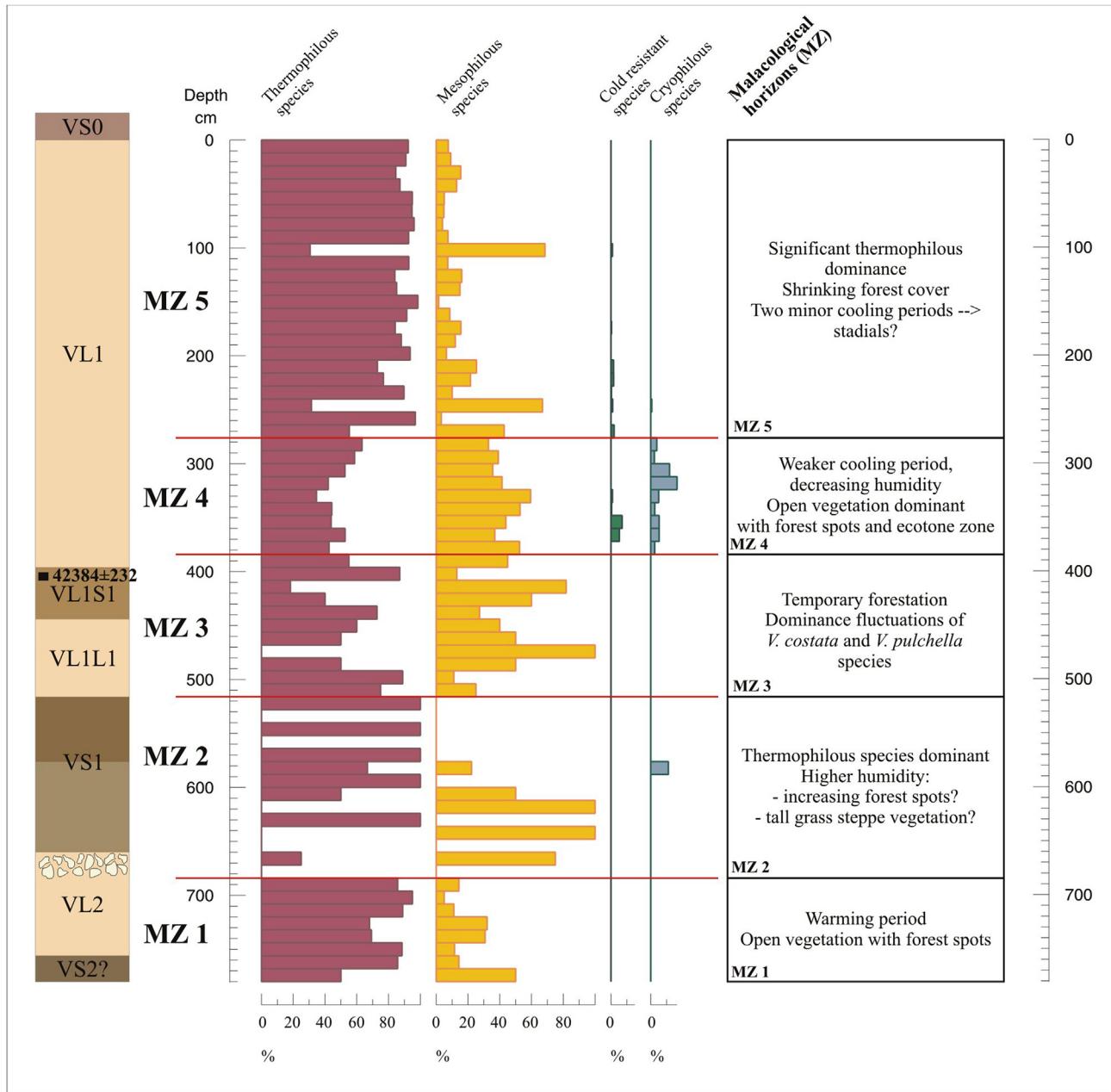


Fig. 4. Results of the malacological examinations in Villánykövesd sequence 2. – dominance relations of the eco-groups, and the description of the reconstructed malacological zones (MZs).

mesophilous (*P. muscorum*) and cold-resistant (*T. hispidus*, *S. oblonga*, *P. sterri*) dominate this zone. At the upper part of the zone, cryophilous species (*V. tenuilabris*, *C. columella*) appear, but the mass dominance of these groups did not exceed the dominance of mesophilous species (Fig. 6). This zone could be a transition between the warmer MZ-5 and the cold MZ-7. The relatively high abundance values of *T. hispidus* indicate an extending forest area in this zone. At the border between MZ-6 and 7, several mesophilous (*V. costata*, *V. pulchella*, *Vitrea crystallina*) and warmth-loving species (*P. triplicata*) appear, which indicates a short warming period, maybe related to the GI 3 stage (Björck et al., 1998; Gibbard and Cohen, 2008) at the borderline of the two MZs.

Cold-resistant species are present in MZ-7 (258–180 cm) with clear dominance of *T. hispidus*. Besides, the mesophilous *P. muscorum*, the cold-resistant *S. oblonga* and *P. sterri* occur with

notable dominance values. The high abundance of *T. hispidus* refers to a cooling climate and emerging forested areas, maybe the most extended areas in the sequence, but the ratio of forest/open environment species was still low.

At MZ-8, between 180 and 12 cm, a strong cooling period could be reconstructed by the dominance relations of snails (Figs. 5 and 6). The lack of warmth-loving species and the lower dominance of mesophilous species (only the *P. muscorum* represents higher values) combined with an increase of cold-resistant (*T. hispidus*, *S. oblonga* and *P. sterri*) and cryophilous species (*V. tenuilabris*, *C. columella* and *Pupilla alpicola*) indicates a strong cooling period in this MZ. The cold climate and the dominance relations of the species indicates mainly open vegetation with small forest spots, and indicates MIS 2 stage, maybe the Heinrich event H1 (Bond et al., 1993; Björck et al., 1998; Hemming, 2004; Gibbard and Cohen,



Fig. 5. Results of the malacological examinations in Máza sequence 1. – dominance relations of the various snail species (1. thermophilous, 2. mesophilous, 3. cold-resistant, 4. cryophilous species, 5. fragment shells).

2008). The thickness of this zone may refer to intensive dust accumulation processes.

The uppermost and youngest MZ-9 contained only one sample but there are clear differences from the fauna of MZ-8. The cryophilous species disappear, from the cold-resistant only *T. hispidus* remained. Besides, mesophilous species appear (*P. muscorum*, *V. pulchella*, *V. costata*, *E. fulvus*, *Limax* sp.) with higher abundance values. These relations point to warming climatic conditions and the expansion of forested areas. This zone may represent the end of the Pleistocene or the beginning of the Holocene period.

5. Discussion

The results of malacological examinations of the Villánykövesd and Máza loess-paleosol sequences were correlated to each other, and were placed into the global timeline to compare the reconstructed paleoenvironmental conditions (Bronger, 2003). The setting of the sequences into the global timeline was made by their radiocarbon age data. Both sequences deposited during the Late Pleistocene period and three global stages (MIS) (Lisiecki and Raymo, 2005; Gibbard and Cohen, 2008) could be recognised (Fig. 7). Going back in time, the MIS 2 stage, or Last Glacial Maximum (LGM) could be revealed in both sequences' L1 layer (VL1 and ML1). By their setting and age, the paleosol layers in the Villánykövesd (VS1) and Máza (MS1) sequences could be placed in the MIS 3 interstadial, between ca. 47,000 and 51,000 cal BP years (Johnsen et al., 1995). The next warm stage is the MIS 5a interstadial (between ca. 75,000 and 83,000 cal BP years), which can only be investigated in the Villánykövesd sequence (VS2 layer; Fig. 7).

Besides the chronological correlation, it is essential to know each sequences' own environmental and climatic conditions. Correlating these, a more detailed chronological-paleoecological system could be established, which contains global and local data of climatic and environmental effects as derived from the

investigated sequences. By the dominance relations of the snail species and the separated MZs, climatic and vegetation (forest coverage) zones, were reconstructed (Fig. 7). The reconstructed MIS stages remark different paleozones in each sequence, showing the local climatic impacts in the investigated area.

During the deposition of the Villánykövesd sequence, particularly warm climatic conditions prevailed (Fig. 7). The highest temperatures reconstructed in MZ-2 represent a paleozone during the MIS 3 interstadial (VS1 paleosol layer). The warm/mild climatic conditions were only once interrupted by cooler conditions in the MZ-4 paleozone, but the malacological results did not show a strong decrease in temperature. In contrast to paleoclimate results, the changes of local forest cover produced much more diversified results. The highest forest cover was reconstructed for MZ-3 (cool climate) and MZ-4 (mild climate) paleozones, yet the lowest forest coverage could be identified in MZ-2 (warm) paleozone.

The reconstructed paleozones in the Máza sequence display much colder climatic conditions than at Villánykövesd. Considering that the sequences were deposited nearby during mostly the same period, the reconstructed temperature difference is apparent (Fig. 7). Two cold, three mild and four cool paleozones could be separated. The MZ-2 and MZ-4 paleozones are chronologically parallel, with the same paleozones of Villánykövesd. The mild zones all correspond with paleosols (related to MS1, ML1S1 and MS0). From the cold periods, MZ-4 refers to Heinrich event 2, MZ-8 corresponds to the LGM period (Bond et al., 1993; Björck et al., 1998; Hemming, 2004; Gibbard and Cohen, 2008). The highest forest cover corresponds to the cool paleozones, however still subordinate in respect to open vegetation.

The chronological and paleoecological correlation of the Villánykövesd and Máza sequences gave the opportunity to correlate these to other similar aged loess-paleosol sequences, such as sequences from the left bank of Danube River, Katymár (Sümegi, 2007) and Madaras (Hupuzci, 2012) from Hungary and Črvenka

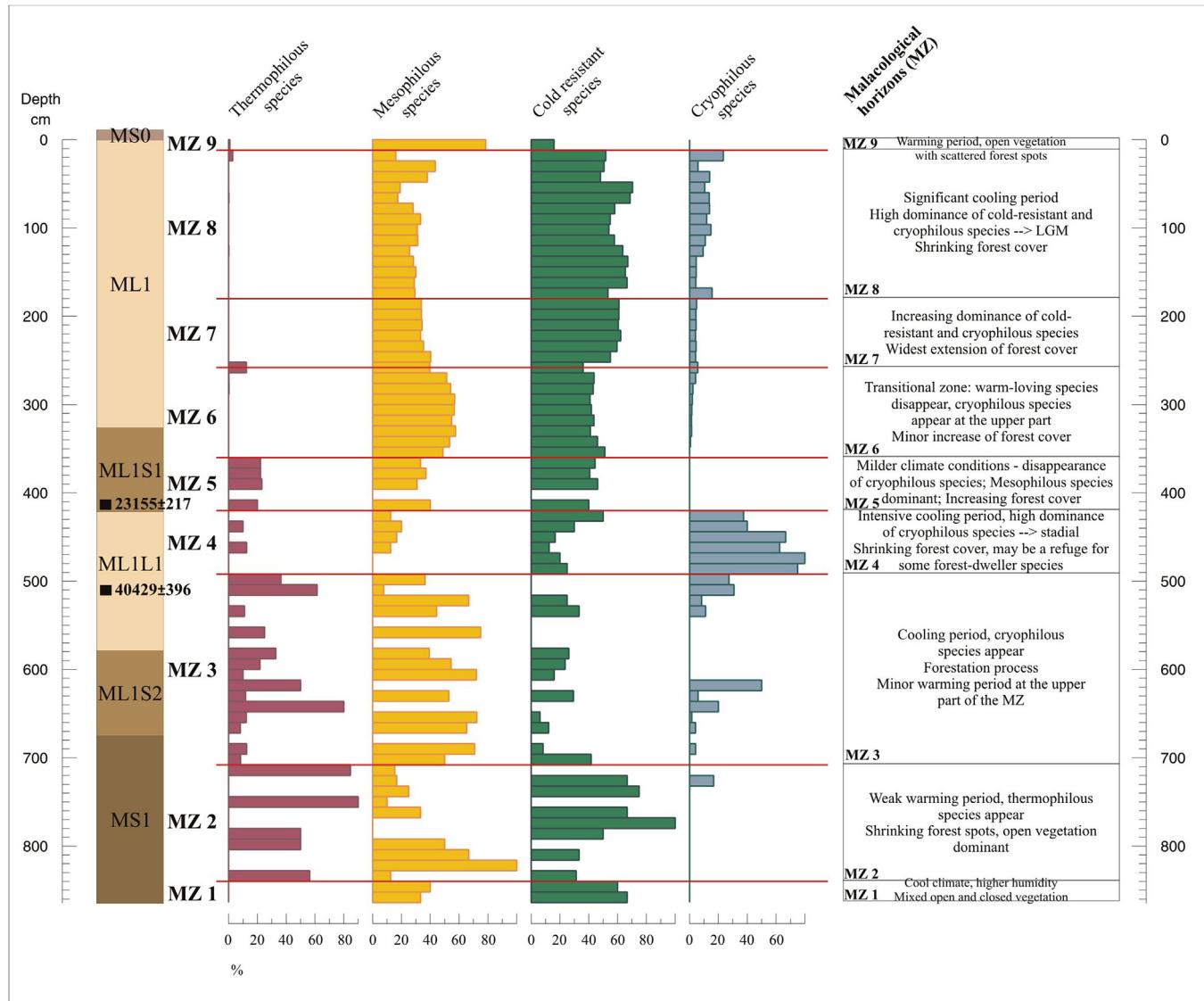


Fig. 6. Results of the malacological examinations in Máza sequence 2. – dominance relations of the eco-groups, and the description of the reconstructed malacological zones (MZs).

(Sümegi et al., 2016) from Serbia. Interesting similarities are noticed in the snail dominance tendencies among the investigated sequences in three periods (Table 1).

In the period younger than 22,000 cal BP years, the clear dominance of *Succinella oblonga*, *Trocholus hispidus*, *Vallonia tenuilabris*, *Columella columella* and *Pupilla muscorum* is noticed in the Máza sequence. A similar dominance can be observed in the Madaras sequence (Hupuczi, 2012), only the dominance of *P. muscorum* is lower. At Katymár, a similar dominance situation is present, although the dominance values of *S. oblonga* are lower. In the Villánykövesd sequence this dominance connection is missing, because of the continuously warmer climatic conditions. Another dominance connection could be established in the period older than 25,000 cal BP years, where the significant dominance of *Pupilla triplicata* and *Vallonia costata* is present in the Villánykövesd, Máza and Črvenka sequences. Only the main dominance of *P. triplicata* could be noticed in Katymár sequence. Unfortunately, the oldest parts of Katymár and Madaras sequences are not older than 35,000 cal BP years, thus older similarities can only be investigated for the Villánykövesd, Máza and Črvenka sequences' 35,000 cal BP years older parts. This relation is the *Pupilla triplicata*, *Vallonia*

costata and *Helicopsis striata* dominance, which demonstrable in all sequences of Villánykövesd, Máza and Črvenka (Table 1).

6. Conclusions

Examining the malacological results of the Villánykövesd and Máza sequences in SW Hungary, several important conclusions can be made. The sedimentary material of the sequences was deposited in a similar period, this means the sequences are of similar age (^{14}C dating, Fig. 7). Despite of the chronological correspondence, the paleoecological reconstruction in both sequences produced different results. Global climatic impacts affected the investigated areas, as the cool zones during MIS 2, and milder zones in MIS 3. However, the number and the climatic and environmental conditions of the paleozones of Villánykövesd and Máza show evidence that the previously verified mosaic-like environmental patterns in the Carpathian Basin (Sümegi, 1995, 1996, 2005, 2007; Sümegi and Kropp, 1995, 2002; Sümegi and Hertelendi, 1998) were present in the area of Villánykövesd and Máza during the Pleistocene as well. This means that a different and unique paleoecological system, the so-called local pattern or scheme (Sümegi, 1996, 2001, 2005),

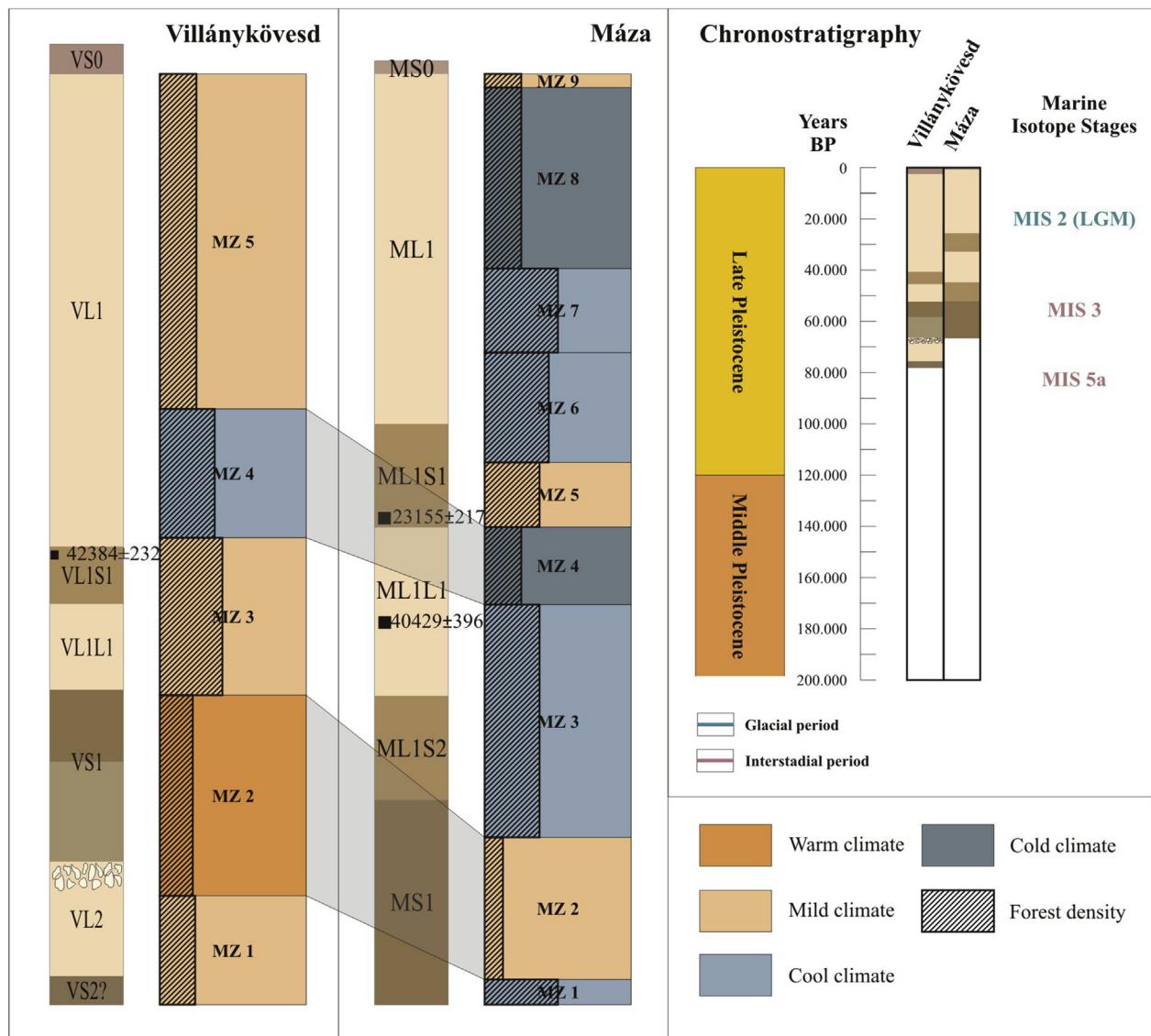


Fig. 7. Results of chronological and paleoecological correlations between Villánykövesd and Máza sequences.

Table 1

Dominance connections between loess-paleosol sequences from the right (Villánykövesd, Máza) and left (Madaras, Katymár, Črvenka) bank of the Danube River.

Age	Sequences				
	Villánykövesd	Máza	Madaras (Hupuczi, 2012)	Katymár (Sümegi, 2007)	Črvenka (Sümegi et al., 2016)
22,000 cal BP yr		<i>S. oblonga</i> <i>T. hispidus</i> <i>V. tenuilabris</i> <i>C. columella</i> <i>P. muscorum</i>	<i>S. oblonga</i> <i>T. hispidus</i> <i>V. tenuilabris</i> <i>C. columella</i>	<i>T. hispidus</i> <i>V. tenuilabris</i> <i>C. columella</i>	
25,000 cal BP yr	<i>P. triplicata</i> <i>V. costata</i>	<i>P. triplicata</i> <i>V. costata</i>		<i>P. triplicata</i>	<i>P. triplicata</i> <i>V. costata</i>
35,000 cal BP yr	<i>P. triplicata</i> <i>V. costata</i> <i>H. striata</i>	<i>P. triplicata</i> <i>V. costata</i> <i>H. striata</i>			<i>P. triplicata</i> <i>V. costata</i> <i>H. striata</i>

formed in each of these two close-by sequences.

The local climatic impacts are influencing the development of the fauna and the flora. At Máza 9 paleoecological zones could be identified, at Villánykövesd only 5. At Villánykövesd, warmer local

climatic conditions resulted in high abundances of thermophilous snails. Only one of them, the *Pupilla triplicata*, had an outstanding dominance in nearly all samples of the sequence (Fig. 3). During the cool period (MZ-4) its dominance values did not decrease lower

than 30–35%, meaning this species was present at the time when the climatic and environmental conditions were unideal for the warmth-loving species (Fig. 3). This means that the area of Villánykövesd was a refuge of *P. triplicata* during the cold period(s) of the Late Pleistocene.

The significant presence of the cold-resistant and the cryophilous species in the Máza sequence indicates generally much lower temperatures than at Villánykövesd. Such cryophilous species appeared in the cold paleozones (*Vallonia tenuilabris*, *Pupilla apicola*), which nowadays occur in high mountainous regions, indicating cold periods in this area during the Late Pleistocene. The geographic situation of the area (on a north-ascending bench; Fig. 2) have influenced the MZs in the sequence, because this area may have functioned as a passage between the higher and lower altitudes, resulting this “passage effect” of the snails.

There are common conformities in the vegetation development. The forest covered areas had the largest extension during cool periods, and covered the smallest areas during cold and warm periods. The high forest density is caused by the increased humidity during cool periods, which enabled the development of closed vegetation areas (forest; Sümegi, 2005; Molnár et al., 2011). However, too warm or cold climate is not favoured by forest development, this is cause for the prevalence of the open vegetation during these periods.

Considering the reconstructed dominance connections with the investigated Sites Madaras, Katymár and Črenka, it can be said that, aside from the local patterns, during diverse periods similar snail communities developed in each sequence. The bed-migration of the Danube River during the Late Pleistocene did apparently not influence the development of these snail communities.

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