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Arthropod-related vehicle collisions increase harvestmen populations along road verges

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ABSTRACT

The expansion of road networks has been instrumental in facilitating human mobility and economic development. However, this infrastructure presents significant challenges to ecological systems. While most research focusses on the ecology of vertebrates, the potential effects on invertebrates remain understudied. This study investigated the impact of roads on the abundance and diversity of ground-dwelling arthropods, specifically harvestmen (Arachnida: Opiliones) and ground beetles (Coleoptera: Carabidae). The results showed that the distance from the road positively influenced the abundance (but not diversity) of beetles, while both the abundance and diversity of the harvestmen were highest near the roads. Further analysis revealed that dead insects were significantly more common near high-speed road sections compared to low-speed sections, probably due to increased road collisions. The abundance of harvestmen (but not beetles) was significantly affected by the presence of dead insects. Mediation analysis showed that high speed roads influence harvestmen abundance indirectly through its effect on dead insects abundance. It seems that the carabid beetles avoided the high-speed sections of the roads. Our findings suggest that roads causes mortality of flying insects via collisions but also serve as an important food source for scavengers such as harvestmen. Thus, road collisions with arthropods generate conditions similar to those observed for vertebrate scavengers feeding on roadkill.

1. Introduction

Road verges constitute up to 0.2 % of land worldwide (Phillips et al., 2020). They become an important element of the landscape solely due to the extent of the area they cover from a global perspective. The impact of roads on biodiversity, particularly invertebrate populations, has become a significant area of ecological research. Roads serve as both physical barriers and sources of environmental stressors, influencing the abundance and diversity of invertebrate communities (Keller and Largiadèr, 2003; Koivula and Vermeulen, 2005; Van Der Ree et al., 2015; Andersson et al., 2017; Markovits et al., 2025). Construction and maintenance of road networks can lead to habitat fragmentation, increased mortality rates from vehicle collisions, and altered microhabitats due to pollution and human activity (Iuell et al., 2003; Skórka et al., 213; Andersson et al., 2017). Collectively, these factors contribute to a decline in species richness and abundance, posing threats to ecological balance and ecosystem functioning.

Invertebrates play crucial roles in ecosystem services, including pollination, nutrient cycling, soil formation, and pest control (Klein et al., 2007; Rader et al., 2016; Langraf et al., 2021). Their sensitivity to environmental changes makes them valuable indicators of ecosystem health (Ortega et al., 2023; Shehzad et al., 2024). Many investigations indicate that roads can alter the natural movement patterns of invertebrates, leading to isolated populations that struggle to maintain genetic diversity (Dunn and Danoff-Burg, 2007; Holderegger and Di Giulio, 2010; Muñoz et al., 2015). Furthermore, studies have shown that increased traffic volumes correlate with higher mortality rates among certain groups of invertebrates, exacerbating declines in local populations (Martin et al., 2018).

Although there is extensive research on vertebrate roadkill, including ungulates, birds, and reptiles (Gunson et al., 2011; Yang et al., 2023; Bénard et al., 2024), studies focussing on invertebrates remain notably scarce. Large-scale datasets and mitigation report consistently prioritise mammals and birds due to their economic impacts and risks to human safety (Heigl et al., 2022). This vertebrate-centric focus persists despite evidence that roads create ecological traps for arthropods

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(Bénard et al., 2024) and the well-documented role of invertebrates in decomposition cycles and their ecosystem services (Lavelle et al., 2006). The ecological implications of insect mortality from vehicle collisions extend beyond direct population impacts, potentially influencing necrophagous invertebrate communities through carrion availability. Although vertebrate scavengers, such as birds and mammals are well-documented beneficiaries of roadkill (Trombulak and Frissell, 2000; Baxter-Gilbert et al., 2015), the role of insect-derived carrion in supporting necrophagous invertebrates remains understudied.

Our study aimed to investigate the effects of expressways on ground-dwelling arthropods, focussing on two main aspects. First, we examined whether there are differences in the diversity and abundance of harvestmen (Opiliones) and ground beetles (Carabidae) relative to their distance from the expressway. Second, we investigated the effects of vehicle speed on arthropod mortality and its potential influence on the diversity and abundance of these groups. Specifically, we compared high-speed and low-speed road sections to assess whether higher vehicle speeds result in greater insect mortality due to collisions. We hypothesized that high-speed road sections would lead to increased insect mortality, which in turn could positively influence the diversity and abundance of harvestmen and ground beetles near the road, potentially altering ecological interactions.

These two groups of invertebrates were chosen because harvestmen (Opiliones) and ground beetles (Carabidae) serve as vital indicators of ecosystem health, including in habitats along roads. Their sensitivity to environmental changes makes them effective bioindicators for assessing habitat quality and anthropic impacts on biodiversity (Rainio and Niemelä, 2003; Stašiov, 2001; Pinto-da-Rocha et al., 2007; Kotze et al., 2011; Gerlach et al., 2013; Merino-Sáinz and Anadón, 2015; Litavský et al., 2018, 2021, 2024). Both taxonomic groups of arthropods are mainly predators of small, soft-bodied arthropods and other invertebrates, though many species are also opportunistic scavengers and some readily consume plant material (Edgar, 1971; Halaj and Cady, 2000; Acosta and Machado, 2007; Elek and Lövei, 2007; Holecová et al., 2012). Harvestmen and ground beetles differ primarily in their ability to disperse. Harvestmen are flightless and less mobile, while most ground beetles are capable of flying, allowing them to migrate more easily to isolated parts of the country. We chose these groups not as universal indicators, but as model taxa to test specific hypotheses about road-related food subsidies (for scavengers) and avoidance behaviour (for predators). Harvestmen are generalist scavengers, allowing us to test the hypothesis that road-killed insects provide a carrion subsidy. In contrast, carabid beetles are predominantly predators with high mobility, making them ideal for assessing the effects of avoiding heavily disturbed habitats.

2. Material and methods

2.1. Study area

The monitored area represents the Nitra - Selenec expressway junction that ensures the connection between the road I/51 and the R1 expressway (Slovakia). Within the study area, eight study sites were established, which differed in terms of distance from the road, plant species richness, and plant coverage (Fig. 1). In the case of the study plots located close to the road, there was a difference in the speed with which the vehicles moved along that section of the road. All study plots are linear transects placed further away from the trees, so the tree layer is absent in all study plots. Young trees, not exceeding a height of 3 m, are present in the surrounding area.

The study plot **P1** is located at the northwestern edge of the observed area, away from the road edge (48°18′36.91″ N, 18° 8′23.33″ E, 153 m a.s.l.). The shrub layer is absent on this plot. The herbaceous layer includes 24 plant taxa with a total coverage of 85 %. The following plant taxa were most represented in the herbaceous layer: *Elytrigia repens*, *Stellaria media* and *Taraxacum* sect. *Taraxacum*.

The plot **P2**, located in the western part of the observed area, is the furthest from the edge of the road (48°18′33.67″ N, 18°8′21.45″ E, 153 m a.s.l.). The plot features a shrub layer with species such as *Acer platanoides* and *Tilia cordata*, as well as a herbaceous layer with 21 plant taxa, dominated by *Trifolium pratense*, *Medicago lupulina*, *Poa pratensis*, *Plantago lanceolata* and *Taraxacum* sect. *Taraxacum*, and *Trifolium repens*. The shrub layer has a total coverage of 6 %, while the herbaceous layer has a total coverage of 100 %.

The study plot **P3** is located near the edge of the low-speed road section, where vehicles travel at an average speed of 68 km/h (48°18′32.45″ N, 18°8′26.02″ E, 159 m a.s.l.). Only the herbaceous layer is present, with a total coverage of 80 % and 28 plant taxa, with the most represented species being *Cerastium brachypetalum*, *Lactuca saligna*, *Veronica arvensis*, and *Veronica persica*.

The plot **P4** is located along the edge of the high-speed road section (expressway), where the maximum permitted speed is 90 km/h for freight vehicles and 130 km/h for passenger vehicles. (48°18′29.33″ N, 18°8′22.83″ E, 158 m a.s.l.). The shrub layer is absent. The herbaceous layer is represented by 19 plant taxa with a total coverage of 80 %. The most dominant plants in this plot: *Festuca rubra* agg., *Bromus hordeaceus*, *Poa pratensis*, and *Achillea millefolium* agg.

The study plot **P5** is isolated from the surrounding landscape by a road (48°18′34.96″ N, 18° 8′27.97″ E, 160 m a.s.l.). It is located in the centre of a circle bounded by a road that leads vehicles to the R1 Expressway. The shrub layer is formed by *Acer pseudoplatanus* with a

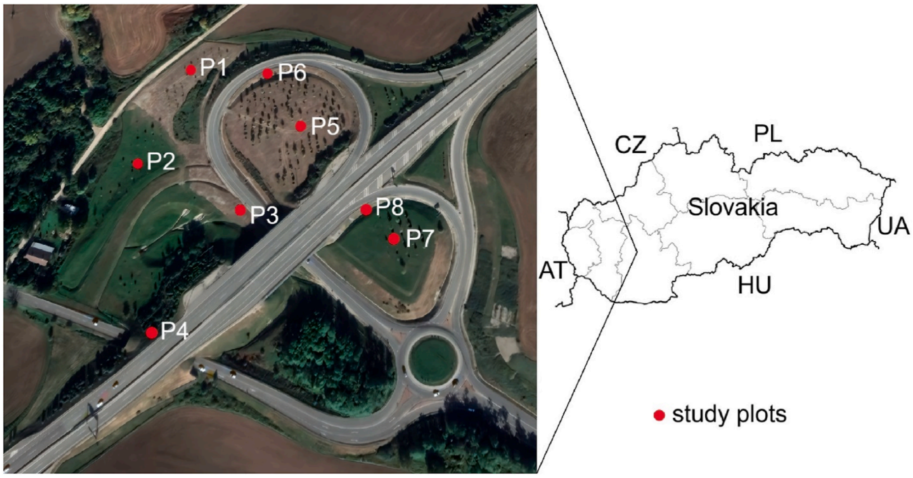

Fig. 1. Illustration showing the study plots within the Nitra - Selenec expressway junction (Slovakia): S1–S10 – study plots, AT – Austria, CZ – Czech Republic, HU – Hungary, PL – Poland, UA – Ukraine.

coverage of 1 %. The herbaceous layer is represented by 37 plant taxa with a total coverage of 70 %. *Cerastium brachypetalum*, *Noccaea perfoliata*, *Veronica arvensis*, and *Veronica persica* are dominant taxa in the herb layer.

The plot **P6**, like the previous plot, is isolated from the surrounding landscape by a road (48°18′36.81″ N, 18°8′26.93″ E, 156 m a.s.l.). It is located near the low-speed road section, where vehicles move at an average speed of 52 km/h. The herb layer has a coverage of 70 % with 31 plant taxa. *Helminthotheca echioides* is the dominant species on this study plot. The shrub layer is absent.

The study plot **P7** is in the centre of a circle, isolated from the surrounding landscape by a road (48°18′31.45″ S, 18°8′31.62″ E, 169 m a.s.l.). The herb layer has a coverage of 90 %, with 19 plant taxa. The most represented plant species are *Trifolium pratense* and *Leontodon hispidus*. The shrub layer is formed by *Acer pseudoplatanus* with a coverage of 1 %.

The study plot **P8** is isolated by a road and is located along the edge of the high-speed road section (expressway), where the maximum permitted speed is 90 km/h for freight vehicles and 130 km/h for passenger vehicles (48°18′32.38″ N, 18°8′30.49″ E, 167 m a.s.l.). The herb layer contains 16 plant taxa, with *Elytrigia repens* as the dominant species, and reaches a coverage of 55 %. The shrub layer is absent.

2.2. *Sampling*

Ground-dwelling arthropods were sampled using pitfall traps, which is the most effective and widely established method for studying epigeic communities of harvestmen and carabid beetles (e.g., Koivula and Vermeulen, 2005; Siewers et al., 2014; Černecká et al., 2017; Jung et al., 2019; Litavský et al., 2018, 2021, 2024; Langraf et al., 2024). This method provides several key advantages: it standardises collection without influence from the collector, operates continuously, and allows for simultaneous, comparable sampling across multiple sites (Stašiov, 2001). Although pitfall traps can have disadvantages, such as a sampling bias against very slow-moving invertebrates (e.g., Isopoda, Diplopoda) (Greenslade, 1964; Adis, 1979), they remain the most suitable and effective method for the targeted taxa in this study (Prasifka et al., 2007; Băncilă and Plăiaşu, 2009; Sabu et al., 2011). In our study, this method was implemented by establishing a single transect of five pitfall traps at each study site. The traps were placed on a line with 5–7 m of spacing between each trap. The lines forming the study plots located near the edges of the roads were oriented parallel to the road, at a distance of 2–3.1 m from the road edge (plots P3, P4, P6, and P8). The lines of traps located farther from the road, in the central parts of the study area, forming plots P1, P2, P5 and P7, were oriented parallel to the main road, the Nitra-Selenec expressway (R1). Plastic cups with a volume of 0.5 L and an inner opening diameter of 9 cm were used as traps. These cups were filled to half of their volume with a 4 % formaldehyde solution. This solution also contained antifreeze (200 ml of Velvana FRIDEX G48 per 1 L of solution) and a few drops of detergent. Each trap was equipped with a cover to prevent flooding the trap, dilution of the solution, drying out, filling with plant material, and access by other animals. The traps were exposed from March 24, 2022, to January 17, 2024. The material from the traps was collected at regular monthly intervals. The samples were sorted in the laboratory, and carabid beetles and harvestmen were subsequently identified using the keys of Martens (1978) and Krajčovičová et al. (2022) for harvestmen and Hůrka (1996) and Müller-Motzfeld (2004) for ground beetles.

To assess arthropod collisions with vehicles, we collected dead arthropods along the edges of the road during each entomological sampling from the pitfall traps. Along four studied plots located near the road edges (areas P3, P4, P6, and P8), we collected dead invertebrates along a 50-m stretch near each plot. The width of the line was 1 m, with dead entomological material collected from 0.5 m along the paved road edge (asphalt, concrete) and 0.5 m along the unpaved road edge (gravel, soil). The material was collected using entomological tweezers and preserved in 75 % ethanol. The collected samples were then sorted into taxonomic groups (orders) and counted. The conditions for conducting this part of the research were favourable weather (no rain and calm). During the winter months from November to the end of February, this part of research was not carried out. The numbers of dead insects collected outside the winter season were included in the statistical analyses. To more accurately determine the speed at which vehicles move on sections of the road near study areas P3 and P6, we drove our own car behind 5 passenger vehicles and 5 freight vehicles (a total of 10 times) and recorded the speed near each study area. From the recorded values, we calculated the average speeds.

We conducted estimates of the cover of shrub and herb layers in all study plots and identified plant species occurring in individual layers, all in a sampling area of 90 m2 (30 m × 3 m) on 19 May 2022. The pitfall traps were located in the central parts of these transects. Trees taller than 3 m were not recorded within the transects studied. The nomenclature of the vascular plants was interpreted following Euro Med, 2025.

2.3. *Statistical analyses*

1. We employed the generalized linear mixed model (GLMM) where the abundance of arthropods or the number of species were defined as dependent variables with Poisson distribution. The location of the traps (centre or edge) was a categorical predictor (supplementary materials). The month of sampling was defined as a continuous predictor, and the year of sampling and the sampling plot were random effects. Because there were several strong correlations between herbs and shrub variables (herb cover and diversity, r = 0.67), shrub cover and diversity of herbs, r = 0.92), shrub diversity and cover of herbs, r = 0.61), we used PCA analysis with Varimax rotation on diversity and coverage of herbs and shrubs to reduce the number of variables and avoid multicollinearity. The resulting factor scores were defined as continuous predictors. Multicollinearity diagnostic showed that all VIF values were lower than 2 in case of harvestmen species diversity. However, the multicollinearity values of certain variables were greater than 2 in the model with harvestmen abundance and overdispersion ratio was also alarmingly high (10.82). We therefore centered continuous predictors and used GLMM with negative binomial distribution. Similar approach was used when carabid abundance was dependent variable. Although multicollinearity did not take place here, overdispersion was high (7.01), thus GLMM with negative binomial distribution was used. We further used a generalized linear model (GLM) with a subset of variables on arthropod abundance or number of species (dependent variables) that were examined specifically at the edge near the expressway. The categorical predictor was the study site (located near high-speed or low-speed road sections), and the continuous predictors were the number of dead insects and PCA scores from herb coverage (shrubs were absent at these sites). Again, we checked models for overdispersion and multicollinearity and used centered continuous variables if necessary. Distribution of dependent variable was checked for each model separately. Inspection of overdispersion and AIC values were critical for whether we decided to proceed with Poisson or negative binomial distribution. We also reduced number of predictors given that the sample was lower (N = 27) in order to increase statistical power. All statistical analyses were performed in R version 4.3.0 (R Core Team, 2023). Generalized Linear Mixed Models (GLMMs) were fitted using the 'lme4' package version 1.1–31 (Bates et al., 2015). Variance Inflation Factors (VIF) were calculated using the 'car' package (Fox and Weisberg, 2019). Additional mediation analysis between road speed, dead insect abundance and harvestmen abundance was confirmed with mediation analysis. **Path a model** regressed dead insect abundance on traffic speed using GLM. **Path b model regressed** harvestmen abundance on both dead insect abundance and traffic speed using a negative binomial GLM. The indirect effect was calculated as the product of the coefficients from paths a and b (a × b). The proportion mediated was calculated as the ratio of the indirect effect to the total effect. All analyses were performed in Python using the statsmodels package (version 0.14.0) for GLM estimation and

custom code for the bootstrap procedure.

3. Results

During our two-year research, we recorded a total of 1192 individuals of ground beetles (Carabidae) belonging to 45 species and 1013 individuals of harvestmen (Opiliones) belonging to 6 species across eight study plots.

The effect of road proximity and plant diversity/cover on arthropod diversity and abundance.

3.1. PCA on herbs and shrub diversity and cover

PCA resulted in two independent factors (PC1 and PC2) with eigenvalues 2.49 and 1.02. These two factors explained 62.3 and 25.5 % of the total variance of the results. Shrub diversity and cover and herb cover loaded to PC1 (hereafter Herbs/Shrubs cover) and Herbs diversity loaded to PC2.

3.2. Harvestmen species diversity

Harvestmen species diversity was significantly higher in roadside plots (mean = 1.23, 95 % CI, 0.99–1.45) than in plots distant from roads (mean = 0.32, 95 % CI, 0.18–0.45) (GLMM, estimate = −0.17 $P < 0.001$). As the season progressed, the number of harvestman species increased significantly (GLMM, estimate = 0,092, $P < 0.05$). The cover of herbs/shrubs and herb diversity did not influence the number of species of harvestmen (GLMM, estimate = 0.270, and 0,269, P = 0.23 and 0.12, respectively).

3.3. Harvestmen abundance

The abundance of harvestmen was significantly higher in roadside plots (mean = 18.6, 95 % CI, 8.89–28.4) than in plots distant from roads (mean = 0.46, 95 % CI, 0.21–0.72) (GLMM, estimate = −3,77, $P < 0.001$). The cover of herbs/shrubs and the diversity of herbs were not significantly associated with a higher number of harvestmen abundance (GLMM, estimate = 0.23 and 0.07, P = 0.53 and 0.78, respectively). Time of season (month) was positively associated with harvestmen abundance (GLMM, estimate = 0.19, $P < 0.05$). The most numerous species of harvestmen was *Opilio saxatilis* with a total abundance of 955 individuals and a dominance of 94.27 %.

3.4. Carabidae species diversity

The number of carabid species was similar in plots distant from roads (mean = 3.81, 95 % CI, 3.25–4.38) and in plots near roads (mean = 2.02, 95 % CI, 1.61–2.43) (GLMM, estimate = 0.45, P = 0.15). The cover of herbs/shrubs, the diversity of herbs and time of season were not significantly associated with the number of carabid species (GLMM, estimate = 0,1, −0,12 and −0.01, all $P > 0.31$, respectively).

3.5. Carabidae abundance

The abundance of carabids was significantly higher in plots distant from roads (mean = 17.8, 95 % CI, 13.1–22.4) than in roadside plots (mean = 4.40, 95 % CI, 3.39–5.41) (GLMM, estimate = 1.51, $P < 0.001$). The effect of cover of herbs/shrubs, herb diversity and time of season were not associated with carabid abundance (GLMM, estimate = −0,15, −0,11 and −0,05, all $P > 0,12$).

4. Effects of collisions on arthropod abundance and diversity

4.1. PCA on herb diversity and cover

The PCA on herb cover and diversity resulted in one factor (PC1) with an eigenvalue of 1.46. This factor explained 73.14 % of the total variance of the results.

4.2. Insect mortality at sites near high-speed (plots P4 and P8) and low-speed (plots P3 and P6) road sections

During our investigation, we collected insects from eight orders that were killed in traffic collisions along the road edges near the study plots P3, P4, P6 and P8. The highest number of dead individuals was recorded from the order Hymenoptera, accounting for 75 %, followed by Diptera (17.5 %) and Coleoptera (4.4 %). The remaining portion consisted of the Dermaptera, Hemiptera, Orthoptera, Neuroptera, and Lepidoptera. GLMM with Poisson distribution showed a high overdispersion (2.71). We therefore removed random effects (year and sampling plot) and time of season which were not significant in an initial analysis. GLM with negative binomial distribution showed that there was 23.8 times lower number of dead insects in sites near low-speed road sections (mean = 1.0, 95 % CI, 0.04–1.96) than in sites near high-speed road sections (mean = 15.4, 95 % CI, 7.78–22.9) (GLM, estimate 3.17, $P < 0.001$). The effect of Herb diversity/cover was not significantly associated with the number of dead insects (GLM, estimate = 0.289, P = 0.938).

4.3. Harvestmen abundance

The harvestmen were significantly more abundant on sites with a higher number of dead insects (GLM with negative binomial distribution, estimate = 0.05, P = 0.002, Fig. 2). The roads (high or low speed sections) and the diversity/cover of herbs did not significantly influence the abundance of harvestmen (GLM, estimate = 0.12 and 0.31, P = 0.88 and 0.36). Due to the high correlations between dead insects abundance and the speed section (r = 0.62) and the diversity/cover of herbs and the speed section (r = −0.78), we run three additional GLMs with each predictor separately. The results showed that dead insects is a significant predictor of Harvestmen Abundance even when analysed independently (p = 0.026). This model also has the lowest AIC (180.93), indicating the best fit among the single-predictor models. Neither Speed nor Herb Diversity/Cover were significant predictors when analysed independently (p = 0.196 and p = 0.943, respectively).

All these calculations suggest that speed influenced the number of dead insects which in turn influences harvestmen abundance (Speed → Dead Insects → Harvestmen Abundance). To confirm the mediation effect of dead insects on harvestmen abundance, we performed mediation analysis. Dead Insects (N) significantly predicts Harvestmen Abundance (coefficient = 0.0478, p = 0.0286) when controlling for Speed. Interestingly, the direct effect of Speed on Harvestmen Abundance becomes negative (−0.3265) and non-significant (p = 0.5313) when controlling for Dead Insects. The indirect pathway was significant ($a \times b = 0.131$, 95 % CI [0.013, 0.313]), showing that dead insect abundance mediating approximately 25 % of the total effect of traffic speed on harvestmen abundance (Fig. 3).

4.4. Harvestmen species diversity

Greater herb diversity/cover was associated with a higher number of harvestmen species (GLM with Poisson distribution estimate = 0.66, P = 0.037). The effects of roads (high or low speed sections), the abundance of dead insects was also significant (GLM, estimate = 1.32, P = 0.03), but the effect of dead insects was not (estimate = 0.005, P = 0.75). Again, due to the same correlations as reported above, we run separate GLM on each predictor. None of predictors was significant when presented alone. However, the full model provides the best fit (lowest AIC), suggesting that the combination of all three predictors explains Harvestmen Species Diversity better than any single predictor alone.

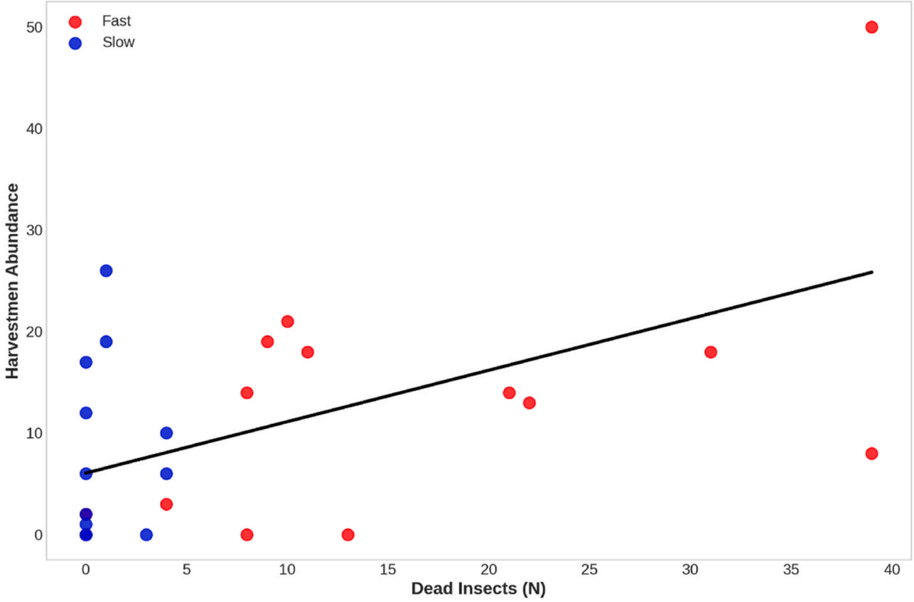

Fig. 2. Significant association between the number of dead insects near roads and harvestmen abundance. Blue dots represent dead insects on slow roads and red dots represent dead insect on fast roads.

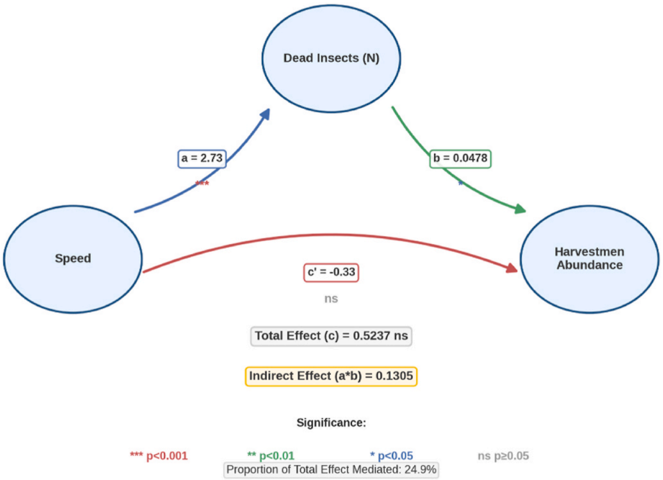

Fig. 3. The effect of Speed on Harvestmen Abundance Through Dead Insect Availability.

4.5. *Carabidae abundance*

There were similar number of carabids at sites near low-speed road sections than at sites near high-speed road sections (GLM with negative binomial distribution, estimate = −1.20, P = 0.17). The diversity/cover of the herbs and the number of dead insects were not associated with the abundance of carabids (GLM, estimate = −0.24 and 0.04, P = 0.52 and 0.14).

4.6. *Carabidae species diversity*

The number of carabid species was not influenced by any of examined variables (GLM with Poisson distribution, effects of roads (high or low speed sections), herb diversity/cover, dead insect abundance, estimate = −0.31, 0.28 and 0.01, all P > 0.30, respectively).

5. Discussion

Our two-year study reveals contrasting impacts of roads on two common ground-dwelling arthropod groups. We found that the abundance and diversity of harvestmen (Opiliones) were highest near the road, whereas carabid beetles (Carabidae) were more abundant in areas farther from the road. Crucially, mediation analysis showed that the abundance of harvestmen near high-speed road sections was indirectly influenced by the increased availability of dead arthropods resulting from vehicle collisions.

5.1. *Roadkill as a food subsidy for scavengers*

Our data indicate that while vehicle collisions pose a threat to insect populations, they may inadvertently contribute to the increase in harvestmen populations by providing a consistent food source through increased insect mortality. The results show that the harvestmen were significantly more abundant at plots with a higher number of dead insects, suggesting that these arachnids benefit from the increased availability of food resources near roadways where insect collisions occur. Although several researchers such as Noordijk et al. (2009), Buchholz et al. (2018) and Phillips et al. (2020) have noted that roadside habitats can serve as important foraging areas for various invertebrates, none have explicitly investigated how car speed on roads affects insect collisions, and subsequently, how the resulting dead insects influence the abundance and richness of ground-dwelling arthropods. For example, Noordijk et al. (2009) during their research on arthropods along 57 road edges in the Netherlands from 1998 to 2008 found that more than half of the total number of known species of ants, orthopterans, spiders, and harvestmen, including several vulnerable and endangered species living in the Netherlands, were also found on the roadside verges. In Berlin, Germany, road edges and urban grasslands hosted 20 % of all carabid species and 23 % of all spider species recorded in the country (Buchholz et al., 2018). Our research, therefore, provides a novel mechanistic understanding of a previously observed pattern by directly linking road speed, collision mortality, and scavenger abundance. While contributing to the existing literature on the benefits of road collisions for carrion-eating vertebrates, but our contribution expands this area of study by focussing on invertebrates.

5.2. *The roles of habitat preference, disturbance, and functional traits*

We also observed that the species diversity of harvestmen (Opiliones) was significantly higher in roadside plots than in plots distant from roads. Samways et al. (1997) presented similar findings, who in their research focused on the species composition and abundance of ants at varying distances from the highway, concluded that the greatest diversity was found in areas very close to the highway (<4 m from the highway), while the lowest diversity was recorded in areas farthest from the highway (32 m). One of the significant factors contributing to the higher diversity of ants closer to roads, according to the authors, is the availability of food resources, particularly in the form of animals killed on the roads. However, there is no direct evidence to support this claim. Kaur et al. (2019) compared the species composition and functional diversity of three groups of arthropods (spiders, ants, and true bugs) in fragmented forest steppe patches, moderately grazed pastures, and road edges in Hungary. The road edges showed a higher species richness of spiders and ants. In spiders, higher functional diversity was also recorded compared to the other areas. Noordijk et al. (2009) studied ground beetles and spiders at six highway edges in the Veluwe region of the Netherlands. The total number of species at the road edges was similar to the values found in nearby nature reserves with comparable vegetation, but Carabidae tended to be more abundant in the reserves. However, compared to nature reserves, there were fewer stenotopic carabid species at the edges of the road and the stenotopic spiders were less numerous.

On the contrary, compared to harvestmen, we recorded that the carabids exhibited a contrasting trend, with greater diversity and abundance found in the centre of the study plots rather than at the edges. This disparity may be attributed to the differing habitat preferences between these two groups; While harvestmen (Opiliones) tend to thrive more in the peripheral parts of the monitored area along high-speed road sections with lower plant species diversity, ground beetles (Carabidae) prefer the more stable central parts of the monitored area (further from the road edges), which offer less disturbed conditions, higher plant diversity, and therefore a greater food supply for the phytophagous (plant-eating) species of ground beetles. Regarding insects, similar findings are also reported by Kimaro and Kisingo (2017), who studied the impact of public roads on the species richness, abundance, and diversity of epigeic insects in Arusha National Park in Tanzania. During this study, the authors recorded a higher species richness in areas of the core zone (far from the edge of the road) compared to the richness found at the edge of the road.

This suggests that for many carabids, the negative impacts of road disturbance (e.g., pollution, vibration, noise) likely outweigh the potential benefits of any food subsidy.

The contrasting responses of harvestmen and carabid beetles can be further interpreted through their fundamental behavioral and morphological differences. Harvestmen are slow-moving, flightless scavengers well-adapted to exploiting clustered, ephemeral resources like roadkill (Pinto-da-Rocha et al., 2007). The preference of some harvestmen species for grassy edge habitats and their tolerance of disturbance likely explains their abundance near roads. In stark contrast, carabid beetles are predominantly predatory and highly mobile, with many species capable of flight (Hůrka, 1996; Müller-Motzfeld, 2004). This mobility likely allows them to actively avoid the disturbances characteristic of high-speed road environments (e.g., noise, vibration, pollution) (Koivula and Vermeulen, 2005), leading to their lower abundance near the road. Furthermore, their flight capability might increase their own risk of collision on high-speed road sections, potentially contributing to the observed patterns.

5.3. *The role of dominant species and microclimate*

Regarding harvestmen and their significant preference for plots near road edges, it would be more appropriate to discuss the most dominant species we recorded, *Opilio saxatilis* (94.27 %) within the study area. This species of harvestman is considered xerotolerant and synanthropic, preferring open spaces such as fields, meadows, gardens, orchards, and forest edges (Martens, 1978; Stašiov, 2004; Wijnhoven, 2009). Litavský et al. (in press) recorded that in areas located in the central parts of this study area (areas P1, P2, P5, and P7), average temperatures were 1.2 °C lower compared to the average temperatures recorded near the edges of the roads (plots P3, P4, P6, and P8). Although we know that *O. saxatilis* is xerotolerant, significantly fewer individuals of this harvestman species were recorded at the edges of low-speed road sections, where the air temperature was higher on average and the traffic speed lower. This clearly confirms that the food supply of insects killed by vehicles is the most likely reason for the presence of a larger population of *Opilio saxatilis* along high-speed road sections. It feeds on aphids and dipterans (Dixon and McKinlay, 1989; Pinto-da-Rocha et al., 2007). Many species of harvestmen, including those of the genus *Opilio*, have been observed feeding on dead insects (Martens, 1978). Given that *Opilio saxatilis* shares ecological and behavioural traits with other *Opilio* species, it is reasonable to infer that it also scavenges dead insects. This fact explains why a higher abundance of this species of harvestman was recorded near the edges of high-speed road sections (expressways), where the most insect specimens were collected from road collisions (study plots SP and P8).

O. saxatilis tolerates anthropogenic influences in the landscape (Stašiov, 2004; Litavský et al., 2024), which is clearly demonstrated in our research, as it is not disturbed by vibrations, dustiness, exhaust fumes, etc., caused by road traffic. Therefore, based on our results, we can conclude that *O. saxatilis* has begun to occur in human-made habitats – road verges, as secondary habitats.

5.4. *The complex role of vegetation and other factors*

An important variable in supporting the species composition and abundance of arthropods is also the complexity of the habitat, which, among other things, is determined by the coverage and species richness of plants in the herbaceous, shrub, and tree layers and their associated structures (Lassau et al., 2005; Uno et al., 2010; Litavský et al., 2021, 2024; Tobisch et al., 2023).

During a study on the effects of plant species composition and environmental factors on insect composition in the federal state of Bavaria (Germany), Tobisch et al. (2023) found that predators, including ground beetles, showed the strongest response to plant species composition. However, this was not confirmed at the road edges in the study by Leonard et al. (2018), possibly because roads provide specific habitats that differ from natural conditions, which can alter the typical responses of insects to environmental factors. The authors examined the effect of habitat complexity on the abundance and species composition of epigeic arthropods in public parks and at road edges using pitfall traps. The effect of habitat complexity within both types of habitats studied had no impact on the composition of key arthropod taxa, including ants, beetles, and spiders. During research focused on identifying factors that influence butterfly mortality along road verges, Skórka et al. (2013) found, among other things, that high plant species richness decreases butterfly road mortality (Lepidoptera).

5.5. *Broader implications and future directions*

Our findings also indicated that sites near high-speed roads had significantly higher numbers of dead insects compared to low-speed road sections. This aligns with previous studies that indicate that traffic intensity correlates with increased mortality rates among roadside fauna (Skórka et al., 213; Baxter-Gilbert et al., 2015; Keilsohn et al., 2018). However, the authors mentioned did not investigate the subsequent impact of insect mortality caused by traffic on invertebrates that inhabit roadside habitats. For this reason, our study represents a significant initial step in researching the impact of traffic on fauna, which deserves greater attention in future studies.

We acknowledge that other mechanisms and factors could be contributing to the observed patterns, such as reduced competition and reduced predation. Other arthropod scavengers are possible to be more susceptible to road-related mortality or avoidance, thus reducing competitive pressure on harvestmen and allowing their populations to increase (competitive release). Our data do not directly test this possibility, but it is a plausible secondary effect. With regard to reduced predation, the road environment may act as an escape from natural enemies if predators (e.g., ground-foraging birds, larger spiders) are also repelled by the road, creating a predator-free space for harvestmen. Finally, we acknowledge that our study is limited to two taxonomic groups. Although harvestmen and carabid beetles are excellent bioindicators, future studies should expand to include other arthropods (e.g. spiders, ants) to understand the full ecological impact of roads. Furthermore, species-level trait analysis could help elucidate the mechanisms behind the community patterns we observed.

6. Conclusion

In summary, our research provides initial evidence that arthropod-related vehicle collisions play a complex role in the formation of arthropod communities—especially harvestmen—along road edges. While they contribute positively to harvestmen populations by increasing food availability, they simultaneously pose significant risks to other insect groups. Future studies should focus on understanding these dynamics more comprehensively and exploring management strategies that improve roadside habitats while minimising vehicular impacts on vulnerable species.

CRediT authorship contribution statement

Juraj Litavský: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Pavol Prokop:** Writing – original draft, Formal analysis, Conceptualization. **Oto Majzlan:** Methodology, Investigation. **Hubert Žarnovičan:** Methodology, Investigation.

Ethical statement

No ethical statement was reported.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2025.104114.

Data availability

Data will be made available on request.

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