



Consequences of *Spiraea tomentosa* invasion in Uropodina mite (Acari: Mesostigmata) communities in wet meadows

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Abstract

Vegetation cover has been consistently reported to be a factor influencing soil biota. Massive spreading of invasive plants may transform native plant communities, changing the quality of habitats as a result of modification of soil properties, most often having a directional effect on soil microorganisms and soil fauna. One of the most numerous microarthropods in the litter and soil is Acari. It has been shown that invasive plants usually have a negative effect on mites. We hypothesized that invasive *Spiraea tomentosa* affects the structure of the Uropodina community and that the abundance and species richness of Uropodina are lower in stands monodominated by *S. tomentosa* than in wet meadows free of this alien species. The research was carried out in wet meadows, where permanent plots were established in an invaded and uninvaded area of each meadow, soil samples were collected, soil moisture was determined and the mites were extracted. We found that Uropodina mite communities differed in the abundance of individual species but that the abundance and richness of species in their communities were similar. *S. tomentosa* invasion led primarily to changes in the quality of Uropodina communities, due to an increase in the shares of species from forest and hygrophilous habitats. Our results suggest that alien plant invasion does not always induce directional changes in mite assemblages, and conclude that the impact of an alien species on Uropodina may cause significant changes in the abundance and richness of individual species without causing significant changes in the abundance and diversity of their community.

Keywords Uropodina · Alien shrub · Arthropods · Biodiversity · Invasive species · Soil biota

Introduction

Invasive plants have strong direct and indirect impacts on invaded ecosystems, particularly due to their effects on the physical and chemical properties of soil substrates (Ehrenfeld 2003; Weidenhamer and Callaway 2010; Gibbons et al. 2017; Stefanowicz et al. 2018). Studies have shown that invasive species increase soil nutrients and increase the rate of

edaphic processes such as litter decomposition and mineralization, possibly accelerating nutrient cycling (Vanderhoeven et al. 2005; Liao et al. 2008; Castro-Díez et al. 2014). Some of them affect soil conditions by increasing the activity of soil enzymes (Zhou and Staver 2019). It is also known that alien plants cause changes in soil structure and in nutrient mobilization and/or chelation (Weidenhamer and Callaway 2010; Kalisz et al. 2021), and some secrete allelopathic compounds from the roots (Chengxu et al. 2011; Wardle et al. 2011; Kalisz et al. 2021). Changes in soil properties induced by invasive plants may affect soil biota (Belnap et al. 2005; Zhang et al. 2019). Though it is known that invasive species affect soil microorganisms (Batten et al. 2006; Xiao et al. 2014; McLeod et al. 2016), there is surprisingly little information about the impact of neophytes on soil mesofauna such as mites.

Acari are one of the most abundant microarthropods in the leaf litter and upper soil layers (Rusterholz et al. 2014). This group plays a key role in decomposition and mineralization of organic material (Seastedt 1984), nutrient cycling (Irmeler 2000; Wickings and Grandy 2011) and soil formation (Persson 1983). Soil mites, especially taxa that are sensitive to all kinds of soil disturbances, are often used in environmental monitoring (van Straalen 1988; Gulvik 2007), useful in studies on the impact of invasive species on ecosystems.

Most studies report changes in the species composition of Acari in invaded areas (Belnap et al. 2005; Pritekel et al. 2006; McGrath and Binkley 2009; Skubała and Mierny 2009; Christopher and Cameron 2012; Gutiérrez-López et al. 2014; Rusterholz et al. 2014; Kohyt and Skubała 2020), but John et al. (2006), Sterzyńska et al. (2017) and Ustinova et al. (2021) found no influence of invasive plants on mite communities, and that their abundance and species richness in soil under invasive and native species were similar. These various data argue against a clear pattern of the influence of invasive species on mites. Many works report lower numbers of Acari in soil of invaded sites (Belnap et al. 2005; Pritekel et al. 2006; Skubała and Mierny 2009; Motard et al. 2015; Kohyt and Skubała 2020) but other studies show the opposite direction of change: an increase in their number (McGrath and Binkley 2009; Christopher and Cameron 2012; Rusterholz et al. 2014). Hence the impact of invasive plants on Acari populations is hard to predict. Here we studied such effects of invasive steeplesbush *Spiraea tomentosa* L. in order to assess the actual interactions of soil fauna with that alien species.

Steeplebush is a North American shrub (Flora of North America 2024; USDA – The Plants Database 2024) which has become one of most successful invasive plants in Europe (Dajdok et al. 2011; Wiatrowska et al. 2020). Its locations were first recorded outside of cultivation in Central Europe at the turn of the 19th/20th centuries (Fiek 1881; Schube 1903). Since that time, *S. tomentosa* has colonized and spread over wetland habitats in eight European countries (Wiatrowska et al. 2020). The shrub has developed many dense monospecific assemblages, especially in wet meadows and transitional and raised bogs (Dajdok et al. 2011; Wiatrowska and Danielewicz 2016), leading to the homogenization of these habitats (Wiatrowska et al. 2023). Steeplebush significantly reduces the number of native plant species (Wiatrowska et al. 2023) and negatively affects several taxonomic groups: spiders (Balkenhol et al. 2018), bees, butterflies and flies, the number and richness of which decrease significantly and linearly with the increase of *S. tomentosa* cover (Wiatrowska et al. 2023). The shrub is characterized by rapid growth (Wiatrowska 2015) and high concentrations of total nonstructural carbohydrates and defence compounds such as condensed tannins and soluble phenols in leaves (Wiatrowska et al. 2018). Its large woody biomass production (Wiatrowska et al. 2022) and its ability to transform plant communities to shru-

bland may alter the parameters of organic material accumulated as litter on the soil surface and in the upper soil horizon. This in turn may create specific conditions for many saprotrophic taxa associated with organic material, including Uropodina mites, which inhabit leaf litter and the upper soil layers (see e.g. Błoszyk 1983; Karg 1993; Koehler 1997, 1999).

There are 137 mite species of the suborder Uropodina (Acari: Mesostigmata) in Poland (Błoszyk 1999, 2008). Most of them (60%) live in forest soil and litter, while other species (30%) inhabit unstable microhabitats such as dead wood, anthills, bird and mammal nests, and animal feces. Only about 10% occur in open habitats such as meadows, dunes and grasslands (e.g. Błoszyk 1999; Błoszyk et al. 2003; Napierała and Błoszyk 2013). Uropodina mites most often form communities with low species diversity, consisting of a few to a dozen species (Athias-Binche 1981a, b; Błoszyk 1999; Napierała et al. 2009). Uropodina occurs in the greatest abundance in places with a high amount of organic matter such as deciduous forest litter (abundance up to 10,000 specimens/m²), dead wood (up to 6,000 specimens/m²) and compost (up to 15,000 specimens/m²) (Koehler 1997, 1999; Błoszyk et al. 2013, 2016). Many species are saprophagous (Karg 1993) and others are mycetophagous (Faasch 1967; El-Banhawy et al. 1998). Most of the Uropodina known from Poland are species with a narrow range of ecological tolerance (stenobiotic or oligobiotic; 70%); only 6% are characterized by wide tolerance to environmental factors (eurybiotic) (Błoszyk 1999; Błoszyk et al. 2003, 2004). In view of these characteristics, Uropodina mites should be ideal indicators of the effects of steeplesbush invasion on soil fauna diversity.

Our literature searches yielded no published information on the impact of *S. tomentosa* on soil biota. In this study we assessed the impact of this invasive shrub on the species number and diversity of mites of the suborder Uropodina in wet meadow soils. We compared the abundance and species richness of Uropodina mites in meadows dominated by *S. tomentosa* and those free of this shrub, and determined whether the structural transformations of wet meadow communities caused by it affected their community composition. Our working hypotheses were that (1) in areas invaded by *S. tomentosa* the abundance and species richness of Uropodina will be lower than in meadows free of this alien species, and that (2) the presence of *S. tomentosa* will transform the structure of Uropodina communities toward more forest-like assemblages. The work was intended to contribute to our understanding of the impact of invasive *S. tomentosa* on the diversity of wet meadow soil fauna.

Materials and methods

Study area

The research was carried out in south-western Poland in a wet meadow complex located in the Zgorzelecko-Osiecznicki Forest. The surface formations in the study area are mainly Pleistocene sands and gravels of fluvio-glacial or fluvial accumulation, heavily washed by the waters of the melting ice sheet, as well as younger, Holocene patches of fluvial accumulation mud (Rzechowski 1994; Forest Data Bank 2024). The dominant habitats in this area are forest habitats, such as mesic coniferous forest (40%) and mesic mixed coniferous forest (34%) (Góral 2005), between which there are numerous complexes of extensively used meadows and low and transitional bogs.

Using present vegetation (Forest Data Bank 2024) and hydrological maps (Bieroński et al. 2000), we selected and found forest meadows with soils periodically saturated with water. All the meadows are located in the Lower Silesian Forests mesoregion (Solon et al. 2018) and have a similar geological history (Rzechowski 1994), climate (Woś 1999) and soil properties, the moisture conditions of which are determined by the groundwater table located just below the soil surface (Forest Data Bank 2024). The meadows are dominated by *Juncus effusus* L. and *Molinia caerulea* (L.) Moench, with a significant proportion of grasses: *Deschampsia caespitosa* (L.) P.B., *Holcus lanatus* L., *Calamagrosti canescens* (Weber) Roth, *Agrostis stolonifera* L.; and herbs: *Filipendula ulmaria* (L.) Maxim., *Cirsium palustre* (L.) Scop., *Lythrum salicaria* L. or *Lotus uliginosus* Schkuhr (see Wiatrowska et al. 2023). All these meadows were maintained mainly as part of regular practices, but when mowing was stopped in some of them *S. tomentosa* spread, completely changing the structure and character of the plant communities (Wiatrowska and Danielewicz 2016; Wiatrowska et al. 2023) (Fig. 1).

Sampling methods

In 2020, eight wet meadow complexes (hereinafter referred to as study sites) were randomly selected for further analyses (Table SI 1). The study sites were at least 1000 ± 830 m apart. Two permanent square plots covering 100 m² were established in each study site: one in a well-preserved meadow with no signs of invasion (“uninvaded plot”), and the other one in a meadow with monodominant stands of *S. tomentosa*, 100% covered by this invasive shrub (“invaded plot”). To exclude or minimize the effect of interaction between invaded and uninvaded plots they were established 50 m apart. Along diagonals of each of the study



Fig. 1 Inflorescence of invasive *Spiraea tomentosa* (a – left), and uninvaded (b – upper right) and invaded (c – lower right) wet meadows in the Lower Silesian Forests (photo by B. Wiatrowska)

plots we collected four 0.5 dm³ soil samples (sampling core: $\phi = 8$ cm, depth = 10 cm) from organic-mineral horizon A. Soil samples were collected at similar intervals (May, August and December 2020), close to each other but not from the same spot, for a total of 192 soil samples. Eight samples from two plots located in the same study site from the sampling effort in May were excluded because of flood damage. The soil moisture of each sample was determined as the weight ratio between the water content and whole fresh samples (Napierała 2008). The mites were extracted with Tullgren funnels for six days and subsequently preserved in 75% ethanol. Permanent and temporary microscope slide preparations were made (using Hoyer's medium) and the specimens were identified with the keys of Kadite and Petrova (1977), Evans and Till (1979), Karg (1989), Błoszyk (1999) and Mašán (2001). The samples are deposited in a soil fauna collection in the Natural History Collections of the Faculty of Biology, Adam Mickiewicz University, Poznań.

Statistical analysis

The abundance and species richness of mites from suborder Uropodina, estimated per soil sample, were tested in relation to three explanatory variables: “plot type” (invaded vs. uninvaded), “sampling period” (May, August, December), and “moisture” as an environmental factor. “Study site” was applied as a random factor. After backward selection of explanatory variables, two were selected for further computations: “plot type” and “sampling period”. “Moisture” as a non-significant factor was excluded from the models, but as it appeared to be a relevant environmental factor for community composition it was applied in ordination analysis. In the second step, to obtain more precise species-specific results the data were analysed separately for the three most abundant uropods (*Olodiscus minima*, *Urodiaspis tecta*, *Trachytes aegrota*) also in relation to “plot type” and “sampling period” as referred to above. Generalized linear mixed-effect (GLMER) models based on a Poisson distribution were applied for analyses. Residuals versus expected values and overdispersion were verified using the DHARMa package (Hartig 2023). In the case of significant deviations in residual diagnostics a negative binomial model was applied. Final results were computed with the ‘Anova’ function using the car package (Fox and Weisberg 2019). Post-hoc analyses were run with the glht function of the multcomp package, applying Tukey's test (Hothorn et al. 2008). We used the r.squaredGLMM function to calculate marginal R^2_M (describes the proportion of variance explained by the fixed factors alone) and conditional R^2_C (describes the proportion of variance explained by both the fixed and random factors) (Nakagawa and Schielzeth 2013) of the MuMIn package (Bartoń 2019). Statistical computations were performed with R v4.2.1 (R Core Team 2022).

The analysis of the Uropodina community was based on the indices of dominance (number of individuals of i th species compared to individuals of all species in all samples) and frequency (number of samples with i th species compared to all samples) (Błoszyk 1999). The dominance and frequency characteristics were computed with data for invaded and uninvaded plots separately, but pooled for all the sampling periods. To test the differences in the structures of dominance, frequency and age between Uropods recorded in invaded and uninvaded plots, the Chi square test (χ^2) was applied to the analysed data.

Our samples were divided into two datasets depending on plot type (uninvaded, invaded). To assess correlations between communities/clusters presented as different datasets representing different plot types, with moisture as an environmental variable, principal compo-

nents analysis (PCA, gradient length=2.7) was performed with CANOCO v.5 (Šmilauer and Lepš 2014). Here the aim of the ordination analysis is to arrange the samples so that those with a similar species composition are located close to each other on the axes, while differing samples are distant from each other.

Results

Spatial and seasonal differences in abundance

The analysed material included 482 specimens representing ten species in various developmental stages (adults, protonymphs, deutonymphs) (Table 1). For all species analysed together the only significant effect that determined the number of Uropodina species recorded in soil samples was sampling period ($\chi^2=7.15$, $df=2$, $P=0.028$, Table 2). The lowest number of species was recorded in August (mean $\pm$ SE, 1.56 ± 0.38) and did not differ significantly from the number recorded in May (2.36 ± 0.46 , Tukey $P=0.106$) but differed significantly from December (2.06 ± 0.38 , Tukey $P=0.024$). There were no significant differences in the number of Uropodina mite species ($\chi^2=0.11$, $df=1$, $P=0.742$, Table 2) between plot types: invaded, 2.09 ± 0.30 ; uninvaded, 1.87 ± 0.36 . However, the number of individuals was also affected by sampling period ($\chi^2=15.78$, $df=2$, $P<0.001$, Table 2): lowest in August (4.50 ± 1.68) and differing significantly from May (13.86 ± 3.7 , Tukey $P=0.001$) and December (13.50 ± 3.90 , Tukey $P=0.002$). There were no significant differences in the number of individuals ($\chi^2<0.01$, $df=1$, $P=0.990$, Table 2) between plot types: invaded, 8.30 ± 1.72 ; uninvaded, 12.65 ± 3.43 .

The most abundant Uropodina mites were *Olodiscus minima*, *Urodiaspis tecta* and *Trachytes* spp. (*Trachytes aegrota* and *T. pauperior* have similar ecology and were pooled together in all analyses, hereafter called *Trachytes* spp.). The number of individuals of those three Uropodina taxa were analysed in relation to plot type and sampling period, showing different patterns in relation to the explanatory variables. The number of *O. minima*

Table 1 Uropodina species recorded in plots invaded by *Spiraea tomentosa* and in uninvaded meadow plots, with the abundance of adults of both sexes and juvenile stages (D – deutonymphs, P – protonymphs) and habitat preferences (F – forest, O – open habitats). Asterisk indicate source: *Błoszyk (1983)

Species	Invaded				Uninvaded				Habitat preferences*
	Adults		Juveniles		Adults		Juveniles		
	♀♀	♂♂	D	P	♀♀	♂♂	D	P	
<i>Olodiscus minima</i>	67	-	26	5	188	1	31	6	F
<i>Trachytes aegrota</i>	33	-	26	5	14	-	11	1	F
<i>Urodiaspis tecta</i>	11	-	1	1	14	-	2	7	F
<i>Uropoda orbicularis</i>	-	-	1	-	-	-	9	-	F/O
<i>Trachytes pauperior</i>	4	-	3	3	3	-	1	-	F
<i>Iphiduropoda penicillata</i>	-	-	-	-	-	1	-	-	F
<i>Oplitis</i> sp.	-	-	-	-	1	-	-	-	F
<i>Uroplitella paradoxa</i>	-	-	-	-	1	-	-	-	O
<i>Uropoda undulata</i>	1	2	-	1	-	-	-	-	O/F
<i>Dinychus perforatus</i>	1	-	-	-	-	-	-	-	F
No. of individuals	117	2	57	15	221	2	54	14	
No. of species	7			8					

Table 2 Relations between dependent variables and fixed effects, showing the response of Uropodina mites to environmental conditions. $P < 0.05$ denoted by asterisk *

Dependent variable				
Number of species (total)				
Random effect		Variance		SD
‘study site’		0.328		0.573
Fixed effects	χ^2	df		P
‘plot type’	0.11	1		0.742
‘period’	7.15	2		0.028*
		$R^2_M = 0.036$		$R^2_C = 0.238$
Number of individuals (total)				
Random effect		Variance		SD
‘study site’		0.821		0.906
Fixed effects	χ^2	df		P
‘plot type’	< 0.01	1		0.990
‘period’	15.78	2		< 0.001*
		$R^2_M = 0.080$		$R^2_C = 0.278$
Number of individuals of <i>O. minima</i>				
Random effect		Variance		SD
‘study site’		3.016		1.737
Fixed effects	χ^2	df		P
‘plot type’	48.25	1		< 0.001*
‘period’	66.28	2		< 0.001*
		$R^2_M = 0.166$		$R^2_C = 0.921$
Number of individuals of <i>U. tecta</i>				
Random effect		Variance		SD
‘study site’		0.360		0.600
Fixed effects	χ^2	df		P
‘plot type’	2.81	1		0.094
‘period’	2.67	2		0.263
		$R^2_M = 0.030$		$R^2_C = 0.094$
Number of individuals of <i>Trachytes aegrota</i> + <i>T. pauperior</i>				
Random effect		Variance		SD
‘study site’		0.159		0.399
Fixed effects	χ^2	df		P
‘plot type’	7.39	1		0.007*
‘period’	3.64	2		0.162
		$R^2_M = 0.065$		$R^2_C = 0.096$

and *Trachytes* spp. was significantly dependent on plot type (Fig. 2; Table 2), but only the genus *Trachytes* had higher abundance in invaded plots (2.78 ± 0.59) than in uninvaded plots (1.13 ± 0.34). However, *O. minima* and *U. tecta* were more abundant in open habitats of uninvaded plots (9.83 ± 2.92 and 1.00 ± 0.35 respectively) than in plots invaded by steplebush (4.26 ± 1.32 and 0.57 ± 0.24 respectively). For sampling period only *O. minima* displayed a significant relation to that variable, reaching minimum abundance in August. The abundance of *U. tecta* was not affected by either of the two fixed effects in the analysis.

Fig. 2 Mean number of individuals (bars), with standard error (whiskers), of the three most abundant taxa of uropods (*Olo-discus minima*, *Urodiaspis tecta*, *Trachytes aegrota* + *T. pauperior*) in relation to uninverted vs. inversed plots covered by *Spiraea tomentosa*

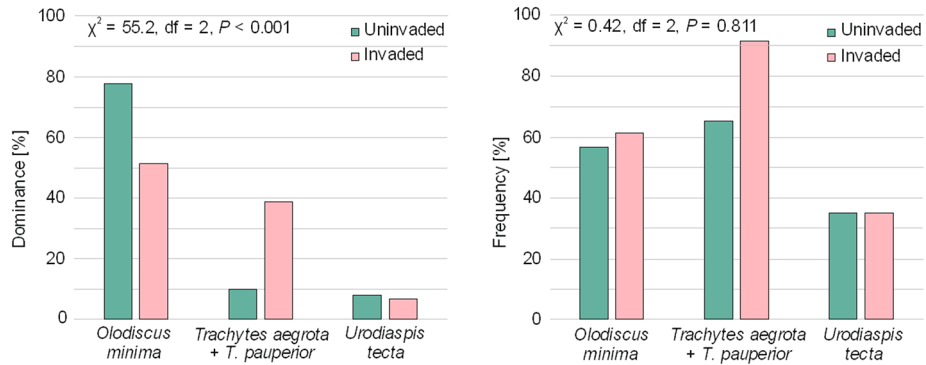
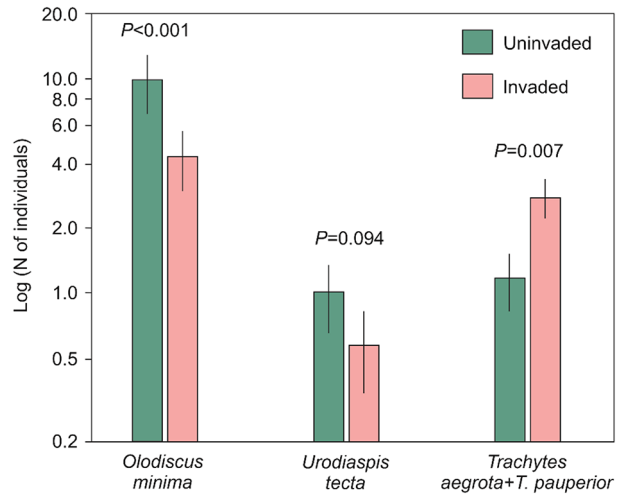


Fig. 3 Structures of dominance (left) and frequency (right) of the three most abundant taxa of uropods in relation to plot type – uninverted vs. inversed by *Spiraea tomentosa*

Dominance and frequency

The Uropodina communities were dominated by the three most numerous taxa in each plot type: *O. minima*, *Trachytes* spp. (*Trachytes aegrota* and *T. pauperior* pooled together) and *U. tecta* (Table 1; Table SI 2), with significant differences in the dominance structure between inversed and uninverted plots ($\chi^2 = 55.2$, $df = 2$, $P < 0.001$, Fig. 3A). In the plots inversed by *S. tomentosa*, *Trachytes* spp. reached higher abundance (38.7%) than in uninverted plots (10.3%). There was an opposite tendency in the dominance structure for *O. minima*, which was more abundant in uninverted plots (inversed, 51.3%; uninverted, 77.7%). The share of *U. tecta* was similar in both plot types (Fig. 3).

The same three taxa were most frequent among the Uropodina communities of both plot types. In inversed plots the share of *Trachytes* spp. was higher (91.3%) than in uninverted ones (65.2%), and exceeded that of *O. minima* (inversed, 60.9%; uninverted, 56.5%), but

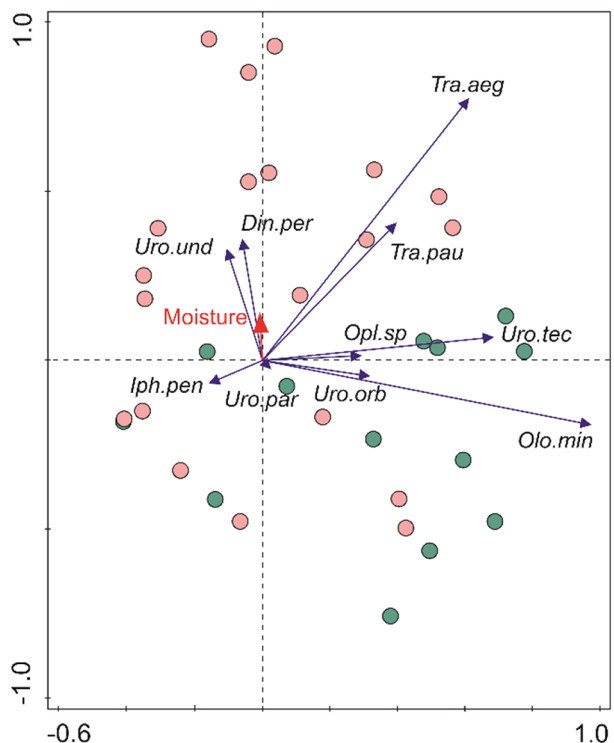
the differences were not significant ($\chi^2=0.42$, $df=2$, $P=0.811$). The share of *U. tecta* was similar in both plot types (Fig. 3).

There were significant differences in the shares of adults and juveniles between plot types. The share of juveniles were significantly higher in invaded (37.7%, $N=72$) than in uninvaded plots (23.4%, $N=68$) ($\chi^2=10.80$, $df=1$, $P=0.001$).

Diversity in community structure

In total, 191 individuals of 7 species were recorded in plots invaded by *S. tomentosa*, in comparison to 291 specimens of 8 species in uninvaded plots. Both groups of samples consisted mostly of the same Uropodina species, common to both uninvaded and invaded plots (e.g., *O. minima*, *T. aegrota*, *T. pauperior*, *U. orbicularis*, *U. tecta*) and forming the core of the whole mite community. PCA analysis showed some qualitative differences between plot types (Fig. 4), manifested in the presence of exclusive species occurring in only one type of plot: *Uropoda undulata* and *Dinychus perforatus* occurred only in plots invaded by *S. tomentosa* (Table 1), whereas *Iphiduropoda penicillata*, *Uroplitella paradoxa* and species of the genus *Oplitis* occurred only in uninvaded plots but their presence was incidental and consisted of only single specimens (Table 1). In the group formed by species common to both plot types the genus *Trachytes* (*T. aegrota* and *T. pauperior*) was more abundant and more frequent in invaded than in uninvaded plots. This group of species formed the upper left part of Fig. 4, representing habitat conditions after the invasion of *S. tomentosa*. *O. minima* and *U. tecta* formed the group preferring uninvaded open habitats (Fig. 4).

Fig. 4 Principal components analysis (PCA) scatterplot showing relationships between Uropodina mite communities from uninvaded and invaded plots on the first two axes. The first and second axes explained 83.7% of variation. Legend: pink dots=plots invaded by *Spiraea tomentosa*; green dots=uninvaded plots. Arrows represent the share of the given species in the assemblage. Species abbreviations: *Din.per*=*Dinychus perforatus*, *Iph.pen*=*Iphiduropoda penicillata*, *Olo.min*=*Olo-discus minima*, *Opl.sp*=*Oplitis* sp., *Tra.aeg*=*Trachytes aegrota*, *Tra.pau*=*T. pauperior*, *Uro.tec*=*Urodiaspis tecta*, *Uro.par*=*Uroplitella paradoxa*, *Uro.orb*=*Uropoda orbicularis*, *Uro.und*=*U. undulata*



Discussion

The impact of invasive species on microarthropod communities can vary greatly (Belnap et al. 2005), so the direction, strength and effects of these changes must be assessed in each particular context. At least three scenarios are known for the response of mite assemblages after invasion: (i) a decline in the abundance and species richness of mites (Belnap et al. 2005; Pritekel et al. 2006; Skubała and Mierny 2009; Motard et al. 2015; Kohyt and Skubała 2020), (ii) a positive effect on the populations of native microarthropod taxa (McGrath and Binkley 2009; Christopher and Cameron 2012; Rusterholz et al. 2014), or (iii) induction of changes in community composition without significant changes in the number of species or individuals (this study). The latter is relatively rare in the ecology of invasions considered on the soil mesofauna level (Wardle et al. 1995; John et al. 2006; Ustinova et al. 2021).

The microarthropod community in litter is shaped by many factors, such as physical soil properties (L'ubomir et al. 2001; Huhta and Ojala 2006), nutrient availability (King and Hutchinson 1980; Lindbert and Persson 2003), litter complexity (Hansen and Coleman 1998), disturbance (Bird et al. 2004; Reynolds et al. 2007; Rola et al. 2017) or plant diversity (Migge et al. 1998; Hansen 2000). These habitat properties are strongly modified by invasive species (Vanderhoeven et al. 2005; Liao et al. 2008; Castro-Díez et al. 2014). Previous studies have indicated a clear directional impact of alien species on the number and richness of soil mesofauna. Belnap et al. (2005) showed that invasion of *Bromus tectorum* causes a rapid decline in the abundance and richness of microarthropods, whereas Skubała and Mierny (2009) reported a reduction in the abundance and richness of saprophagous and fungivorous mites in areas completely dominated by *Reynoutria sachalinensis* as compared to areas free of this perennial. Lower abundance and richness of mites was found in the litter of alien *Quercus rubra* as compared to litter of the native oak *Q. robur* (Kohyt and Skubała 2020). Increasing density of *Ailanthus altissima* was accompanied by a decrease of litter detritivore abundance (Motard et al. 2015). Other research has shown a negative impact of invasive plant species on the number and abundance of mites. Invasion of *Lonicera maackii* in a deciduous forest had a positive effect on Acari abundance in litter (Christopher and Cameron 2012), and litter under the invasive grass *Microstegium vimineum* in upland forests showed greater abundance of mites than litter from the surrounding forest floor (McGrath and Binkley 2009). According to Rusterholz et al. (2014), in the litter of areas invaded by *Impatiens glandulifera* there were 10–33% more mites than in areas where the plant was removed or in areas not invaded, and this tendency also applied to Uropodina analysed separately. Most studies suggest that the effects of invasion are usually clear and extreme – they illustrate clear negative or positive reactions of indigenous mesofauna communities (Ustinova et al. 2021).

We found that *S. tomentosa* invasion induced some changes in the composition of Uropodina communities, although steeplebush did not have a significant effect on their quantitative characteristics, such as total abundance and species richness. Even though *S. tomentosa* is considered a transforming species (Wiatrowska et al. 2023), the lack of significant changes in the quantitative characteristics of the whole Uropodina mite community means that our first working hypothesis about a clear negative impact of this shrub on the total abundance and species richness of Uropodina should be rejected. Our results are in line with those from other research. Wardle et al. (1995) showed that mite populations generally do not respond to *Senecio jacobaea* infestation in pastures. The abundance of mites was not altered by inva-

sion of *Solidago gigantea* in wet meadows (Sterzyńska et al. 2017) and urban wasteland (Ustinova et al. 2021). Nor were there differences in the number and abundance of mites in areas dominated by native and invasive grass species (John et al. 2006). The effect of an invasive species on mites may be ambiguous and is not always directional. Interpretation of such effects is complicated by the very small number of detailed studies characterizing the ecology and general distribution patterns of mites, including Uropodina. However, some general conclusions can be drawn from research on the impact of invasive species on ecosystems.

It is known that the impact of invasive plants is context-dependent and shaped by the ecological setting (Hejda et al. 2009; Pyšek et al. 2012; Hulme et al. 2013). The structure of soil food webs is controlled by plant inputs and by internal dynamics between trophic levels (Belnap and Phillips 2001), which means that changes in plant cover due to the spread and impact of an alien species can be buffered by habitat properties such as those related to the local structure of the food web in the soil. Wet meadows, like other wetland habitats, are known for their buffering properties (Mander et al. 1996). It is therefore possible that, despite transformations occurring in the meadow ecosystem as a result of *S. tomentosa* invasion, the buffering properties of these habitats (and therefore the amounts of key resources available to mites in the invaded habitats) are similar to those in uninvaded habitats. With an increase in the cover of *S. tomentosa* there is a very significant decrease in plant diversity (Wiatrowska et al. 2023), which, as a consequence of the homogenization of the plant communities, may lead to a reduction in the availability of habitats for Uropodina (Napierała et al. 2006). At the same time, the high biomass production of *S. tomentosa* (Wiatrowska et al. 2022), may increase the food base for mites (or vice versa), and this may help maintain the numbers and species richness of Uropodina.

As a result of steppelush invasion, two parallel processes can be observed in the Uropodina community: changes in the dominance structure of the most numerous species, and the entry or numerical increase of Uropodina typical of forest habitats (Błoszyk 1983, 1999). A real and rarely analysed effect of the studied invasion seems to be expressed in some qualitative changes in Uropodina mite communities in the habitats invaded by *S. tomentosa*; this allows us to positively verify our second hypothesis, that *S. tomentosa* affects mite community structure. We found that all the studied sites were dominated by Uropodina soil parthenogenetic species, such as *O. minima*, *T. aegrota* and *U. tecta*, which are common and widely distributed in both forest and open areas of Europe (Błoszyk 1983, 1999; Błoszyk et al. 2003). However, the presence of *T. aegrota* and *T. pauperior* was much more marked in invaded plots. Under monodominant stands of *S. tomentosa*, *T. aegrota* reached the eudominant class, and although the differences were not significant, its frequency was much higher there (euconstant). *Trachytes aegrota* is a eurytopic species, found in almost all types of habitats but most frequently and numerously inhabiting forest litter (Błoszyk 1983, 1999). The second species of the genus *Trachytes* – *T. pauperior* – is also typical of forest habitats (Błoszyk 1983, 1999). The greater abundance of both species and the differences in the dominance structure between invaded and uninvaded sites possibly are promoted by the more “forest-like” features of meadows covered by *S. tomentosa*. It is known that the spread of woody species on grasslands and meadows causes significant changes in the structure of the plant community (Hobbs and Mooney 1986; Costello et al. 2000), resulting, for example, in greater shading of the soil surface (Kudo et al. 2011) and lower daytime temperature (Shen et al. 2022), which leads to changes in arthropod communities (Litt et al. 2014;

Woodworth et al. 2020; Lalk et al. 2021). The greater abundance of typical forest dwellers such as *T. pauperior* and *T. aegrota* under *S. tomentosa* indicates slow transformation of the Uropodina communities from those of open-like habitats to more forest-specific ones.

A crucial factor that may affect qualitative differences in the structure of Uropodina communities in invaded and uninvaded sites is moisture content. Although we found that the occurrence of most of the analysed Uropodina species generally was independent of the moisture gradient, two species found only in monodominant stands of *S. tomentosa* showed a preference for wetter habitats than the others. One of them, *U. undulata*, is a rare and sparse hygrophilous species often found in peat bogs, alder forests and riparian forests, while the other, *D. perforatus*, occurs in multi-species deciduous forests and alder forests (Błoszyk 1983, 1999). It seems that, as in the case of other invasive species (McGrath and Binkley 2009), the dense litter layer developed by *S. tomentosa* (Balkenhol et al. 2018) may promote moisture retention, increasing the stability of the habitat (McGrath and Binkley 2009) and favouring hygrophilous species.

Beside moisture changes, the qualitative characteristics of the studied Uropodina communities may also be influenced by significant structural and functional simplification of the plant communities (Wiatrowska et al. 2023) as a result of invasion. In our research we found that such Uropodina mites as *I. penicillata*, a very rare species associated with microhabitats such as rotten stumps, hollows or mammalian nests, and *U. paradoxa*, a species rarely found in xerothermic peat bogs and grasslands (Błoszyk 1983), or *Oplitis* sp., occurred only in meadows free of *S. tomentosa*. It is known that mite communities are strongly determined by the diversity of microhabitats (Hansen 2000; John et al. 2006), and many species of Uropodina, including rare species, are associated with specific microhabitats (Bajerlein and Błoszyk 2004; Napierała et al. 2016, 2021). The homogenization of plant communities caused by the invasion of *S. tomentosa* (Wiatrowska et al. 2023) may limit the number of microhabitats available to rare natives (Seabloom et al. 2006), which often occupy narrow environmental or functional niches (Flather and Sieg 2007).

Conclusion

The management of invasive plants should always be supported by studies of their impact on the ecosystem (Barney 2016), because their influence is difficult to predict and is not uniform across species (Vilà et al. 2011; Litt et al. 2014; Schirmel et al. 2016). We found that despite profound changes in the ecosystem caused by *S. tomentosa* invasion, the mass spread of the shrub did not lead to significant directional changes in the number and species richness of Uropodina communities living in the leaf litter and upper soil layers of wet meadows. Our results support the suggestion that the structure of aboveground vegetation is not the only factor determining the stability of soil microarthropod communities (John et al. 2006); disturbances caused by the invasion of an alien species may not affect their quantitative characteristics. However, we did find that the invasion of the shrub affected the qualitative features of Uropodina communities. The conditions prevailing in the monodominant stands of *S. tomentosa* seem to favour shade-tolerant and hygrophilous species, initiating a slow transformation process in Uropodina communities toward more forest-like assemblages. Since various environmental factors may be responsible for the observed patterns, these results should be treated with caution. More studies should be done to determine the

impact of *S. tomentosa* on microorganisms (bacteria, fungi) and other groups of soil fauna, to yield a more complete picture of the impact of the shrub on soil biota and on the wide range of ecosystem services and the productivity of invaded ecosystems.

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Declarations

Competing interests The authors declare no competing interests.

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