

Ph.D. thesis

**Impacts of biological invasion and overwintering on spider
fauna in plantation forest**

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1. Introduction

As a consequence of agricultural intensification and urbanisation since the mid-20th century, biological diversity has declined considerably throughout the world but particularly in European countries, resulting in mosaic landscapes. The spatial distribution of organisms in such habitat complexes is influenced by numerous habitat and landscape scale factors and presumably also by the complex interactions among them. It is therefore, relevant to identify the drivers of diversity and assemblage composition for assessing patterns of biodiversity in the remaining semi-natural habitats.

The anthropogenic land use changes including intensive agriculture, urbanization etc., result in the habitat fragmentation and further be responsible for the loss of biological diversity throughout the globe (Belcik *et al.*, 2020; Wilson *et al.*, 2016). Traditionally, species richness or taxonomic diversity has been considered as one of the most commonly used indices of biodiversity. There are many studies investigated the impact of habitat fragmentation on taxonomic, phylogenetic and functional diversity metrics (Belcik *et al.*, 2020; Chesson, 2000). The functional diversity approach offers a useful tool to assess ecosystem functions and services (Díaz & Cabido, 2001). Numerous studies showed that increasing species richness and diversity can enhance ecosystem functioning (Cardinale *et al.*, 2012), however, large part of the variation may remain unexplained (McGill *et al.*, 2006). Functional diversity measures relative abundance, range, and dispersion of functionally meaningful life-history trait values (Díaz *et al.*, 2007). It describe how ecosystems work and how it adapt to change (Petchey & Gaston, 2006). Functional diversity is considered more sensitive to environmental changes than taxonomic diversity (Woodcock *et al.*, 2014). However, the quantification of functional diversity requires a number of complex and precise measures on functional traits (Cardoso *et al.*, 2011). Databases of functionally important traits, especially of less studied invertebrate taxa, are scarce and usually incomplete (Moretti *et al.*, 2017). The functional diversity of arthropods in semi natural habitats is still not studied deeply (Woodcock *et al.*, 2010). With this, increase in overall functional diversity in the plantation forests may enhance resistance and resilience of ecosystems (Ares *et al.*, 2010; Gallé *et al.*, 2018).

The majority of the invertebrate species has well defined habitat requirements; therefore their species diversity and composition are sensitive indicators to landscape structure and habitat change. Ground-dwelling arthropod assemblages are generally diverse and abundant, and therefore may be collected in large numbers with relatively little effort. Spiders are among the most diverse taxa of the invertebrate macrofauna in all terrestrial ecosystems, representing polyphagous predators. The high number of species and abundance make their assemblages suitable for ecological studies (Schowalter, 2006).

1.1 Effect of tree plantation on arthropods

The intensive forest management during the last century has transformed a significant portion of European natural forests as well as Pannonian sand forest-steppes into even-aged plantations, monocultures of deciduous or coniferous tree species. In Hungary, the area covered by forests is approximately 22.5% and is increasing by 0.5% per annum (Gallé *et al.*, 2017); however, 75% of the forests are primarily under intensive management focusing almost entirely on wood production (Magura *et al.*, 2015).

The landscape of the Southern Kiskunság region is dominated by different aged plantation forests under intensive management. The most widespread tree species include black locust, pines (*Pinus* spp.) and silver poplar. There is evidence that intensive forestry management of short-rotation forests is reducing microhabitat diversity and changes vegetation composition, which in turn reduces the number of species, especially the number of habitat specialists (Klimes *et al.*, 2012). However, numerous studies demonstrated the capacity of plantation forests to provide habitat for native forest species (Gallé *et al.*, 2014b; Oxbrough *et al.*, 2012).

The land cover of commercial tree plantations is increasing worldwide, replacing natural forests and sometimes open habitats. These secondary forests include native and non-native, mainly coniferous tree plantations. The plantation of non-native trees for commercial use (e.g. timber production) may be responsible for alteration of hydrologic regimes (Urcelay *et al.*, 2017), increasing soil acidity (Selvi *et al.*, 2017), loss of soil fertility (Augusto *et al.*, 2002) and organic matter (Henneron *et al.*, 2015). Tree species have a significant effect on sunlight exposure of the understory in forests and may also affect the microclimate (Messier *et al.*, 1998). Intensive forestry management of short-rotation forest plantations reduces microhabitat

diversity and changes vegetation composition. Although international pressure is increasing to tackle the negative environmental effects of such plantations, tree plantation covers more than 7% of total forest area worldwide (Payn *et al.*, 2015).

The expansion of tree plantations can have severe ecological impacts on native biota, such as alteration of plant and animal community compositions (Brockerhoff *et al.*, 2008; Moreira-Arce *et al.*, 2015) and ecosystem functioning (Spirito *et al.*, 2014). However, plantations may also have a positive impact on local biodiversity by providing secondary habitats for rare and threatened species (Brockerhoff *et al.*, 2008). Deciduous tree plantations, such as poplar in central Europe, have dense understory vegetation similar to natural forests (Calviño-Cancela *et al.*, 2012) which can reduce extreme microclimatic conditions (Harms *et al.*, 2000) and favorable for forest specialist arthropods (Barton *et al.*, 2017; Carvalho *et al.*, 2011). All these changes affect understory vegetation which regulates the ground surface microclimate (Finch, 2005) and provides various habitats for arthropods (Rodrigues & Mendona Jr., 2012). Replacement of a native tree species to a non-native species has a large impact on biodiversity as a consequence of structural and compositional changes in understory vegetation affecting the invertebrate fauna (Ennos *et al.*, 2019). Furthermore, non-native evergreen plantations provide moister and more sheltered forest floor compared to broadleaf forests (Humphrey *et al.*, 2004). These differences results in lower invertebrate diversity in non-native coniferous plantation than natural forests (Brockerhoff *et al.*, 2008).

Pine plantations are common in Europe; they are among the most widespread tree plantations in Hungary, as well. They are generally used for timber production. *Pinus sylvestris* is the most widely distributed Eurasian conifer. It occurs on different soils, and under different climates condition from arid, mountainous areas of Southern Europe to subarctic forests of Siberia. Its natural distribution started to expand after the last glacial period from the ice-free Southern European regions. Scots pine has isolated natural population in Carpathian Mountain range and scattered populations in mixed forest stands, in the western Pannonian Basin at the foothills of the Alps (Tóth *et al.*, 2017). Pine species (*P. sylvestris* and *P. nigra*) were introduced to the Hungarian Great Plain in the 19th century to prevent of soil erosion. Pine species were considered to effective sand-binding trees due to the dense root system (Cseresnyés & Tamás, 2014). The layer of pine needles on forest floor makes the soil acidic (Selvi *et al.*, 2017), and the change in chemical and physical properties of the soil results in loss

of fertility (Augusto *et al.*, 2002). These processes are responsible for the changes in understory vegetation structure and microhabitat diversity (Chiarucci & De Dominicis, 1995), and in turn, lower species diversity of arthropods compared to natural forests (Brockerhoff *et al.*, 2008; Gallé *et al.*, 2018). Species richness and diversity of predatory invertebrates are generally lower in pine plantations than in forest plantations of native forests (Bonham *et al.*, 2002; Gallé *et al.*, 2014b; Samways *et al.*, 1996).

The ground-dwelling spider fauna of both poplar and pine plantations comprises of mainly active hunter Lycosid and Gnaphosid spiders such as the dominant species *Pardosa alacris* (C. L. Koch, 1833), *Arctosa lutetiana* (Simon, 1876), *Zelotes apricorum* (L. Koch, 1876). In addition, several thomisid spiders are frequent ground level of lowland forest plantations (e.g. *Ozyptila praticola* (C. L. Koch, 1837) and *Xysticus luctator* L. Koch, 1870). *Zodarion germanicum* (C. L. Koch, 1837) is a common spider in old plantations with dense ant communities. The dominant species are similar in poplar and pine plantations; however, the species richness is higher in poplar than in in plantations (Gallé *et al.*, 2014a, 2014b, 2017, 2018).

1.2. Plant invasions and the effect on arthropods

In ecological research, the effect of invasive plant species has become a hot topic due to their increasing number worldwide (Seebens *et al.*, 2017). The threat of invasive plants to native biodiversity is considered as second after habitat destruction (Mack *et al.*, 2000; Wilcove *et al.*, 1998); which makes it a serious ecological and economic problem and a significant component of global change (Sala *et al.*, 2000; Vitousek *et al.*, 1997).

Invasiveness of plants is major threat not only to native species assemblages but also to overall natural habitats (Vitousek *et al.*, 1997). Most of the arthropods are closely associated with the native vegetation or its microhabitats (Gratton & Denno, 2005). Alteration of habitat's physical characteristics has been responsible for negative consequences on the indigenous fauna. As native insects have different evolutionary history with exotic plants, it is quite difficult for them to get adapted for consumption of these plants as a food resources (Tallamy, 2004). The herbivore insects count 37% of all animal species, transfer energy from plants to higher trophic levels (Wilson, 1987) such as predatory insects. Not all exotic plants become invasive but the reason for invasiveness of exotic plants is losing several important enemies

from their native locations during the colonization in the new land (Colautti *et al.*, 2004). It is reported that invasive plant species incurred lesser enemy loads than native plants in the invaded ranges (Dostál *et al.*, 2013; Han *et al.*, 2008). However, it is still unclear that on which extent the natural enemies can the invasibility of non-native plants (Han *et al.*, 2008). This might result in increasing population growth (Roy *et al.*, 2011) and spreading of exotic species with increasing their impact on native communities (Mitchell & Power, 2003). However, exotic plants can become alternative food source for few insects (Hill & Kotanen, 2009) and may also get infected by native fungal communities (Agrawal *et al.*, 2005; Parker & Gilbert, 2007). This can limit the spread of an exotic plant species in invaded communities (Levine *et al.*, 2004).

The geographical location of Hungary makes it more sensitive for the invasion of exotic plant species because it is situated in a biogeographical transition zone between the deciduous forest and the steppe areas. In this zone several species reach their distribution borders and made it as a gateway for invasion (Török *et al.*, 2003a). This zone may provide favorable environment which is susceptible to certain exotic species invasions. Many exotic plant species are reported as invasive in Hungary, such as *Ambrosia artemisiifolia*, *Aster spp*, *Celtis occidentalis*, *Ailantus altissima*, *Asclepias syriaca*, *Vitis riparia*, etc (Török *et al.*, 2003a).

Exotic plant species in Hungary are first reported from 19th century, the invasions are suspected to be began long before that (Török *et al.*, 2003b). The first serious impact of an invasion is generally on the local vegetation as aggressive spreading property of invasive plants can dominate the community. The spreading of exotic plants with high reproduction output, density, population size, seed bank size is a serious problem for nature conservation (Hinz & Schwarzlaender, 2004). These properties make exotic plant species hard to control (Ducs *et al.*, 2016).

The common milkweed (*Asclepias syriaca*) is originated from northern America. Populations of milkweed are declining in its original distribution area, as a result of land use change (Lark *et al.*, 2015; Pleasants, 2017). Milkweed is the host plant of monarch butterfly in eastern North America. The decline of milkweed has a negative effect on monarch butterfly populations. However, common milkweed in Europe spreads aggressively and is found in 11 European countries (Szitar *et al.*, 2018). It establishes dense populations in disturbed habitats (Kelemen *et al.*, 2016; Pysek *et al.*, 2012), and may change the composition of existing vegetation and form novel ecosystems (Kelemen *et al.*, 2016; Szitár *et al.*, 2016). The plant was

introduced into Europe in the 17th century (Bukovinszky *et al.*, 2014; Gaertner, 1979) from eastern North America and into Hungary in the 18th century by beekeepers (Balogh *et al.*, 2007; Csontos *et al.*, 2009). Currently, *A. syriaca* endangers the semi-natural and natural vegetation of sandy regions (Ducs *et al.*, 2016), has become one of the most abundant invasive plant species in Hungarian lowland forest plantations, and represents a major problem in conservation areas (Szitár *et al.*, 2016). The poisonous cardenolide content present in the white latex in *A. syriaca* can hinder top-down control of native generalist herbivores (Van Zandt & Agrawal, 2018), and have a negative effect on native specialist herbivores by loss of native vegetation due to the invasion of *A. syriaca* (Litt *et al.*, 2014). Generally, plant invasion is responsible for the reduction of herbivore abundances (Cronin *et al.*, 2015; Simao *et al.*, 2010). However, its negative effects are not always straightforward (Somogyi *et al.*, 2017; Szitár *et al.*, 2016).

Invasive plants had a strong effect on the species composition of terrestrial arthropods (Greenwood *et al.*, 2004). Due to the mechanical disturbance of the soil, altered microclimate and soil properties, plantation forests are prone to invasion by non-native herbaceous plant species (Henneron *et al.*, 2015) such as *A. syriaca*. However, in some extent, invertebrate communities remain unchanged even the vegetation structure changed (Harris *et al.*, 2003). *A. syriaca* attracts many insects, particularly pollinators, because of the open structure of its flowers. As such, it serves as a continuous resource for pollinators day and night, attracting both diurnal and nocturnal pollinators (Southwick, 1983). The high density of pollinators, in turn, may attract predatory arthropods. The effect of plant invasion on arthropod assemblage structure is still not well defined, and is crucial in understanding terrestrial ecosystem ecology (Bezemer *et al.*, 2014).

Spiders play important role in the regulation of terrestrial arthropod communities, as they affect lower trophic levels by top down effects on the food webs (Scott *et al.*, 2006), however the effect of invasive plants on spiders remains relatively understudied. It may alter the native spider abundance, diversity, assemblage patterns. For example, invaded sites by *Chromolaena odorata* are found with lower diversity and species richness of spiders than in not invaded sites. Although spiders do not show direct interactions with non-native plant species, any change in spider community can reflected the changes in arthropod herbivore community on which spiders are dependent for food (Mgobozi *et al.*, 2008).

1.3. Effect of winter on arthropods

Arthropods avoid cold habitats according to the ‘warmer is better’ hypothesis (Frazier *et al.*, 2006) as increasing temperature and a longer growing season positively affect metabolism and reproduction (Groffman *et al.*, 2012; Penczykowski *et al.*, 2017). The temperate winter is generally challenging for many arthropods to survive. Forests are likely to be important overwintering habitats for arthropods at the landscape scale (Roume *et al.*, 2011). Hibernation in the soil or in leaf litter is common behaviour of arthropods (Kirchner, 1987). The quality and quantity of leaf litter are important factors in the formation of appropriate hibernation sites. Selection of habitats which buffer temperature fluctuations (freezing avoidance) and physiological adaptations to resist cold are the most common strategies to cope with winter (Roume *et al.*, 2011). The cold resistance of invertebrates is based on freezing tolerance; usually they have a cryoprotective dehydration strategy (Convey *et al.*, 2015; Everatt *et al.*, 2015). However, numerous arthropod species are active during winter (Korenko & Pekár, 2010; Petráková *et al.*, 2016). Winter active arthropods are capable of moving and feeding at low temperatures. Below a threshold temperature, feeding ceases, although activity may continue corresponding to ice nucleation temperature (Aitchison, 1987). Winter active Springtails and Psyllids, such as *Cacopsylla* are the major prey source of these spiders throughout the winter (Pekár *et al.*, 2015).

The most abundant winter food for ground-dwelling predatory arthropods of the forest floor is Collembola which can tolerate sub-zero temperatures and available in large numbers on snow covered surfaces and in their microhabitats under the snow, as well (Hågvar, 2010; Hao *et al.*, 2020; Zhang *et al.*, 2014).

1.4. Forest type, plant invasions and overwintering affect spiders

Spiders are a diverse group of arthropods; they are abundant generalist predators in almost all terrestrial ecosystems, including tree plantations (Munévar *et al.*, 2018; Nyffeler & Birkhofer, 2017; Pearce & Venier, 2006). They also play a key role in directly regulating the invertebrate populations of soil-surface and vegetation in forests and have a cascading effect on several ecosystem functions such as pollination, litter decomposition (Lawrence & Wise, 2000; Liu *et al.*, 2016).

Diversity of ground-dwelling spiders is affected by biotic interactions and the characteristics of understory habitats (Gallé *et al.*, 2016, 2017; Samu *et al.*, 2014; Schuldt *et al.*, 2008). Spider diversity depends on the microhabitat structure of the forest floor (Castro & Wise, 2009; Pearce *et al.*, 2004). In poplar plantations, the floor is generally more complex than in pine plantations due to the presence of a thick layer of deciduous leaves (Gallé *et al.*, 2014b), while in pine forests, the floor is covered by pines needles, forming a homogeneous microhabitat structure (Selvi *et al.*, 2017).

Spiders as at the top of their terrestrial arthropod communities, they only interact with exotic plants indirectly. The plant invasion can be resulted in a decrease of the numerically dominant spiders, and make changes in the assemblage pattern, species richness and diversity (Mgobozi *et al.*, 2008) due to the disturbance of food web connections and flow of energy in invaded habitats (Tallamy, 2004). For instance, the invasive plant, Himalayan balsam (*Impatiens glandulifera*) in Central Europe attracts native pollinators through its widespread floral resources (Davis *et al.*, 2018), and in turn have a strong negative effect on the diversity and abundance of foliage-dwelling arthropod predators such as spiders (Bauer *et al.*, 2021; Tanner *et al.*, 2013). The progressive invasion of Triffid weed (*Chromolaena odorata*) in South Africa was responsible to make changes in spider abundance, species composition and also in estimated spider species richness (Mgobozi *et al.*, 2008). The invasion of American goldenrods (*Solidago Canadensis* and *S. gigantean*) in protected areas and in abandoned arable fields, affected pollinators negatively due to simplification of floral resources (Fenesi *et al.*, 2015). This may affect ambush hunters such as crab spiders (Thomisidae) negatively as they lurk on flowers of invasive plants for visiting pollinators. Many spiders are habitat specialists with a fast reaction to environmental changes and stress (Buchholz *et al.*, 2015, 2018), however, the effects of plant invasion on spider communities are appear to be mostly reversible (Mgobozi *et al.*, 2008; Palmer *et al.*, 1997).

The diversity of spiders in plantations and native forests are already compared in numerous studies (Gallé *et al.*, 2014b; Samu *et al.*, 2014; Sanders *et al.*, 2008), but the winter activity of spiders in poplar and pines tree plantations has not been studied until now. Microclimatic pattern during winter and presumably species composition of spider communities differs from summer conditions. It has already been demonstrated that winter-active spiders have a significant suppressing effect on their prey populations (Pekár *et al.*,

2015; Sigsgaard, 2007) and thus presumably have an indirect effect on several ecosystem functions, such as herbivory and decomposition in forests (Sitvarin *et al.*, 2016). The rate of successful overwintering is determined by body condition and is thus linked to prey availability in the overwintering habitat type (Gunnarsson, 1988; Lee, 1991). Large spiders may have higher chances of survival than small individuals of the same species (Schneider, 1995; Walker *et al.*, 2003), but this correlation is not always clear (Gunnarsson, 1988; Kotiaho *et al.*, 1996). Besides body size, numerous indices have been proposed for assessing the body condition of invertebrates (Jakob *et al.*, 1996). However, fat reserves in arthropods are considered good estimators of body condition (Contreras-Garduño *et al.*, 2006), since age and nutrition intake determine the protein and lipid content of arthropods (Bednaski *et al.*, 2015; Cappelari *et al.*, 2009). Good body condition and rapid growth of an arthropod predator are presumably due to an increase in the quantity and quality of consumed prey, which is linked to habitat quality. In complex habitats, the amount of prey available to predatory arthropods is higher than in simple habitats (Copley & Winchester, 2010). Prey availability, together with predation risk by other vertebrate and invertebrate predators, influences active foraging behaviour and microhabitat selection of predatory arthropods (Roume *et al.*, 2011). According to my knowledge, the effects of overwintering on spider body condition and behaviour in semi natural and exotic habitats have not yet been studied. My dissertation focuses on the locomotory activity and body condition of a wolf spider (*P. alacris*). Wolf spiders are among the most abundant predatory arthropods in many terrestrial ecosystems. Instead of building a web, they move the ground to hunt for their prey. *Pardosa* species are relatively small wolf spiders, with flexible life history pattern and significant winter activity. *P. alacris* and *Pardosa lugubris* Walckenaer, 1802 are the most common species in deciduous forests in Central and Eastern Europe, however only *P. alacris* occurs in the natural and plantation forests of the Kiskunság, this species is associated with relatively open canopy of dry forests.

Most spiders spend the winter in a state of dormancy, they reduce growth, movement, feeding, and metabolism (Danks, 2006). Diapause is a form of dormancy, the main stimulus entering diapause is the reduced day length and it cannot be immediately terminated even if favorable conditions for development appear (Tougeron, 2019). In contrast quiescence is an immediate response to cold temperatures and metabolism resumes if favorable conditions return allowing a more flexible winter activity pattern (Denlinger,

1991). Winter activity has several advantages including the ability to locate habitat, food resources (Aitchison, 1987). While prey availability is typically low in the winter, the competition is also reduced (Aitchison, 1987), furthermore feeding during winter can improve survival rates.

2. Aims and objectives

The main aim of my work was to reveal how plantation forest tree species, plant invasions in plantation forests and overwintering affects spiders.

The knowledge gap

The effect of habitat structure of forests on arthropods has been documented (Corcuera *et al.*, 2016; Dalzochio *et al.*, 2018; Gallé *et al.*, 2018); however, the majority of this work focuses on species diversity patterns (Kuuluvainen *et al.*, 2012), with few studies focusing on functional diversity of spiders (Gallé *et al.*, 2018; Magura, 2017). Furthermore, there is limited information on how arthropod assemblages and functional diversity is affected by plant invasion in different forest types and how forest type affects winter active spiders. Furthermore, the effects of overwintering on spider body condition and behaviour in plantation forests have not yet been studied.

The present dissertation covers three studies to fill the above knowledge gaps

1. In first study we assessed the effect of *A. syriaca* invasion on species richness, and species composition of spiders in the poplar and pine plantation forests. We also applied the functional diversity concept to link diversity patterns with ecosystem processes and functioning. Hypotheses for this study were:

(1) Species richness is higher in poplar plantations compared to pine plantations, and tree species have an effect on species functional diversity and composition of spider assemblages.

(2) Functional diversity and abundance of spiders is higher in the forests which were invaded by *A. syriaca* as this plant may attract more pollinators, herbivores, therefore may offer more potential food, more structured habitat for spiders.

(3) *A. syriaca* has a different effect on spider diversity in poplar and pine plantations. In poplar forests the spider diversity is higher than in pine plantations.

2. The aim of second part of my thesis was to reveal the differences in the species richness and community composition of spiders in the poplar and pine plantation during winter. Hypothesis for this study was:

(1) Poplar plantations have higher winter active species richness and abundance than pine plantation forests and spider species composition of winter active assemblages are different in the poplar plantation and in pine plantation forests.

3. Finally, we aimed to test the effects of winter on the behaviour and body condition of spiders collected from poplar and pine plantations. More specifically, we hypothesized that:

(1) Winter has a significant negative effect on the fat reserves of spiders. Spiders collected in spring have lower body fat content the spiders collected before winter.

(2) Effect of winter on spiders is mediated by habitat type. We assumed that the more diverse food available in poplar plantations may have a positive effect on the body condition of winter active spiders.

(3) Habitat and body condition of the spiders affect their behaviour. Spiders of poplar plantations have better body condition and may move less to decrease the risk of predation.

3. Materials and methods

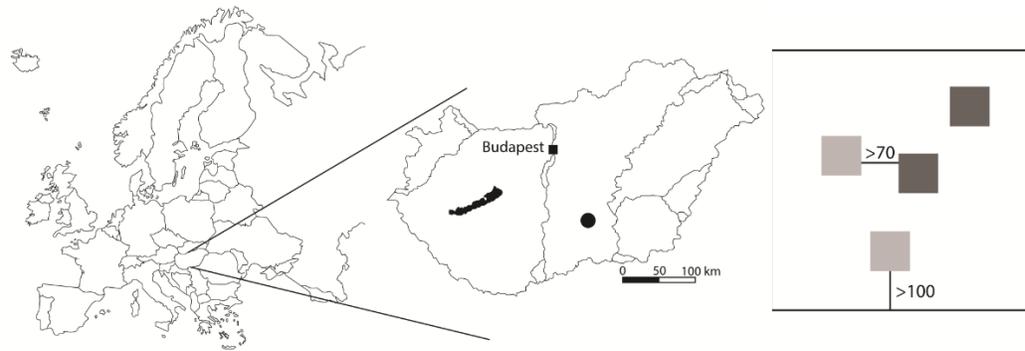
3.1 Study area

The present study was carried out in the Kiskunság region, in the southern part of the Great Hungarian Plain (46° 42 ' N, 19° 36 ' E). The dominant land use types are plantation forests and agricultural land. Small patches of natural vegetation – forest-steppe habitats – are embedded in this matrix (Gallé *et al.*, 2018). The plantation forests are generally poplar and pines forests. The soil is calcareous coarse sand. The study area is characterized by semi-arid temperate continental climate with mean annual precipitation in the ranges between 550 – 600 mm. The mean annual temperature ranges from 10.2– 10.8°C, daily temperature ranges between 0–5°C in winter and 21–28°C in summer (Domonkos & Tar, 2003; Török *et al.*, 2003a).

3.2 Effect of *A. syriaca* and different tree species

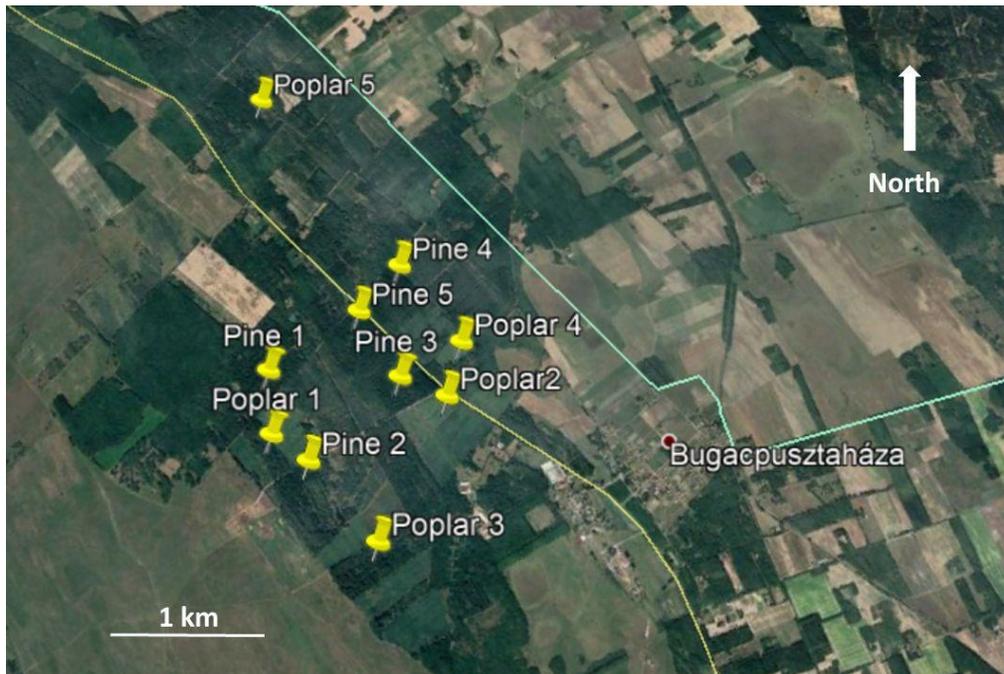
3.2.1 Study design and sampling

We selected 5 poplar and 5 pine plantation forests for spider sampling. We surveyed ground-dwelling spiders at 4 sampling sites in each of the 10 forests, for a total of 40 sampling sites (Fig. 1). Sites were selected according to tree species (*Populus alba* and *Pinus sylvestris*) and common milkweed density (invaded vs. non-invaded sites) in a full factorial design resulting in 10 replicates per treatment combination. All sampled plantations were mature forests with no recent intensive forestry activity. The diameters of trees at breast height were 25.77 ± 12.17 (mean \pm SD) for poplar trees and 25.48 ± 4.57 (mean \pm SD) for pine trees (10 randomly chosen trees measured in each forest). Sampling sites were located at least 70 m distance from each other, and each sampling site was located more than 100 m from the forest edges. We assessed *A. syriaca* quantity in four 1 m² quadrates at each invaded sampling site; the density of *A. syriaca* stems was 7.33 ± 3.86 stems/m² (mean \pm SD), and its cover was $30.31\% \pm 17.05$ (mean \pm SD). We characterized the habitat structure at the sampling sites by the approximate percentage cover of herbaceous plants (excluding *A. syriaca*), the average height of the vegetation and by the cover of leaf litter.



(a)

(b)



(c)

Figure 1. Map and satellite image of the study region. (a) location of the study region, (b) sampling design, (c) satellite image of sampling sites

Pitfall traps method is selective, catches are biased toward mobile invertebrates, the method measures activity-density of the fauna and does not provide reliable density data. Pitfall trap catches depend on both the density of a population and the species activity, thus pitfall trap measure quantity referred to as activity-density (Thomas *et al.*, 1998). However, the method is useful when comparing the spider fauna of similar habitat types. Pitfall trap catches also dependent on the exact type of the traps, therefore we used the same type, traps were supplied with funnel and roof in both the first and second study. I include this information in the

dissertation. We used 3 pitfall traps for collecting spiders at each site. The traps were plastic cups with a diameter of 8.5 cm species (Császár *et al.*, 2018). Traps were arranged in a triangle, we kept 8 m distance between them. We supplied the traps with plastic funnels and we placed a metal roof above them. Traps were filled with a 50% water-ethylene-glycol solution to which we had added a few drops of detergent. Traps were open for three 7-day sampling periods: May 23 - 30, 2017; June 26 - July 3, 2017; and Oct 2 - 10, 2017. Pitfall traps are the most widely used tools for sampling ground-dwelling arthropods. This method has several favourable attributes such as simultaneous sampling at many locations, it yields a large number of species, however, the species inventory is biased towards ground-dwelling species (Császár *et al.*, 2018).

3.2.2. Data analysis

From the habitat structure data, mean values were calculated for each variable at each site. To detect possible differences in herbaceous cover, average height of the vegetation and the cover of leaf litter, we applied generalized linear mixed models (GLMMs) with binomial error terms. Forest type (i.e., poplar, pine), presence of *A. syriaca* (i.e. invaded, non-invaded sites) were fixed factors. Sampling site nested in plantation forest was used as random effect.

We chose 4 attributes to characterize for functional role of spiders. We classified species according to: shading tolerance, ranging from 1 (open) to 4 (shaded); moisture preference, ranging from 1 (very dry) to 5 (very humid habitats); feeding, 0 (active hunter) and 1 (web builder); and size, as a continuous variable in mm (Bell *et al.*, 2005; Blandenier, 2009; Buchar & Ruzicka, 2002; Nentwig *et al.*, 2017). If a species was assigned to more than 1 category, the values were averaged. Spiders were considered as generalists if they were assigned to more than 3 categories in the case of shading tolerance and moisture preference. They were also considered generalist species if they were present at both extremes of the given categories, and their score was excluded from further analyses. We calculated community-weighted mean (CWM) values for each trait at each sampling site; functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) to characterize the functional diversity of spider assemblages, using FD package in R (Laliberté *et al.*, 2014). The FDis index characterizes how the communities respond to disturbances, a decrease in FDis means that the community composition shifted towards functionally similar species, indicating a loss of resilience

(Laliberté *et al.*, 2010). The RaoQ index was useful for detecting assembly rules, habitat filtering (trait convergence) and limiting similarity (trait divergence; (Botta-Dukat *et al.*, 2016)). We applied GLMMs, where forest type (i.e., poplar, pine), presence of *A. syriaca* (i.e. invaded, non-invaded sites) were fixed factors. Sampling site nested in plantation forest was used as random effect. We used the Poisson error term for species richness data, negative binomial error term for abundance data to account for over-dispersion of the data and Gaussian error terms for RaoQ and CWM values (glmer and lmer functions, “lme4” package, (Aisenberg *et al.*, 2009)).

We explored the multivariate response of spider assemblages to tree species and the presence of *A. syriaca* with non-metric multidimensional scaling (NMDS) using Bray-Curtis distance measure. We tested the effect of the above variables on spider assemblage composition with non-metric multivariate analysis of variance (PERMANOVA), using the Bray-Curtis distance measure, 10000 permutations and the vegan analysis package (Oksanen *et al.*, 2015). Where significant correlation with tree species and *A. syriaca* invasion was found, we used indicator value analysis to detect characteristic spider species (IndVal; (Dufrene & Legendre, 1997)) with the ‘labdsv’ package (Roberts & Roberts, 2016).

3.3. Effect of tree species on winter fauna

3.3.1 Study design and sampling

We used the sampling sites described in section 3.2 with the same collecting method and same arrangement of traps. We conducted sampling in two consecutive winters (182 trap days); traps were open for three one-month sampling periods in two years (emptied three times in both years, once every month each of the three months), from December 2017 to February 2018 and from December 2018 to February 2019.

Habitat structure in the sampling sites was characterised in four 1x1 metre quadrates at each sampling sites. Quadrates were spaced at least 8 m apart. We assessed the average percentage cover of leaf litter, mosses, herbaceous vegetation and shrubs. We assessed the microclimatic differences using data loggers (Optin ADL TH3-32), and one logger was placed randomly in each of the plantations and recorded hourly temperature data. Loggers were exposed for 12 days.

3.3.2 Data analysis

We determined the effect of forest type on habitat structural characteristics (percentage cover of leaf litter, mosses, herbaceous vegetation and shrubs) by using linear mixed effect models. We used plantation type (pine or native) as fixed factor, whereas spatial distribution of sampling sites (forest ID) was considered as a random factor. We determined the effect of forest type and habitat structure on species richness, adult activity density and total number of collected spiders, including juveniles, using generalized linear mixed effect models. The variable ‘activity density’ is defined as the activity divided by the range over which it took place (Kafkafi & Elmer, 2005). Plantation type and habitat structural characteristics with no significant correlation with plantation type were used as fixed factors and forest ID was considered as a random factor. We used the Poisson error term for species richness and negative binomial error term for activity density and total number of spiders, after checking for overdispersion of the data.

The indicator species concept helps to identify characteristic species for a given habitat type (Dufrene & Legendre, 1997). We used indicator value analysis to identify the characteristic species of spiders in pine and poplar forests, with “labdsv” package in R (Roberts and Roberts 2016). High indicator value means that almost all individuals of a species are collected in a single habitat type and, that the species occurs in almost all sampling sites of that habitat type (Dufrene & Legendre, 1997). As a result of the analysis, spiders were grouped into three categories (1) spiders of poplar plantations; (2) spiders of pine plantations; (3) non-characteristic species, with no strong association with plantation type.

3.4. Effect of forest type on spider behaviour and condition

3.4.1 Study design and sampling

We studied the wolf spider *Pardosa alacris* C.L. Koch, 1833 (Lyosidae, Araneae), a very common species in central European forests (Michalko *et al.*, 2016). The species belongs to the ground-dwelling active hunter guild and shows a sit-and-move hunting strategy (Cardoso *et al.*, 2011; Samu, 2003). The species has a clear preference to dry deciduous forests with an open canopy and forest steppes (Michalko *et al.*, 2016), but it also occurs in pine forests (Gallé *et al.*, 2014b).

The specimens used in the present study were collected in six forest plantations using the ground hand collecting method (Sørensen *et al.*, 2002). We selected six plantations of the above 10, three poplar and three pine. We collected 15 sub-adult *P. alacris* spiders in the second half of November 2016, shortly before overwintering, and again in early March 2017, when the activity of *P. alacris* increases after winter, in each of the sampling sites (Eliašová *et al.*, 2015). The 180 spiders were housed individually in plastic containers (4.5 cm in diameter and 7 cm height) with blotting-paper as substrate. We kept the individuals at a constant temperature of 10°C and a 12:12 h photoperiod in the climate chamber and provided them with water *ad libitum* overnight.

3.4.2 Locomotory behaviour trials

We studied the cursorial locomotion of *P. alacris* by tracking their movements in a white circular plastic arena (25 cm in diameter) at 20°C of temperature. The floor of the arena was covered with blotting-paper. The spider was placed into a small black plastic cylinder (3 cm in diameter) in the centre of the arena; it was allowed to acclimatise for 60 s before the cylinder was removed. The spider could freely move in the arena for 180 s. The movement of the spider was recorded with a Fuji ® finepix HS 50EXR camera from 100cm above the arena.

The locomotory activity of individuals within the arena was determined by digitalising their path using the SMART video tracking software version 2.5.2 (Panlab). The following parameters were measured: (1) total distance travelled (cm); (2) total moving time during the 180 s of observation (s); (3) average speed of the individuals when moving (cm/s) (Csata *et al.*, 2017).

3.4.3 Body size and fat percentage

Spiders were fixed by freezing, and they were stored in a freezer at -15°C. The gender of the spiders was identified, and the total body length and prosoma length of spiders were determined using an Olympus SZ40 stereo microscope. Spiders were subsequently dried at 60°C for four days and then we recorded dry weight to the nearest 0.0001 g with an OHAUS Explorer® Proscale. The spiders were then moved to glass vials (2 cm diameter), and the fat was extracted with 4 ml petroleum-ether (boiling range 40–70°C; Molar Chemicals®). We closed the vials with plastic lids and kept them at room temperature. The spiders were left in

the petroleum-ether for three days; we then changed the petroleum-ether, and spiders were kept in the new liquid for further three days. Spiders were subsequently dried again at 60°C for four days and their weight was measured. The fat proportions of spiders were calculated by the ratio of final mass and dry mass.

3.4.4 Data analysis

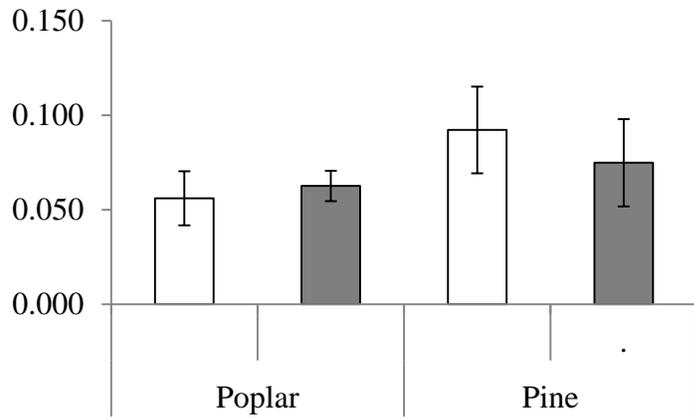
To test if season (autumn/spring), forest type (poplar/pine), gender and their second order interaction had significant effects on the size or fat content of *P. alacris* spiders, we used mixed effect linear models and model averaging. We also added percentage fat content as a fixed effect in the models where total distance covered and speed were the dependent variables. We used mixed-effect linear models (lmer function, “lme4” package, (Aisenberg *et al.*, 2009)) with a Gaussian error term, and the random effect term was “forest ID”. For total distance covered and speed models, sex was used as a random effect, in order to control for potential multicollinearity between gender specific locomotory activity and sex (Framenau, 2005). All possible linear combinations of the above fixed effects were considered and ranked according to Akaike’s information criteria corrected for small sample sizes (AICc) The models with <10 Δ AICc of the best model (i.e. the model with the lowest AICc) were used for model averaging with the R package MuMIn (Bartón, 2015).

4. Results

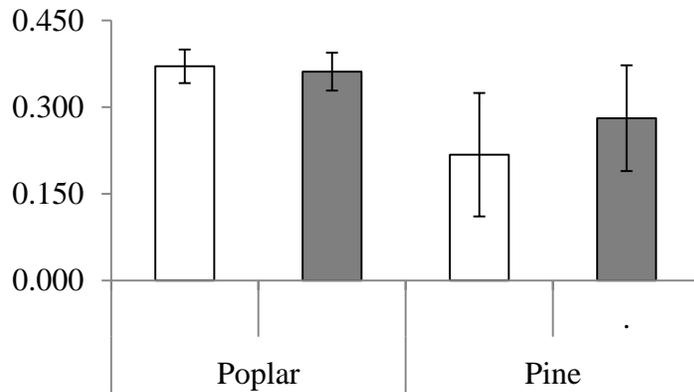
4.1. Effect of *A. syriaca* and tree species

We collected 1621 adult spider specimens from 53 species. The most abundant species in total catch were *Arctosa lutetiana* (Simon, 1876), *Pardosa alacris* (C. L. Koch, 1833) and *Zelotes apricorum* (L. Koch, 1876) with 256, 241 and 221 individuals, respectively; all 3 species are abundant in dry forests with relatively open canopies (Buchar & Ruzicka, 2002).

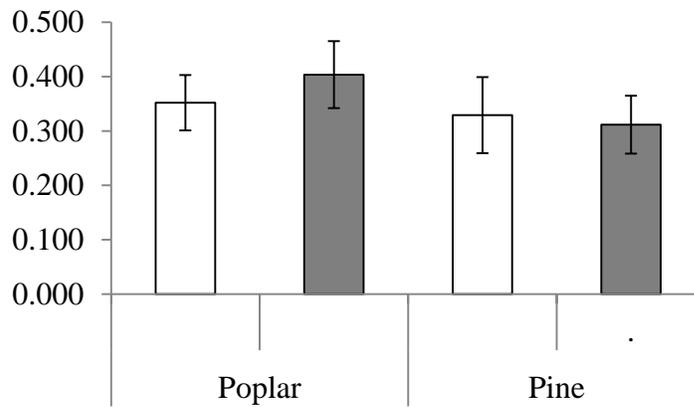
We did not find a significant effect of tree species or *A. syriaca* invasion on the species richness and abundance of spider assemblages (Table 1). There was a significant effect of *A. syriaca* on FDis and RaoQ of spiders, with the invaded sites having lower functional diversity than non-invaded sites. The significant interaction effect of forest types and invasion of *A. syriaca* on FDis and RaoQ of spiders indicated that invasion had a more pronounced effect in pine than in poplar forests (Fig. 2a). Spider species were larger (Fig. 2b) and web building spiders were more abundant (Fig. 2c) in poplar forests than in pine plantations; however, there was no significant effect of moisture and shading (Table 1).



(a)



(b)



(c)

Figure 2. Effect of forest type and *Asclepias syriaca* invasion on functional diversity. Open circles: non-invaded; black dots: invaded sites. (a) RaoQ index; (b) Community weighted mean (CWM) of hunting strategy; (c) CWM value of spider body sizes.

Table 1. The effect of tree species and *Asclepias syriaca* invasion on species richness, abundance and functional diversity measures of spiders according to mixed models, parameter estimates \pm 95% confidence intervals and (z/t values) are given. Significant p-values are presented in bolds. Abbreviations: ep: exotic pine; np: native poplar; i: invaded; n: non invaded sites.

	Tree (np/ep)	Type (n/i)	Tree: Type
Species richness ¹	0.052 \pm 0.256 (0.396)	-0.149 \pm 0.245 (-1.189)	0.140 \pm 0.358 (-0.767)
Abundance ²	-0.143 \pm 0.231 (-0.210)	-0.171 \pm 0.182 (- 1.800)	1.176 \pm 0.260 (1.320)
FDis	0.034 \pm 0.197 (0.336)	-0.21795 \pm 0.197 (- 2.137) *	0.372 \pm 0.282 (2.586) *
RaoQ ³	0.012 \pm 0.015 (1.431)	-0.017 \pm 0.013 (-2.223)*	-0.023 \pm 0.021 (-2.166)*
Shading CWM ³	-0.015 \pm 0.070 (-0.436)	0.063 \pm 0.058 (0.770)	-0.072 \pm 0.084 (1.023)
Hunting CWM ³	-0.080 \pm 0.068 (-2.284)*	0.063 \pm 0.058 (2.037)	-0.072 \pm 0.084 (1.656)
Moisture CWM ³	0.034 \pm 0.052 (1.288)	-0.028 \pm 0.035 (-1.556)	0.018 \pm 0.029 (0.711)
Size CWM ³	-0.091 \pm 0.027 (-3.318)**	-0.017 \pm 0.049 (-0.683)	0.069 \pm 0.071 (-1.907)

¹ Models were fitted with Poisson distribution

² Models were fitted with negative binomial distribution

³ Models were fitted with normal distribution

Significance levels: *: <0.05, **: <0.01, ***: <0.001.

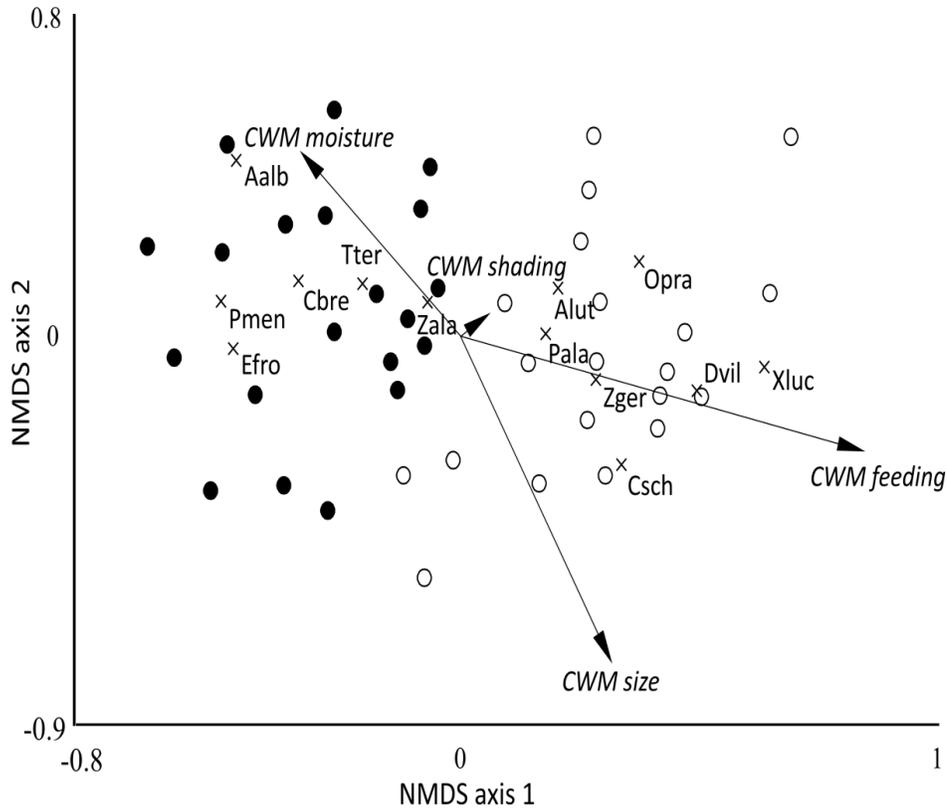


Figure 3. NMDS ordination plot of sampling sites (dots), and significant indicator species (crosses), community weighted mean values (CWM) are fitted onto the ordination plot (arrows). Black dots: pine plantations, open circles: poplar plantations. Species names are abbreviated with the first letter of genus name and the first three letters of species names, please see Table 2. for further details.

Spider assemblages of the two forest types clearly separated according to the NMDS (Fig. 3). Non-metric multivariate ANOVA indicated a significant difference in composition of spider assemblages from poplar and pines forests ($R^2 = -0.227$, $p < 0.001$). We found 7 species associated with pine plantations and 6 species associated with poplar plantations, according to indicator value analysis (Table 2).

4.2. Effect of tree species on winter fauna

We collected 1,337 spiders, out of which 735 were adults from 26 species (Table 2). The most abundant species were *Centromerus sylvaticus* (Blackwall, 1841) (Linyphiidae) and *Trochosa terricola* (Thorell, 1856) (Lycosidae), with 401 and 106 individuals, respectively.

Table 2. List of collected species and indicator values for significant indicator species to its maximum class. *P <0.05, **P <0.01, ***P<0.001

	Pine		Poplar		Indicator value
	Invaded	Non-invaded	Invaded	Non-invaded	
Species richness	31	35	32	34	
Abundance	360	428	418	415	
<i>Pholcus opilionoides</i> (Schrank, 1781)	0	0	1	0	
<i>Harpactea rubicunda</i> (C. L. Koch, 1838)	0	0	0	2	
<i>Eresus kollari</i> Rossi, 1846	0	0	1	0	
<i>Asagena phalerata</i> (Panzer, 1801)	1	3	4	2	
<i>Episinus truncatus</i> Latreille, 1809	1	1	1	0	
<i>Euryopis flavomaculata</i> (C. L. Koch, 1836)	0	0	0	3	
<i>Platnickina tinctoria</i> (Walckenaer, 1802)	0	0	1	0	
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	3	1	0	0	
<i>Ceratinella brevis</i> (Wider, 1834)	15	17	2	1	pine, 0.640***
<i>Linyphia triangularis</i> (Clerck, 1757)	0	1	0	0	
<i>Metopobactrus ascitus</i> (Kulczyński, 1894)	0	0	0	1	
<i>Minicia marginella</i> (Wider, 1834)	0	0	1	0	
<i>Mioxena blanda</i> (Simon, 1884)	0	0	0	1	
<i>Panamomops mengei</i> Simon, 1926	9	21	0	2	pine, 0.468**
<i>Tapinocyba insecta</i> (L. Koch, 1869)	0	2	0	0	
<i>Walckenaeria alticeps</i> (Denis, 1952)	3	4	1	1	
<i>Alopecosa sulzeri</i> (Pavesi, 1873)	20	37	54	26	
<i>Arctosa figurata</i> (Simon, 1876)	1	1	0	0	

<i>Arctosa lutetiana</i> (Simon, 1876)	42	53	80	81	poplar, 0.628**
<i>Aulonia albimana</i> (Walckenaer, 1805)	8	3	0	0	pine, 0.300*
<i>Pardosa alacris</i> (C. L. Koch, 1833)	41	54	69	77	poplar, 0.605*
<i>Trochosa ruricola</i> (De Geer, 1778)	0	0	0	1	
<i>Trochosa terricola</i> Thorell, 1856	58	41	10	22	pine, 0.755***
<i>Agelena labyrinthica</i> (Clerck, 1757)	0	0	0	1	
<i>Eratigena agrestis</i> (Walckenaer, 1802)	0	3	0	0	
<i>Hahnia nava</i> (Blackwall, 1841)	1	1	0	0	
<i>Argenna patula</i> (Simon, 1874)	0	1	0	0	
<i>Brommella falcigera</i> (Balogh, 1935)	0	0	1	0	
<i>Titanoeca schineri</i> L. Koch, 1872	15	20	32	20	
<i>Zora pardalis</i> Simon, 1878	0	0	0	1	
<i>Zora spinimana</i> (Sundevall, 1833)	2	0	0	1	
<i>Agroeca cuprea</i> Menge, 1873	4	2	3	2	
<i>Phrurolithus festivus</i> (C. L. Koch, 1835)	8	19	10	2	
<i>Phrurolithus minimus</i> C. L. Koch, 1839	34	36	39	42	
<i>Zodarion germanicum</i> (C. L. Koch, 1837)	6	7	20	25	poplar, 0.543*
<i>Callilepis schuszteri</i> (Herman, 1879)	0	0	4	4	poplar, 300*
<i>Drassodes pubescens</i> (Thorell, 1856)	0	1	2	2	
<i>Drassyllus praeficus</i> (L. Koch, 1866)	2	4	3	1	
<i>Drassyllus villicus</i> (Thorell, 1875)	1	2	8	19	pine, 0.585***
<i>Haplodrassus signifer</i> (C. L. Koch, 1839)	1	1	0	0	
<i>Haplodrassus silvestris</i> (Blackwall, 1833)	0	0	0	1	
<i>Phaeoecus braccatus</i> (L. Koch, 1866)	0	0	1	0	
<i>Trachyzelotes pedestris</i> (C. L. Koch, 1837)	3	2	1	2	
<i>Zelotes apricorum</i> (L. Koch,	65	64	43	49	pine,

1876)					0.583**
<i>Zelotes electus</i> (C. L. Koch, 1839)	1	3	1	0	
<i>Zelotes latreillei</i> (Simon, 1878)	1	2	0	0	
<i>Ozyptila atomaria</i> (Panzer, 1801)	1	3	0	0	
<i>Ozyptila praticola</i> (C. L. Koch, 1837)	0	0	4	8	poplar, 0.250*
<i>Xysticus luctator</i> L. Koch, 1870	2	0	14	11	poplar, 0.555***
<i>Euophrys frontalis</i> (Walckenaer, 1802)	11	17	6	2	pine, 0.583**
<i>Myrmarachne formicaria</i> (De Geer, 1778)	0	0	0	2	
<i>Neon reticulatus</i> (Blackwall, 1853)	0	1	0	0	
<i>Pseudicius encarpatus</i> (Walckenaer, 1802)	0	0	1	0	

Pine plantations maintained a more temperate microclimate than poplar plantations (Fig. 2) Percentage cover of leaf litter and mosses were positively related with pine plantations (leaf litter: parameter estimate (\pm 95%CI): 0.160 ± 0.094 , $t = 3.333$, $p = 0.002$; mosses: parameter estimate (\pm 95% CI): 0.140 ± 0.052 , $t=5.268$, $p<0.001$), however we found no effect of plantation type on percentage cover of shrubs (parameter estimate (\pm 95% CI): 0.021 ± 0.171 , $t= 1.056$, N.S.) and on cover of herbaceous vegetation (parameter estimate (\pm 95%CI): 0.023 ± 0.081 , $t= 0.565$, N.S).

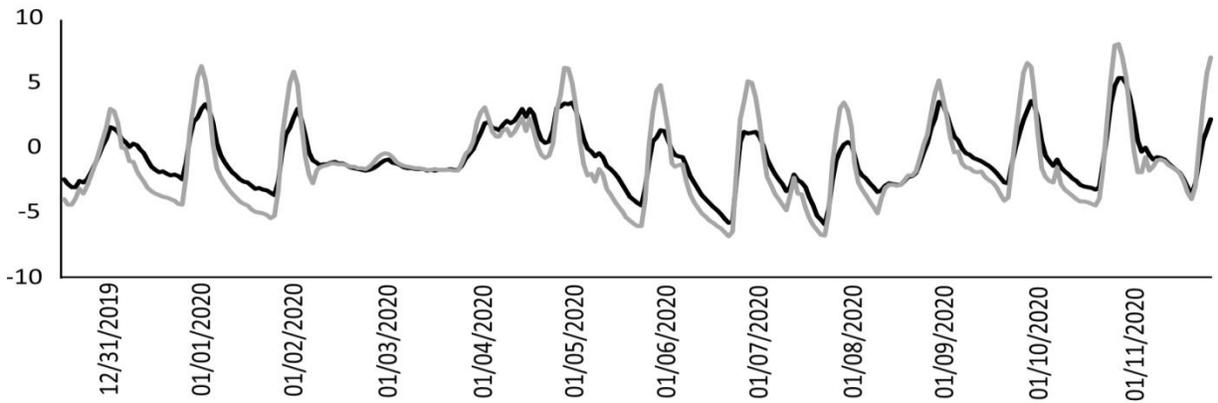


Figure 2. Temperature data. Lines represent the average values of five data loggers, black line: pine plantation, grey line: poplar plantation.

We found higher species richness and activity density in pine plantations than in the poplar forests. Percentage coverage of shrubs had a significant negative effect on adult spider activity density; however, we found no significant effect of herbaceous vegetation cover (Table 3).

Table 3. Effect of forest type and habitat structure on species richness, adult spiders and total number of collected spiders according to mixed models.

Parameters	Type (pine/poplar)	Shrub cover	Vegetation cover
Species richness ^a	-0.494 ± 0.289 (-3.324)***	-0.832 ± 2.395 (-0.723)	0.161 ± 1.068 (0.294)
Adult spiders ^b	-0.651 ± 0.217 (-5.880)***	-1.859 ± 1.524 (2.231)*	0.120 ± 0.806 (0.770)
Spiders including juveniles ^b	-0.848 ± 0.323 (-5.050)***	2.064 ± 2.324 (1.669)	0.417 ± 1.235 (0.666)

Parameter estimate ± 95% confidence intervals and (z/t) values are represented. Significance results are shown in bold. e: pine forest; n: poplar forest. (Significance level: **: <0.01, ***: <0.001. ^a : Model fitted with Poisson distribution. ^b : models fitted with negative binomial distribution)

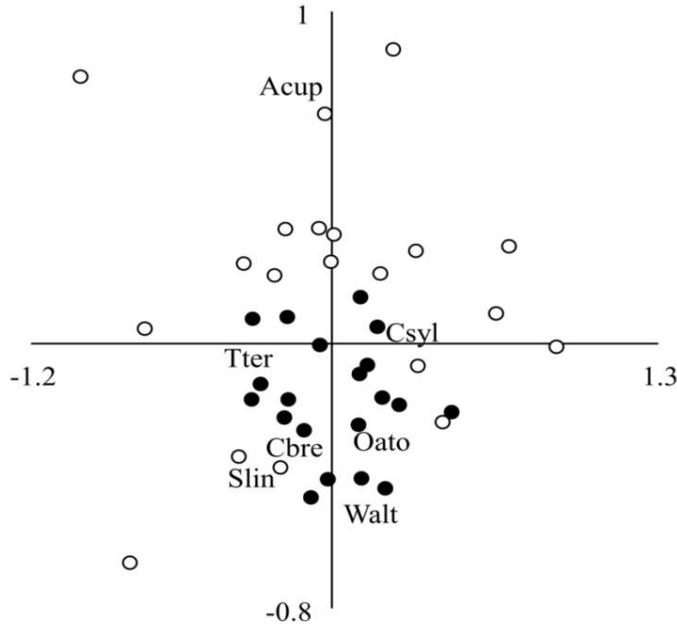


Figure 3. NMDS plot of the spider communities in poplar and pine plantations and significant indicator species. Open circles: poplar forest and black dots: pine forest. Csyl = *Centromerus sylvaticus*, Cbre = *Ceratinella brevis*, Tter = *Trochosa terricola*; Oato = *Ozyptila atomaria*; Slin = *Stemonyphantes lineatus*; Walt = *Walckenaeria alticeps*; Acup = *Agroeca cuprea*. Please refer to Table 4. for further details.

Table 4. List of collected species. Activity density data of forest types were pooled.

	2017-2018 winter		2018-2019 winter		Abundance /trap/day
	poplar	pine	poplar	pine	
Web builders					
Araneidae					
<i>Cercidia prominens</i> (Westring, 1851)	0	0	1	0	4.57 E-05
Linyphiidae					
<i>Agyreta rurestris</i> (C. L. Koch, 1836)	2	2	0	0	1.83 E-04
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	66	207	36	92	1.83 E-02
<i>Ceratinella brevis</i> (Wider, 1834)	5	26	7	19	2.60 E-03
<i>Mioxena blanda</i> (Simon, 1884)	0	1	0	0	4.57 E-05
<i>Sintula spiniger</i> (Balogh, 1935)	2	6	7	10	1.14 E-03
<i>Stemonyphantes lineatus</i> (Linnaeus, 1758)	4	13	3	12	1.46 E-03

<i>Tapinocyba insecta</i> (L. Koch, 1869)	0	3	0	1	1.83 E-04
<i>Walckenaeria alticeps</i> (Denis, 1952)	0	15	0	0	6.86 E-04
<i>Walckenaeria antica</i> (Wider, 1834)	0	0	0	2	9.15 E-05
<i>Mermessus trilobatus</i> (Emerton, 1882)	0	0	0	1	4.57 E-05
<i>Canariphantes nanus</i> (Kulczyński, 1898)	0	0	4	0	1.83 E-04
<i>Improphantes geniculatus</i> (Kulczyński, 1898)	0	0	0	1	4.57 E-05
<i>Mecopisthes peusi</i> Wunderlich, 1972	0	0	1	0	4.57 E-05
Theridiidae					
<i>Asagena phalerata</i> (Panzer, 1801)	0	0	0	3	1.37 E-04
Agelenidae					
<i>Eratigena agrestis</i> (Walckenaer, 1802)	0	0	1	2	1.37 E-04
Hahnidae					
<i>Hahnia nava</i> (Blackwall, 1841)	0	0	0	1	4.57 E-05
Active hunters					
Lycosidae					
<i>Alopecosa sulzeri</i> (Pavesi, 1873)	0	1	0	0	4.57 E-05
<i>Arctosa lutetiana</i> (Simon, 1876)	7	3	2	3	6.86 E-04
<i>Alopecosa mariaae</i> (Dahl, 1908)	0	0	1	1	9.15 E-05
<i>Trochosa terricola</i> Thorell, 1856	4	20	28	54	4.85 E-03
Liocranidae					
<i>Agroeca cuprea</i> Menge, 1873	13	3	9	2	1.23 E-03
<i>Agroeca lusatica</i> (L. Koch, 1875)	0	1	1	0	9.15 E-05
Thomisidae					
<i>Ozyptila atomaria</i> (Panzer, 1801)	0	3	4	15	1.00 E-04
Philodromidae					
<i>Thanatus formicinus</i> (Clerck, 1757)	0	1	0	0	4.57 E-05
Gnaphosidae					
<i>Zelotes apricorum</i> (L. Koch, 1876)	0	0	1	2	1.37 E-04

The species composition of spiders in pine and poplar plantations differed significantly according to the PERMANOVA ($F = 7.298$, $p < 0.001$), however we found no significant effect of shrub ($F = 0.876$, $p = 0.478$) and herbaceous vegetation cover ($F = 0.459$, $p = 0.871$). Spiders communities of pine and poplar plantations did not clearly separate according to the NMDS plot and species composition of pine plantations were less variable than that of the poplar plantations (Fig. 3). We identified 6 and 1 significant indicator species for pine and poplar forests, respectively (Fig. 3, Table 3). All of the indicator species in pine plantations preferred

humid habitats; however, poplar forest indicator species preferred dry and partly shaded habitats (Buchar & Ruzicka, 2002).

Table 3. List of indicator species of spiders in pine and poplar plantations.

Species	Forest type	Indicator value	P value
<i>Centromerus sylvaticus</i> (Blackwall, 1841)	pine	0.7456	<0.001
<i>Ceratinella brevis</i> (Wider, 1834)	pine	0.6711	<0.001
<i>Trochosa terricola</i> (Thorell, 1856)	pine	0.6632	<0.001
<i>Ozyptila atomaria</i> (Panzer, 1801)	pine	0.4500	0.008
<i>Stemonyphantes lineatus</i> (Linnaeus, 1758)	pine	0.4297	0.024
<i>Walckenaeria alticeps</i> (Denis, 1952)	pine	0.3000	0.021
<i>Agroeca cuprea</i> Menge, 1873	poplar	0.4481	0.015

4.3. Effect of forest type on spider *P. alacris* behaviour and condition

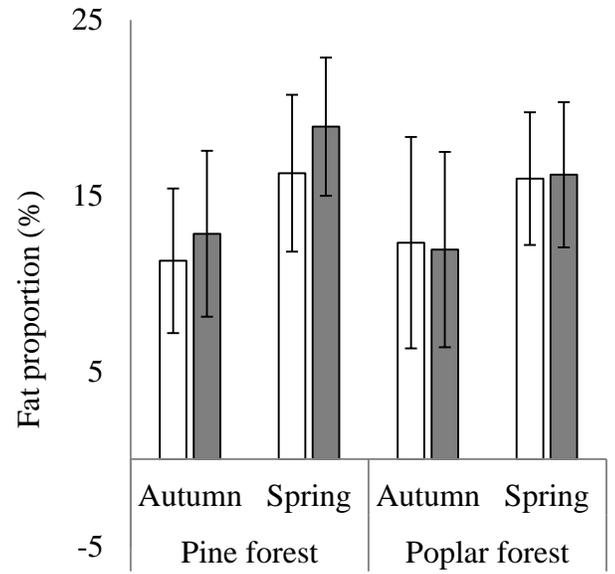
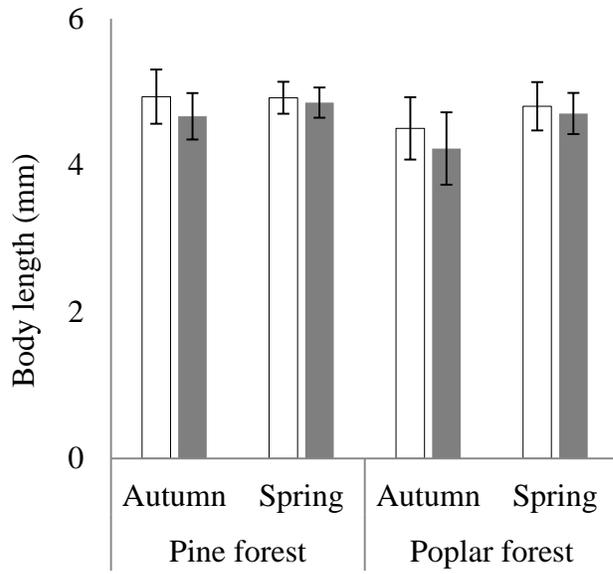
Subadult female spiders (4.77 ± 0.38 mm; mean \pm SD) were larger than subadult males (4.63 ± 0.38 mm) and subadult spiders collected from poplar forests (4.57 ± 0.42 mm) were smaller than from pine forests (4.83 ± 0.30 mm). We found a significant interaction effect of forest type and season on body length, suggesting a more pronounced effect in poplar forests (autumn: 4.40 ± 0.46 mm; spring: 4.74 ± 0.29 mm) than in pine forests (autumn: 4.78 ± 0.36 mm; spring: 4.89 ± 0.21 mm). Furthermore, the significant interaction effect of season and gender indicated that the difference between body length in autumn (4.49 ± 0.44 mm) and spring (4.76 ± 0.26 mm) in subadult males was greater than that of the subadult females (Table 4, Fig. 4a) in autumn (4.67 ± 0.45 mm) and spring (4.87 ± 0.26 mm), respectively.

The percentage of fat content ($16.72 \pm 4.21\%$) was significantly higher in spring spiders than in autumn spiders (fat content: $12.17 \pm 5.15\%$).

Total distance covered (1.04 ± 0.54 m) and speed (0.022 ± 0.004 m/s) were significantly lower in spring spiders than in autumn spiders (total distance covered: 1.39 ± 0.68 m; speed 0.025 ± 0.006 m/s) (Table 4, Fig. 4b-d). Spiders with higher fat content moved slower (Table 4, Fig.5).

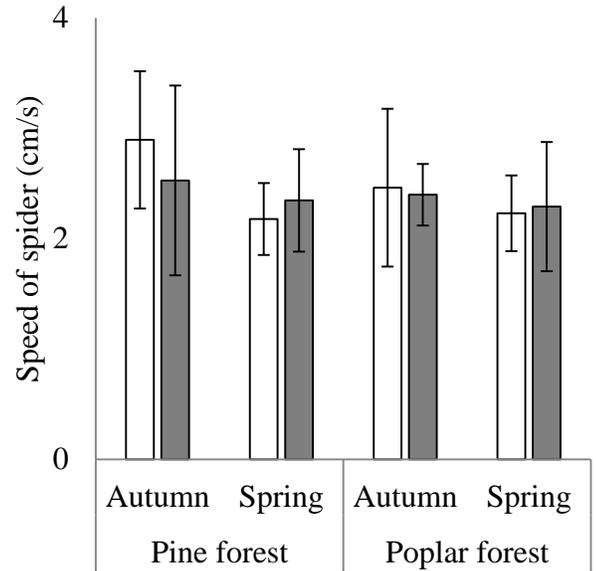
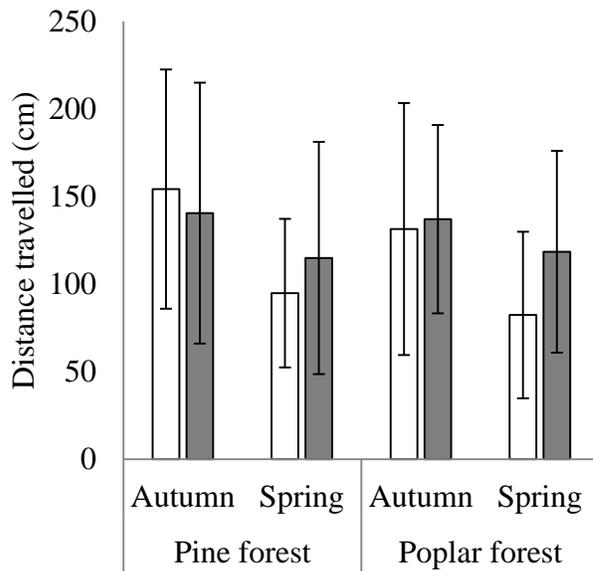
Table 4. Summary of the effect of overwintering, habitat type and gender on spider body condition and behaviour after GLMMs and model averaging.

Model	Variable	Relative importance (%)	Multimodel estimate \pm 95 % CI
Length (mm)	Gender (Female/Male)	100%	-0.224 \pm 0.164**
	Forest (pine/poplar)	100%	-0.417 \pm 0.170***
	Season (Autumn/Spring)	95%	0.043 \pm 0.207
	Season * Forest	89%	0.311 \pm 0.200***
	Season * Gender	44%	0.219 \pm 0.200*
	Forest * Gender	7%	-0.004 \pm 0.200
	Prosoma length	Forest (pine/poplar)	99%
Season (Autumn/Spring)		2%	-0.010 \pm 0.046
Season (Autumn/Spring)		100%	5.138 \pm 2.134***
Fat content (%)	Forest (pine/poplar)	92%	0.811 \pm 2.411
	Gender (Male/Female)	92%	1.576 \pm 2.384
	Forest * Gender	71%	-2.286 \pm 2.614
	Season * Forest	64%	-1.593 \pm 1.713
	Season * Gender	51%	0.428 \pm 2.762
	Season (Autumn/Spring)	100%	-39.145 \pm 26.818**
Distance (m)	Forest (pine/poplar)	100%	-10.414 \pm 25.400
	Season: Forest	95%	11.781 \pm 36.504
	Fat content	53%	-0.766 \pm 1.989
	Season (Autumn/Spring)	95%	-0.299 \pm 0.184 **
Speed (m/s)	Forest (pine/poplar)	16%	-0.140 \pm 0.222
	Season: Forest	5%	0.252 \pm 0.336
	Fat content	4%	-0.020 \pm 0.019 *



(a)

(b)



(c)

(d)

Figure 4. The effect of overwintering, habitat type and gender on: a) spiders body length (mm); b) fat proportion (relative to dry mass, %); c) total distance travelled (cm); and d) speed (cm/s). White bars represent subadult females and grey bars represent subadult males. Mean \pm SD values are presented.

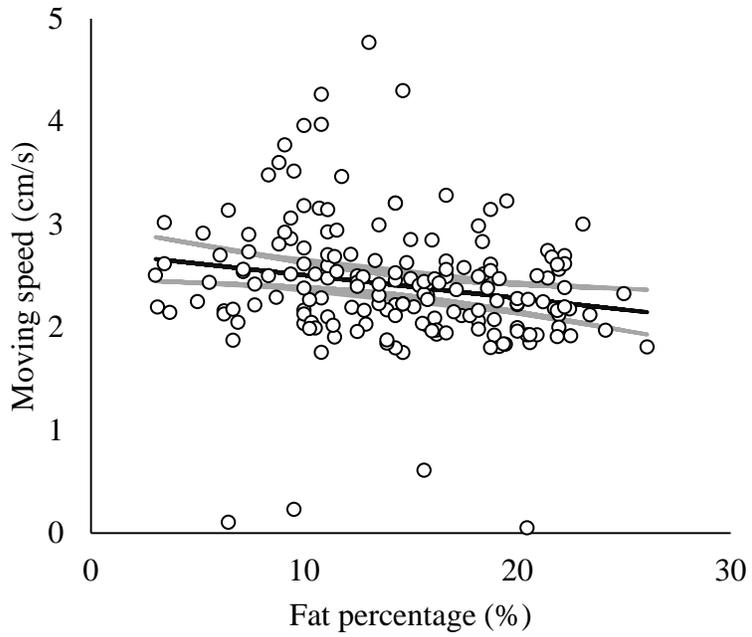


Figure 5. Relationship between fat proportion (relative to dry mass, %) and moving speed (cm/s). Confidence intervals (97%) are given in grey around the estimated regression lines (black).

5. Discussion

5.1. Effect of *A. syriaca* and tree species

In accordance with hypothesis (1), we found different species compositions for poplar and pine forests. Furthermore, we found a higher proportion of web-building spiders and larger species in poplar forests than in pine forests. In contrast to hypothesis (2), functional diversity was higher in non-invaded sites than in invaded sites; however, we found no effect of *A. syriaca* invasion on the abundance of spiders. Supporting hypothesis (3), *A. syriaca* had a negative effect on functional diversity in pine forests, while its effect was less pronounced in poplar forests.

Canopy closure is among the most important determinants of spider species richness and assemblage composition, because it can affect the soil microclimate and understory vegetation development (Finch, 2005; Lange *et al.*, 2011). The thick moss-litter layer, shrub-rich understory vegetation, and coarse woody debris together with variation in light regimes due to the gaps in dense canopy layer may determine spider assemblages directly and via prey abundance (Finch, 2005; Uetz, 1991). Herbaceous vegetation structure depends on the light availability at the forest floor. As deciduous plant, poplar forests have more open canopies than pine forests and more sunlight reach the forest floor. Due to this, there are more chances of growth of diverse herbaceous understory vegetation in poplar plantations than in pine plantations with their closed canopies (Balandier *et al.*, 2006). Our study focused only on mature plantations, which usually have relatively dense understory vegetation (Calviño-Cancela *et al.*, 2012) and well-developed canopies which can reduce extreme microclimatic variation (Harms *et al.*, 2000). Dense vegetation offers several micro-habitats, which have an important role in regulating the species composition of spider assemblages (Rodrigues & Mendona Jr., 2012).

Complex vegetation structure might offer plentiful prospective of the web attachments for web-building spider species (Schirmel *et al.*, 2012). Spiders are generally sensitive to structural conditions of the vegetation and habitat heterogeneity (Gallé *et al.*, 2014b; Wise, 1993). The web builders are connected to more heterogeneous environments with increased structural complexity, a higher density of web-builder spider species reported from structurally

more complex forests than from simple habitats (Schirmel *et al.*, 2012, 2016). Decreasing structural complexity of forest floor in turn may result in a decline in spiders diversity due to the reduction of microhabitat diversity and resources (Finch, 2005; Willett, 2001). The relatively uniform microhabitat conditions may result in a uniform spider species composition (Schultz, 1997). In this study, we found that species composition differed between forest types, as indicated by the significant results of multivariate ANOVA and the clear separation by NMDS ordination. The high number of significant indicator species also underpinned the marked differences in spider assemblages of pine and poplar forests, even though we detected no differences in herbaceous vegetation cover between the plantations types. However, the species composition differs and diversity of vegetation is lower in pine than in poplar plantations (Ingle *et al.*, 2020). Probably different soil conditions and lower light availability developed a diverse herbaceous understory vegetation in coniferous forests than in deciduous forests (Barbier *et al.*, 2008).

The abundance of litter-dwelling invertebrates is expected to be related to the amount of leaf litter, as well. The leaf litter quality and quantity determines the structure of microhabitat of the forest floor, which can further have an effect on the diversity of spiders (Castro & Wise, 2009; Pearce *et al.*, 2004). The thick layer of deciduous leaf litter in poplar forests generates a more complex forest floor than in pine forests (Gallé *et al.*, 2014a). The leaf litter in pine plantations consists of pine needles which reduces soil pH and may change the physical properties of the soil, as well (Selvi *et al.*, 2017). Thick layer of needle-litter pines and other coniferous trees has chemical and physical effects on soil through the acidification process and this leads to the loss of soil fertility (Augusto *et al.*, 2002; Burgess *et al.*, 2015; Cumming & Kelly, 2007).

Spider diversity and density is mainly organized bottom-up forces in food webs, (Lange *et al.*, 2011; Price, 2002). Many studies explore spiders role in the top-down control of herbivores and detritivores (Finke & Denno, 2005; Michalko *et al.*, 2019; Schmitz *et al.*, 2000). Spiders may change their diet according to environmental constraints. For example, they may shift to protein-rich prey after winter for their growth and development from lipid-rich prey in their pre-overwintering diet enhancing their energy reserves (Bressendorff & Toft, 2011). The relative abundances of alternative prey can also determine the feeding preference of spiders (Michalko *et al.*, 2019). For example, wolf spider *Pardosa milvina* (Hentz) found to utilize

dipterans less frequently when they were abundant, but more frequently when they were rare (Schmidt *et al.*, 2012). As spiders are food-limited, the importance of Collembola and other fungivore abundance as a potential food source can strongly influence the spider population density and dynamics in both forest types (Wise, 1993).

The major part of diet of ground-dwelling spiders in forests is Collembola (Block & Zettel, 2003; Wise, 2004), which are abundant and diverse in forest soils (Bolger *et al.*, 2013; Kováč *et al.*, 2005). However, their species composition varies in coniferous and deciduous forests. In boreal coniferous forest soils the density of Collembola was recorded higher than in temperate deciduous forests (Petersen & Luxton, 1982). They are a major components of the forest biodiversity, they occupy various microhabitats, and they have an important functional roles in decomposition (Faber & Verhoef, 1991; Lavelle *et al.*, 1995). Collembola is affected by the introduction of exotic species and they are found more abundant in native forests than in plantations (Bolger *et al.*, 2013; Kováč *et al.*, 2005). For example, afforestation program with exotic tree species in Portugal affected strongly Collembola assemblages (Pinto *et al.*, 1997; Sousa *et al.*, 1997). Collembola offer an easily accessible food source for ground-dwelling spiders (Ingle *et al.*, 2018) in poplar forests, and may result in increase in the abundance of larger species of spiders. In the present study, we also found larger CWM size values in poplar forests than in pine forests.

Many invasive plant species significantly affect the architecture of vegetation (Simao *et al.*, 2010; De Souza & Martins, 2005) and therefore, habitat structure which further modifies the ground surface micro-habitat (Pétillon *et al.*, 2005b). Invasive plants have a significant negative effect on invertebrates, as well (Standish, 2004; Toft *et al.*, 2001), particularly on arthropod abundance and diversity (Herrera & Dudley, 2003; Slobodchikoff & Doyen, 1977). They affect species composition of spider assemblages (Bultman & DeWitt, 2008; Mgobozi *et al.*, 2008), and the behavior and density of spider species (Gallé *et al.*, 2015; Pearson, 2009).

However, the invasion of a non-native plant and changes in habitat structure do not necessarily affect the density of every spider species (Pétillon *et al.*, 2005a). The changes in the abundances and assemblage composition of species can be explicated by differences in structure and condition of vegetation, microclimate and alteration in the food supply in invaded sites (Pétillon *et al.*, 2005b; Schirmel & Buchholz, 2013).

Invasive plants may offer novel food resources to various native herbivore arthropods (Bezemer *et al.*, 2014), which can affect the potential prey abundance for spiders. The native distribution area of *A. syriaca* is North America, where 457 insect species from 8 orders are reported to be associated with it, which are mainly pollinators and specialist herbivores (Dailey *et al.*, 1978). For the pollinators, the continuously open flowers of *A. syriaca* are a relatively large and stable food resource (Dafni *et al.*, 1997). However, to be associated a plants, a herbivore or pollinator may require a common evolutionary history with the invasive plant (Tallamy *et al.*, 2010). Pollinators also serve as an important food resource for spiders (Wise, 1993). Pollinator interactions may be changed due to invasive plants in both ways, either positively or negatively (Bartomeus *et al.*, 2008; Fenesi *et al.*, 2015; Larson *et al.*, 2006). Invasive plant species can weaken the relationship between the native plants with their pollinators (Aizen *et al.*, 2008), thus reducing pollinator abundances and change assemblage structure.

The non-invaded sites in pine plantations had similar species richness and higher functional diversity (FD_{is} and RaoQ indices) which suggested that traits values are less similar than in invaded sites. In contrast, the invaded sites had lower functional diversity, and thus a uniform trait state composition. Invaded pine forests only preferred a certain trait state combination, which implied that environmental filtering played an important role in species sorting (Cornwell *et al.*, 2006; Kraft *et al.*, 2015). This precluded the colonization of several species of the original forest-steppe fauna. In a novel habitat, species need specific functional traits to encounters a specific set of environmental conditions of that habitat (Mammola *et al.*, 2020).

5.2. Effect of tree species on winter fauna

In contrast with our hypothesis (1), we found higher species richness in pine plantations than in the poplar plantations. However, our results supported our second hypothesis that spider species composition of winter-active communities is different in poplar and pine plantations; we also identified significant indicator spider species for both plantations.

Microclimatic factors, such as temperature and moisture have an effect species richness and activity density of spiders (Chen *et al.*, 1999). Temperature on the floor is dependent on penetration of sunlight through the canopy (Hardy *et al.*, 2004). The architecture of forest

canopy is formed by presence of tree elements and gaps can strongly influence the solar radiation (Hardy *et al.*, 2004). Forest canopy opening is a major driver of community structure of ground-dwelling invertebrates (Černecká *et al.*, 2020; Perry *et al.*, 2018; Thorn *et al.*, 2016). Gaps in canopy are found to have either positive (Seibold *et al.*, 2016) or negative (Gandhi *et al.*, 2008) effect or no impact (Černecká *et al.*, 2017) on invertebrates. Thus species composition and richness of trees of forests can also affect the spider richness, abundance and community composition (Korenko *et al.*, 2011; Samu *et al.*, 2014). As poplar is a deciduous tree, it drops the leaves before the winter and it results in higher solar transmission in the poplar plantation than in the pine plantations during the winter (Ingle *et al.*, 2019). Forest floor temperature in poplar forest was higher during the day than during night compared with in pine plantation (Fig. 2). However, reverse condition during the night due to drastic drops in temperature in poplar plantations. Thick canopy in the pine plantations can provide a thermal insulation effect throughout day and night and maintain a more temperate microclimate (Weng *et al.*, 2007). This may provide a possibility of survival to many spider species and result in higher species richness in pine plantation than in poplar plantation.

Soil and litter moisture affect the composition of spider communities during autumn (Ziesche & Roth, 2008). Wind flow together with canopy closure in the forests can determine the moisture of the forest floor (Gálhidy *et al.*, 2006; Ritter *et al.*, 2005). The layer of litter may also regulate the moisture level of soil indirectly by reducing capillary rise and evaporation (Bezkorovainaya & Yashikhin, 2003; Sakaguchi & Zeng, 2009). The moisture condition in pine plantations and in poplar plantations are different which may also contribute to the differences in spider species composition. This can result in a higher species richness of spiders in pine forest than in poplar forest. Several collected species of the family Linyphiidae with a preference for moisture and shading (e.g., *Cenromerus sylvaticus*, *Ceratinalla brevis* and *Walckenaeria alticeps*, Buchar and Ruzicka 2002) were found as significant indicator species of pine forests.

Poplar plantations may provide higher quality habitats for the spiders than pine plantations (Gallé *et al.*, 2014b). Such complex habitat structures are expected to provide a variety of prey organisms in a large abundance. For web builders, it can provide more attaching points for webs and shelters (Oxbrough *et al.*, 2006). However, we found no effect of structural

parameters on winter active spiders. Presumably, the effects of microclimatic parameters overrode the effect of microhabitat heterogeneity.

5.3. Effect of forest type on spider behaviour and condition

We analyzed the effect of forest type and overwintering on body condition and locomotory activity of the diurnal wolf spider *P. alacris*. In contrast to our hypothesis concerning the negative effect of overwintering on fat reserves (hypothesis 1), overwintering had significant positive effect on the fat reserves of spiders; however, it had no effect on the body length of *P. alacris*. We also hypothesised, that habitat type and gender would affect overwintering spiders (hypothesis 2); in line with this, we found a significant positive interaction effect of season and forest type, and season and gender on the length of spiders, indicating that the effect of overwintering is mediated by habitat type and gender. Concerning our hypothesis on the movement pattern of spiders (hypothesis 3), spiders collected in spring moved less and moved slower than spiders collected in autumn and spiders with high fat content moved slower.

We collected smaller spiders in the poplar forests than in the pine plantations, and the significant interaction effect indicated that the difference in body length of autumn and spring spiders was more pronounced in poplar forests than in pine plantations. Habitat type affect the overwintering of ants, and this effect is mediated by the energy reserve of body fat content (Sorvari & Hakkarainen, 2009; Sorvari *et al.*, 2011). Many insects and other organisms from temperate and boreal zones have evolved to tackle the problem of low food availability during winter by using winter dormancy to save energy by lowering their metabolic activity (Guppy & Withers, 1999; Leather *et al.*, 1993). The energy resources such as body fat may be consumed more rapidly during the winter.

Deciduous forests presumably offer favorable conditions for overwintering due to the transmission of solar radiation during daytime which results in a warmer floor temperature; advantageous for foraging activity of spiders. In case of subzero temperature, forest-dwelling spiders predominantly pursue refuge under the lowest leaf layer which can reduce the variations in temperature and low thermal conductivity and decrease their activity (Whitney *et al.*, 2014). This can restrict the risks of spontaneous freezing (Whitney *et al.*, 2014). The presence of coarse woody debris in the poplar plantation also increases in the structural

complexity of forest floor directly and indirectly by improving the leaf litter accumulation and forming overwintering microhabitats for spiders (Castro & Wise, 2009, 2010)

We collected larger subadult female than subadult male spiders, and the difference between body length of subadult males in autumn and spring was greater than that of subadult females. Seasonal activity pattern in wolf spiders can differ according to sex due to the different energetic requirements of egg production for females and mate searches for males (Framenau, 2005). This characteristic sexual dimorphism results in a gender-specific seasonal developmental pattern. The larger body size in female spiders may result in higher reproductive success through a fecundity advantage as female fecundity changes with mass (Framenau, 2005; Prenter *et al.*, 1999).

Spiders collected in spring had greater fat content than spiders collected in autumn. Gunnarsson (1988) showed a significant increase in size and body mass in winter active spiders. Larger size of body might be gained through fast growth rate or by prolonging the growth period. At high quality habitats spiders forage more and reach adult body size faster (Vollarath, 1987). In the temperate zone many spider species forage in winter days prolonging their growth period (Aitchison, 1984).

We found that the spiders from poplar plantations were smaller than in pine forests. Furthermore, we found that in poplar forests overwintering had a more positive effect on body size than in pine plantations. Spiders primarily overwinter in a state of diapause, but some species are winter-active and exhibit only temporary quiescence when temperatures fall below a given threshold (Schaefer, 1977). They may successfully prey on other winter active invertebrates on the forest floor during winter. On the other hand, the success of survival in overwintering is depending on the good body condition such as high fat percentage. The spiders with good body condition might had a higher rate of survival and successful overwintering (Sorvari *et al.*, 2011). However, combination of certain cryoprotectants cause physiological restrictions on arthropods by hampering locomotary and active foraging ability (Vanin *et al.*, 2008; Whitney *et al.*, 2014) Furthermore, prey consumption may compromise the cold hardiness by increasing ice particles in the gut (Sømme, 1982).

Intraguild predation is very common mortality factor for wolf spiders (Korenko & Pekár, 2010), and its effect on spider abundance is well documented (Wise & Chen, 1999). The activity-density of *P. alacris* and larger bodied wolf spiders such as *Alpoecosa* and *Trochosa*

species are higher in the poplar forests than in pine forests during the spring (Gallé *et al.*, 2014a). Large lycosids use movement signals of small invertebrates to identify their prospective prey and they may prey on *P. alacris*. It may result in reduction of movement speed of *Pardosa* species in the presence of larger spiders (Barnes *et al.*, 2002). Predation pressure thus affects the behavior of ground-dwelling spiders, because they need to forage under the risks of being encountered by predators (Pruitt, 2010). We also found that spring spiders were slower than autumn spiders and they covered less distances. However, increased immobility duration during winter may result in reduction of feeding efficiency and further may be responsible for weight loss (Persons *et al.*, 2002).

The hunting insectivorous predators such as birds may also reduce the densities of terrestrial arthropod assemblages through feeding (Mäntylä *et al.*, 2011). At least 20% of the total winter mortality of spiders are due to avian predators in which particularly the large spiders were found to be affected (Askenmo *et al.*, 1977; Gunnarsson, 1983). Avian predator risk is higher for repeatedly moving individuals than sedentary spiders (Avery & Krebs, 1984; Gunnarsson, 2007). For early spring nesting bird species, spiders and other arthropods are among the most important food resources. This may have indirectly negatively affected spider speed and mobility during spring to avoid the risk of bird predation.

6. Conclusion

In conclusion, plantation type and invasion of *A. syriaca* affected different elements of functional diversity of spiders. There is difference in spider species composition of pine forests and poplar forest assemblages in terms of functional diversity. This might also affect arthropod food web structure. The impact invasion of *A. syriaca* on the trait composition of spiders in pine forest, suggested that strong habitat filtering and the generation of low-quality secondary habitats for the original spider fauna. This may have further top-down effects on the broader invertebrate herbivore and detritivores community. The information on the effect of pine plantations and *A. syriaca* invasion on biodiversity is critical for forestry and conservation management.

Spiders probably actively forage and move more for shelter in evergreen pine forest than in deciduous poplar forests, and this can be resulting in higher number of catches in the pitfall trap in the pine plantations. However, our study showed that there was almost no effect of structural parameters on spiders. Presumably, during winter, the effects of microclimatic parameters override the effect of microhabitat heterogeneity. Moreover, an underrepresentation of web builders in pitfall trap data may also contribute to this pattern. Relatively little is known about the winter-active arthropod fauna of plantation forests. We found that plantation type affected species richness, activity density, and community composition of spiders; however, habitat structure did not play a significant role in shaping winter-active fauna. We conclude that the effect of microclimatic differences and prey availability presumably overrides the effect of habitat structure on winter-active spiders.

In the conclusion of third part of our study, before winter, spiders in poplar forests were smaller than spiders of pine forests, but during winter, spiders in poplar forests grew more than spiders in pine forests. We also showed an effect of season on cursorial locomotion, but moving may increase the risk of predation. Our study improved the understanding of effects of overwintering on the body condition and behavior of *P. alacris*. We found that spiders collected in spring were fat than collected in autumn, which further emphasizes the major role of winter foraging in the development of *P. alacris*.

7. Key findings of research

1. We found different species compositions for poplar and pine forests. Furthermore, we found a higher proportion of web-building spiders and larger species in poplar forests than in pine forests. With this, the functional diversity was higher in non-invaded sites than in invaded sites; however, we found no effect of *A. syriaca* invasion on the abundance of spiders. *A. syriaca* had a negative effect on functional diversity in pine forests, while its effect was less pronounced in poplar forests.
2. We found higher numbers of winter active species in pine plantations than in the poplar plantations. Furthermore, spider species composition of winter-active assemblages is different in poplar and pine plantations; we also identified significant indicator species for both plantations.
3. We found that the overwintering had significant positive effect on the fat reserves of spiders; however, it had no effect on the body length of *P. alacris*. We also found a significant positive interaction effect of season and forest type, and season and gender on the length of spiders, indicating that the effect of overwintering is mediated by habitat type and gender. The movement pattern of spiders was different before and after winter. Spiders collected in spring moved less and moved slower than spiders collected in autumn and spiders with high fat content moved slower.

List of articles on thesis (MTMT No: 10070640)

1. Ingle, K., Gallé-Szpisjak, N., Kaur, H., & Gallé, R. (2019). Forest type interacts with milkweed invasion to affect spider communities. *Insect Conservation and Diversity*, *12*, 321–328. (IF- 2.92)
2. Ingle, K., Horváth, Á., Gallé-Szpisjak, N., Gellért, L., Csata, E., & Gallé, R. (2018). The effects of overwintering and habitat type on body condition and locomotion of the wolf spider *Pardosa alacris*. *Acta Oecologica*, *89*, 38–42. (IF 1.65)
3. Ingle, K., Kaur, H., Gallé-Szpisjak, N., Bürgés, J., Szabó, Á., & Gallé, R. (2020). Winter-active spider fauna is affected by plantation forest type. *Environmental Entomology*, *49*, 601–606. (IF- 1.58)

Other Articles

4. Gallé, R., Császár, P., Makra, T., Gallé-Szpisjak, N., Ladányi, Z., Torma, A., Ingle, K., Szilassi, P. (2018). Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites. *Landscape Ecology*, *33*, 1435–1446. (IF- 4.51)
5. Ingle, K., Vitkin, E., Robin, A., Yakhini, Z., Mishori, D., & Golberg, A. (2018). Macroalgae biorefinery from *Kappaphycus alvarezii*: conversion modeling and performance prediction for India and Philippines as examples. *BioEnergy Research*, *11*, 22–32. (IF- 2.58)
6. Ingle, K., Polikovsky, M., Chemodanov, A., & Golberg, A. (2018). Marine integrated pest management (MIPM) approach for sustainable seagrass agriculture. *Algal Research*, *29*, 223–232. (IF- 3.99)
7. Ingle, K., Traugott, H., & Golberg, A. (2020). Challenges for marine macroalgal biomass production in Indian coastal waters. *Botanica Marina*, *1*, 1–15. (IF- 1.38)

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Summary

The anthropogenic land use changes are resulted in habitat destruction and fragmentation worldwide, that is responsible highly for the loss of biological diversity. For instance, in Hungary, the area covered by forests is approximately 22.5% and is increasing by 0.5% per annum; however, 75% of the forests are primarily under intensive management focusing almost entirely on wood production. The expansion of tree plantations can have severe ecological impacts on native biota, such as alteration of plant and animal community compositions and ecosystem functioning. Although international pressure is increasing to tackle the negative environmental effects of such plantations, tree plantation covers more than 7% of total forest area worldwide. Deciduous tree plantations, such as poplar in central Europe, have dense understory vegetation similar to natural forests which can reduce extreme microclimatic conditions and favorable for forest specialist arthropods. However, in pine plantations, the floor is covered by pines needles, forming a homogeneous microhabitat structure.

Due to increasing transportation activities, occurrence and spread of non-native species considerably increased. Biological invasion is also considered as serious threat for biodiversity and related ecosystem functioning. Most of the arthropods are closely associated with the native vegetation. Alteration of habitat's physical characteristics is responsible for negative consequences on the indigenous fauna.

Overwintering in temperate regions is a considerable mortality risk for arthropods. To avoid extremely low temperatures, arthropods overwinter in habitats that buffer temperature fluctuations. Some species may even be active at temperatures below freezing levels and search for food when other species have become inactive. Winter activity has several advantages including the ability to locate habitat, food resources. While prey availability is typically low in the winter, the competition is also reduced; furthermore, feeding during winter can improve survival rates.

The effect of habitat structure of forests on spiders has been documented; however, the majority of this work focuses on species diversity patterns, with few studies focusing on functional diversity of spiders. There is limited information on how arthropod assemblages and functional diversity is affected by plant invasion in different forest types and how forest type

affects winter active spiders. Furthermore, the effects of overwintering on spider body condition and behaviour in plantation forests have not yet been studied.

The present dissertation covers three studies to fill the above knowledge gaps. All studies were carried out in the Kiskunság region, in the southern part of the Great Hungarian Plain. The dominant land use types are plantation forests and agricultural land under intensive management. The secondary forests include pine and poplar tree plantations.

The aim of the first study was to reveal the effect of plantation tree species and plant invasion on the spider fauna

We the first and second study selected total 40 sampling sites in 10 plantation forests according to tree species (5 are of poplar and 5 are of pine plantations). two sites in each plantation were invaded by common milkweed (*Asclepias syriaca*) and two were non-invaded. We collected samples by using 3 pitfall traps in each site for three 7 days period in May, June-July and October of 2017 and then we pooled the data.

Our main result of this study was follows,

1. We found a significant effect of *A. syriaca* invasion on spider functional diversity (Rao's quadratic entropy), with invaded sites having a lower functional diversity than non-invaded sites. A larger effect of invasion with *A. syriaca* on the RaoQ of spiders was observed in pine compared to poplar plantations.
2. Spider species were larger, and web-building spiders were more frequent in poplar forests than in pine plantations.

We found no effect of *A. syriaca* invasion on species richness or abundance of spiders, however species composition of spider assemblages in the two forest types was clearly separated according to non-metric multidimensional scaling. We identified seven species associated with pine plantations and six species associated with poplar plantations. In conclusion, plantation type and invasion of *A. syriaca* affected different elements of spider functional diversity.

The aim of second part of my thesis was to reveal the differences in the species richness and community composition of spiders in the poplar and pine plantation during winter.

We used the same study design for this study as previous study. We assessed the average height of vegetation and percentage cover of leaf litter, mosses, herbaceous vegetation, and shrubs to characterize habitat structure.

The main result of this study was as follows,

1. We found higher species richness and activity density of spiders in the pine plantations compared to the poplar plantations, presumably due to the more temperate microclimate in pine than in poplar plantations. However, there was no significant effect of habitat structure and its interaction with forest type on species richness and activity density of spiders.
2. Species composition of non-poplar and poplar plantation forests differed significantly.

The plantation type affected species richness, activity density, and community composition of spiders; however, habitat structure did not play a significant role in shaping winter-active fauna. We conclude that the effect of microclimatic differences and prey availability presumably overrides the effect of habitat structure on winter-active spiders.

For final study, we aimed to test the effects of winter on the behaviour and body condition of spiders collected from poplar and pine plantations.

We selected total 6 plantations sites (3 of pines and 3 of poplars) from previous plantations, and collected 15 sub-adult spiders *P. alacris* in each site by hand catch method before and after winter. We studied the locomotory behaviour of *P. alacris* by tracking their movement in a white circular plastic arena and recording them by camera individually. We analysed the films by using video editing software for calculate the total distance travel, total time of travelling and speed of travelling. We measured total body length and prosoma length, and exact total fat content by using petrol-ether method. The results of this study were as follows.

1. We found that plantation type and sex had significant effects on body length. Fat content was significantly higher in the spring than in autumn, and spiders covered larger distances and were faster in autumn than in spring.
2. Spiders in poplar forests were smaller but grew more during the winter than in pine plantations.

3. Fat spiders with better body condition moved less, and were thus less detectable by predators. However the low movement rate may result in a low rate of encountering prey items, thus lowering feeding efficiency.

In conclusion, season, gender and forest type affects body condition and behavior of spiders. This indicated that the effect of overwintering is mediated by habitat type and gender.

In conclusion, plantation type and invasion of *A. syriaca* affected different elements of functional diversity of spiders. There is difference in spider species composition of pine forests and poplar forest assemblages in terms of functional diversity. The information on the effect of pine plantations and *A. syriaca* invasion on biodiversity is critical for forestry and conservation management. We also conclude that the effect of microclimatic differences and prey availability are important for successful overwintering of spiders and the effects of these parameters presumably override the effect of habitat structure on winter-active spiders.