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Invasive occurrence and abundance changes of *Armadillidium vulgare* (Latreille, 1804) in Hungarian roadside verges

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Abstract

Background and purpose: *The impact of invasive species in ecosystems is an important problem worldwide and the spreading of invader species are affected exceedingly by linear infrastructure. Primarily the aim of our investigation was to studied how the invasion of the species impacts the isopod diversity of roadside verges. Secondly, we determined what attributes of linear infrastructure affect on mass occurrence by the species.*

Materials and methods: *Double-glass pitfall traps were established 30 localities along highways and 4 localities along main roads in Hungary between 2011 and 2016. To studied what attributes of roads affect the abundance of* A. vulgare *we considered seasons, adjacent areas, road edge proximity, leaf-litter depth, the age of highway, vegetation type and mowing.*

Results: *We collected a total of 18 isopod species. The* A. vulgare *was the most abundant and frequently encountered species in both road types, which represented 89% of the total isopod catches. The high abundance of the species negatively correlated with isopod diversity. The invasive nature of this species is promoted by summer season, the proximity of arable fields, intermediate distance from the road, leaf-litter at a depth of 0 cm and the young age of highways. On mainroad verges the highest abundance was in the non-mown sections of the arid grassland sites.*

Conclusions: *Our results suggest that this species is likely to adversely impact ecosystem function of roadside verges in Hungary. Different land use, water supply, surrounding landscapes, habitat structure, vegetation, biogeographical context and human activities along road verges influence the invasiveness of* A. vulgare.

INTRODUCTION

Roadside verges function as prime habitats for several native, exotic and invasive animal and plant species *(1, 2, 3, 4)*. Roads provide not only refuges for protected and endangered species in agriculturally-dominated landscapes but also function as invasion pathways for arthropods *(5, 6, 7, 8)*. However, roads also exert significant negative effects on communities, wildlife populations and ecosystems of surrounding habitats *(9)*. The presence of roads and traffic may alter the chemical environment, modify animal behaviourand provide dispersal routes for species *(1)*. Linear infrastructure, vehicles and roadside verges may be important elements in determining the spatial spread of an organism's distribution *(6, 10)*. In heavily disturbed and modified habitats such as highways, invasive species have a chance to adapt and spread along roadsides by the green corridor effect *(11)*. The distribution of other species is reduced or becomes isolated to facilitate the expeditious spread of invasive species *(12)*. However, not all new species can adapt and spread in the new area after entering and become invasive, as the „tens rules" by Williamson & Fitter *(13)* illustrates well. In the new habitats, 10% of imported species can escape to the wild, 10% of occasionally colonizing species become naturalized, and only 10% of naturalized species become invasive. Over recent decades the spread of invasive species is related to climate change and the ever-increasing development of international commerce *(14)*. The appearance of a new invasive species into an ecosystem often does not result in an immediate impact, furthermore, in many cases, it is difficult to estimate which species are essential to ecosystem functioning and which are redundant *(15)*. The presence of invasive species in ecosystems is a remarkable problem worldwide because they have an impact on the structure and function of ecosystems, and biodiversity and the loss of habitats, and invader species can cause serious environmental, economic or social damage *(16)*. Clavero & García-Berthou *(17)* showed that overgrowth of invasive species contributed to 54% of extinction of animal species.

Firstly, the main objectives of this study were to investigate the invasive occurrence of *A. vulgare* along Hungarian highways, and we studied how the invasion of the species impacts the isopod diversity of highway verges.

1) We hypothesised that *A. vulgare* has a negative effect on the diversity of the isopod communities because of the species invasiveness. Secondly, we explored what attributes of roads (seasons, adjacent areas, road edge proximity, leaf-litter depth, highway age, vegetation and mowing) affect the abundance of *A. vulgare*.

2) We compared the abundance of *A. vulgare* based on seasons in highway verges. We assumed that the maximum number of individuals will peak abundance in autumn because of its semelpar reproduction *(18)*.

3) We studied the effect of adjacent areas of highway verges on *A. vulgare* abundance. Our hypothesis was that this species prefers disturbed open habitats compared to other isopod species which prefer wet forested habitats, because of the species is an indicator of anthropogenic impacts.

4) We analysed the effects of road edge proximity on highways and we expected that the highest abundance of *A. vulgare* would occur at an intermediate distance from the road, because of the intermediate disturbance hypothesis.

5) We compared the abundance of *A. vulgare* in highway sampling sites based on leaf-litter depth between 0–5 cm intervals. We hypothesised that the species abundance would increase with leaf-litter depth, because of the species contribution to decomposition processes.

6) We assessed differences between sampling sites based on highway age. We hypothesised that there would be a decrease in the abundance of the species from the oldest sites to the youngest sites, because of the invasive nature of this species.

7) In main roads we examined the effect of the main Hungarian vegetation types and we expected the highest abundance of *A. vulgare* in open habitats, such as grasslands.

8) Finally, we analysed the effect of mowing on the abundance of *A. vulgare* on main roads. Our hypothesis was that the mowing would negatively affect the number of individuals.

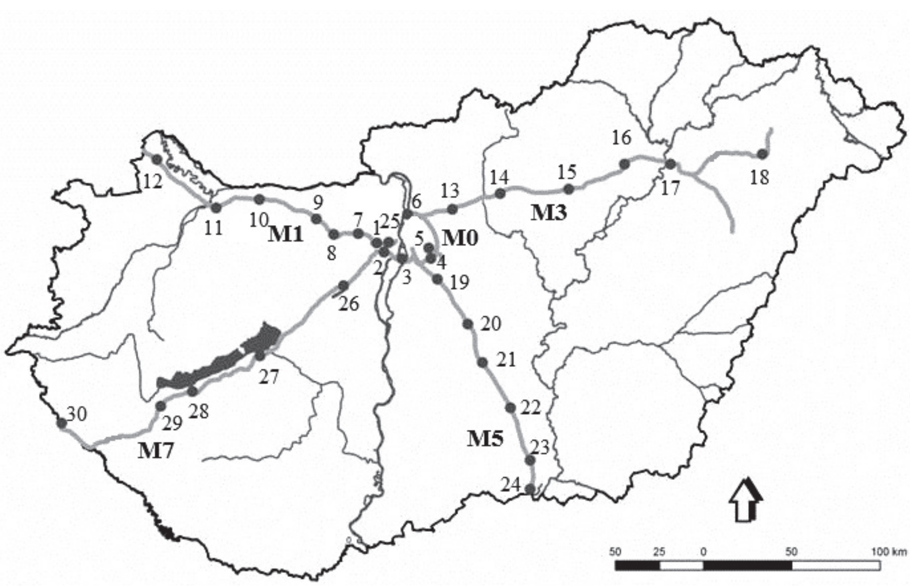

Figure 1. *Map of highways and the sampling sites. The code of sampling sites can be found in Table 1*

Table 1. *Characterization of sampling sites along highway*

Highway	Code	Sampling sites	Adjacent area	Leaf litter cover (%)	Leaf litter depth (cm)	Soil
M0	1	0 km sos	urban	15	3	construction debris
	2	Anna-hegy	orchard	15	1	gravelly
	3	Csepel	urban	40	2	sand
	4	Alacska	grassland	30	1	sand
	5	Ferihegy	grassland	10	4	gravelly, clastic
	6	Dunakeszi	forest	20	3	clastic
M1	7	Zsámbék	arable land	95	1	light loess
	8	Óbarok	forest	98	0.5	light loess
	9	Turul	orchard	98	6	light loess
	10	Bábolna	arable land	75	2	dark humus
	11	Arrabona	arable land	100	5	humic sand
	12	Moson	arable land	40	0.5	dark gravelly
M3	13	Kisbag	forest	10	1	sand
	14	Ecséd	orchard	10	1	black loose
	15	Rekettyés	arable land	0	0	black loam
	16	Gelej	arable land	5	1	black loam
	17	Polgár	arable land	5	1	sand
	18	Nyíregyháza	arable land	10	4	loessal
M5	19	Inárcs	sand grass	20	0.5	sand
	20	Örkény	forest	20	0.2	light sandy
	21	Kecskemét	arable land	80	0.2	dark humus
	22	Petőfiszállás	arable land	100	0.2	dark humus
	23	Szatymaz	grassland	100	1	dark humus
	24	Röszke	sand grass	100	5	sand
M7	25	Budaörs	urban	100	0.2	darl loess
	26	Velence	orchard	100	5	light loess
	27	Törek	arable land, forest	98	1	brown, loessal
	28	Táska	grassland	50	0.2	light sandy
	29	Szegerdő	arable land	2	0.2	light gravelly
	30	Letenye	forest	98	0	gravelly, loam

MATERIAL AND METHODS

Study sites and sampling procedure

Highways

Data collection was done along 5 Hungarian highways (M0, M1, M3, M5, M7) (Figure 1). Highway M0 is considered to be the main road but it is managed as a highway in Hungary, because the traffic intensity on the main road is the same as that of highways. Thirty sampling points were selected in the highway verges that were located among neighbouring habitats with different type of vegetation and various level of disturbance. Along each highway we selected 6-6 sampling points (Table 1) where a total of 180 double-glass pitfall traps made of 3 dl plastic cups filled with a 65% aqueous solution of ethylene glycol were established. Sampling sites were selected next to the lay-bys along highway where isopods were sampled using 6-6 pitfall traps at each site and the distance between traps was 5 m. The traps were deployed three times (spring, summer, autumn) over a three-week period each year. On highways, we studied the effects of seasons, ad-

Table 2. *Sampling sites along highways used to examine the effect of adjacent areas and road edge proximity*

Types of adjacent areas		Highway	Sampling site	Distance from the road (~)
Natural and semi-natural	Grasslands	M5	Röszke	20 m
		M0	Ferihegy	40 m
		M7	Táska	90 m
	Forest	M5	Örkény	20 m
		M3	Kisbag	40 m
		M1	Óbarok	90 m
Disturbed	Urban	M0	0 km	20 m
		M7	Budaörs	40 m
		M0	Csepel	90 m
	Orchard	M3	Ecséd	20 m
		M1	Turul	40 m
		M7	Velence	90 m
	Arable land	M7	Szegerdő	20 m
		M3	Polgár	40 m
		M5	Kecskemét	90 m

Table 3. *Sampling sites along highways used to examine the effect of leaf-litter depth*

Highways	Sampling sites	Leaf litter depth (cm)
M7	Letenye	0
M3	Rekettyés	
M0	Alacska	1
M3	Gelej	
M0	Csepel	2
M1	Bábolna	
M0	Dunakeszi	3
M0	0 km	
M0	Ferihegy	4
M3	Nyíregyháza	
M5	Röszke	5
M1	Arrabona	

jacent areas, road edge proximity, leaf litter depth and the age of highways on the abundance of *A. vulgare*. Selection of sampling sites and coordination of sampling methods were occurred by the Center of Agricultural Research, Hungarian Academy of Sciences, Plant Protection Institute. When we analysed the effect of different factors on the abundance of *A. vulgare*, we did not consider the data of all 30 sampling sites except for annual and seasonal examination. To examine the effect of adjacent areas and

Table 4. *Sampling sites along highways used to examine the effect of age of highway*

Sampling sites	Highways	Year of establishment
Arrabona	M1	1977
Bábolna	M1	
Turul	M1	1982
Óbarok	M1	
Kecskemét	M5	1989
Őrkény	M5	
Polgár	M3	2002
Gelej	M3	
Ferihegy	M0	2008
Szegerdő	M7	

road edge proximity, we selected 15 sampling sites (see Table 2). To assess the effect of leaf litter depth, we considered 12 sampling sites (see Table 3). To examine the effect of age of highways, we selected 10 sampling sites (see Table 4).

Main roads

Along Hungarian main roads data was collected at four sampling sites representing the main types of verge habitats between 2014–2016 (Figure 2). Verge types were categorised based on the vegetation type of neighboring habitats. Sampling area Pilisjászfalu (Road No. 10) consisted of arid grassland with some small bushes. Mány (Road No. 1) was situated in the lowlands and hilly landscapes of Hungary, and was bordered by 2 roads running through agricultural land. Herceghalom (Road No.1) was situated next to a forest. Agárd (Road No. 7) crosses a wetland area in the west section of Lake Velence. All localities included three sections representing *(1)* no maintenance (non mown) *(2)* normal maintenance (mown once a year) and *(3)* enhanced maintenance (mown twice or three times a year). The distance between 2 sections was 100 m. In each section five pitfall traps were established 5 meters apart, and they were located 1,5 meters from the roads. Double glass pitfall traps filled with ethylene glycol were used which were left in the fields for three weeks and three times a year in different seasons (spring, summer and autumn). We collected samples after first mowing in between May and June. After the second mowing the field experiment was repeated twice in August and September. Trapped specimens were preserved in 75 percent alcohol. Sampling methods made it possible to study the effects of vegetation type and mowing on abundance of *A. vulgare.* Selection of sampling sites and coordination of sampling methods were occured by the Centre for Ecological Research, Hungarian Academy of Sciences, Danube Research Institute.

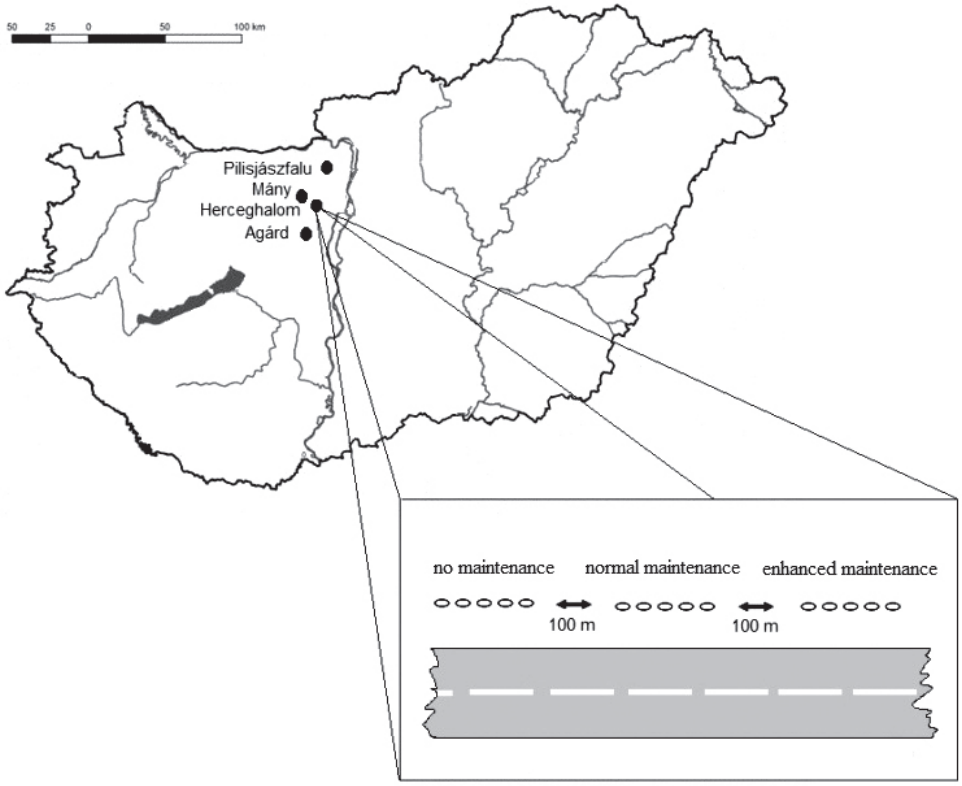

Figure 2. *Sampling sites and treatment along main roads*

Data analysis

We used the PAST Paleontological Statistic suite for data analysis *(19)*. Besides a number of individuals, we computed Shannon-Wiener diversity in order to analyse the invasive patterns of *A. vulgare*. The Shannon-Wiener index is more sensitive to the frequency of rare species *(20, 21, 22)*. Species with the highest abundance have the greatest influence on the Simpson's index *(20, 21, 22)*. The characterization of the *A. vulgare* population was based on relative abundance (Ar) and frequency (F). The years were the replications, except for the case of the annual population dynamics, when sampling dates were the replications. One-Way ANOVA was applied to assess the differences between the number of individuals of A. *vulgare* in relation to years, seasons, adjacent areas, road edge proximity, leaf-litter depth and highway age. We used the keys of Hopkin *(23)*, Schmidt *(24)*, and Farkas & Vilisics *(25)* for identification of isopod specimens. Species' names were applied according to Schmalfuss *(26)*.

RESULT

γ-diversity

Along main roads, we collected 6 isopod species and on highway verges 18 species. During our study *A. vulgare* was the most abundant isopod species (highways: Ar =89% of a total number of individuals collected, main roads: Ar = 89%) and frequent species (highways: F = 94%, main roads: F = 100%). A total of 52361 specimens of *A. vulgare* were collected along roads, composed of 45626 individuals on highway verges and 6735 individuals on main road verges.

Highways

We examined the annual population dynamics along highways and we found no significant differences (p=0.416) in abundance of *A. vulgare*. The number of *A. vulgare*, the relative abundance and the frequency increased with years (Figure 3). Simultaneously, the values of Shannon-Wiener diversity of isopods along highways decreased with years, beacause it was significantly lower (p= 0.049) in 2013 compared to 2011 (Figure 4).

Significant differences were no found between number of *A. vulgare* (p=0.287) in relation to season. The number of the species was the highest in summer and the lowest was in autumn. The highest relative abundance and frequency of the species also were in summer, while the lowest was in autumn (Figure 5).

We found statistically significant differences in number of *A. vulgare* (p=0.013) in relation to adjacent areas of highways. Abundance of *A. vulgare* was significantly higher next to arable lands compared to verges next to forests, urban areas and orchards. The relative abundance of the species was lowest next to urban areas than the other verges, while the frequency of the species was 100% in each verges (Figure 6).

Significant differences were found between number of the species (p=0.045) in relation to road edge proximity. The number of *A. vulgare* was significantly higher at 40 m from the road than at 20 m from the road. The relative

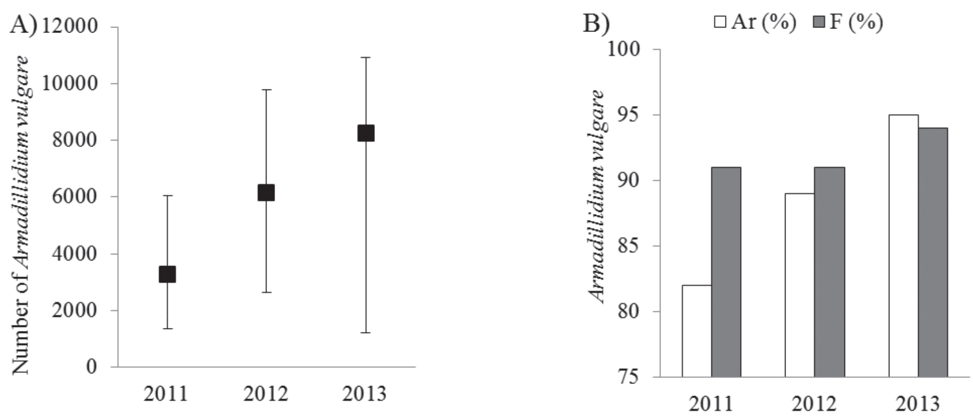

Figure 3. *Annual population dynamics of abundance (A), and relative abundance and frequency (B) of* A. vulgare *(average ± S.E.).*

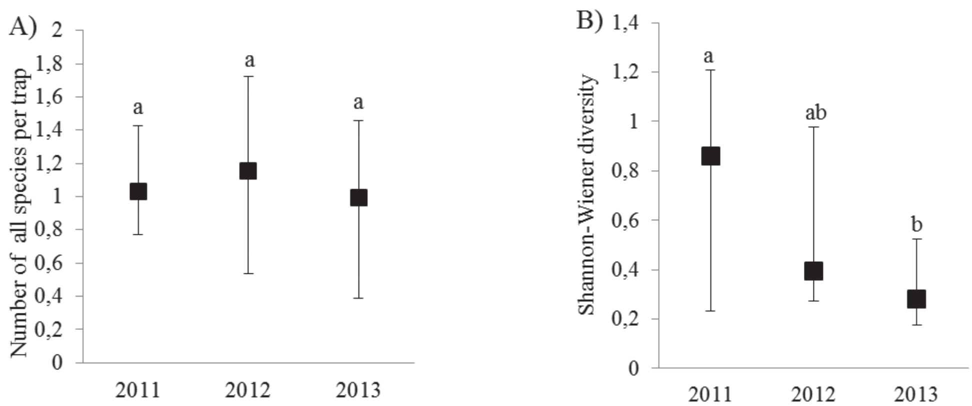

Figure 4. *Annual population dynamics of species richness (A) and Shannon-Wiener diversity (B) of isopod assemblages in highway verges (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)*

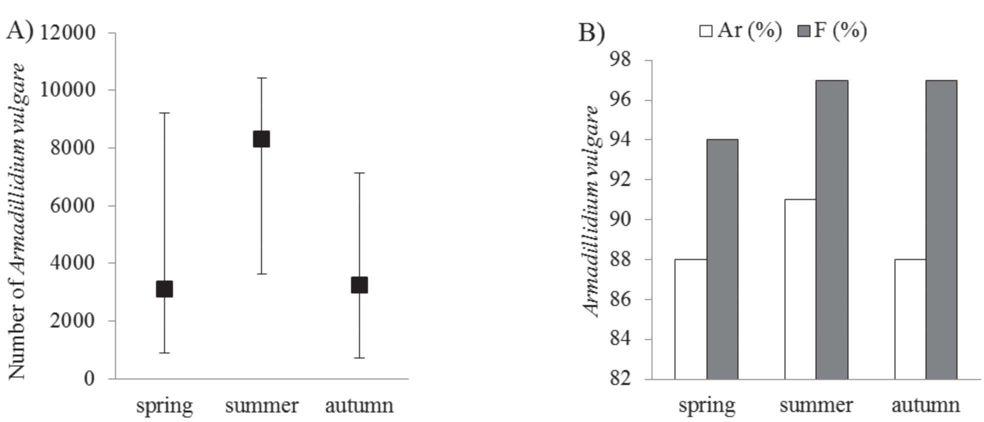

Figure 5. *Abundance (A) and relative abundance and frequency (B) of* A. vulgare *in highway verges in relation to season (average ± S.E.).*

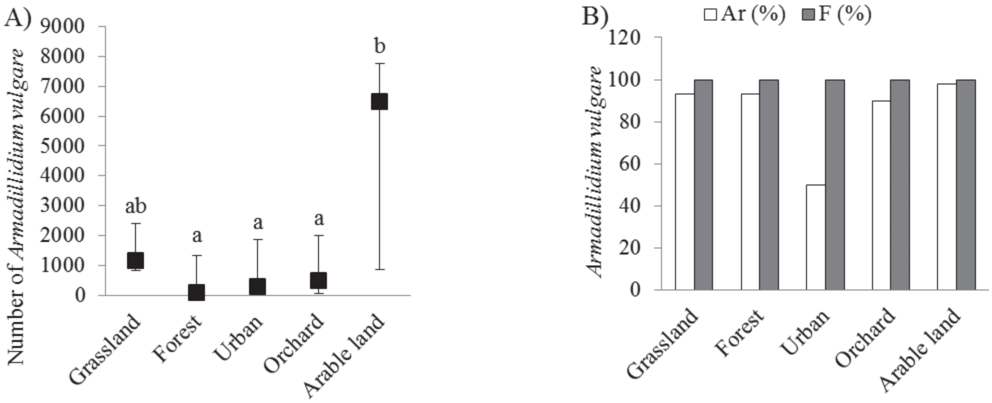

Figure 6. *Abundance (A) and relative abundance and frequency (B) of* A. vulgare *in highway verges in relation to adjacent areas (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)*

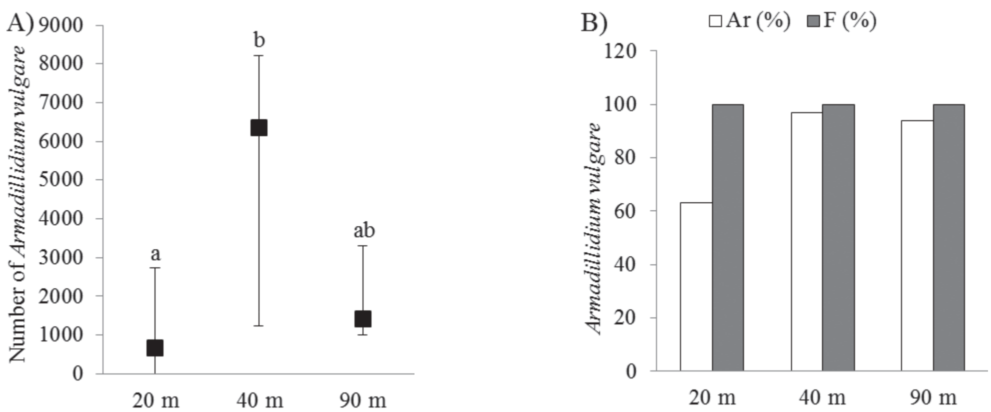

Figure 7. *Abundance (N) and relative abundance and frequency (B) of* A. vulgare *in highway verges located at different distances (20 m, 40 m and 90 m) from roads (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)*

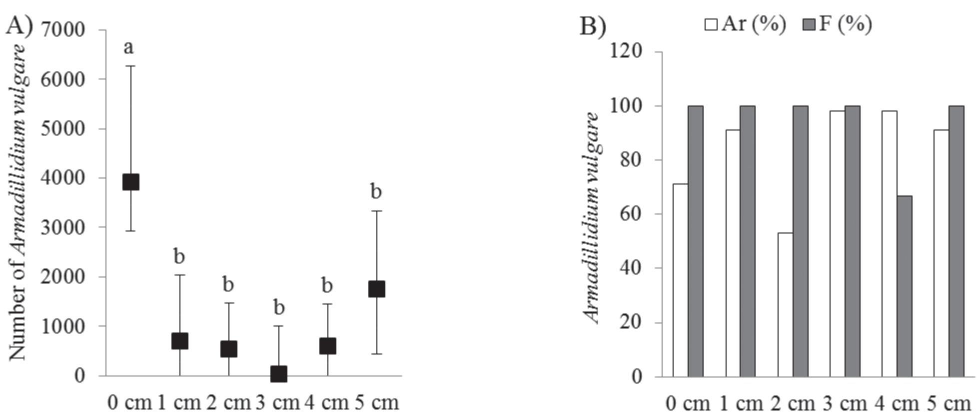

Figure 8. *Abundance (N) and relative abundance and frequency (B) of* A. vulgare *in highway verges relative to leaf-litter depth in the verges that were examined (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)*

abundance of *A. vulgare* was lowest at 20 m from the road and the frequency of the species was equal in each distance from the road (Figure 7).

There were significant differences (p=0.00016) in abundance *of A. vulgare* in relation to leaf-litter depth. The number of *A. vulgare* was significantly highest in sam-

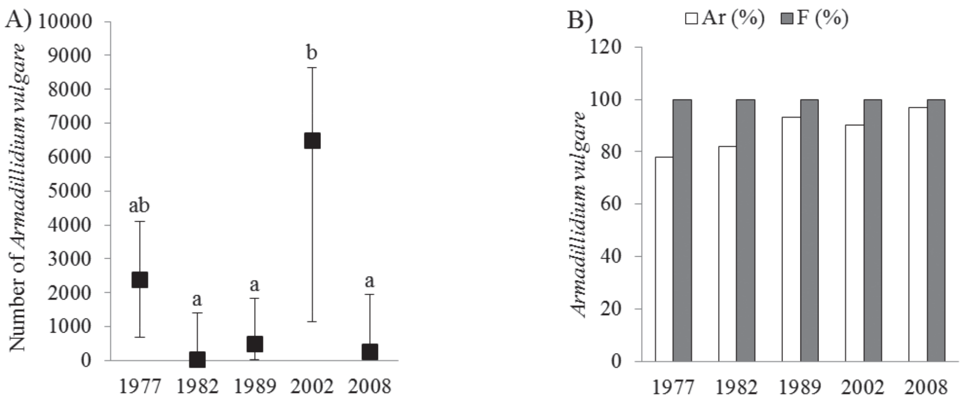

Figure 9. *Abundance (N) and relative abundance and frequency (B) of* A. vulgare *in highway verges relative to the year when highway have been finished (average ± S.E.). Different letters indicate significant (p<0.05) differences (one-way ANOVA)*

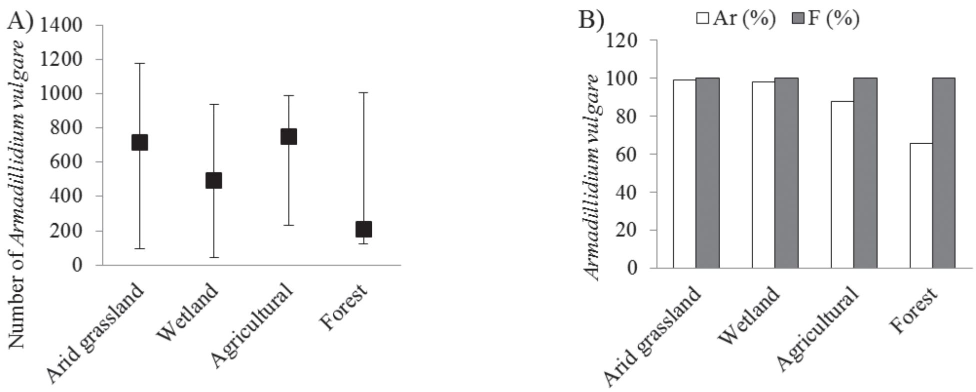

Figure 10. *Abundance (N) and relative abundance and frequency (B) of* A. vulgare *in mainroad verges relative to the vegetation type (average ± S.E.).*

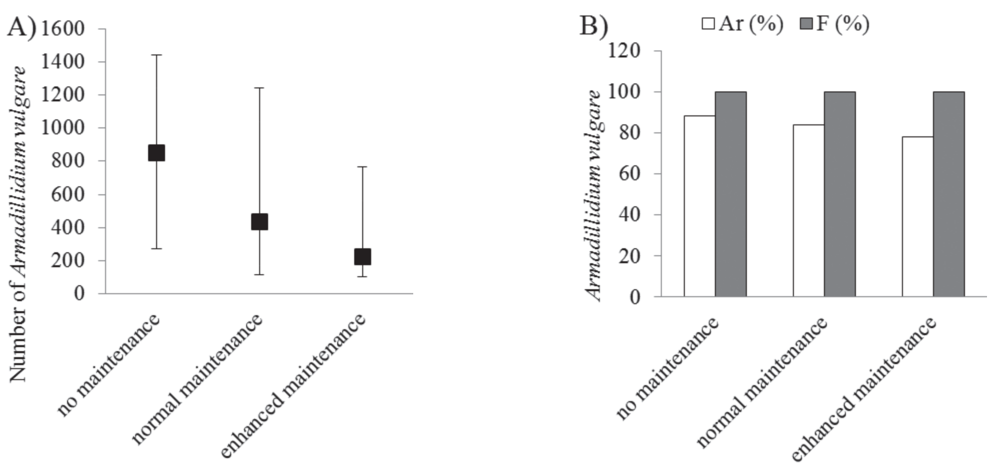

Figure 11. *Abundance (N) and relative abundance and frequency (B) of* A. vulgare *in mainroad verges relative to mowing intensity (average ± S.E.).*

pling sites at 0 cm leaf-litter depth, and it was significantly lowest in sampling sites with 3 cm leaf-litter depth compared to sampling sites with 5 cm leaf-litter depth. The relative abundance of *A. vulgare* was lowest in sampling sites at 2 cm leaf-litter depth and the frequency of the species was equal in each verges except for the sites at 4 cm leaf-litter depth (Figure 8).

We observed statistically significant differences in number of *A. vulgare* (p=0.010) in relation to years when highway have been finished. The abundance of the species was significantly highest in verges that were established in 2002 compared to other verges. The relative abundance of *A. vulgare* increased from old verges to young verges and the frequency of the species was equal in each verge types (Figure 9).

Main roads

Statistically significant differences were no found between number of *A. vulgare* (p=0.886) in relation to vegetation type of main roads. The highest number of relative abundance of *A. vulgare* were in arid grassland and in wetland, while the lowest was in the forested verges (Figure 10).

Finally, along main roads, significant differences were no found between number of *A. vulgare* (p=0.370) in relation to mowing intensity. The mowing negatively affected the number of individuals and the relative abundance of *A. vulgare*. The highest number of specimens and relative abundance of the species were recorded in the no maintenance sections, whereas the lowest number was in enhanced maintenance sections (Figure 11).

DISCUSSION

Highways

The isopod fauna of roadside verges are not typically the focus of zoological research, and there are few published studies on this taxon. We are the first researchers to examine the isopod fauna along roads in Hungary. The holomediterranean *A. vulgare*, which is a typical indicator of anthropogenic impacts *(27)*, probably originated in the eastern mediterranean region *(28)*. In Hungary, *A. vulgare* was initially discovered by Csiki Endre in 1926 in Budapest, Bodajk and Pápa *(29)*. This widely distributed species can be found in most parts of the world, and is associated with high human activity and has a broad ecological tolerance *(28)*. This life history may explain why this species can colonise disturbed habitats such as roadsides. The high abundance of *A. vulgare* reflects the environmental tolerance and invasive nature of this species. *A. vulgare* is one of the most common species of isopod in Hungary *(25)*. The abundance of *A. vulgare* was observed to be similar to other habitats in Hungary. Our results compare well to Szlávec *(30)* in Hortobágy National Park, Farkas *(31, 32)* in Somogy county, in Baranya county *(33)* and in Tolna county *(34) A. vulgare* was one of the most frequent and abundant species in the areas examined. Hornung *et al. (12, 35)* studied isopods in Budapest and other cities and observed that *A. vulgare* was the widest spread and common species.

The high number of traps we deployed along highways made it possible to assess the relationship between isopod diversity and the high abundance of *A. vulgare*. Our results support our hypothesis that *A. vulgare* has a negative effect on the diversity of the isopod communities. Davis *(36)* examined isopods in a dune grassland and observed that *A. vulgare* showed a sudden increase in aggregation in 1968 and 1973. Similarly, by examining the annual population dynamics, we found that the increasing abundance of *A. vulgare* was related to the decreasing isopod diversity on highways. Horváth *et al. (37)*, Magura *et al. (38)* and Bogyó *et al. (39)* concluded that while the populations of species that are successful adapters increase, the distribution and occurrence of less-adaptive species decreases.

Our results based on seasonality do not support the hypothesis that the highest abundance of *A. vulgare* is in autumn. The high abundance of species in summer on highway verges might be explained by the high reproductive potential *(40)*, excellent adaptation ability and dehydration tolerance *(41)*. In isopods, the main mechanism for water loss is evaporation from the respiratory organs and the body surface *(42)*. Isopods differ expressly in their ability to tolerate dry conditions *(43)*. Arid-tolerant-species have a complex structural respiratory system and thick cuticle *(44)*. Among the examined Hungarian *Armadillidium* species (*A. zenkeri*, *A. nasatum*, *A. versicolor*, *A. vulgare*), *A. vulgare* has the thickest cuticle and an extremely structured respiratory system *(41)*, and is able to take up 94% of its normal oxygen requirement in dry air with a dry integument *(45)*. According to many published studies, the long-day photoperiods *(46)* and the warm temperatures *(47)* stimulate the reproduction and the growth of the offspring *(48)* of *A. vulgare*. This species produced larger offspring when the food supply of females is reduced, for example, in summer when food availability and quality is low *(49)*. Moreover, females may not produce offspring until the third year, which will be smaller in size *(48)*.

The larger difference between the fragmented and the adjacent land in vegetation structure is expected to lead to microclimate differences and hence, a greater edge effect *(50)*. To test our hypotheses we compared highway sampling sites based on adjacent areas. Our results clearly demonstrate that sites near arable fields proved to be more advantageous to *A. vulgare.* Human activity stresses soil communities due to heavy fertilizer use, frequent biocide treatment and export of nutrient and organic matter *(51)*. Conversely, many studies show that the margins of arable fields rapidly produce biodiversity benefits for the soil macrofauna *(52, 53)*. The high abundance of *A. vulgare* recorded near arable fields reflects the species' ability to adapt to disturbed and open habitats. Wolters & Ekschmitt *(51)* showed that although the abundance and diversity of isopods in arable lands is very low, marginal habitats adjacent to arable lands have the highest abundance.

Our data showed that *A. vulgare* abundance was highest at intermediate (40 m) distances from the road, which supported our hypothesis. Roadside verges have a specific flora and fauna, contained within an ecotone *(54)*.

Delgado *et al. (55)* showed that the highest frequency of litter invertebrate species occurred close to a road (10 and 20 m from the edge).

We expected that the highest number of *A. vulgare* would be observed in sampling sites that had the thickest leaf-litter, but our result does not support this hypothesis. It is known that isopods are responsible for most of the decomposition of organic matter, mostly leaf litter decomposition *(56)*. The leaf-litter and its microorganisms serve as food sources for isopods. Moreover, the surfaces of plant residues have much more active microbial biomass than in the soil *(57)*. However, we found that the 0 cm thick leaf-litter provided the most suitable habitat for *A. vulgare.* Thick leaf-litter has increased CO_2 levels, which has a negative effect on the fertility of isopods *(58).* Panlasigui *(27)* showed that *A. vulgare* displays a preference for leaf-litter with a water content of 0.39 compared to litter with a water content 0.53.

Because the regeneration of natural vegetation going on 30–40 years, we expected the highest abundance on the oldest highway sampling site, but our hypothesis was not supported by this result. Several studies show that many invader plant and animal species'colonies have expanded along roads where the age of roads has an impact on the diversity and abundance of organisms *(7, 59, 60, 61, 62, 63).* Similarly, we found an increase in the relative abundance of *A. vulgare* that probably reflected the invasive patterns of the species. Along with Hungarian highways, Fetykó *(64)* observed only a slight increase in the number of scale insects in the old sampling sites, but Lengyel *et al. (63)* provided evidence for a growing population of spotted wing drosophila at such sites.

Main roads

The highest abundance of *A. vulgare* was in arid grasslands, which confirmed our original hypothesis. We conclude that *A. vulgare* is a typical and common species of drier areas *(65, 45, 66).* Miller & Cameron *(67)* showed that survivorship of *A. vulgare* in Texas was highest in grassland areas. Roadside verges of Hungary typically consist of grassy vegetation, habitats that may be facilitating the invasion and spread of *A. vulgare*. The road stretches examined are located in lowland areas that bypass the mountain regions, which may also explain the high biomass of *A. vulgare* on roadside verges. According to our data, abundance of *A. vulgare* was highest in grassy verges of main roads compared to other verge types. According to Farkas & Vilisics *(25)*, this cosmopolitan species has a ubiquitous distribution in Hungary, except for protected hardwood forests. Our findings concur with Farkas & Vilisics *(25)* in addition, the relative abundance of *A. vulgare* was lowest in the forested verges of main roads and highway verges near forests. Few studies have examined isopod communities in Hungarian mountainous areas. In the North-Vértes Mountains, and in Hungarian Northern Mountains, Kontschán *(68, 69)* observed that *A. vulgare* was not common. In Mátra Mountains, Vona-Túri & Szmatona-Túri *(70)* found that the species was not dominant. Vilisics & Hornung *(71)* examined many regions in Hungary: Great Plains, Little Plains, Western Hungary, Transdanubian Hills, Transdanubian Mountain Range, Northern Mountain Range, Aggtelek National Park and Budapest. According to their studies *A. vulgare* dominated the isopod communities, but the species was not detected in the Northern Mountain Range. Accordingly, the biogeographical context and habitat structure are likely impacting the spread of *A. vulgare* along roads.

Mowing has a positive effect on floral diversity which contributes to a diverse habitat structure and increasing animal and plant species richness *(72, 73, 74)*. Responses of isopods to mowing are not well known but studies about other soil-dwelling arthropods suggest that grassland management can alter soil humidity, vegetation structure and lighting conditions *(75)*, factors that likely influence isopod communities. Our result concerning the high abundance on non-mowing sections confirms our hypothesis. Although *A. vulgare* adapt well to dry conditions and disturbance, mowing has a negative effect on the species' abundance.

Conclusion

Our results demonstrate that the terrestrial isopod *A. vulgare* was common and widespread in Hungarian roadside verges. The ability of this species to successfully colonize open vegetation and its tolerance of dry conditions can be attributed mostly to its anatomical features. Besides roads and traffic, biogeographical context, different land use, water supply, surrounding landscapes, habitat structure and vegetation significantly influence the abundance of *A. vulgare*. The increasing abundance of *A. vulgare* in Hungary is related to the decreasing species diversity of other isopods on highways. Consequently, this invasive species is likely to be a strong determinant of invertebrate community composition and as such may influence ecosystem function along roadside verges in Hungary.

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REFERENCES

1. TROMBULAK S C, FRISSELL C 2000 A. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14: 18-30. https://doi.org/10.1046/j.1523-1739.2000.99084.x
2. HANSEN M J, CLEVENGER A P 2005 The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biol. Conserv. 125 (2): 249–259. https://doi.org/10.1016/j.biocon.2005.03.024
3. PAUCHARD A, ALABACK P B 2006 Edge type defines alien plant species invasions along Pinus contorta burned, highway and clearcut forest edges. For. Ecol. Manage.223: 327–335. https://doi.org/10.1016/j.foreco.2005.11.020
4. KNAPP M, SASKA P, KNAPPOVÁ J, VONIČKA P, MORAVEC P, KURKA A, ANDEL P 2013 The habitat-specific effects of highway proximity on ground-dwelling arthropods: implications for biodiversity conservation. Biol. Conserv. 164: 22–29. https://doi.org/10.1016/j.biocon.2013.04.012
5. TIKKA P M, HOGMANDER H, KOSKI P S 2001 Road and railway verges serve as dispersal corridors for grassland plants. Landsc. Ecol. 16 (7): 659–666. https://doi.org/10.1023/A:1013120529382
6. HAWBAKER T J, RADELOFF V C, CLAYTON M K, HAMMER R B, GONZALES-ABRAHAM C E 2006 Road development, housing growth and landscape fragmentation in northern Wisconsin: 1937-1999. Ecol. Appl. 16: 1222-1237. https://doi.org/10.1890/1051-0761(2006)016[1222:RDHGAL]2.0.CO;2
7. BRISSON J, DE BLOIS S, LAVOIE C 2010 Roadside as invasion pathway for common reed (Phragmites australis). Inv. Plant. Sci. Manag. 3 (4): 506–514. https://doi.org/10.1614/IPSM-09-050.1
8. HOLDEREGGER R, DI GIULIO M 2010 The genetic effects of roads: a review of empirical evidence. Basic Appl. Ecol. 11 (6): 522–531. https://doi.org/10.1016/j.baae.2010.06.006
9. VAN DER REE R, JAEGER J A G, VAN DER GRIFT E A, CLEVENGER A P 2011 Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving towards larger scales. Ecol. Soc. 16 (1): 48. https://doi.org/10.5751/ES-03982-160148
10. MARTINEZ J J I, WOOL D 2006 Sampling bias in roadsides: the case of galling aphids on Pistacia trees. Biodivers. Conserv. 1–13. https://doi.org/10.1007/s10531-004-6685-2
11. ALARUIKKA D M, KOTZE D J, MATVEINEN K, NIEMELÄ J 2002 Carabid and spider assemblages along an urban to rural gradient in Southern Finland. J. Insect Conserv. 6: 195–206. https://doi.org/10.1023/A:1024432830064
12. HORNUNG E, VILISICS F, SZLÁVECZ K 2007 Hazai szárazföldi ászkarák fajok (Isopoda, Oniscidea) tipizálása két nagyváros, Budapest és Baltimore (ÉK Amerika) összehasonlításának példájával (Standardization of Hungarian terrestrial isopods comparing two big cities, Budapest and Baltimore (North America)). Termvéd Közl.13: 47–58
13. WILLIAMSON M H, FITTER A 1996 The characters of successful invaders. Biol. Conserv. 78(1-2): 163-170. https://doi.org/10.1016/0006-3207(96)00025-0
14. THUILLER W, RICHARDSON D M, MIDGLEY G F 2007 Will Climate Change Promote Alien Plant Invasions? In: Nentwig W (ed.) Biological Invasions. (Ecological Studies Vol. 193).Springer-Verlag, Berlin p. 197–211. https://doi.org/10.1007/978-3-540-36920-2_12
15. LOWE S, BROWNE M, BOUDJELAS S, DE POORTER M 2000 100 of the World's Worst Invasive Alien Species. A selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN) p. 12.
16. CHARLES H, DUKES J S 2007 Impacts of Invasive Species on Ecosystem Services. In: Nentwig W. editor. Biological invasions (Ecological Studies Vol. 193). Springer-Verlag, Berlin, p. 217–237. https://doi.org/10.1007/978-3-540-36920-2_13
17. CLAVERO M, GARCÍA-BERTHOU E 2005 Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20: 110. https://doi.org/10.1016/j.tree.2005.01.003
18. HASSALL M, HELDEN A, BENTON T 2003 Phenotypic plasticity and interpopulation differences in life history traits of *Armadillidium vulgare* (Isopoda: Oniscidea). Oecologia 137: 85–89. https://doi.org/10.1007/s00442-003-1325-1
19. HAMMER O, HARPER DAT, RYAN PD 2001 PAST: Paleontological Statistics software package for education and data analysis. Palaeontol. Electron. 4 (1): 9
20. NAGENDRA H 2002 Opposite trends in response for the Shannon and Simpson indices of landscape diversity. Appl. Geogr. 22 (2): 175–186. https://doi.org/10.1016/S0143-6228(02)00002-4
21. HILL T C J, WALSH K A, HARRIS J A, MOFFETT B F 2003 Using ecological diversity measures with bacterial communities. FEMS Microbiol. Ecol. 43 (1): 1–11. https://doi.org/10.1111/j.1574-6941.2003.tb01040.x
22. MAGURRAN A E 2003 Measuring Biological Diversity. Blackwell Publishing Oxford. 264 p.
23. HOPKIN S P 1991 A Key to the Woodlice of Britain and Ireland. AIDGAP, Field Studies7, England p. 599–650
24. SCHMIDT C 1997 Revision of the European species of thegenus Trachelipus Budde-Lund, 1908 (Crustacea: Isopoda: Oniscidea). Zool. J. Linn. Soc. 121: 129–244. https://doi.org/10.1111/j.1096-3642.1997.tb00337.x
25. FARKAS S, VILISICS F 2013 Magyarország szárazföldi ászkarák faunájának határozója (Isopoda: Oniscidea) (A Key to the Terrestrial Isopods of Hungary). Nat. Somogy. 23: 89–124
26. SCHMALFUSS H 2003 World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgart: Beitr. Naturk. Ser. A. Nr.; 654: 341 p.
27. PANLASIGUI S 2011 Choosy Crustaceans: Habitat Preference of the Terrestrial Isopod, *Armadillidium vulgare* (Isopoda: Oniscidea). Terrestrial Isopod Habitat Preferencen. pag. Nature. berkeley. edu.
28. SCHMALFUSS H 2000 Distributional patterns in the Greek species of the terrestrial isopod genus Armadillidium Brandt, 1833. Belg. J. Zool. 130 (Supplement): 77–82
29. FORRÓ L, FARKAS S 1998 Checklist, preliminary distribution maps, and bibliography of woodlice in Hungary. Misc. Zool. Hung. 12: 21–44
30. SZLÁVECZ K 1991 The terrestrial isopod fauna of the Hortobágy National Park. Misc. Zool. Hung. 6: 61-66
31. FARKAS S 1998 A Rinya-ártér Isopoda faunája I. Bakháza (The Isopoda fauna of the Rinya region. Bakháza (Hungary). Nat. Somogy. XIII. 257-262
32. FARKAS S 2004 Data to the knowledge of the terrestrial Isopod (Isopoda: Oniscidea) fauna of Somogy county (Hungary: South Transdanubia). Nat. Somogy. 16: 313-323
33. FARKAS S 2005 Data to the knowledge of the terrestrial Isopod (Isopoda: Oniscidea) fauna of Baranya county (Hungary: South Transdanubia). Acta Kaposvariensis 9 (1): 67-86
34. FARKAS S 2006 Tolna megye szárazföldi ászkarákfaunájának (Isopoda: Oniscidea) alapvetése. (Data to the knowledge of the terrestrial Isopod (Isopoda: Oniscidea) fauna of Tolna county (Hungary: South Transdanubia)). *Állattani Közl*. 91 (1): 29-42
35. HORNUNG E, VILISICS F, SÓLYMOS P 2009 Ászkarák együttesek (Crustacea, Isopoda, Oniscidea) felhasználhatósága élőhelyek minősítésében (The use of woodlice assemblages (Crus-

tacea, Isopoda, Oniscidea) in the assessment of habitat naturalness). Termvéd *Közl.* 15: 381–395

36. DAVIS R C 1984 Effects of Weather and Habitat Structure on the Population Dynamics of Isopods in a Dune Grassland. Oikos 42: 387-395. https://doi.org/10.2307/3544409

37. HORVÁTH R, MAGURA T, TÓTHMÉRÉSZ B 2012 Ignoring ecological demands masks the real effect of urbanization: a case study of ground-dwelling spiders along a rural-urban gradient in a lowland forest in Hungary. Ecol. Res. 27: 1069–1077. https://doi.org/10.1007/s11284-012-0988-7

38. MAGURA T, NAGY D, TÓTHMÉRÉSZ, B 2013 Rove beetles respond heterogeneously to urbanization. J. Insect Conserv. 17: 715-724. https://doi.org/10.1007/s10841-013-9555-y

39. BOGYÓ D, MAGURA T, SIMON E, TÓTHMÉRÉSZ B 2015 Millipede (Diplopoda) assemblages alter drastically by urbanisation. Landsc. Urban Plan. 133: 118–126. https://doi.org/10.1016/j.landurbplan.2014.09.014

40. QUADROS A F, CAUBET Y, ARAUJO P B 2009 Life history comparison of two terrestrial isopods in relation to habitat specialization. Acta Oecol. 35: 243–249. https://doi.org/10.1016/j.actao.2008.10.007

41. CSONKA D, HALASY K, MRAK P, ŠTRUS J, HORNUNG E 2012 *Armadillidium*-fajok (Isopoda: Oniscidea) élőhelyi adaptációjának morfológiai háttere (The morphological background of the habitat adaptation of *Armadillidium* (Isopoda: Oniscidea) species). Termvéd. *Közl.* 18: 115–126

42. KUENEN D J 1959 Excretion and water balance in some land isopods. Entomol. Exp. Appl. 2: 287– 294. https://doi.org/10.1111/j.1570-7458.1959.tb00442.x

43. SMIGEL J T, A G Gibbs 2008 Conglobation in the pill bug, Armadillidium vulgare, as water conservation mechanism. J. Insect. Sci. 8 (1): 44. https://doi.org/10.1673/031.008.4401

44. PAOLI P, FERRARA F, TAITI S 2002 Morphology and evolution of the respiratory apparatus in the family Eubelidae (Crustacea, Isopoda, Oniscidea). J. Morphol. 253: 272–289. https://doi.org/10.1002/jmor.10008

45. CLOUDSLEY-THOMPSON J L 1977 The Water and Temperature Relations of Woodlice. Meadowfield Press, England, p. 84

46. MOCQUARD J P, JUCHAULT P, SOUTY-GROSSET C 1989 The role of environmental factors (temperature and photoperiod) in the reproduction of the terrestrial isopod *Armadillidium vulgare* (Latreille, 1804). Monitore Zool. Ital. 4: 455-475

47. MADHAVAN K, SHRIBBS J M 1981 Role of photoperiod and low temperature in the control of ovigerous molt in the terrestrial isopod *Armadillidium vulgare* (Latreille, 1804). Crustaceana 41: 263 – 270. https://doi.org/10.1163/156854081X00840

48. HELDEN A J, HASSALL M 1998 Phenotypic plasticity in growth and development rates of *Armadillidium vulgare* (Isopoda: Oniscidea). Israel J. Zoo.44: 379-394

49. BRODY M S, LAWLOR L R 1984 Adaptive variation in offspring size in the terrestrial isopod, *Armadillidium vulgare*. Oecologia 61 (1): 55-59. https://doi.org/10.1007/BF00379089

50. RIES L, FLETCHER R J, BATTIN J, SISK T D 2004 Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu. Rev. Ecol. Evol. Syst. 35:491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

51. WOLTERS V, EKSCHMITT K 1997 Gastropods, Isopods, Diplopods, and Chilopods: Neglected Groups of Decomposer Food Web. In: Benckiser G (ed.) Fauna in Soil Ecosystems: recycling processes, nutrient fluxes, and agriculture production. Marcel Dekker, Inc. New York, p. 279-281

52. MEEK B, LOXTON D, SPARKS T, PYWELL R, PICKETT H, NOWAKOWSKI M 2002 The effect of arable field margin composition on invertebrate biodiversity. Biol. Conserv. 106, 259-271. https://doi.org/10.1016/S0006-3207(01)00252-X

53. SMITH J, POTTS S, EGGLETON P 2008 The value of sown grass margins for enhancing soil macrofaunal biodiversity in arable systems. Agric. Ecosyst. Environ.127:119-125. https://doi.org/10.1016/j.agee.2008.03.008

54. RISSER P G 1995 The status of the science examining ecotones. BioScience 45:318–325. https://doi.org/10.2307/1312492

55. DELGADO J D, ARROYO N L, ARÉVALO J R, FERNÁNDEZ-PALACIOS J M 2013 The responses of leaf litter invertebrates to environmental gradients along road edges in subtropical island forests. Pedobiology 56:137–146. https://doi.org/10.1016/j.pedobi.2013.01.003

56. ABD EL-WAKEIL K F 2015 Effects of terrestrial isopods (Crustacea: Oniscidea) on leaf litter decomposition processes. J. Basic Appl. Zool. 69:10-16. https://doi.org/10.1016/j.jobaz.2015.05.002

57. WEST A W, SPARLING G P 1986 Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of different water contents. J. Microbiol. Methods. 5:177–189. https://doi.org/10.1016/0167-7012(86)90012-6

58. DAVID J, GILLON D 2009 Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. Glob. Change Biol. 15: 156–165. https://doi.org/10.1111/j.1365-2486.2008.01711.x

59. GELBARD J L, BELNAP J 2003 Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv. Biol. 17: 420–432. https://doi.org/10.1046/j.1523-1739.2003.01408.x

60. CHRISTEN D, MATLACK G 2006 The role of roadsides in plant invasions: a demographic approach. Conserv. Biol. 20: 385–391. https://doi.org/10.1111/j.1523-1739.2006.00315.x

61. JODOIN Y, LAVOIE C, VILLENEUVE P, THERIAULT M, BEAULIEU J, BELZILE F 2008 Highways as corridors and habitats for the invasive common reed Phragmites australis in Quebec, Canada. J. Appl. Ecol. 45:459–466. https://doi.org/10.1111/j.1365-2664.2007.01362.x

62. MEUNIER G, LAVOIE C 2012 Roads as Corridors for Invasive Plant Species: New Evidence from Smooth Bedstraw (Galium mollugo). Inv. Plant. Sci. Manag. 5 (1): 92-100. https://doi.org/10.1614/IPSM-D-11-00049.1

63. LENGYEL G D, OROSZ S, KISS B, LUPTÁK R, KÁRPÁTI ZS 2015 New records and present status of the invasive spotted wing drosophila, *Drosophila suzukii* (Matsumura, 1931) (Diptera) *Drosophila suzukii* (Matsumura, 1931) (Diptera) in Hungary. Acta Zool. Hung. 61 (1): 73–80. https://doi.org/10.17109/AZH.61.1.73.2015

64. FETYKÓ K G 2014 Scale insect communities (Hemiptera: Coccoidea) of Hungarian highways: biocoenology and ecology. PhD thesis Gödöllő

65. PARIS O H 1963 The ecology of *Armadillidium vulgare* (Isopoda: Oniscoidea) in California grassland: food, enemies, and weather. Ecol. Monogr. 33 (1): 1–22. https://doi.org/10.2307/1948475

66. WRIGHT J C, TING K 2006 Respiratory physiology of the Oniscidea: Aerobic capacity and the significance of pleopodal lungs. Comp. Biochem. Physiol. 145: 235– 244. https://doi.org/10.1016/j.cbpa.2006.06.020

67. MILLER R H, CAMERON G N 1983 Intraspecific variation of life history parameters in the terrestrial isopod, *Armadillidium vulgare*. Oecologia 57: 216-226. https://doi.org/10.1007/BF00379583

68. KONTSCHÁN J 2001 Adatok Majk (Észak-vértes) magasabbrendű rák (Crustacea: Amphipoda et Isopoda et Decapoda) faunájához (Data of crustacean fauna (Crustacea: Amphipoda et Isopoda et Decapoda) of Majk (North-Vértes Mts.). Fol. His. Nat. Mus. Matraensis 25: 65–68

69. KONTSCHÁN J 2004 Néhány adat az Északi-középhegység ászkarák faunájához (Crustacea: Isopoda: Oniscidea) (Some data to

the woodlice fauna of the Hungarian Northern Mountains). Fol. His. Nat. Mus. Matraensis 28: 91–93

70. VONA-TÚRI D, SZMATONA-TÚRI T 2012 Adatok a Mátra-hegység ászkarák (Crustacea: Isopoda: Oniscidea) faunájához, különös tekintettel az út menti élőhelyekre (New data to the terrestrial isopoda (Crustacea, Isopoda, Oniscidea) fauna of Mátra-mountains, especially the wayside regions). Termvéd. *Közl.* 18: 537–548

71. VILISICS F, HORNUNG E 2010 Újabb adatok Magyarország szárazföldi ászkarákfaunájához (Crustacea, Isopoda, Oniscidea) (New data to the terrestrial isopod (Crustacea, Isopoda, Oniscidea) fauna of Hungary). *Állattani Közl.* 95 (1): 87–120

72. BUTTLER A 1992 Permanent plot research in wet meadows and cutting experiment. Vegetatio 103 (2): 113–124

73. TEWS J, BROSE U, GRIMM V 2004 Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31 (1): 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

74. MALUMBRES-OLARTE A, VINK CJ, ROSS J G, RUICKSHANK R H, PATERSON A. M 2013 The role of habitat complexity on spider communities in native alpine grasslands of New Zealand. Insect Conserv. Divers. 6 (2): 124–134. https://doi.org/10.1111/j.1752-4598.2012.00195.x

75. SZMATONA-TÚRI T, VONA-TÚRI D, MAGOS G, URBÁN L 2017 The effect of grassland management on diversity and composition of ground-dwelling spider assemblages in the Mátra Landscape Protection Area of Hungary. Biologia Section Zoology 72(6): 642-651. https://doi.org/10.1515/biolog-2017-0075