The effect of the invasive *Asclepias syriaca* on the ground-dwelling arthropod fauna

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Abstract: The management of natural and seminatural systems often leads to disturbance associated with the appearance of non-native species. The spread of these species is increasing due to global environmental changes combined with local management interventions. These non-native species may establish self-sustaining populations influencing ecosystem functions, including the habitat use of native species. Here we explore the response of diplopods, spider and ant assemblages and the activity-density of individual species to the establishment of the non-native plant species, *Asclepias syriaca* in a disturbed poplar forest in Hungary. The relationship between the species richness of spiders and ants and the structural features of *A. syriaca* was weak. We found a significant relationship between the structural features of *A. syriaca* stands and the density and activity of the diplopod *Megaphyllum unilineatum*. We explain this relationship by the modified microclimate and litter quality of the habitats invaded by *A. syriaca*. The species composition of ant and spider assemblages was sensitive to *A. syriaca*. *Asclepias syriaca* had a negative local effect on the abundance of two spider species which were common in the studied forest. However, *A. syriaca* positively influenced the abundance of two ant species, most probably via indirect trophic relationships, as they feed on aphids living on *A. syriaca*. Our study shows that invasive plants can have mixed effects on local invertebrate assemblages. It is therefore crucial to understand how native assemblages respond to these changes in order to better manage these novel ecosystems and maximize their biodiversity benefits.

Key words: spider; ant; millipede; poplar forest; Araneae; Formicidae; Diplopoda

Introduction

Most habitats which were once natural are now under some form of management in Europe. These interventions usually create a disturbance regime from which many species can profit. However, these disturbances also create niches for the establishment of non-native species especially plants. Currently wide areas of Europe are invaded by non-native plant species (Gordon 1998), which are now forming novel, self-sustaining ecosystems (*sensu* Hobbs et al. 2009). Invasion of exotic plants is one of the most significant threats to native species assemblages and have been reported to be responsible for the degradation of natural and semi-natural habitats (Vitousek et al. 1997; Gratton & Denno 2005). Exotic plants can alter the habitat structure due to their impact on vegetation diversity and composition (Hejda et al. 2009), biotic interactions and ecosystem functioning (Schirmel & Buchholz 2013). Even small-scale invasions can influence the native ground-dwelling arthropod fauna (Schirmel et al. 2011). These negative effects on ecosystems may remain even after the removal of the non-native species (Hobbs et al. 2006). Eradicating invasive species is often a difficult and contra productive task therefore first we need to understand how native species interact with non-natives in order to maximize the potential benefits of non-native

species to native biodiversity elements (Hobbs et al. 2009).

European forests are good model systems to study the establishment and biodiversity effects of non-native species because most of these forests are under some form of exploitation management practices (Paillet et al. 2010). These interventions affect not only the tree community structure and heterogeneity of the forests but also represent a disturbance regime which is different from the natural ones (Vanberger et al. 2005; Paillet et al. 2010). These disturbed forest patches represent ideal environment for the establishment of non-native plant species (Gordon 1998).

The common milkweed (*Asclepias syriaca*) is originally from North-America and was introduced to Hungary in the 18th century (Balogh et al. 2007; Csontos et al. 2009). As a successful invader, *A. syriaca* has become one of the most abundant invasive plant species in sandy grasslands, fallow lands and forest plantations in the Hungarian Great Plain (Bagi 2008; Török et al. 2003a).

Several former studies found close relationship between *A. syriaca* and various arthropod species (e.g., Chien & Morse 1998; Molnár et al. 2010; Abdala-Roberts et al. 2012), however, very little is known about the effects of *A. syriaca* invasion on the ground-dwelling arthropod fauna (Ernst & Cappuccino 2005). Our study focuses on spiders (Araneae), ants (Formicidae) and

Table 1. Description of environmental variables used to characterise the study sites.

Parameter group	Habitat parameter	Description	Mean ± SD
Structure	Total vegetation cover	The cover of the vegetation (%)	47.67 ± 11.84
	Vegetation cover (10 cm)	The cover of stems reaching 10 cm above ground (%)	42.37 ± 11.07
	Vegetation cover (40 cm)	The cover of stems reaching 40 cm above ground (%)	5.97 ± 3.32
	Vegetation height	The average height of the stems (cm)	46.45 ± 10.23
	Shrub cover	The cover of shrubs (%)	3.34 ± 3.49
	Leaf litter	The cover of leaf litter (%)	67.91 ± 20.89
Shading	Canopy closure	Assessed using digital photographs of the canopy of each site (%)	58.59 ± 14.04
Invasive plant	A. syriaca cover	The cover of A. syriaca (%). Relatively low values were measured as stems were not full-grown at the sampling period	19.55 ± 16.04
	A. syriaca density	The number of A. syriaca stems within the 5 × 5 m quadrates	86.43 ± 59.93

millipedes (Diplopoda) for several reasons. Both spiders and ants are good groups to address the potential effects of non-native plants on the community structure and habitat use of invertebrates. First, both are generally diverse and abundant groups of arthropods (Hölldobler & Wilson 1990; Foelix 2010). Second, they occupy specific trophic levels (with spiders as predators and ants as omnivores) (Hölldobler & Wilson 1990; Wise 1993).Third, both groups are sensitive to vegetation structure (Wise 1993; Wang et al. 2001). Saprophagous diplopods are a major component of soil fauna (Voigtländer 2011). In forest habitats millipedes are influenced by litter and soil parameters (e.g., humidity, humus type, pH) and the age of the forest stands (Stasiov 2009).

The major goal of this study was to explore the relationship between the structural features and the density of the invasive A. syriaca and its effects on species richness and composition of the spider and ant assemblages and the activity-density of diplopods.

Material and methods

Study site and sampling method
The study was conducted in the Kiskunság region of the Hungarian Great Plain. The landscape consists of mainly agricultural fields, semi-natural forest plantations and small patches of the original steppe and forest steppe habitats. The basic substrate of this region is calcareous coarse sand. The climate is semiarid with a mean annual precipitation of 550–600 mm and with an annual mean temperature of 10.2–10.8 °C (Török et al. 2003b).The sampling sites were located in a 38 years old poplar (*Populus alba*) forest plantation near the village of Bugacpusztaháza (46°41′36″ N, 19°36′45″ E).

Invertebrates were sampled with pitfall traps consisting of plastic cups (6.5 cm in diameter and 10 cm in depth) driven into the ground so that the lips were in the level of the soil surface. Ethylene glycol was used as preservative, because it does not affect invertebrate catches (Topping & Luff 1995).

Pitfall traps measure the activity-density of ground-dwelling arthropods, as the probability of falling into a pitfall trap depends on the activity, density and trappability of invertebrates. However, pitfall traps offer a relatively good alternative to compare ground-dwelling arthropod assemblages, assuming that the number of individuals of each species captured reflects their real proportions in the assemblages (Schmidt et al. 2005; Borgelt & New 2006; Öberg et al. 2007). Although microhabitat structure can affect movement behaviour and thus the trappability of invertebrates (Topping & Sunderland 1992), the vegetation density biases pitfall trap samples significantly only when the ground cover is very dense (Melbourne 1999). Presumably in our situation no such bias was present.

A total of 32 sites were sampled in the poplar forest interior (approximately 0.5 km²), and each sampling site was located at least 150 m from the forest edge. The distance between the sampling sites was ≥40 meters. The number of A. syriaca stems within a 5 × 5 m quadrate ranged from 5 to 276 (86.59 ± 59.71, mean ± SD). At each site 5 pitfall traps worked between 12.V.2011 and 24.VI.2011. The traps were emptied in every two weeks. The traps were arranged in circles with 5 m in diameter. Before data analysis we pooled the data of the traps for each sampling site.

The habitat characteristics were assessed visually for three 1 × 1 m quadrates in each sampling site. The three main groups were: (i) structure, (ii) shading and (iii) the abundance of the invasive plant (Table 1).

Data analysis
We explored how the species richness of spider and ant assemblages and the density of diplopods related to the habitat parameters with generalized linear models (GLM). Poisson distribution was used for the species richness and negative binomial for the density data. The influential points were identified with the Cook's distance plot and were excluded from further analysis. To select the appropriate models, we ranked them by their Akaike's information criterion (AIC) in the forward selection procedure. Based on the estimation of variance inflation factors (VIF) (Stine 1995) there was no high collinearity between the explanatory variables (VIF ranging from 1.25 to 7.41).

The relationship between the activity-density of the frequent spider and ant species and the two variables of A. syriaca abundance was analysed with negative binomial GLMs. For this analysis we considered only those species which were represented by more than 100 individuals in our sites.

The relationship between the community composition of spiders and ants and the habitat characteristics was explored with canonical correspondence analysis (CCA). In the case of spiders species with relative abundance below 1% were considered 'accidental' and were excluded from the analysis. However all ant species were considered in the multivariate analyses, as the presence of a worker in the samples presumes the presence of the nest in the sampling site. Abundance data were normalized with *log* transformation (Petillon et al. 2008). To reduce the number of constraints in the final CCA model and to identify important habitat parameters we applied stepwise selection on the basis of the AIC (Oksanen et al. 2011). The marginal effect of the habitat parameters included in the final CCA was tested with Monte Carlo permutation tests using 5000 permutations.

The similarity of species assemblages was explored with non-metric multidimensional scaling (NMDS) using Bray-Curtis similarity measure. The influential habitat parameters suggested by the CCA were fitted passively onto the NMDS ordination plot.

All analyses were carried out using the free software R 2.13.1 (R Development Core Team 2011) and Vegan package (Stevens & Wagner 2011).

Results

We recorded 43 species and 5,952 (4,939 adult and 1,012 juvenile) individuals of spiders, 20 species and 10,162 individuals of ants and 3,802 individuals of the diplopod *Megaphyllum unilineatum* (see Appendix 1 for the species list). Since juvenile spiders could not be identified to species level, they were not included in the analysis.

In the present study the only diplopod species collected was *M. unilineatum* (C.L. Koch, 1838). This xerotolerant species is widespread in Central Europe and typical for grasslands, fallows and open woodlands with dry and warm microclimate (Loksa 1966; Hornung & Vajda 1988; Voigtländer 2011). We found no relationship between the habitat parameters and the species richness of spiders and ants respectively, according to the GLMs and the subsequent forward selection. However, a number of parameters influenced the amount of collected diplopod individuals, indicating a coarse-grained response of *M. unilineatum* to the habitat struc-

Table 2. The results of the general linear model followed by stepwise selection between the microhabitat parameters and the activity-density of the diplopod *Megaphyllum unilineatum*.

Habitat parameter	z-value	P-Value
Vegetation cover (10 cm above ground)	3.149	0.0016
Vegetation cover (40 cm above ground)	−1.659	n.s.
Vegetation height	2.717	0.006
Canopy closure	2.142	0.032
Leaf litter	2.338	0.019
A. syriaca cover	4.678	<0.001

ture (Table 2). The activity-density of two frequent spider species, namely *Alopecosa sulzeri* (Pavesi, 1873) and *Callilepis schuszteri* (Herman, 1879) correlated negatively with *A. syriaca* density ($z = -2.10$, $P = 0.035$, $z = -2.095$, $P = 0.036$, respectively), however the relationship proved to be positive in the case of two ants, namely *Formica fusca* (L., 1758) and *Formica sanguinea* (Latreille, 1798) ($z = 22.81$, $P < 0.001$, $z = 4.11$, $P < 0.001$, respectively).

Species composition of spiders correlated closely with both the habitat parameters and the density of *A. syriaca* according to the CCA models (Table 3). We found close relationship between the leaf litter cover and the ant assemblages. We did not find distinct groups of the sampling sites but the NMDS scatterplot indicated smooth transition between the spider and ant assemblages of the sampling sites with different *A. syriaca* densities (Figs 1, 2.)

Discussion

Our results can be summarized as follows: (i) habitat structure exerts an effect on epigaeic spiders diplopods, and ants (ii) we found that the abundances of several invertebrate species and species composition of spiders correlated with *A. syriaca* density.

Even in the case of small scale spatial heterogeneity of invasive plant density presented in this study, we found that *A. syriaca* has a significant effect on the ground dwelling fauna. Positive relationships have been

Table 3. The marginal contribution of the habitat parameters in explaining the composition of spider and ant assemblages assessed by canonical correspondence analysis and the subsequent model selection. Only species represented by >1% of the total abundance were included, data were log (activity density +1) transformed.

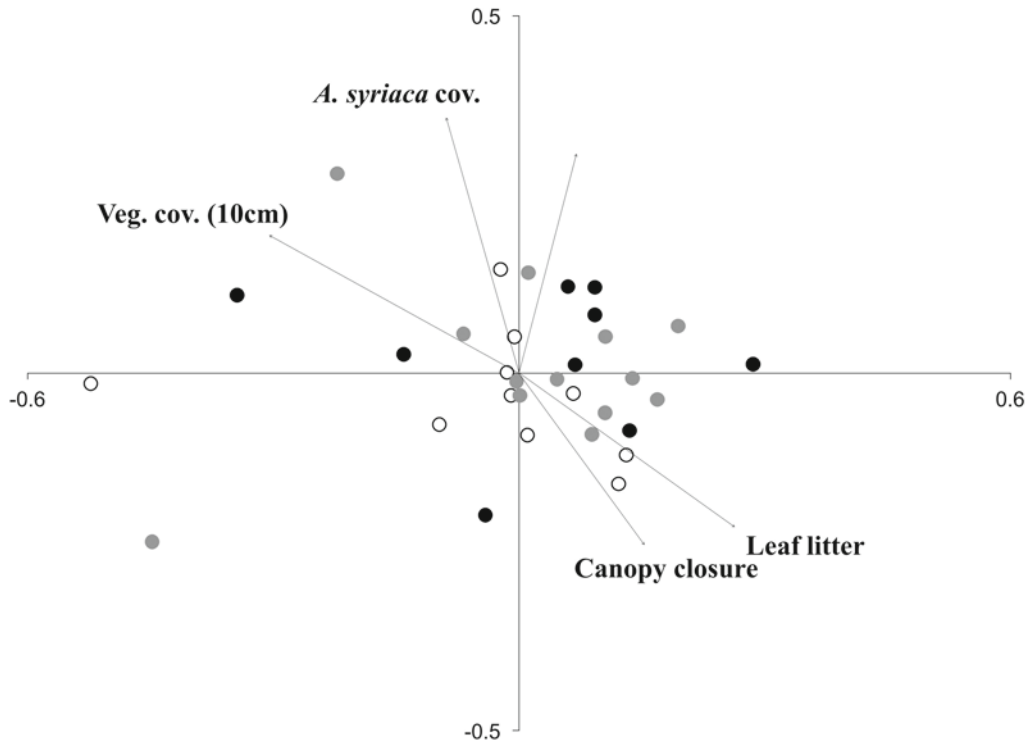| Habitat parameter	Spiders			Ants		
	Chi-sq.	F	P-value	Chi-sq.	F	P-value
Total vegetation cover	0.013	3.343	0.004		*Not entered*	
Vegetation cover (10 cm)		*Not entered*			*Not entered*	
Vegetation cover (40 cm)	0.006	1.702	n.s.		*Not entered*	
Vegetation height	0.011	3.050	0.008		*Not entered*	
Shrub cover		*Not entered*			*Not entered*	
Leaf litter	0.012	3.225	0.004	0.0462	1.9410	0.0451
Canopy closure	0.009	2.443	0.020		*Not entered*	
A. syriaca cover	0.012	3.298	0.003		*Not entered*	
A. syriaca density		*Not entered*			*Not entered*	

Fig. 1. Non-metric multidimensional scaling (NMDS) of spider assemblages (stress value: 16.47). The habitat parameters are passively included and represented by arrows. Their relative effect is indicated by the length and direction of the arrows. Filled circles, grey circles and open circles indicate sites with high (more than 25%), medium (between 10% and 25%) and low (less than 10%) *A. syriaca* coverage, respectively.
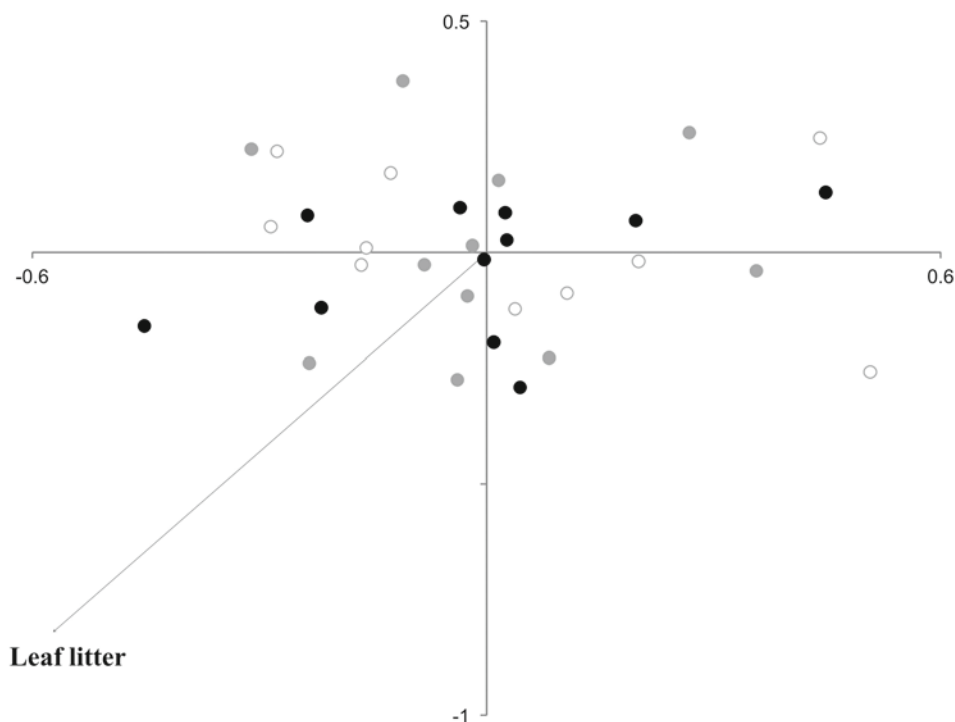

Fig. 2. Non-metric multidimensional scaling (NMDS) of ant assemblages (stress value: 17.84).The leaf litter cover is passively included and represented by the arrow. Filled circles, grey circles and open circles indicate sites with high (more than 25%), medium (between 10% and 25%) and low (less than 10%) *A. syriaca* coverage, respectively.

documented between density and impact of some non-native species (Ricciardi et al. 2013). Former studies demonstrated the significant effect of invasive plants on invertebrates (Toft et al. 2001; Standish 2004). Most of them found that arthropod abundance and diversity decline with the increasing density of non-native herbaceous plants (Slobodchikoff & Doven 1977; Herrera & Dudley 2003), presumably because these plants modify

the ground surface micro-habitat (e.g., Langellotto & Denno 2004; Petillon et al. 2005) and they even lack the associated diversity of herbivores that are present in their original ecosystems (Strong et al. 1984).

Spiders

Terrestrial arthropod diversity is commonly thought of as being positively correlated with the structural diversity of the vegetation (Southwood et al. 1979; Lawton 1983; Siemann 1998).

The density and the structure of the vegetation have previously been identified as factors important in determining spider assemblages (Gibson et al. 1992; Malumbres-Olarte et al. 2012). A more complex vegetation or habitat structure may sustain a higher diversity of spiders (Rypstra et al. 1999; Jimenez-Valverde & Lobo 2007). On the basis of the CCA the composition of spider assemblages was affected by the vegetation structure and shading, which is consistent with several studies in other ecosystems (e.g., Scheidler 1990; Entling et al. 2007; Petillon et al. 2008). However, when summarizing the data on the assemblages in a single variable such as species richness, the loss of information may diminish the effect of habitat parameters (Jeanneret et al. 2003). This is in accordance with the results of the present study, as we did not identify significant influence of habitat parameters on the species richness of spiders. Gallé & Torma (2009) and Gallé et al. (2010) also found that different habitat patches may have spider assemblages with similar species number, but with different species composition on the Hungarian Great Plain. Invasive plants may substantially alter the forest floor spider assemblages. Bultman & DeWitt (2008) found that the invasive *Vinca minor* significantly reduced the total activity-density and species diversity of spiders, however, species richness was not affected.

Out of the most abundant spider species one lycosid (*A. sulzeri*) and one gnaphosid (*C. schuszteri*) spider species showed significantly negative relationship with *A. syriaca* density (Table 2). Our results are in accordance with Schirmel et al. (2011), as they found that activity densities of ground-dwelling wolf spiders were lower in invaded sites. They conclude that, in the case of high exotic plant density, the invasion might have a strong impact on typical arthropod species. However, contrary indirect effects may occur when invasive plants increase habitat heterogeneity (Pearson 2009). Petillon et al. (2005) found that the activity-density of the native diurnal and nocturnal wanderers decreased in invaded areas compared to natural areas. However, the changes in habitat structure due to the invasion of a non-native plant do not necessarily affect the density of every spider species to the same extent, owing to the differences in their habitat requirements (Petillon et al. 2005).

Shifts in species abundances and assemblage composition can be explained by differences in the vegetation structure, microclimate conditions and most likely an altered food supply in invaded sites (Petillon et al. 2005; Schirmel et al. 2011). Large catches of *A. sulzeri* and *C. schuszteri* in sparser vegetation were possibly due to increased activity and preferences for a warmer microclimate (Honek 1988), as both species prefer open forests and warm microhabitat conditions (Buchar & Ruzicka 2002).

Ants

In the case of ants the collected number of individuals must have been affected by the proximity of the nests and the foraging trails to food resources (Wilkie et al. 2007). However, pitfall trap method is widely used to collect ants, as the cruising radius of workers can reach 150 m, although the nests are fixed in space. Andersen (1996a) compared quadrate samples with pitfall traps and found significant correlation between the two data sets. Thus pitfall trap method is a relatively good alternative to compare the assemblage structure of ants (Schlick-Steiner et al. 2006).

Habitat and biotic parameters regulating ant assemblages have been well studied (e.g., Savolainen & Vepsalainen 1988; Gallé et al. 1998; Lessard et al. 2009) and it is well-known that competition can play a major role in shaping ant assemblages (Hölldobler & Wilson 1990; Cerda et al. 2013). However, numerous studies emphasize that habitat structure is also important in determining the structure of ant assemblages (Alvarado 2000; Arnan et al. 2009; Gibb 2011). We found no significant effect of the habitat parameters on the species richness and assemblage structure of ants. In the case of the present study the biotic interactions (i.e., competition and trophic interactions) presumably blur the effect of the habitat parameter variations.

Wilkie et al. (2007), who investigated the effect of the invasion of the non-native bitou bush (*Chrysanthemoides monilifera*), reported temporally stable ant assemblage structures in the long run, suggesting that the species composition of ant assemblages is stable. In contrast to spiders and diplopods, ants are social insects living in colonies, which involve territoriality and may persist for long periods of time (Hölldobler & Wilson 1990), thus they may give a fine-grained response to the small-scale structural heterogeneity of the forest floor brought about by different *A. syriaca* densities. This is in accordance with our results as the constrained ordination failed to establish significant relationship between the density of *A. syriaca* and the assemblage composition of ants. However, the activity-density of several abundant ant species was affected by the density of *A. syriaca*, confirming the conclusion proposed by Samways et al. (1996) that non-native species have their greatest effect not on the assemblage but on the species level.

Indirect effects of non-native species are common and often significant to the structure and function of ecosystems (Simberloff 2011; Ricciardi et al. 2013). Several studies emphasize the importance of the mutualistic relationship between aphids and ants (Hölldobler & Wilson 1990; Smith et al. 2008). Ants are attracted to honeydew as a predictable, renewable food resource and protect the honeydew-producing hemipterans from

predators and parasitoids (Styrsky & Eubanks 2007). Several ant species also feed on aphids (Andersen 1991b; Stadler & Dixon 2005), also reported from the Kiskunság, the study region of the present paper (Gallé 1978). Aphids are among the most abundant herbivores feeding on *A. syriaca* (Molnár et al. 2010), so these ant – hemipteran interactions can alter the structure of ant assemblages by increasing the abundances of hemipteran-tending and -eating species (e.g., *Formica* spp.) (Renault et al. 2005; Abdala-Roberts et al. 2012). Ants may have either indirect negative effect on *A. syriaca*, when tending the sap-sucking aphids or indirect positive effect, when feeding on them.

Furthermore, some ant species (for example *Temnothorax* sp.) in these poplar forests may form their nests in the dry stems of this invasive species, affecting their abundance and occurrence (I.M. unpublished data).

Diplopods

The diplopod abundance was closely related to the habitat structure, shading and the cover of the invasive plant. Diplopods usually prefer moist conditions, the Eastern European *M. unilineatum* having a broad tolerance for moisture often becomes numerically dominant on arable fields, fallows and warm, open forests (Loksa 1966; Haacker 1968; Korsós 1991). In the present study the number of collected individuals was affected by numerous habitat parameters. Several former studies emphasize the importance of soil characteristics, microclimate and the coverage and depth of litter on diplopods (Branquart et al. 1995; Smith et al. 2006; Stasiov 2009). The linear model also confirmed the positive relationship between litter coverage and diplopod abundance. It is well known that diplopods are closely related to leaf litter quality (Grelach et al. 2012). According to David & Handa (2010) the invasion of non-native plant species and the subsequent changes in plant community structure can change the composition of litter, and thus can significantly affect its structure and the nutrient resources available to the diplopod fauna. The coarse-grained response of *M. unilineatum* to the density of *A. syriaca* is possibly due to the low dispersal rate of the species, which does not exceed a few meters (Voigtländer 2011).

The effect of canopy closure and understory vegetation structure is possibly due to their effect on the microclimate. A closed canopy and well developed understory vegetation determine the litter temperature and effectively protects the ground-dwelling fauna from high microclimatic variations, which in turn influence the diplopods (Martius 2004). Korsós (1991) found bimodal seasonal activity pattern of *M. unilineatum,* the first activity peak of the species starts in April and it declines at the end of Jun with a second activity peak in the autumn. Despite their nocturnal activity during hot weather conditions they search for microhabitats with stable and relatively moist microclimate (Korsós 1991).

Conclusion: implications for understanding the effect of non-native species

The effect of the invasion of the non-native plant *A. syriaca* on the ground-dwelling spiders, ants and diplopods was detectable even in the case of our small-scale study, emphasising that the invasion of *A. syriaca* severely affects the distributional pattern of ground-dwelling arthropods, hence threatens their diversity and alters the interactions between species (e.g. competition and trophic interactions), resulting in a novel ecosystem with lower conservation value.

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