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Diversity and Abundance of Isopods (Isopoda: Oniscidea) on Hungarian Highway Verges

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Abstract: We examined the spatiotemporal distribution of isopods along four Hungarian highways (M1, M3, M5, M7) while accounting for sampling years and seasons in relation to climate conditions of highways. Isopods were collected with double-glass pitfall traps from 24 sites over three years. Isopod abundance followed the temporal trend of increasing average temperature and precipitation. Conversely, isopod diversity followed a different trend in all sampling years, which clearly demonstrated the effects of annual and seasonal change of climate. Examining isopods spatial distribution we found that high temperature had a positive effect on isopod diversity. The studied ecological parameters in different sampling years and seasons varied strongly in relation to locality of highways, because of ecological factors characterising the landscape surrounding the highways. The number of generalists decreased, while the number of specialists increased with sampling years. Highway verges had special isopod communities that consisted of coloniser species and displaced native species. Our results show decreasing diversity and increasing isopod abundance on highway verges influenced by adventive species, temperature, precipitation, adjacent areas and disturbance level.

Key words: roads, woodlouse, macroepigeon, colonisers, displaced species

Introduction

Terrestrial isopods are not important arthropods for nature conservation in Hungary, but their contribution to ecosystem services is very important. Isopods contribute to decomposition processes, especially the fragmentation and mineralisation of organic matter contributing to the maintenance of energy transfer in soil (Wolters 2000). Isopod activity and abundance is affected by biotic (Woodin 1976) and abiotic factors, such as warming and climate change (Swift et al. 1998). Disturbance level and vegetation also determine the composition of isopod communities along highways (Vona-Túri et al. 2017). Habitat alteration changes soil structure and hydrological conditions, which in turn influence the activity of soil arthropods. In previous studies, we explored the effect of highway location (Vona-Túri et al. 2015), adjacent areas of roads and road edge proximity (Vona-Túri et al. 2017) on isopod communities.

The main objective of this study was to explore the effects of environmental variables on the spatiotemporal distribution of isopods, species richness, abundance, diversity, evenness, species composition and the contribution of species differentiation (beta

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diversity) among sampling years, seasons and location of Hungarian highways. Firstly, we examined environmental factors that may affect the temporal distribution of isopods. According our hypothesis, temperature and precipitation have effects on isopod temporal distribution, sithence warm temperature provides suitable conditions for generalist species contributing to high regional abundance, while species with low cold tolerance prefer colder areas (Castañeda et al. 2004, Bozinovic at al. 2014). Secondly, we determined how environmental factors impact on isopod spatial distribution and isopod diversity. Our hypothesis was that location and climate conditions of highways would influence the isopod spatial distribution because isopods respond differently to light, temperature and moisture conditions in the soil (Davis 1984, Wartburg 1987). Finally, we explored which isopod species are able to adapt and spread on the green corridor along highways. Based on the introduced species hypothesis (Vilisics et al. 2007), we hypothesised that exotic and invasive species would be more likely to colonise the altered habitats and become naturalised, while the distribution of sensitive native forest species could be reduced.

Materials and Methods

Sampling areas and methods

Data collection was conducted along four Hungarian highways (M1, M3, M5, M7) between 2011-2013. Along each highway, we selected six sampling points (Table 1) where double-glass pitfall traps made of 3 decilitre plastic cups filled with a 65% aqueous solution of ethylene glycol were established and enclosed by fences. Sampling sites were selected next to the lay-bys along highway, where isopods were sampled using six pitfall traps at each site and the distance between traps was 5 m (Vona-Túri et al. 2013, 2015, 2017). The traps were located at different distances from the edge of the roads and next to different types of adjacent areas (Vona-Túri et al. 2017). Habitats in all verges were represented by uncharacteristically dry and semi-dry grasslands or closed sand steppes. Verges are regularly mowed and maintained but since many companies are responsible for maintaining the highway sections, coordination of maintenance on overall area is very hard. The traps were deployed three times (May, July and September) over a three-week period each year. We studied the effects of climate conditions on the diversity and abundance of isopods, i.e. the average temperature and precipitation of Hungary during the sampling years (2011-2013) and sampling seasons (spring, summer, autumn; Fig. 1-2). Maps and diagrams of the average temperature and precipitation of Hungary were taken from the National Meteorological Service (https://met.hu). We used the keys of Hopkin (1991), Schmidt (1997), Berg & Wijnhoven (1998) and Farkas & Vilisics (2013) for identification of woodlice specimens. Species names were according Schmalfuss (2003). The habitat preference of isopods (generalist, natural-frequent species, disturbed-rare species and natural-rare species) followed the classification by Hornung et al. (2007, 2009) and Vilisics & Hornung (2010).

Statistical analyses

For data analysis we used the PAST Paleontological Statistic suite (Hammer et al. 2001). One-Way ANOVA was applied to assess the differences between the number of species, number of individuals and diversity of isopods in relation to years, seasons and location of highways. The characterisation of isopod communities was based on relative abundance (Ar), number of individuals (N), species richness (S), Shannon-Wiener diversity (H) and Pielou's evenness index (E). The value of species turnover was characterised with Wilson & Shmida's Beta diversity index (βT). We computed the Whittaker's β-diversity index (βW) in order to evaluate the level of complementarity of habitats between sampling years and seasons. Community separation was represented with Detrended Correspondence Analysis. Cluster analysis was performed using Jaccard Similarity Index for presentation of similarities of species and similarities of sites. We used the Jaccard similarity index for pairwise comparison of similarities of sampling years and seasons and highways, based on species composition.

Results

γ and α diversity

A total of 14 isopod species (Table 2) comprising 49,965 individuals were collected at 24 sampling sites. We found no significant differences between average number of species per trap (p=0.84) and average number of individuals per trap (p=0.63), but we found significant differences between isopod diversity (p=0.04) in relation to sampling years. The number of species was highest in 2012, when the average temperature exceeded the long-term average (1971-2000) temperature by 1.4 C°. The number of individuals increased with years, but the Shannon-Wiener diversity of isopods was significantly lower in 2013 than in 2011 (Fig. 3). No significant differences were found between average number of species per trap (p=0.86), number of individuals per trap (p=0.64) and isopod diversity (p=0.81) in rela-

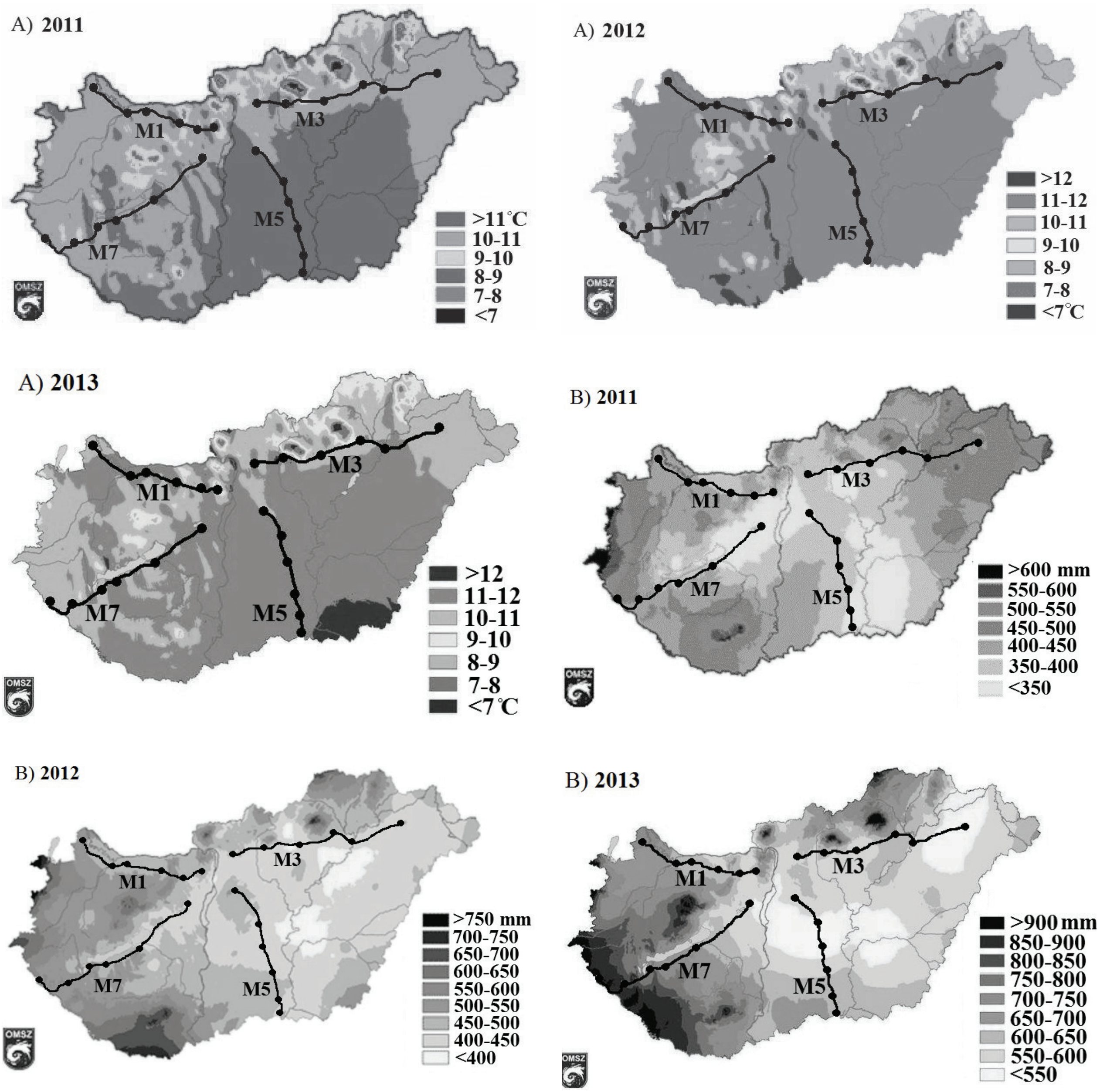

Fig. 1. Map of highways, sampling sites, average temperature (A) and precipitation (B) of Hungary during sampling years (2011-2012)

tion to season. Summer seasons were characterised by the highest number of species and individuals. The highest was the Shannon-Wiener diversity in spring (Fig. 4). We found no significant differences between number of species (p=0.92) and of individuals (p=0.79) during the three sampling seasons of each sampling years. In each year, summer was characterised by the highest number of species. In 2011 and 2012, the lowest average number of individuals per trap was in spring, while in 2013 it was in autumn. The values of Shannon-Wiener diversity did not follow the trend of species richness and abundance. In 2011 and 2012, the highest diversity was in spring, while in 2013 it was in autumn (Fig. 5). We found no statistically significant differences in the average number of species per trap (p=0.70) and average number of individuals per trap (p=0.44), but we found significant differences in isopod diversity (p=0.004) in relation to location of highways. The lowest was the number of species on the eastern highways M3 and M5, while the highest was on the western highways M1and M7. The highest number of individuals was found along highway M3. The lowest was along highway M5. Isopod diversity was significantly higher along highway M1 compared to highway M3 (Fig. 6). The abundance and diversity of isopods varied strongly at all 24 sites. The highest number of individuals was found in Polgár (M3) and

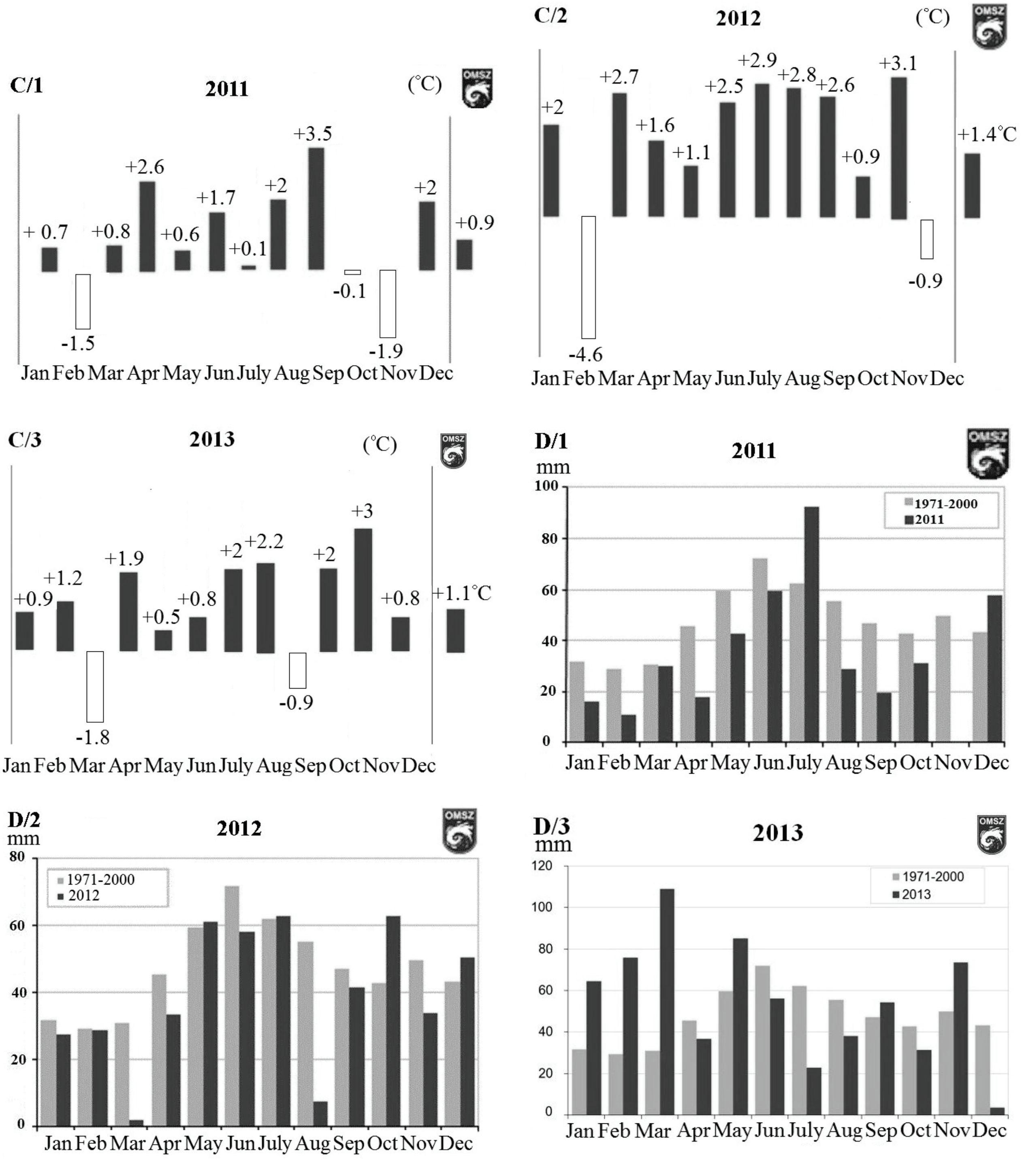

Fig. 2. The deviation of the national monthly average temperature (C) and precipitation (D) from the long-term average (1971-2000-es) in the sampling years

Letenye (M7), followed by Arrabona (M1), Sormás (M7) Zsámbék (M1) and Bábolna (M1). Conversely, isopod diversity was low in Polgár and Letenye and the highest diversity was found in Nyíregyháza (M3), Törek (M7), Röszke (M5), Moson (M1), Bábolna (M1) and Sormás (M7). Inárcs (M5) and Petőfiszállás (M5) were characterised by the lowest isopod abundance and diversity (Fig. 7).

The studied ecological parameters varied strongly in different sampling years in relation to climate conditions and were influenced by highway location. Along all highways, the species richness decreased slightly between 2011 and 2013, except for highway M3, where the number of species increased between 2012 and 2013. Conversely, between 2011 and 2012, the abundance of isopods increased, and

Table 1. Characterisation of sampling sites

	Sampling site	Adjacent area	Leaf litter cover (%)	Leaf litterdepth (cm)	Soil
M1	Zsámbék	arable land	95	1	light loess
	Óbarok	forest	98	0,5	light loess
	Turul	orchard	98	6	light loess
	Bábolna	arable land	75	2	dark humus
	Arrabona	arable land	100	5	humic sand
	Moson	arable land	40	0,5	dark gravelly
M3	Kisbag	forest	10	1	sand
	Rekettyés	arable land	0	0	black loose
	Gelej	arable land	5	1	black loam
	Polgár	arable land	5	1	black loam
	Nyíregyháza	arable land	10	4	sand
	Ecséd	arable land	10	1	loessal
M5	Inárcs	sandgrass	20	0,5	sand
	Örkény	forest	20	0,2	light sandy
	Kecskemét	arable land	80	0,2	dark humus
	Petőfiszállás	arable land	100	0,2	dark humus
	Szatymaz	grassland	100	1	dark humus
	Röszke	sandgrass	100	5	sand
M7	Velence	orchard	100	5	darl loess
	Táska	grassland	50	0,2	light loess
	Törek	arable, forest	98	1	brown, loessal
	Szegerdő	arable land	2	0,2	light sandy
	Sormás	grassland	10	0	light gravelly
	Letenye	forest	98	0	gravelly, loam

between 2012 and 2013, abundance decreased or stagnated in all highways, except for highway M1 where it increased. Along all highways, the values of Shannon-Wiener diversity decreased with sampling year. Pielou's evenness indices were highest in 2012 along all highways except for highway M5 where the evenness was lowest (Fig. 8). The studied ecological parameters varied strongly among different seasons in relation to climate conditions and were influenced by highway location. Along all highways, species richness was highest in spring, except for the highway M3, where the highest species richness was in summer and the lowest was in spring. Isopod abundance was the highest in summer along all highways, except for highway M7, where the highest isopod abundance was in autumn. The

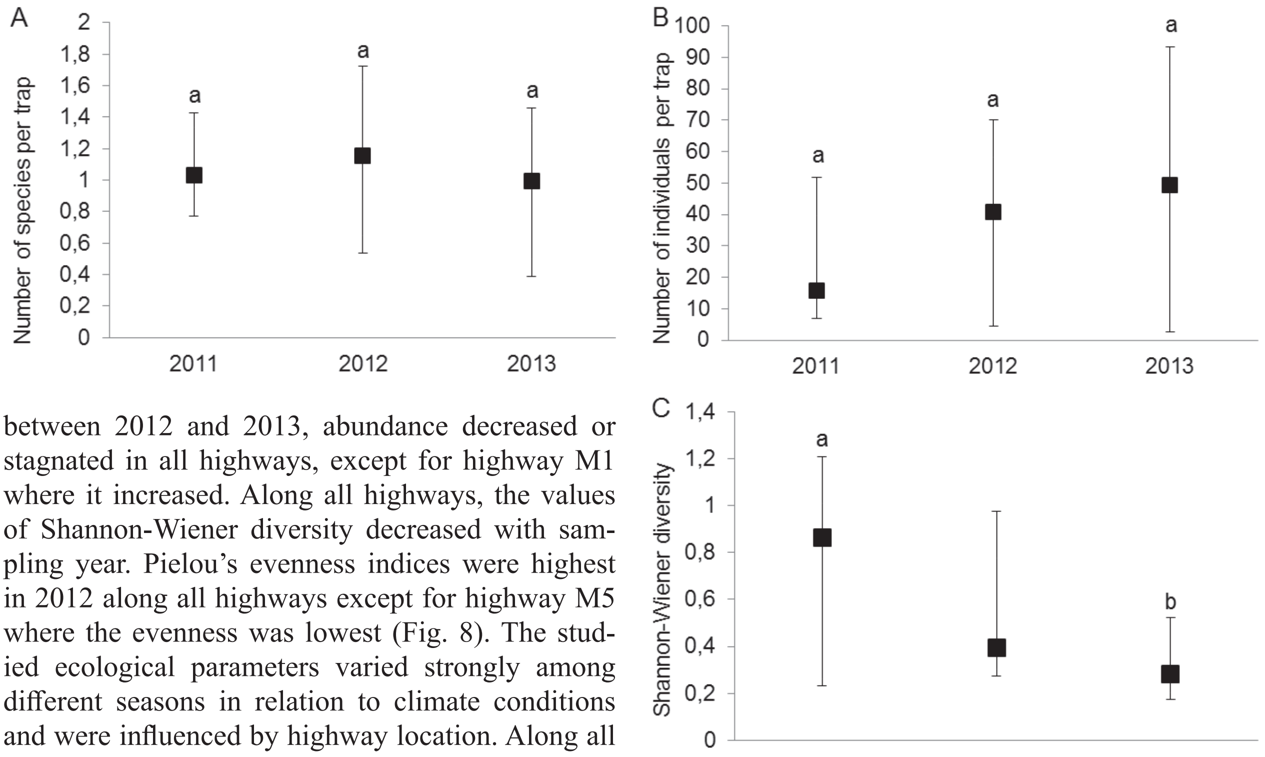

Fig. 3. The changes of average number of isopod species per trap (A), average number of individuals per trap (B) and Shannon-Wiener diversity (C) in sampling years (average ± S.E.). Different letters indicate significant ($p<0.05$) differences (one-way ANOVA)

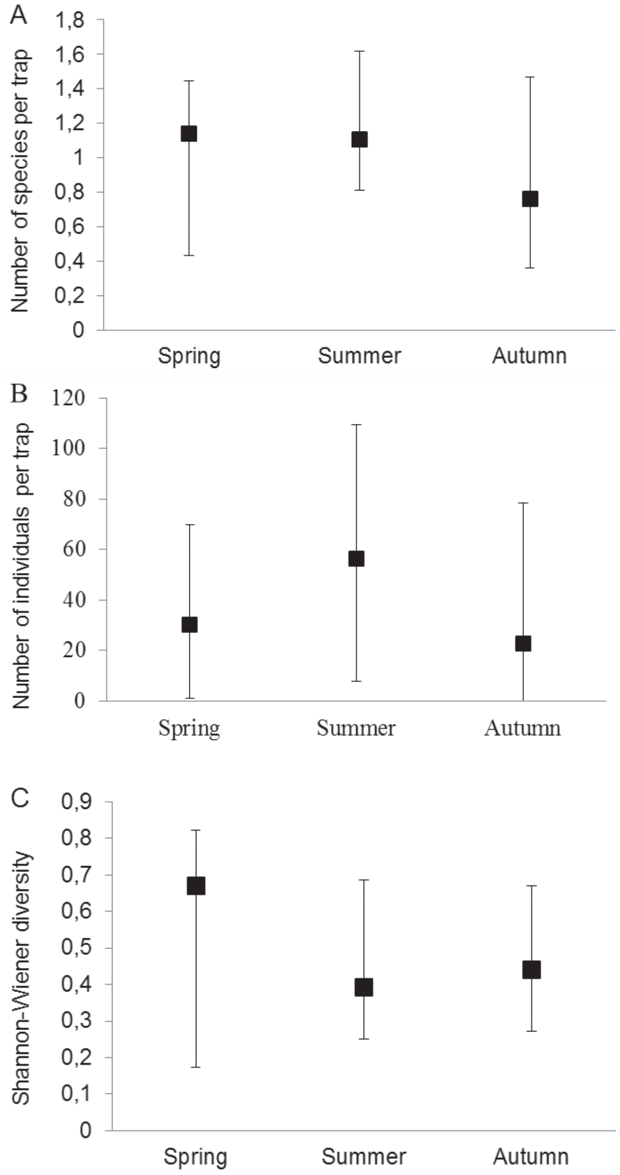

Fig. 4. The changes of average number of isopod species per trap (A), average number of individuals per trap (B) and Shannon-Wiener diversity (C) in sampling seasons (average ± S.E.)

high isopod abundance observed along highway M7 likely resulted in a reduction in diversity in autumn. The values of Shannon-Wiener diversity clearly demonstrated the effects of highway location on the seasonal distribution of isopods on highways. Along highways M1 and M3, diversity was lowest in summer, unlike highway M7 where the highest diversity was in summer. Along highway M5, isopod diversity increased from spring to autumn. The Pielou's evenness followed the same trend (Fig. 9).

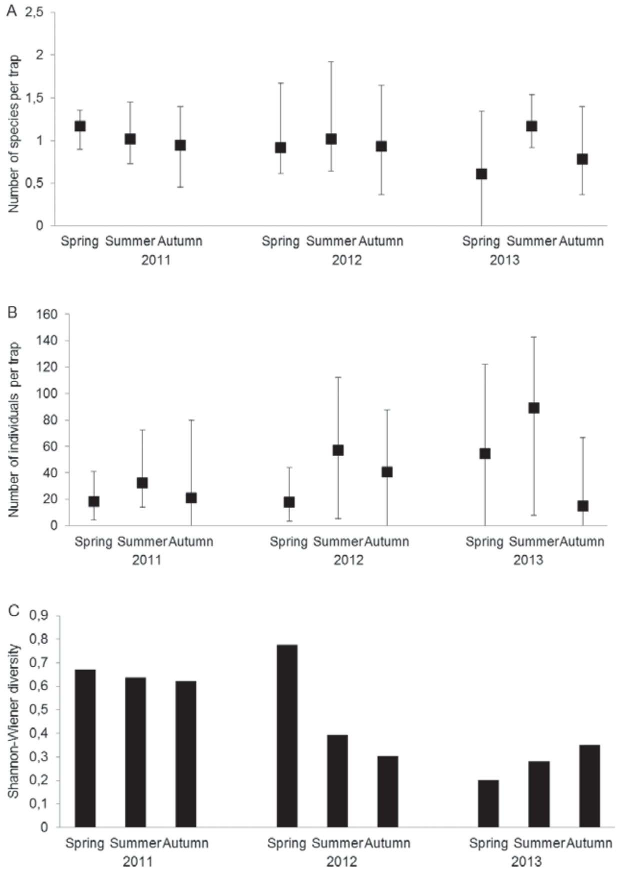

Fig. 5. Average number of isopod species per trap (S), average number of individuals per trap (N) and values of Shannon-Wiener index (H) in different sampling years and seasons

Community assemblages and abundance

The composition of isopod assemblages varied in relation to sampling year. The year 2011 was characterised by the highest number of generalist species and a reduction in the number of specialist species (5 generalists/3 specialists). By 2012, the number of generalist species decreased and the number of specialists increased compared to year 2011 (5 generalists/4 specialist). By 2013, the number of specialists exceeded the number of generalists (4 generalists/6 specialist). The abundance of *P. collicola* was highest in 2012, while the relative abundance of the cosmopolitan species *A. vulgare* increased. The relative abundance of the native *T. nodulosus*, *T. rathkii* and *T. ratzeburgii* decreased with sampling year. *L. minutus* and *O. planum* were observed only in 2012. *Ligidium hypnorum, A. zenkeri* and also the rare *A. nasatum* and *A. versicolor* were collected only in 2013 (Table 2, 3; Fig. 10). The highest number of species with special preferences was found in spring, while the rarest species were recorded in spring and autumn. Spring seasons were characterised by high species richness of generalists and the highest number of specialist (5 generalists/6 specialists). In summer seasons, the number of generalist and specialist species was equal (4 generalists/4 specialists). By

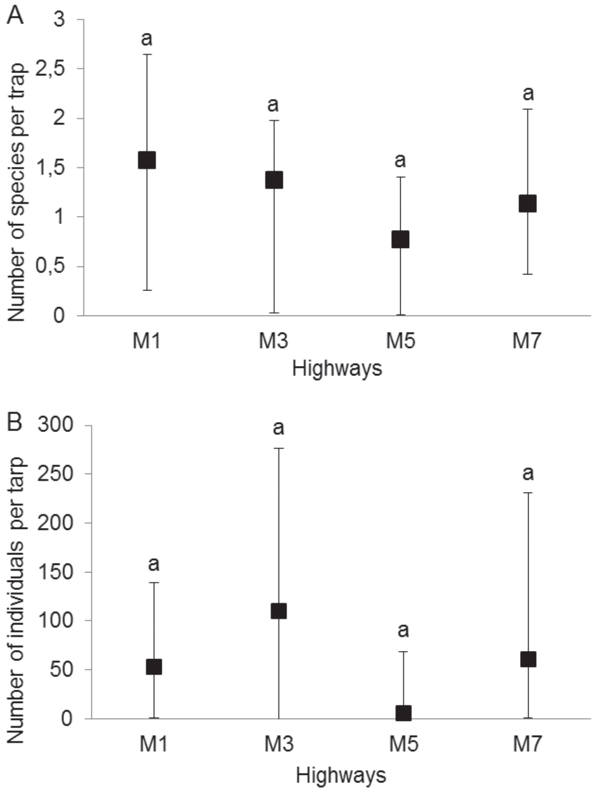

Fig. 6. The changes of average number of isopod species per trap (A), average number of individuals per trap (B) and Shannon-Wiener diversity (C) in relation to location of highways (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)

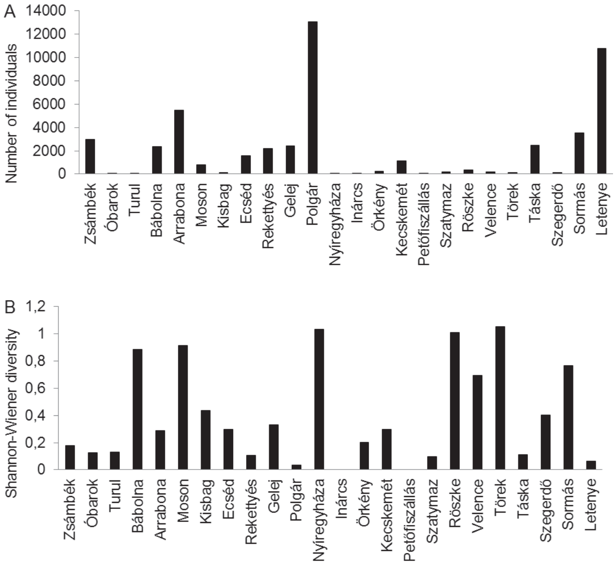

Fig. 7. Number of individuals (A) and Shannon-Wiener diversity (B) in all 24 sampling sites along highways

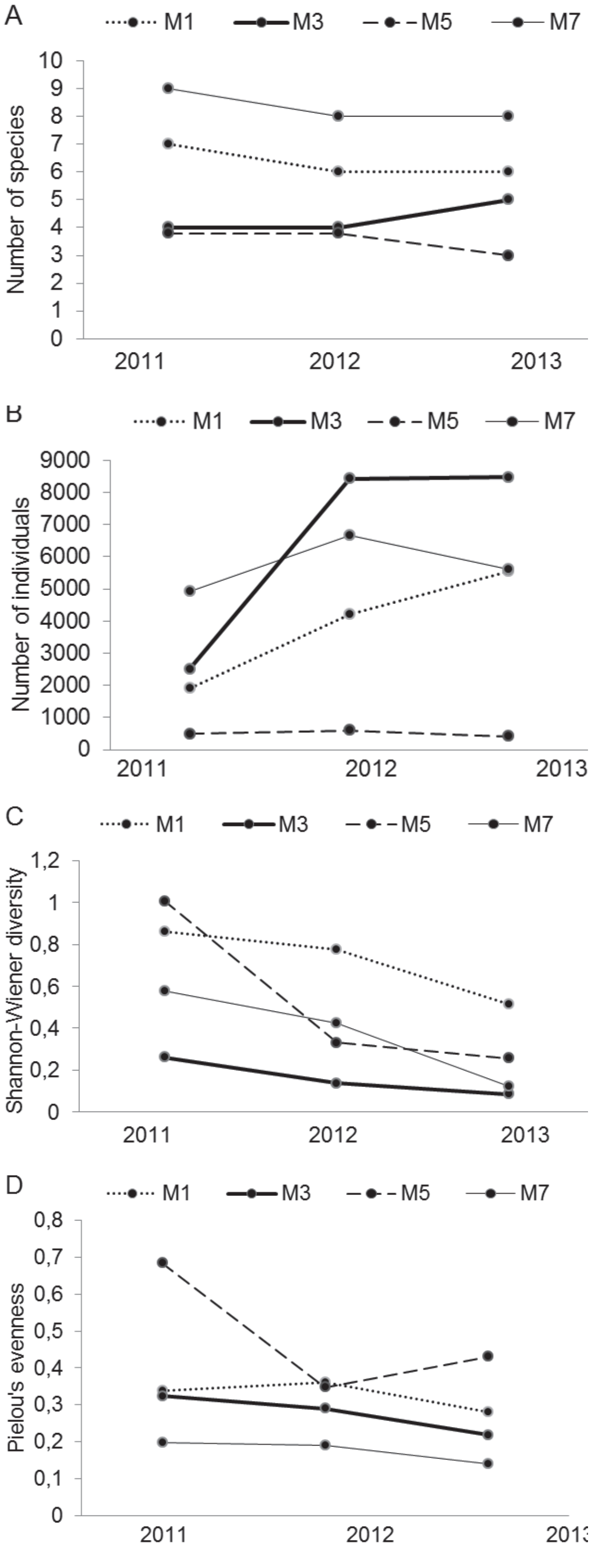

Fig. 8. Number of species (S), number of individuals (N), values of Shannon-Wiener index (H) and Pielou evenness (E) in different sampling years in relation to location of highways

autumn, the number of generalist increased (5 generalists/4 specialists). The number of individuals of *A. vulgare, P. collicola* and *T. rathkii* were highest in summer, while the number of *T. nodulosus* was highest in spring. Conversely, the relative abundance of *A. vulgare, P. collicola* and *T. rathkii* was highest in spring, while the number of *T. nodulosus* was highest in summer. *Ligidium hypnorum* was observed only in spring, *O. planum* was found only in summer and *A. versicolor* was collected only in autumn (Tables

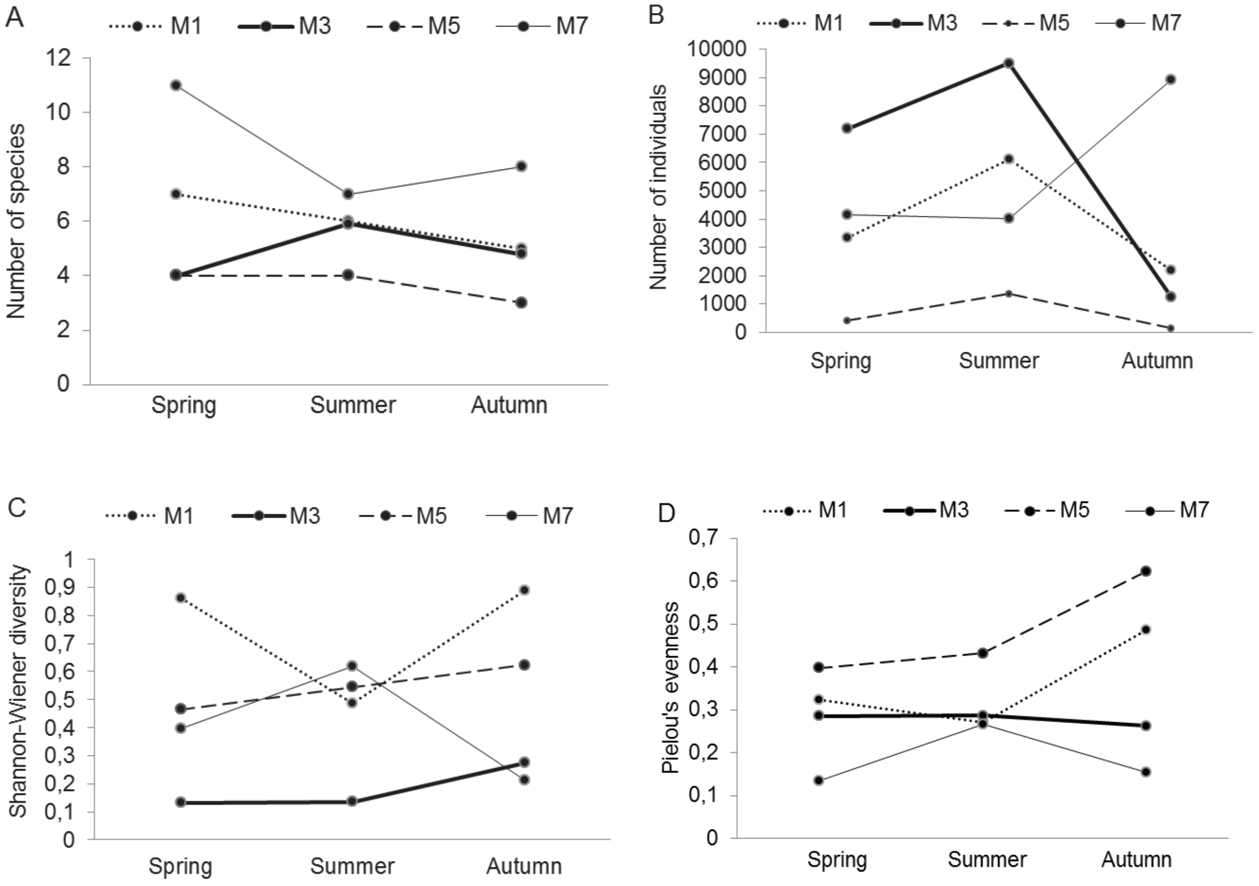

Fig. 9. Number of species (S), number of individuals (N), values of Shannon-Wiener index (H) and Pielou's evenness (E) in different sampling seasons in relation to the situation of highways

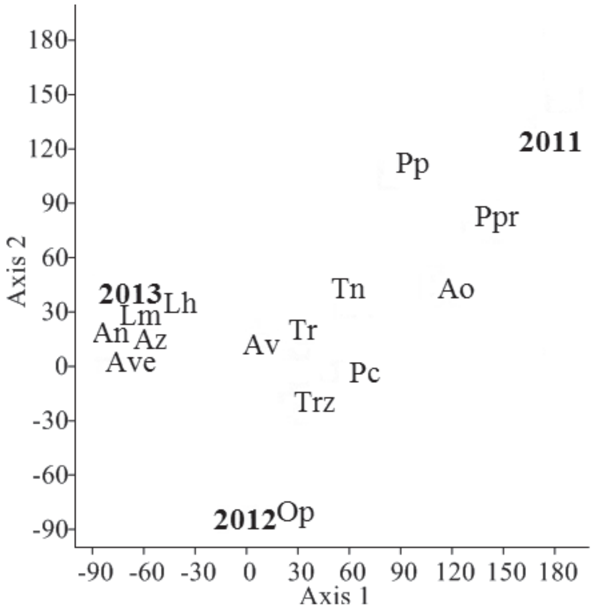

Fig. 10. The separation among the highway verges in relation to sampling years using Detrended Correspondence Analysis (see abbreviations of species in Table 2.)

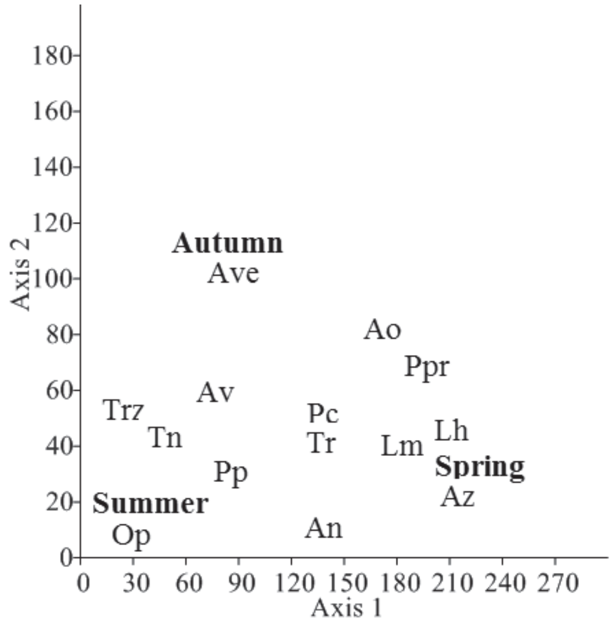

Fig. 11. Separation among the verges in relation to seasons using Detrended Correspondence Analysis (see abbreviations of species in Table 2.)

Table 2. List of species with their habitat preference, annual and seasonal distribution, including species abbreviations (*Hp.-habitat preference, I.- spring, II. summer, III. autumn, G-generalist, NF-natural-frequent species, DR-disturbed-rare species and NR-natural-rare species)

Abb.	Species	Hp.	2011			2012			2013		
			I.	II.	III.	I.	II.	III.	I.	II.	III.
Lh	*Ligidium hypnorum* (Cuvier, 1792)	NF	-	-	-	-	-	-	X	-	-
Hr	*Hyloniscus riparius* (C. Koch, 1838)	G	X	-	X	-	-	-	X	-	-
Tp	*Trichoniscus pusillus* Brandt, 1833,	G	X	-	X	-	-	-	-	-	-
Pc	*Porcellium collicola* (Verhoeff, 1907)	G	X	X	X	X	X	X	X	X	X
Tn	*Trachelipus nodulosus* (C. Koch, 1838)	G	X	X	X	X	X	X	X	X	X
Tr	*Trachelipus rathkii* (Brandt, 1833)	G	X	X	X	X	X	X	X	X	X
Trz	*Trachelipus ratzeburgii* (Brandt, 1833)	NF	-	-	X	-	X	X	-	X	X
Lm	*Lepidoniscus minutus* (C. Koch, 1838)	NF	-	-	-	X	-	-	-	-	-
Pp	*Protracheoniscus politus* (C. Koch, 1841)	NF	X	X	X	-	-	-	-	X	-
Op	*Orthometopon planum* (Budde-Lund, 1885)	NF	-	-	-	-	X	-	-	-	-
Ppr	*Porcellionides pruinosus* (Brandt, 1833)	G	X	-	-	-		X	-	-	-
Av	*Armadillidium vulgare* (Latreille, 1804)	G	X	X	X	X	X	X	X	X	X
An	*Armadillidium nasatum* Budde-Lund, 1885	DR	-	-	-	-	-	-	X	X	-
Ao	*Armadillidium opacum* (C. Koch, 1841)	NR	-	-	X	X	-	-	-	-	-
Az	*Armadillidium zenkeri* Brandt, 1833	NF	-	-	-	-	-	-	X	-	-
Ave	*Armadillidium versicolor* Stein, 1859	NR	-	-	-	-	-	-	-	-	X

*Hp.-habitat preference, I.- spring, II. summer, III. autumn, G-generalist, NF-natural-frequent species, DR-disturbed-rare species and NR-natural-rare species

2, 3; Fig. 11). The highest number of generalist and specialists was found along the western highways, while the lowest was along the northern highways. The north-western highway M1 was characterised by high number of generalist species and low number of specialist species (5 generalists/3 specialists). Along the north-eastern highway M3 and south-eastern highway M5, lower number of both species types (4 generalists/1 specialist species) was found. The number of specialists exceeded the number of generalists (5generalists/7 specialists) on highway M7. The number of individuals of *A. vulgare* was the highest on the north-eastern highway M3, while the number of *T. nodulosus* was highest on the south-western highway M7 and the highest number of individuals of *Trachelipus rathkii* and *Porcellium collicola* was found along the north-western highway M1 (Fig. 12).

Table 3. Relative abundance (Ar) of isopod species in each sampling year and season

Species	Relative abundance (Ar%)					
	2011	2012	2013	spring	summer	autumn
L.hypnorum	-	-	0.01	0.01	-	-
H. riparius	0.03	-	0.01	0.02	-	0.007
T. pusillus	0.02	-	-	0.006	-	0.007
P. collicola	1.48	1.51	0.39	1.65	0.69	0.95
T. nodulosus	10.75	4.91	2.17	2.49	6.36	5.57
T. rathkii	4.47	3.50	2.53	5.32	2.55	2.33
T. ratzeburgii	0.02	0.02	0.01	-	0.009	0.02
L. minutus	-	0.009	-	0.01	-	-
P. politus	0.03	-	0.01	0.006	0.01	0.007
O. planum	-	0.009	-	-	0.009	-
P. pruinosus	0.02	0.004	-	0.01	-	0.007
A. vulgare	83.14	89.97	94.83	90.44	90.31	69.75
A. nasatum	-	-	0.01	0.006	0.004	-
A. opacum	0.02	0.009	-	0.01	-	0.01
A. zenkeri	-	-	0.005	0.006	-	0.01
A. versicolor	-	-	0.01	-	-	0.01

β-diversity and similarity

Regarding annual dynamics, we observed the highest species turnover between 2012 and 2013, and the lowest turnover between 2011 and 2012 (Table 4). According to Jaccard's similarity index, the highest similarity was observed between 2011 and 2012 (Table 4). Regarding seasonal dynamics, the Wilson & Shmida's Beta diversity index was highest between spring and summer, and the lowest between spring and autumn (Table 5). Regarding location of highways, we found the highest species turnover between M3 and M7, and the lowest turnover between M3 and M5 (Table 6.) The highest similarity was observed between M3 and M5, while the lowest

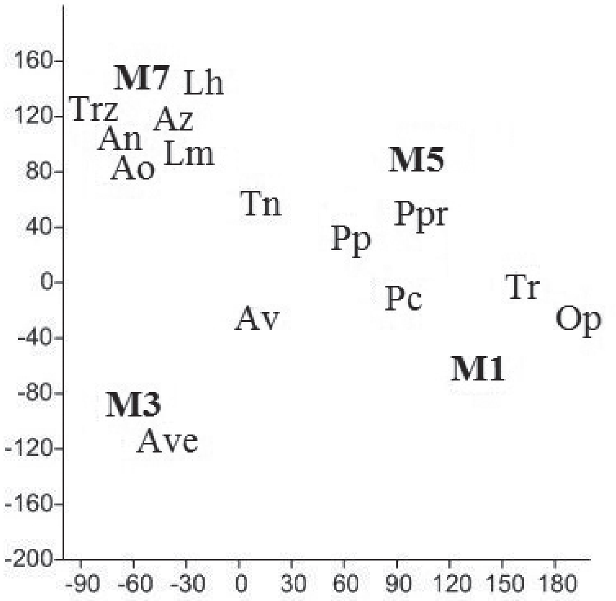

Fig. 12. Separation among the verges in relation to location of highways using Detrended Correspondence Analysis (see abbreviations of species in Table 2.)

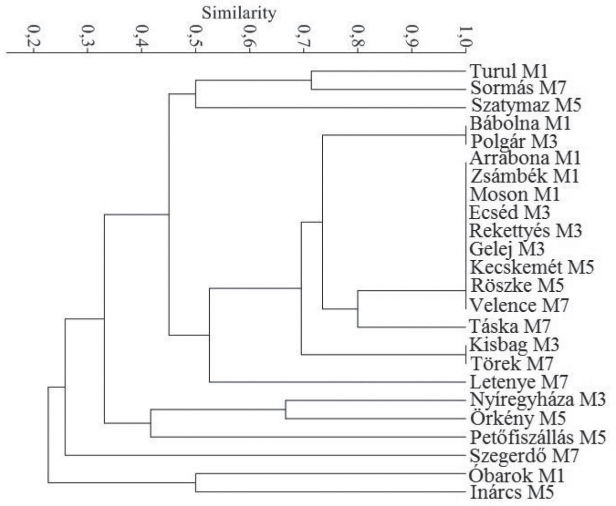

Fig. 13. Similarity of all sites of highway verges using Jaccard' similarity index

Table 4. Species turnover between different sampling years along highways using the Wilson & Shmida ß-diversity index and similarity of highway verges in relation to sampling year using Jaccard' similarity index

		2011	**2012**
Wilson & Shmida' ß diversity index	**2012**	0.26	0
	2013	0.33	0.50
Jaccard's similarity index	**2012**	0.58	1
	2013	0.50	0.46

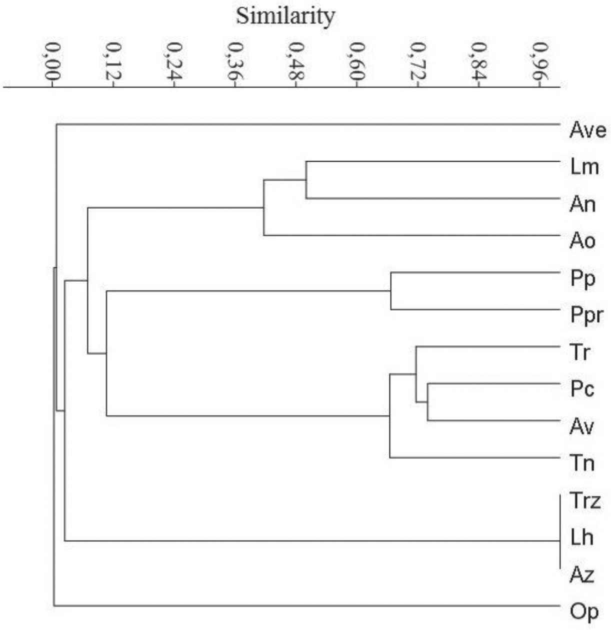

Fig. 14. Similarity of isopod species of highway verges using Jaccard' similarity index

Table 5. Species turnover between different sampling seasons along highways using the Wilson & Shmida ß-diversity index and similarity of highway verges in relation to sampling season using Jaccard' similarity index

		spring	**summer**
Wilson & Shmida's ß diversity index	**summer**	0.42	0
	autumn	0.25	0.36
Jaccard's similarity index	**summer**	0.40	1
	autumn	0.60	0.46

Table 6. Species turnover between different highways using the Wilson & Shmida ß-diversity index and similarity of the four highway using Jaccard' similarity index

		M1	**M3**	**M5**
Wilson & Shmida's ß diversity index	**M3**	0.46		
	M5	0.42	0.11	
	M7	0.25	0.57	0.55
Jaccard's similarity index	**M3**	0.36		
	M5	0.40	0.80	
	M7	0.60	0.26	0.28

was between M3 and M7 (Table 6). We found low complementarity of species between years (50%), seasons (46%) and highways (51%) which was demonstrated by the low Whittaker's β diversity. Hierarchical clustering indicated major similarities between sites, showing 100% similarity between some sites of highways M1, M3 and M5 (Fig. 13). Three frequent forest species (*L. hypnorum, T. ratzeburgii*, *A. zenkeri*) separated from other species. The most abundant species (*P. collicola*, *T. nodulosus*, *T. rathkii* and *A. vulgare*) formed a distinct group, clearly separated from the other species (Fig. 14.)

Discussion

The high number of traps we deployed along highways made it possible to assess the relationship between isopod abundance and diversity. Temperature and precipitation maps and diagrams clearly represented differences between climate conditions of sampling years, seasons and areas. Our results support our hypothesis that temperature and precipitation have effects on isopod temporal distribution. Our findings concur with Khemaissia et al. (2017) who suggest that the highest diversity in spring may be caused by the low temperature. Hornung et al. (2015) concluded that the soil temperature in early spring and later the increasing temperature and decreasing soil moisture, affected the dynamics of isopod populations. Isopod diversity was associated with the number of microhabitats in addition to climate (Lopes et al. 2005). We found that the high isopod abundance due to high summer temperatures led to a reduction in diversity. Similarly, Khemaissia et al. (2017) observed the highest isopod abundance in summer. On the other hand, several studies showed that summer might cause significant mortality of isopods (Sutton 1968, Al Dabbagh & Block 1981, Zimmer 2004). The seasonal activity of isopods followed a different trend in all sampling years, which clearly demonstrated the effects of annual climate change, such as temperature and precipitation, on isopod seasonal activity along highways. The seasonal variation of number of individuls followed the trend of seasonal changes of precipitation, namely in 2011 and 2012 the isopod abundance was lower in spring when precipitation was also lower but in 2013, the increasing spring precipitation resulted in the highest isopod abundance. While the high autumn (in 2011) and summer (in 2012) temperature led to higher isopod abundance, the lower autumn temperature from the long-term average in 2013 caused a great reduction in abundance. Conversely, the seasonal changes of isopod diversity correlated negatively with the seasonal changes of temperature and precipitation. Similarly, Chelazzi & Farrara (1978) noticed that moisture affected isopod distribution. Ma et al. (1991) showed that air temperature was the major cause of the seasonal variation in population density of isopods. Temperature and moisture are among the main factors for the survival of isopods (Warburg 1987, Hornung et al. 2015).

Roadside verges may have other microclimate and anthropogenic impacts compared with the original native habitats (Báldi 1999). Furthermore, the road-effect zone also changes light conditions and soil moisture (Daigle 2010). Soil moisture is very important for the migration of isopods to deeper soil and moss layers (Khemaissia et al. 2017) and their distribution (Dias et al. 2013). Our results support our hypothesis that climate conditions along highways affect also isopod spatial distribution. Hornung & Warburg (1993) noticed that photoperiod and increased temperature have positive effects on isopod reproduction. Moreover, Hornung et al. (2015) found that isopod activity and density were positively correlated with soil temperature. Examining the climate conditions of each highway and considering highway location, high temperatures along highways M5 and M3 exhibited positive effects on isopod diversity. Highway M5 is located in the warmest and driest part of Hungary; highway M3 is located in a cold-temperature belt compared to the other highways which are in a warm-temperature belt (Szelepcsényi et al. 2009) (Figs. 1-2). Isopods showed not only annual but also seasonal variation in their spatial distribution. The effects of temperature and precipitation on isopod diversity and abundance were more pronounced along M7. Bozinovic at al. (2014) observed that heat tolerance isopods exhibited little variation relative to latitude and temperatures, but cold tolerance species showed a large variability. The highest number of individuals was found in two areas with different climates (Polgár and Letenye). We believe that not only climate conditions but also other factors affect isopod abundance and diversity. In a previous study, we found that landscape type and the road edge proximity influenced isopod diversity along highways. Namely, species richness and isopod diversity was lowest in arable land, while urban areas supported the highest isopod diversity (Vona-Túri et al. 2017).

We need to examine each species separately because patterns may not be immediately evident when using species composition data. Our results concur with those of Magura et al. (2006), who found that each isopod species responded differently to various environmental factors, largely due to their anatomical characteristics. According to Verhoeff (1931), some species prefer wet habitats, while others are more abundant in drier areas. Beyer (1964) noticed that habitat selection of isopods was dependent on the moisture condition of microhabitats. *A. vulgare* was characterised by increasing populations and high summer activity maybe owing to the Mediterranean origin of this species. According to Thuiller et al. (2007), constantly rising temperatures provide suitable conditions for Mediterranean species. Nasu et al. (2018) suggest that the urban specialist *A. vulgare* is commonly found in urban areas. The high abundance of *A. vulgare* in summer on highway verges might be explained by its high reproductive potential (Quadros et al. 2009), as well as adaptation ability and tolerance to dehydration that depends on evaporation from the respiratory organs and the body surface (Kuenen 1959). Moreover, Ott et al. (2012) reported that high temperatures have a positive effect on nutritional rates of isopod.

The relative abundance of *T. rathkii, T. nodulosus* and *T. ratzeburgii* decreased with years. Gurnell et al. (2004) found that coloniser species had a negative effect on sensitive native species, which led to a reduction in diversity. Furthermore, we should consider the extreme environmental conditions along highways that negatively affect the distribution of specialist species. Several studies have shown that landscape fragmentation, especially forest fragmentation, is the most serious threat to the loss of sensitive species and biodiversity (Andrew 1990, Forman & Alexander 1998, Seiler 2001, Forman et al. 2002, Daigle 2010). Besides fragmentation, invasive species are another major cause of a reduction in biodiversity (Nentwig 2007). Our results confirm the introduced species hypothesis that the adventive species (e.g. *A. vulgare*) are more likely to colonise the altered habitats and become naturalised, while the distribution and abundance of native specialist species (*T. rathkii, T. nodulosus* and *T. ratzeburgii*) is reduced. According to Andrews (1990), high abundances of widespread species are often observed along roadside verges.

Roadside verges are important habitats for biodiversity conservation, especially in agricultural areas and for habitat expansion in mainly grassy habitats and it is important to prevent the reduction of biodiversity and species loss therein. Our results demonstrate that temperature and precipitation have effects on isopod diversity and distribution and that coloniser species are likely to be strong determinants of isopod communities along roads, and may ultimately influence ecosystem functioning. Temperature and precipitation are determinant factors in the distribution of isopods along highways, but we should also consider the surrounding landscape type and disturbance level. Consequently, we should expect that coloniser species to be involved in processes that cause further changes to the biodiversity along roads.

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