

1

2

**Forest type interacts with milkweed invasion to affect spider communities**

3

4 Ingle, Kapilkumar<sup>1,2</sup>, Gallé-Szpisjak, Nikolett<sup>3</sup>, Kaur, Hardeep<sup>1</sup>, Gallé, Róbert<sup>3, 1\*</sup>5 <sup>1</sup> Department of Ecology, University of Szeged, Hungary6 <sup>2</sup> Doctoral School of Environmental Sciences, University of Szeged, Rerrich Béla tér 1, H-6720

7 Szeged, Hungary

8 <sup>3</sup> MTA ÖK Lendület Landscape and Conservation Ecology Research Group, Hungary

9 \* Corresponding author

10

11 Short title: Spiders of invaded plantation forests

12

13

14 **Abstract.**

15 1. Non-native tree plantations constitute a large part of forestation worldwide. Plantations are  
16 prone to invasion by exotic herbaceous plant species due to habitat properties, including understory  
17 vegetation structure.

18 2. We established 40 sampling sites in 10 plantation forests. Sites were selected according  
19 to tree species (native poplar forests, exotic pine plantations) and common milkweed (*Asclepias*  
20 *syriaca*) density (invaded, non-invaded sites) in a full factorial design. We collected spiders with  
21 pitfall traps.

22 3. We found a significant effect of *A. syriaca* invasion on spider functional diversity (Rao's  
23 quadratic entropy), with invaded sites having a lower functional diversity than non-invaded sites  
24 A larger effect of invasion with *A. syriaca* on the RaoQ of spiders was observed in pine compared

25 to poplar plantations. Spider species were larger and web building spiders were more frequent in  
26 poplar forests than in pine plantations. We found no effect of *A syriaca* invasion on species  
27 richness or abundance of spiders.

28 4. Species composition of spider assemblages in the two forest types were clearly separated  
29 according to non-metric multidimensional scaling. We identified 7 species associated with pine  
30 plantations and 6 species associated with poplar plantations.

31 5. The similar species richness and the higher functional diversity of non-invaded sites  
32 suggested that these trait states were less similar than invaded sites, and that functionally different  
33 species were present. In contrast, the invaded sites had lower functional diversities, and thus more  
34 uniform trait state compositions, suggesting that environmental filtering played an important role  
35 in species sorting, making invaded plantations low quality secondary habitats for the original  
36 spider fauna.

37

38 **Key words.** Plantation, forest, invasion, spider, Araneae, functional diversity, species  
39 composition, pine, poplar, *Asclepias syriaca*.

40

## 41 **Introduction**

42

43 The land cover of commercial tree plantations is increasing worldwide, replacing natural forests.  
44 These secondary forests include native and non-native tree plantations. Generally, they have a  
45 negative impact on the original native ecosystems (Vitousek *et al.*, 1996; Gratton & Denno, 2006;  
46 Spirito *et al.*, 2014), Although international pressure is increasing to tackle the negative  
47 environmental effects of such plantations, tree plantation covers more than 7% of total forest area  
48 worldwide (Payn *et al.*, 2015). However, plantations may also have a positive impact on local  
49 biodiversity by providing secondary habitats for rare and threatened species (Brockerhoff *et al.*,  
50 2008).

51 Pine plantations are common in Europe, where they are generally used for timber  
52 production. Pine trees can alter hydrologic regimes (Urcelay *et al.*, 2017), microclimate and soil

53 properties. The layer of pine needles on forest floor makes the soil acidic (Selvi *et al.*, 2017), and  
54 the change in chemical and physical properties of the soil results in loss of fertility (Augusto *et al.*,  
55 2002). These processes are responsible for the changes in understory vegetation structure and  
56 microhabitat diversity (Chiarucci & De Dominicis, 1995), and in turn, lower species diversity of  
57 arthropods compared to natural forests (Brockerhoff *et al.*, 2008; Gallé *et al.*, 2018).

58 Due to altered microclimate and soil properties, plantation forests are prone to invasion by  
59 non-native herbaceous plant species (Henneron *et al.*, 2015). In turn, invasive plants alter  
60 vegetation diversity (Knops *et al.*, 1999) and biotic interactions (Bezemer *et al.*, 2014). A high  
61 density of invasive plants changes the physical properties of a habitat by altering its structure,  
62 including its microclimatic conditions, such as the light intensity and temperature of the invaded  
63 area (Carter *et al.*, 2015). These changes may lead to changes in ecosystem functioning (Schirmel  
64 & Buchholz, 2013; Gomes *et al.*, 2017).

65 Common milkweed (*Asclepias syriaca*) in Europe spreads aggressively and is found in 11  
66 European countries (Szitar *et al.*, 2018). It establishes dense populations in disturbed habitats  
67 (Pysek *et al.*, 2012; Kelemen *et al.*, 2016), and may change the composition of existing vegetation  
68 and form novel ecosystems (Kelemen *et al.*, 2016; Sztár *et al.*, 2016). Milkweed was introduced  
69 into Europe in the 17<sup>th</sup> century (Gaertner, 1979; Bukovinszky *et al.*, 2014) from eastern North  
70 America and into Hungary in the 18<sup>th</sup> century by beekeepers (Balogh *et al.*, 2007; Csontos *et al.*,  
71 2009). Currently, *A. syriaca* endangers the semi-natural and natural vegetation of sandy regions  
72 (Ducs *et al.*, 2016), has become one of the most abundant invasive plant species in Hungarian  
73 lowland forest plantations, and represents a major problem in conservation areas (Sztár *et al.*,  
74 2016). However, its negative effects are not always straightforward (Sztár *et al.*, 2016; Somogyi  
75 *et al.*, 2017). *A. syriaca* attracts many insects, particularly pollinators, because of the open  
76 structure of its flowers. As such, it serves as a continuous resource for pollinators day and night,  
77 attracting both diurnal and nocturnal pollinators (Southwick, 1983). The high density of  
78 pollinators, in turn, may attract predatory arthropods. The effect of plant invasion on arthropod  
79 assemblage structure is still not well defined, and is crucial in understanding terrestrial ecosystem  
80 ecology (Bezemer *et al.*, 2014).

81 Although there are reports on the ecology of forest invertebrates in the context of changes in quality  
82 (reviewed by Kuuluvainen *et al.*, 2012, Lassauce *et al.*, 2011, Schulze *et al.*, 2016). The majority  
83 of this work focuses on species diversity patterns (Kuuluvainen *et al.*, 2012), with few studies

84 focusing on functional diversity of spiders (Magura, 2017, Gallé *et al.*, 2018). The concept of  
85 functional diversity helps to explain how ecosystems react to environmental change (Petchey &  
86 Gaston, 2006; Cardoso *et al.*, 2011). Changes in habitat quality may act as a filter, structuring the  
87 community with functionally similar species (Cardinale *et al.*, 2012, Dalzochio *et al.*, 2016).

88 The effect of habitat structure of forests on functional diversity of arthropods has been documented  
89 (Corcuera *et al.*, 2016; Dalzochio *et al.*, 2018; Gallé *et al.*, 2018); however, there is limited  
90 information on how arthropod assemblages and functional diversity is affected by plant invasion  
91 in different forest types. In the present study, we focused on spider assemblages as the ideal  
92 indicators of the impact of plantation tree species and non-native plants on assemblage structure  
93 of invertebrates due to their sensitivity to vegetation structure (Mgobozi *et al.*, 2008).

94 In this study we assessed the effect of *A. syriaca* invasion on species richness, and species  
95 composition of spiders in the native and exotic plantation. We also applied the functional diversity  
96 concept to link diversity patterns with ecosystem processes and functioning. Hypotheses for this  
97 study were: (1) species richness would be higher in native forests compared to exotic forests, and  
98 tree species would have an effect on species functional diversity (i.e. functional richness and  
99 evenness, Rao's quadratic entropy and community weighted mean trait values) and composition  
100 of spider assemblages; (2) functional diversity and abundance of spiders would be higher in the  
101 forests which were invaded by *A. syriaca* as this plant would attract more pollinators, herbivores  
102 and associated predators; and (3) *A. syriaca* would have a different effect on spider diversity in  
103 native and exotic forests. We assumed, that changes in habitat structure by *A. syriaca* in the low  
104 quality exotic pine habitat may have a more pronounced deterioration effect on spider communities  
105 than in native forests.

106

## 107 **Materials and methods**

108

### 109 *Study area*

110 The present study was carried out in the Kiskunság region, in the southern part of the Great  
111 Hungarian Plain (Appendix 1.). The landscape was dominated by agriculture and semi-natural  
112 forest plantations, with small patches of the original forest-steppe habitats (Gallé *et al.*, 2018). The  
113 soil was calcareous coarse sand and the climate was semiarid with mean annual precipitation and  
114 temperatures in the ranges 550 – 600 mm and 10.2 – 10.8 °C, respectively (Török *et al.*, 2003).

115

116 *Study design and sampling*

117 We selected 5 poplar and 5 pine plantation forests for spider sampling. We surveyed ground-  
118 dwelling spiders at 4 sampling sites in each of the 10 forests, for a total of 40 sampling sites. Sites  
119 were selected according to tree species (native poplar forests vs. exotic pine plantations) and  
120 common milkweed density (invaded vs. non-invaded sites) in a full factorial design resulting in 10  
121 replicates per treatment combination. All sampled plantations were mature forests with no recent  
122 intensive forestry activity. Sampling sites were located at least 70 m distance from each other, and  
123 each sampling site was located more than 100 m from the forest edges. We assessed *A. syriaca*  
124 quantity in four 1 m<sup>2</sup> quadrates at each invaded sampling site; the density of *A. syriaca* stems was  
125  $7.33 \pm 3.86$  stems/m<sup>2</sup> (mean  $\pm$  SD), and its cover was  $30.31\% \pm 17.05$  (mean  $\pm$  SD). We  
126 characterized the habitat structure at the sampling sites by the approximate percentage cover of  
127 herbaceous plants (excluding *A. syriaca*), the average height of the vegetation and by the cover of  
128 leaf litter.

129 We used 3 pitfall traps for collecting spiders at each site. The traps were plastic cups with  
130 a diameter of 8.5 cm (Császár *et al.*, 2018). We supplied the traps with plastic funnels and we  
131 placed a metal roof above them. Traps were filled with a 50% water-ethylene-glycol solution to  
132 which we had added a few drops of detergent. Traps were open for three 7-day sampling periods:  
133 May 23 - 30, 2017; June 26 - July 3, 2017; and Oct 2 - 10, 2017.

134

135 *Data analysis*

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

141 We chose 4 attributes for functional categorization of spiders. We classified species according to:  
142 shading tolerance, ranging from 1 (open) to 4 (shaded); moisture preference, ranging from 1 (very  
143 dry) to 5 (very humid habitats); feeding, 0 (active hunter) and 1 (web builder); and size, as a  
144 continuous variable in mm (Buchar & Ruzicka 2002, Bell *et al.*, 2005, Blandenier 2009, Nentwig  
145 *et al.*, 2017). If a species was assigned to more than 1 category, the values were averaged. Spiders

146 were considered as generalists if they were assigned to more than 3 categories in the case of  
147 shading tolerance and moisture preference. They were also considered generalist species if they  
148 were present at both extremes of the given categories, and their score was excluded from further  
149 analyses, as their distribution is determined by other factors. We calculated community-weighted  
150 mean (CWM) values for each trait at each sampling site; Functional richness (FRic), Functional  
151 evenness (FEve) and Rao's quadratic entropy (RaoQ) to characterize the functional diversity of  
152 spider assemblages, using FD package in R (Laliberté *et al.*, 2014). The FRic index describes the  
153 dispersion of all species in a trait space without information on relative abundances, the FEve  
154 index the combines distribution of species traits and evenness of species relative abundances  
155 (Laliberté and Legendre, 2010). The RaoQ index was useful for detecting assembly rules, habitat  
156 filtering (trait convergence) and limiting similarity (trait divergence; Botta-Dukat & Czucz, 2016).  
157 We used the Poisson error term for species richness data, negative binomial error term for  
158 abundance data to account for over-dispersion of the data and Gaussian error terms for RaoQ and  
159 CWM values.

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

168

169

## 170 **Results**

171

172 Herbaceous plant cover was higher in non-invaded than in invaded sites ( $z = 2.257$ ,  $p = 0.024$ ).  
173 However, leaf litter cover was higher in invaded than in non-invaded sites ( $z = -2.032$ ,  $p = 0.042$ ),  
174 and it was higher in poplar compared to pine plantations ( $z = 2.547$ ,  $p = 0.011$ ). No difference was  
175 found in the height of the vegetation.

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

180 We did not find a significant effect of tree species or *A. syriaca* invasion on the species  
181 richness and abundance of spider assemblages (Table 1). There was a significant effect of *A.*  
182 *syriaca* on RaoQ of spiders, with the invaded sites having lower functional diversity than non-  
183 invaded sites. The significant interaction effect of forest types and invasion of *A. syriaca* on RaoQ  
184 of spiders indicated that invasion had a more pronounced effect in pine than in poplar forests (Fig.  
185 1a). We did not find a significant effect of tree species or *A. syriaca* invasion on FRic and FEve  
186 indices. Spider species were larger (Fig. 1b) and web building spiders were more abundant (Fig.  
187 1c) in poplar forests than in pine plantations; however, there was no significant effect of moisture  
188 and shading (Table 1).

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

194

## 195 **Discussion**

196

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

203 Canopy closure is among the most important determinants of spider species richness and  
204 assemblage composition, because it can affect the soil microclimate and understory vegetation  
205 development (Finch, 2005; Lange *et al.*, 2011). Vegetation structure provides various micro-  
206 habitats (Rodrigues & Mendonça Jr, 2012), which in turn, determine the species composition of

207 spider assemblages. In the present study, both poplar and pines forests were commercially mature.  
208 Mature plantation forests generally have dense understory vegetation (Calviño-cancela *et al.*,  
209 2012) and well-developed canopies that reduce extreme microclimatic variation (Harms *et al.*,  
210 2000). Herbaceous vegetation structure depends on the light availability at the forest floor. Poplar  
211 forests have relatively open canopies and sunlight penetrates to the forest floor, favoring more  
212 diverse herbaceous understory vegetation than for pine plantations with their closed canopies  
213 (Balandier *et al.*, 2006). The resulting complex vegetation structure might provide numerous  
214 potential web attachments for web-building spider species (Schirmel *et al.*, 2012). We found that  
215 species composition differed between forest types, as indicated by the significant results of  
216 multivariate PERMANOVA and the clear separation by NMDS ordination. The high number of  
217 significant indicator species also underpinned the marked differences in spider assemblages of  
218 pine and poplar forests, even though we detected no differences in herbaceous vegetation cover  
219 between the plantations types.

220         The quality and quantity of leaf litter determined the microhabitat structure of the forest  
221 floor, thus having an effect on the diversity of spiders (Pearce *et al.*, 2004; Castro & Wise, 2009).  
222 The thick layer of deciduous leaf litter in poplar forests creates a more complex forest floor than  
223 in pine forests (Gallé *et al.*, 2014). Furthermore, the leaf litter in pine plantations consists of pines  
224 needles which reduces soil pH and may change the physical properties of the soil, as well (Selvi  
225 *et al.*, 2017). Coniferous forests generally provide less diversified herbaceous understory  
226 vegetation than deciduous forests due to different soil conditions and lower light availability  
227 (Barbier *et al.*, 2008). The resulting relatively uniform microhabitat conditions of pine plantations  
228 may result in a uniform spider species composition (Schultz, 1997). Besides habitat structure, leaf  
229 litter also influences the abundance of decomposer organisms, and therefore, potential food  
230 sources for spiders. Springtails (Collembola) provide a large part of the diet of ground-dwelling  
231 spiders in forests (Block & Zettel, 2003; Wise, 2004). Springtails are more abundant in native  
232 forests than in exotic plantations (Kováč *et al.*, 2005; Bolger *et al.*, 2013), offering an easily  
233 accessible food source for ground-dwelling spiders in poplar forests, and may enhance the  
234 colonization and increase the abundance of larger species of spider. In the present study, we also  
235 found larger CWM size values in poplar forests.

236         Invasive plants affect species composition of spider assemblages (Bultman & DeWitt,  
237 2008; Mgobozi *et al.*, 2008), and the behavior and density of spider species (Gallé *et al.*, 2015;



238 Pearson, 2009). Invasive plant species may have a direct effect on spiders, as they affect the  
239 architecture of vegetation (Souza & Martins, 2005; Simao *et al.*, 2010) and therefore, habitat  
240 structure. Included in these changes are a variety of shelters and structural supports for web  
241 building (Litt *et al.*, 2014).

242 Plant invasion may provide herbivore arthropods with novel food resources (Bezemer *et*  
243 *al.*, 2014), thus affecting the potential prey abundance for spiders. In North America, where *A.*  
244 *syriaca* is a native plant, 457 insect species from 8 orders are associated with it, mainly as  
245 pollinators and specialist herbivores (Dailey *et al.*, 1978). The continuously open flowers are a  
246 relatively large and stable food resource for pollinator insects (Dafni & Kevan, 1997). However,  
247 association as herbivores or pollinators may require a common evolutionary history with the  
248 invasive plant (Tallamy *et al.*, 2010). The poisonous cardenolide content of its white latex hinders  
249 top-down control of native generalist herbivores (Zandt & Agrawal, 2018), and specialist native  
250 herbivores are presumably negatively affected by loss of native vegetation due to the invasion of  
251 *A. syriaca* (Litt *et al.*, 2014). Several authors found that herbivore abundance was reduced due to  
252 plant invasion (Simao *et al.*, 2010; Cronin *et al.*, 2015).

253 Plant invasion may also change plant–pollinator relations, either positively or negatively  
254 (Larson *et al.*, 2006; Bartomeus *et al.*, 2008; Fenesi *et al.*, 2015). Furthermore, invasive plant  
255 species can weaken the relationship between native plants and their pollinators (Aizen *et al.*, 2008),  
256 resulting in significant changes in pollinator abundances and assemblage structure. In accordance  
257 with Bezemer *et al.*, (2014), we did not find a significant indirect effect of altered prey availability  
258 of invaded sites on spider species richness and abundance. This was in line with Groot *et al.*,  
259 (2007), who suggested that profiles of predatory arthropods such as spiders were not closely related  
260 to plant species composition, and were less vulnerable to the effects of invasive plants. However,  
261 we found that *A. syriaca* had a negative effect on the functional diversity of spiders, and this effect  
262 was larger in pine plantations than in poplar forests.

263 In pine plantations, the similar species richness and the higher functional diversity (RaoQ  
264 index) of non-invaded sites suggest that traits values are less similar than in invaded sites, and  
265 functionally different species are present in the assemblage (Schirmel & Buchholz, 2013). In  
266 contrast, the invaded sites had lower functional diversity, and thus a uniform trait state  
267 composition. Invaded pine forests only favored certain trait state combinations, which implied that

268 environmental filtering played an important role in species sorting. This presumably precluded the  
269 colonization of several species of the original forest-steppe fauna.

270 In conclusion, plantation type and invasion of *A. syriaca* affected different elements of  
271 spider functional diversity. Spider species composition of exotic forests was different from that of  
272 native forest assemblages, and they were not functionally equivalent. This might also affect  
273 arthropod food web structure (Gratton & Denno, 2006). In exotic plantations, invasion of *A.*  
274 *syriaca* had an effect on the trait composition of spiders, suggesting strong habitat filtering and the  
275 generation of low quality secondary habitats for the original spider fauna. This may have further  
276 top-down effects on the broader invertebrate herbivore and detritivore community. The  
277 information on the effect of pine plantations and *A. syriaca* invasion on biodiversity is critical for  
278 forestry and conservation management (Mgobozi *et al.*, 2008).

279

#### 280 Acknowledgement

281

282 This work was supported by the Hungarian National Research, Development and Innovation  
283 Office (Grant Id: NKFIFK-124579) and the "Lendület" program of the Hungarian Academy of  
284 Sciences. KI and HK are supported by Stipendium Hungaricum Scholarship of Tempus Public  
285 foundation. Authors have no conflict of interest.

286

287

288 **References**

- 289 Aizen, M.A., Morales, C.L., & Morales, J.M. (2008) Invasive mutualists erode native pollination  
290 webs. *PLoS Biology*. **6**, 396–403.
- 291 Augusto, L., Ranger, J., Binkley, D., & Rothe, A. (2002) Impact of several common tree species  
292 of European temperate forests on soil fertility. *Annals of Forest Science* **59**, 233–253.
- 293 Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., & Zedaker, S.M. (2006) Designing forest  
294 vegetation management strategies based on the mechanisms and dynamics of crop tree  
295 competition by neighbouring vegetation. *Forestry*. **79**, 3–27.
- 296 Balogh, L., Dancza, I., & Király, G. (2007) Preliminary report on the grid-based mapping of  
297 invasive plants in Hungary. In : *In Rabitsch, W., F. Essl & F. Klingenstein (Eds.).*  
298 *Biological Invasions – from Ecology to Conservation*. 105–114.
- 299 Barbier, S., Gosselin, F., & Balandier, P. (2008) Influence of tree species on understory  
300 vegetation diversity and mechanisms involved- a critical review for temperate and boreal  
301 forests. *Forest Ecology and Management*. **254**, 1–15.
- 302 Bartomeus, I., Vila, M., & Santamaría, L. (2008) Contrasting effects of invasive plants in plant-  
303 pollinator networks. *Oecologia*. **155**, 761–770.
- 304 Bell, J.R., Bohan, D.A., Shaw, E.M., & Weyman, G.S. (2005) Ballooning dispersal using silk:  
305 world fauna, phylogenies, genetics and models. *Bulletin of Environmental Research*. **95**,  
306 69–114.
- 307 Bezemer, T.M., Harvey, J.A., & Cronin, J.T. (2014) Response of native insect communities to  
308 invasive plants. *Annual Reviews in Entomology* **59**, 119–141.
- 309 Blandenier, G. (2009) Ballooning of spiders (Araneae) in Switzerland: general results from an  
310 eleven-year survey. *Bulletin of British Arachnological Society* **14**, 308–316.
- 311 Block, W., & Zettel, J. (2003) Activity and dormancy in relation to body water and cold  
312 tolerance in a winter-active springtail (Collembola). *European Journal of Entomology*.  
313 **100**, 305–312.
- 314 Bolger, T., Kenny, J., & Arroyo, J. (2013) The Collembola fauna of Irish forests—a comparison  
315 between forest type and microhabitats within the forests. *Soil Organisms*. **85**, 61–67.
- 316 Botta-Dukat, Z., & Czucz, B. (2016) Testing the ability of functional diversity indices to detect  
317 trait convergence and divergence using individual-based simulation. *Methods in Ecology*  
318 *and Evolution*. **7**, 114–126.
- 319 Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., & Sayer, J. V (2008) Plantation forests  
320 and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**, 925–951.
- 321 Buchar, J., & Ruzicka, V. (2002) Catalogue of spiders of the Czech Republic. Peres, Prague.

- 322 Bukovinszky, T., Gols, R., Agrawal, A.A., Roge, C., Bezemer, T.M., Biere, A., & Harvey, J.A.  
323 (2014) Reciprocal interactions between native and introduced populations of common  
324 milkweed, *Asclepias syriaca*, and the specialist aphid, *Aphis nerii*. *Basic and Applied*  
325 *Ecology*. **15**, 444–452.
- 326 Bultman, T.L., & DeWitt, D.J. (2008) Effect of an invasive ground cover plant on the abundance  
327 and diversity of a forest floor spider assemblage. *Biological Invasions*. **10**, 749–756.
- 328 Calviño-cancela, M., Rubido-bará, M., & Etten, E.J.B. Van (2012) Do eucalypt plantations  
329 provide habitat for native forest biodiversity? *Forest Ecology and Management*. **270**,  
330 153–162.
- 331 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,  
332 Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace,  
333 J.B., Larigauderie, A., Srivastava, D., Naeem, S. (2012) Biodiversity loss and its impact  
334 on humanity. *Nature*. **486**, 59–67.
- 335 Cardoso, P., Pekar, S., Jocque, R., & Coddington, J.A. (2011) Global patterns of guild  
336 composition and functional diversity of spiders. *PLoS One*. **6**.
- 337 Carter, E.T., Eads, B.C., Ravesi, M.J., & Kingsbury, B.A. (2015) Exotic invasive plants alter  
338 thermal regimes: implications for management using a case study of a native ectotherm.  
339 *Functional Ecology*. **29**, 683–693.
- 340 Castro, A., & Wise, D.H. (2009) Influence of fine woody debris on spider diversity and  
341 community structure in forest leaf litter. *Biodivers Conserv*. **18**, 3705–3731.
- 342 Chiarucci, A., & De Dominicis, V. (1995) Effects of pine plantations on ultramafic vegetation of  
343 central Italy. *Israel journal of plant sciences*. **43**, 7–20.
- 344 Corcuera, P., Valverde, P.L., Jimenez, M.L., Ponce-Mendoza, A., Rosa, G.D. la, Nieto, G.  
345 (2016) Ground Spider Guilds and Functional Diversity in Native Pine Woodlands and  
346 Eucalyptus Plantations. *Community and Ecosystem Ecology*. **45**, 292–300.
- 347 Cronin, J.T., Bhattarai, G.P., Allen, W.J., & Meyerson, L.A. (2015) Biogeography of a plant  
348 invasion: plant-herbivore interactions. *Ecology*. **96**, 1115–1127.
- 349 Császár, P., Torma, A., Gallé-Szpisjak, N., Tölgyesi, C., & Gallé, R. (2018) Efficiency of pitfall  
350 traps with funnels and/or roofs in capturing ground-dwelling arthropods. *European*  
351 *Journal of Entomology*. **115**, 15–24.
- 352 Csontos, P., Bozsing, E., Cseresnyes, I., & Penksza, K. (2009) Reproductive potential of the  
353 alien species *Asclepias syriaca* (Asclepiadaceae) in the rural landscape. *Polish Journal of*  
354 *Ecology*. **57**, 383–388.
- 355 Dafni, B.A., & Kevan, M.L.P.G. (1997) Spatial flower parameters and insect spatial vision.  
356 *Biological Reviews*. **72**, 239–282.

- 357 Dailey, P.J., Graves, R.C., & Kingsolver, J.M. (1978) Survey of coleoptera collected on the  
358 common milkweed, *Asclepias syriaca*, at one site in Ohio. *The Coleopterists Bulletin*. **32**,  
359 223–229.
- 360 Dalzochio, M.S., Baldin, R., Stenert, C., Maltchik, L. (2016) How does the management of rice  
361 in natural ponds alter aquatic insect community functional structure? *Marine Freshwater*  
362 *Research*. **67**, 1644–1654.
- 363 Dalzochio, M.S., Périco, E., Renner, S., Sahlén, G. (2018). Effect of tree plantations on the  
364 functional composition of Odonata species in the highlands of southern Brazil.  
365 *Hydrobiologia*, **808**, 283–300.
- 366 Ducs, A., Kazi, A., Bilkó, Á., & Altbäcker, V. (2016) Milkweed control by food imprinted  
367 rabbits. *Behavioural Processes*. **130**, 75–80.
- 368 Duftrne, M., & Legendre, P. (1997) Species assemblages and indicator species: the need for a  
369 flexible asymmetrical approach. *Ecological Monographs*. **67**, 345–366.
- 370 Fenesi, A., Vágási, C.I., Beldean, M., Földesi, R., Kolcsár, L., Teresa, J., & Török, E. (2015)  
371 *Solidago canadensis* impacts on native plant and pollinator communities in different-aged  
372 old fields. *Basic and Applied Ecology*. **16**, 335–346.
- 373 Finch, O.-D. (2005) Evaluation of mature conifer plantations as secondary habitat for epigeic  
374 forest arthropods (Coleoptera: Carabidae; Araneae). *Forest Ecology and Management*.  
375 **204**, 21–34.
- 376 Gaertner, E. (1979) The history and use of milkweed (*Asclepias syriaca* L.). *Economic Botany*.  
377 **33**, 119–123.
- 378 Gallé, R., Erdélyi, N., Szpisjak, N., Csaba, T., & Maák, I. (2015) The effect of the invasive  
379 *Asclepias syriaca* on the ground-dwelling arthropod fauna. *Biologia*. **70**, 104–112.
- 380 Gallé, R., Kanizsai, O., Ács, V., & Molnár, B. (2014) Functioning of ecotones – spiders and ants  
381 of edges between native and non-native forest plantations. *Polish Journal of Ecology*,  
382 815–820.
- 383 Gallé, R., Szabó, Á., Császár, P., & Torma, A. (2018) Forest Ecology and Management Spider  
384 assemblage structure and functional diversity patterns of natural forest steppes and exotic  
385 forest plantations. *Forest Ecology and Management*. **411**, 234–239.
- 386 Gomes, M., Carvalho, C., & Gomes, P. (2017) Invasive plants induce the taxonomic and  
387 functional replacement of dune spiders. *Biological Invasions*.
- 388 Gratton, C., & Denno, R. (2006) Arthropod food web restoration following removal of an  
389 invasive wetland plant. *Ecological Applications*. **16**, 622–631.
- 390 Groot, M. De, Kleijn, D., & Jogan, N. (2007) Species groups occupying different trophic levels  
391 respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*.

- 392 *Biological Conservation*. **136**, 612–617.
- 393 Harms, W.R., Whitesell, C.D., & DeBell, D.S. (2000) Growth and development of loblolly pine  
394 in a spacing trial planted in Hawaii. *Forest Ecology and Management*. **126**, 13–24.
- 395 Henneron, L., Aubert, M., Bureau, F., Dumas, Y., Ningre, F., Perret, S., Richter, C., Balandier,  
396 P., & Chauvat, M. (2015) Forest management adaptation to climate change: a Cornelian  
397 dilemma between drought resistance and soil macro-detritivore functional diversity. *J.*  
398 *Appl. Ecol.* **52**, 913–927.
- 399 Kelemen, A., Valk, O., Kroel-Dulay, G., Deak, B., Torok, P., Toth, K., Miglecz, T., &  
400 Tothmeresz, B. (2016) The invasion of common milkweed (*Asclepias syriaca*) in sandy  
401 old-fields – is it a threat to the native flora? *Applied Vegetation Science*. **19**, 218–224.
- 402 Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie,  
403 M.E., Howe, K.M., Reich, P.B., Siemann, E., & Groth, J. (1999) Effects of plant species  
404 richness on invasion dynamics, disease outbreaks, insect abundances and diversity.  
405 *Ecology Letters*. **2**, 286–293.
- 406 Kováč, L.U., Kostúrová, N., & Miklisová, D. (2005) Comparison of collembolan assemblages  
407 (Hexapoda, Collembola) of thermophilous oak woods and *Pinus nigra* plantations in the  
408 Slovak Karst (Slovakia). *Pedobiologia*. **49**, 29–40.
- 409 Kuuluvainen, T., Tahvonen, O., & Aakala, T. (2012) Even-aged and uneven-aged forest  
410 management in Boreal Fennoscandia: a review. *AMBIO*. **41**, 720–737.
- 411 Laliberté, E., Legendre, P., & Shipley, B. (2014) FD: measuring functional diversity from  
412 multiple traits, and other tools for functional ecology. R package version 1.0-12.
- 413 Laliberté, E., Legendre, P. (2010) A distance-based framework for measuring functional  
414 diversity from multiple traits. *Ecology* **91**, 299–305.
- 415 Lange, M., Weisser, W.W., Gossner, M.M., Carlos, J., Fonseca, R., Kowalski, E., & Tu, M.  
416 (2011) The impact of forest management on litter-dwelling invertebrates: a subtropical-  
417 temperate contrast. *Biodiversity and Conservation* **20**, 2133–2147.
- 418 Larson, D.L., Royer, R.A., & Royer, M.R. (2006) Insect visitation and pollen deposition in an  
419 invaded prairie plant community. *Biological Conservation*. **130**, 148–159.
- 420 Lassauce, A., Paillet, Y., Jactel, H. & Bouget C. (2011) Deadwood as a surrogate for forest  
421 biodiversity: meta-analysis of correlations between deadwood volume and species  
422 richness of saproxylic organisms. *Ecological Indicators*. **11**, 1027–1039.
- 423 Litt, A.R., Cord, E.E., Fulbright, T.E., & Schuster, G.L. (2014) Effects of invasive plants on  
424 arthropods. *Conservation Biology*. **28**, 1532–1549.
- 425 Magura, T. (2017) Ignoring functional and phylogenetic features masks the edge influence on  
426 ground beetle diversity across forest-grassland gradient. *Forest Ecology and*

- 427           *Management*. **384**, 371–377.
- 428 Mgobozi, M., Somers, M.J., & Dippenaar-schoeman, A.S. (2008) Spider responses to alien plant  
429 invasion : the effect of short- and long-term *Chromolaena odorata* invasion and  
430 management. *Journal of Applied Ecology*. **45**, 1189–1197.
- 431 Nentwig, W., Blick, T., Gloor, D., Hanggi, A., & Kropf, C. (2017) Spiders of Europe. [online].  
432 Available from: [www.araneae.unibe.ch](http://www.araneae.unibe.ch) [Accessed March 9, 2018].
- 433 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson,  
434 G.L., Solymos, P., Stevens, H.M.H., & Wagner H. (2015) vegan: Community Ecology  
435 Package. R package version 2.3-0.
- 436 Payn, T., Carnus, G., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez,  
437 L., Silva, L., & Wingfield, M. (2015) Changes in planted forests and future global  
438 implications. *Forest Ecology and Management*. **352**, 57–67.
- 439 Pearce, J.L., Venier, L.A., Eccles, G., Pedlar, J., & Mckenney, D. (2004) Influence of habitat and  
440 microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiversity  
441 and Conservation*. **13**, 1305–1334.
- 442 Pearson, D.E. (2009) Invasive plant architecture alters trophic interactions by changing predator  
443 abundance and behavior. *Oecologia*. **159**, 549–558.
- 444 Petchey, O.L., & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward.  
445 *Ecology Letters*. **9**, 741–758.
- 446 Pysek, P., Jarosik, V., Hulme, P., Pergl, J., Hejda, M., Schaffner, U., & Vila, M. (2012) A global  
447 assessment of invasive plant impacts on resident species, communities and ecosystems:  
448 the interaction of impact measures, invading species’ traits and environment. *Global  
449 Change Biology*. **18**, 1725–1737.
- 450 Roberts, D.W., & Roberts, M.D.W. (2016) Package ‘labdsv’. Ordination and Multivariate.
- 451 Rodrigues, E.N.L., & Mendonça Jr, M. de S. (2012) Spider guilds in the tree-shrub strata of  
452 riparian forests in southern Brazil. *The Journal of Arachnology*. **40**, 39–47.
- 453 Schirmel, J., Blindow, I., & Buchholz, S. (2012) Life-history trait and functional diversity  
454 patterns of ground beetles and spiders along a coastal heathland successional gradient.  
455 *Basic and Applied Ecology*. **13**, 606–614.
- 456 Schirmel, J., & Buchholz, S. (2013) Invasive moss alters patterns in life-history traits and  
457 functional diversity of spiders and carabids. *Biological Invasions*. **15**, 1089–1100.
- 458 Schultz, R. (1997) *Loblolly pine- the ecology and culture of Loblolly pine (Pinus taeda L.)*. US  
459 Government printing office.
- 460 Schulze, E. D., Aas, G., Grimm, G. W., Gossner, M. M., Walentowski, H., Ammer, C., & Von

- 461 Gadow, K. (2016) A review on plant diversity and forest management of European beech  
462 forests. *European journal of forest research*. **135**, 51-67.
- 463 Selvi, F., Carrari, E., Colzi, I., Coppi, A., & Gonnelli, C. (2017) Responses of serpentine plants  
464 to pine invasion: vegetation diversity and nickel accumulation in species with contrasting  
465 adaptive strategies. *Science of the Total Environment*. **595**, 72–80.
- 466 Simao, M.C.M., Flory, S.L., & Rudgers, J.A. (2010) Experimental plant invasion reduces  
467 arthropod abundance and richness across multiple trophic levels. *Oikos*. **119**, 1553–1562.
- 468 Somogyi, A.A., Gabor, L., Kovacs, J., & Maak, I.E. (2017) Structure of ant assemblages in  
469 planted poplar (*Populus alba*) forests and the effect of the common milkweed (*Asclepias*  
470 *syriaca*). *Acta Zoologica Academiae Scientiarum Hungaricae*. **63**, 443–457.
- 471 Southwick, E.E. (1983) Nectar biology and nectar feeders of common milkweed , *Asclepias*  
472 *syriaca* L. *Bulletin of the Torrey Botanical Club*. **110**, 324–334.
- 473 Souza, T. De, Martins, P. (2005) Foliage density of branches and distribution of plant-dwelling  
474 spiders. *Biotropica*. **37**, 416–420.
- 475 Spirito, F., Yahdjian, L., Tognetti, P.M., & Chaneton, E.J. (2014) Soil ecosystem function under  
476 native and exotic plant assemblages as alternative states of successional grasslands. *Acta*  
477 *Oecologica*. **54**, 4–12.
- 478 Szitar, K., Kroel-dulay, G., & Torok, K. (2018) Invasive *Asclepias syriaca* can have facilitative  
479 effects on native grass establishment in a water- - stressed ecosystem. *Applied Vegetation*  
480 *Science*. **21**, 607-614.
- 481 Szitár, K., Ónodi, G., Somay, L., Pándi, I., Kucs, P., & Kröel-dulay, G. (2016) Contrasting  
482 effects of land use legacies on grassland restoration in burnt pine plantations. *Biological*  
483 *Conservation*. **201**, 356–362.
- 484 Tallamy, D.W., Ballard, M., & Amico, V.D. (2010) Can alien plants support generalist insect  
485 herbivores? *Biological Invasions*. **12**, 2285–2292.
- 486 Török, K., Halassy, M., & Szabó, R. (2003) Restoration strategy for endemic grasslands in a low  
487 productive region of Hungary. In *Proceedings of the VIIth International Rangelands*  
488 *Congress*. 1132–1138.
- 489 Urcelay, C., Longo, S., Geml, J., Tecco, P.A., & Nouhra, E. (2017) Co-invasive exotic pines and  
490 their ectomycorrhizal symbionts show capabilities for wide distance and altitudinal range  
491 expansion. *Fungal Ecology*. **25**, 50–58.
- 492 Vitousek, P.M., D'Antonio, C.M., Loope, L.L., & Westbrooks, R. (1996) Biological invasions as  
493 global environmental change. *American Scientist*, 218–228.
- 494 Wise, D.H. (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-  
495 floor food web. *Pedobiologia*. **48**, 181–188.



496 Zandt, P.A. Van, & Agrawal, A.A. (2018) Specificity of induced plant responses to specialist  
497 herbivores of the common milkweed *Asclepias syriaca*. *Oikos*. **104**, 401–409.

498

499 Figure legends

500

501 Figure 1. Effect of forest type and *Asclepias syriaca* invasion on spider functional diversity. Open  
502 circles: non-invaded; black dots: invaded sites. (A) RaoQ index; (B) Community weighted mean  
503 (CWM) of hunting strategy; (C) CWM value of spider body sizes.

504

505 Figure 2. NMDS ordination plot of spider samples (dots), with significant indicator species  
506 (crosses), and community weighted mean values (CWM) also fitted (arrows). Black dots: pine  
507 plantations, open circles: poplar plantations. Species names are abbreviated with the first letter of  
508 genus name and the first three letters of species names, please see Appendix 2. for further details.

509

1

2

**Forest type interacts with milkweed invasion to affect spider communities**

3

4 Ingle, Kapilkumar<sup>1,2</sup>, Gallé-Szpisjak, Nikolett<sup>3</sup>, Kaur, Hardeep<sup>1</sup>, Gallé, Róbert<sup>3, 1\*</sup>5 <sup>1</sup> Department of Ecology, University of Szeged, Hungary6 <sup>2</sup> Doctoral School of Environmental Sciences, University of Szeged, Rerrich Béla tér 1, H-6720

7 Szeged, Hungary

8 <sup>3</sup> MTA ÖK Lendület Landscape and Conservation Ecology Research Group, Hungary

9 \* Corresponding author

10

11 Short title: Spiders of invaded plantation forests

12

13

14 **Abstract.**

15 1. Non-native tree plantations constitute a large part of forestation worldwide. Plantations are  
16 prone to invasion by exotic herbaceous plant species due to habitat properties, including understory  
17 vegetation structure.

18 2. We established 40 sampling sites in 10 plantation forests. Sites were selected according  
19 to tree species (native poplar forests, exotic pine plantations) and common milkweed (*Asclepias*  
20 *syriaca*) density (invaded, non-invaded sites) in a full factorial design. We collected spiders with  
21 pitfall traps.

22 3. We found a significant effect of *A. syriaca* invasion on spider functional diversity (Rao's  
23 quadratic entropy), with invaded sites having a lower functional diversity than non-invaded sites.  
24 A significant effect of *A. syriaca* on functional diversity (Rao's quadratic entropy) was indicated by

25 ~~GLMMs, with invaded sites having a lower functional diversity than non-invaded sites.~~ A larger  
26 effect of invasion with *A. syriaca* on the RaoQ of spiders was observed in pine compared to poplar  
27 plantations. Spider species were larger and web building spiders were more frequent in poplar  
28 forests than in pine plantations. ~~;~~ We found no effect of *A syriaca* invasion on species richness or  
29 abundance of spiders. ~~however, we found no effect on species richness and abundance.~~

30 4. Species composition of spider assemblages in the two forest types were clearly  
31 composition of the 2 forest types clearly separated according to non-metric multidimensional  
32 scaling. We identified 7 species associated with pine plantations and 6 species associated with  
33 poplar plantations.

34 5. The similar species richness and the higher functional diversity of non-invaded sites  
35 suggested that these trait states were less similar than invaded sites, and that functionally different  
36 species were present. In contrast, the invaded sites had lower functional diversities, and thus more  
37 uniform trait state compositions, suggesting that environmental filtering played an important role  
38 in species sorting, making invaded plantations low quality secondary habitats for the original  
39 spider fauna.

40

41 **Key words.** Plantation, forest, invasion, spider, Araneae, functional diversity, species  
42 composition, pine, poplar, *Asclepias syriaca*.

43

## 44 **Introduction**

45

46 The land cover of commercial tree plantations is increasing worldwide, replacing natural forests.  
47 These secondary forests include native and non-native tree plantations. Generally, they have a  
48 negative impact on the original native ecosystems (Vitousek *et al.*, 1996; Gratton & Denno, 2006;  
49 Spirito *et al.*, 2014), Although international pressure is increasing to tackle the negative  
50 environmental effects of such plantations, tree plantation covers more than 7% of total forest area  
51 worldwide (Payn *et al.*, 2015). However, plantations may also have a positive impact on local

52 biodiversity by providing secondary habitats for rare and threatened species (Brockerhoff *et al.*,  
53 2008).

54 Pine plantations are common in Europe, where they are generally used for timber  
55 production. Pine trees can alter hydrologic regimes (Urcelay *et al.*, 2017), microclimate and soil  
56 properties. The layer of pine needles on forest floor makes the soil acidic (Selvi *et al.*, 2017), and  
57 the change in chemical and physical properties of the soil results in loss of fertility (Augusto *et al.*,  
58 2002). These processes are responsible for the changes in understory vegetation structure and  
59 microhabitat diversity (Chiarucci & De Dominicis, 1995), and in turn, lower species diversity of  
60 arthropods compared to natural forests (Brockerhoff *et al.*, 2008; Gallé *et al.*, 2018).

61 Due to altered microclimate and soil properties, plantation forests are prone to invasion by  
62 non-native herbaceous plant species (Henneron *et al.*, 2015). In turn, invasive plants alter  
63 vegetation diversity (Knops *et al.*, 1999) and biotic interactions (Bezemer *et al.*, 2014). A high  
64 density of invasive plants changes the physical properties of a habitat by altering its structure,  
65 including its microclimatic conditions, such as the light intensity and temperature of the invaded  
66 area (Carter *et al.*, 2015). These changes may lead to changes in ecosystem functioning (Schirmel  
67 & Buchholz, 2013; Gomes *et al.*, 2017).

68 Common milkweed (*Asclepias syriaca*) in Europe spreads aggressively and is found in 11  
69 European countries (Szitar *et al.*, 2018). It establishes dense populations in disturbed habitats  
70 (Pysek *et al.*, 2012; Kelemen *et al.*, 2016), and may change the composition of existing vegetation  
71 and form novel ecosystems (Kelemen *et al.*, 2016; Szitár *et al.*, 2016). Milkweed was introduced  
72 into Europe in the 17<sup>th</sup> century (Gaertner, 1979; Bukovinszky *et al.*, 2014) from eastern North  
73 America and into Hungary in the 18<sup>th</sup> century by beekeepers (Balogh *et al.*, 2007; Csontos *et al.*,  
74 2009). Currently, *A. syriaca* endangers the semi-natural and natural vegetation of sandy regions  
75 (Ducs *et al.*, 2016), has become one of the most abundant invasive plant species in Hungarian  
76 lowland forest plantations, and represents a major problem in conservation areas (Szitár *et al.*,  
77 2016). However, its negative effects are not always straightforward (Szitár *et al.*, 2016; Somogyi  
78 *et al.*, 2017). *A. syriaca* attracts many insects, particularly pollinators, because of the open  
79 structure of its flowers. As such, it serves as a continuous resource for pollinators day and night,  
80 attracting both diurnal and nocturnal pollinators (Southwick, 1983). The high density of  
81 pollinators, in turn, may attract predatory arthropods. The effect of plant invasion on arthropod

82 assemblage structure is still not well defined, and is crucial in understanding terrestrial ecosystem  
83 ecology (Bezemer *et al.*, 2014).

84 Although there are reports on the ecology of forest invertebrates in the context of changes in quality  
85 (reviewed by Kuuluvainen *et al.*, 2012, Lassauce *et al.*, 2011, Schulze *et al.*, 2016). The majority  
86 of this work focuses on species diversity patterns (Kuuluvainen *et al.*, 2012), with few studies  
87 focusing on functional diversity of spiders (Magura, 2017, Gallé *et al.*, 2018). The concept of  
88 functional diversity helps to explain how ecosystems react to environmental change (Petchey &  
89 Gaston, 2006; Cardoso *et al.*, 2011). Changes in habitat quality may act as a filter, structuring the  
90 community with functionally similar species (Cardinale *et al.*, 2012, Dalzochio *et al.*, 2016).

91 The effect of habitat structure of forests on functional diversity of arthropods has been documented  
92 (Corcuera *et al.*, 2016; Dalzochio *et al.*, 2018; Gallé *et al.*, 2018); however, there is limited  
93 information on how arthropod assemblages and functional diversity is affected by plant invasion  
94 in different forest types. In the present study, we focused on spider assemblages as the ideal  
95 indicators of the impact of plantation tree species and non-native plants on assemblage structure  
96 of invertebrates due to their sensitivity to vegetation structure (Mgobozi *et al.*, 2008).

97 In this study we assessed the effect of *A. syriaca* invasion on species richness, and species  
98 composition of spiders in the native and exotic plantation. We also applied the functional diversity  
99 concept to link diversity patterns with ecosystem processes and functioning. Hypotheses for this  
100 study were: (1) species richness would be higher in native forests compared to exotic forests, and  
101 tree species would have an effect on species functional diversity (i.e. functional richness and  
102 evenness, Rao's quadratic entropy and community weighted mean trait values) and composition  
103 of spider assemblages; (2) functional diversity and abundance of spiders would be higher in the  
104 forests which were invaded by *A. syriaca* as this plant would attract more pollinators, herbivores  
105 and associated predators; and (3) *A. syriaca* would have a different effect on spider diversity in  
106 native and exotic forests. We assumed, that changes in habitat structure by *A. syriaca* in the low  
107 quality exotic pine habitat may have a more pronounced deterioration effect on spider communities  
108 than in native forests.

109

## 110 **Materials and methods**

111

112 *Study area*

113 The present study was carried out in the Kiskunság region, in the southern part of the Great  
114 Hungarian Plain (Appendix 1.). The landscape was dominated by agriculture and semi-natural  
115 forest plantations, with small patches of the original forest-steppe habitats (Gallé *et al.*, 2018). The  
116 soil was calcareous coarse sand and the climate was semiarid with mean annual precipitation and  
117 temperatures in the ranges 550 – 600 mm and 10.2 – 10.8 °C, respectively (Török *et al.*, 2003).

118

### 119 *Study design and sampling*

120 We selected 5 poplar and 5 pine plantation forests for spider sampling. We surveyed ground-  
121 dwelling spiders at 4 sampling sites in each of the 10 forests, for a total of 40 sampling sites. Sites  
122 were selected according to tree species (native poplar forests vs. exotic pine plantations) and  
123 common milkweed density (invaded vs. non-invaded sites) in a full factorial design resulting in 10  
124 replicates per treatment combination. All sampled plantations were mature forests with no recent  
125 intensive forestry activity. Sampling sites were located at least 70 m distance from each other, and  
126 each sampling site was located more than 100 m from the forest edges. We assessed *A. syriaca*  
127 quantity in four 1 m<sup>2</sup> quadrates at each invaded sampling site; the density of *A. syriaca* stems was  
128  $7.33 \pm 3.86$  stems/m<sup>2</sup> (mean  $\pm$  SD), and its cover was  $30.31\% \pm 17.05$  (mean  $\pm$  SD). We  
129 characterized the habitat structure at the sampling sites by the approximate percentage cover of  
130 herbaceous plants (excluding *A. syriaca*), the average height of the vegetation and by the cover of  
131 leaf litter.

132 We used 3 pitfall traps for collecting spiders at each site. The traps were plastic cups with  
133 a diameter of 8.5 cm (Császár *et al.*, 2018). We supplied the traps with plastic funnels and we  
134 placed a metal roof above them. Traps were filled with a 50% water-ethylene-glycol solution to  
135 which we had added a few drops of detergent. Traps were open for three 7-day sampling periods:  
136 May 23 - 30, 2017; June 26 - July 3, 2017; and Oct 2 - 10, 2017.

137

### 138 *Data analysis*

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

144 We chose 4 attributes for functional categorization of spiders. We classified species according to:  
145 shading tolerance, ranging from 1 (open) to 4 (shaded); moisture preference, ranging from 1 (very  
146 dry) to 5 (very humid habitats); feeding, 0 (active hunter) and 1 (web builder); and size, as a  
147 continuous variable in mm (Buchar & Ruzicka 2002, Bell *et al.*, 2005, Blandenier 2009, Nentwig  
148 *et al.*, 2017). If a species was assigned to more than 1 category, the values were averaged. Spiders  
149 were considered as generalists if they were assigned to more than 3 categories in the case of  
150 shading tolerance and moisture preference. They were also considered generalist species if they  
151 were present at both extremes of the given categories, and their score was excluded from further  
152 analyses, as their distribution is determined by other factors. We calculated community-weighted  
153 mean (CWM) values for each trait at each sampling site; Functional richness (FRic), Functional  
154 evenness (FEve) and Rao's quadratic entropy (RaoQ) to characterize the functional diversity of  
155 spider assemblages, using FD package in R (Laliberté *et al.*, 2014). The FRic index describes the  
156 dispersion of all species in a trait space without information on relative abundances, the FEve  
157 index the combines distribution of species traits and evenness of species relative abundances  
158 (Laliberté and Legendre, 2010). The RaoQ index was useful for detecting assembly rules, habitat  
159 filtering (trait convergence) and limiting similarity (trait divergence; Botta-Dukat & Czucz, 2016).  
160 We used the Poisson error term for species richness data, negative binomial error term for  
161 abundance data to account for over-dispersion of the data and Gaussian error terms for RaoQ and  
162 CWM values.

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

171

172

## 173 **Results**

174



175 Herbaceous plant cover was higher in non-invaded than in invaded sites ( $z = 2.257$ ,  $p = 0.024$ ).  
176 However, leaf litter cover was higher in invaded than in non-invaded sites ( $z = -2.032$ ,  $p = 0.042$ ),  
177 and it was higher in poplar compared to pine plantations ( $z = 2.547$ ,  $p = 0.011$ ). No difference was  
178 found in the height of the vegetation.

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

183 We did not find a significant effect of tree species or *A. syriaca* invasion on the species  
184 richness and abundance of spider assemblages (Table 1). There was a significant effect of *A.*  
185 *syriaca* on RaoQ of spiders, with the invaded sites having lower functional diversity than non-  
186 invaded sites. The significant interaction effect of forest types and invasion of *A. syriaca* on RaoQ  
187 of spiders indicated that invasion had a more pronounced effect in pine than in poplar forests (Fig.  
188 1a). We did not find a significant effect of tree species or *A. syriaca* invasion on FRic and FEve  
189 indices. Spider species were larger (Fig. 1b) and web building spiders were more abundant (Fig.  
190 1c) in poplar forests than in pine plantations; however, there was no significant effect of moisture  
191 and shading (Table 1).

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

197

## 198 **Discussion**

199

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

206 Canopy closure is among the most important determinants of spider species richness and  
207 assemblage composition, because it can affect the soil microclimate and understory vegetation  
208 development (Finch, 2005; Lange *et al.*, 2011). Vegetation structure provides various micro-  
209 habitats (Rodrigues & Mendonça Jr, 2012), which in turn, determine the species composition of  
210 spider assemblages. In the present study, both poplar and pines forests were commercially mature.  
211 Mature plantation forests generally have dense understory vegetation (Calviño-cancela *et al.*,  
212 2012) and well-developed canopies that reduce extreme microclimatic variation (Harms *et al.*,  
213 2000). Herbaceous vegetation structure depends on the light availability at the forest floor. Poplar  
214 forests have relatively open canopies and sunlight penetrates to the forest floor, favoring more  
215 diverse herbaceous understory vegetation than for pine plantations with their closed canopies  
216 (Balandier *et al.*, 2006). The resulting complex vegetation structure might provide numerous  
217 potential web attachments for web-building spider species (Schirmel *et al.*, 2012). We found that  
218 species composition differed between forest types, as indicated by the significant results of  
219 multivariate PERMANOVA and the clear separation by NMDS ordination. The high number of  
220 significant indicator species also underpinned the marked differences in spider assemblages of  
221 pine and poplar forests, even though we detected no differences in herbaceous vegetation cover  
222 between the plantations types.

223 The quality and quantity of leaf litter determined the microhabitat structure of the forest  
224 floor, thus having an effect on the diversity of spiders (Pearce *et al.*, 2004; Castro & Wise, 2009).  
225 The thick layer of deciduous leaf litter in poplar forests creates a more complex forest floor than  
226 in pine forests (Gallé *et al.*, 2014). Furthermore, the leaf litter in pine plantations consists of pines  
227 needles which reduces soil pH and may change the physical properties of the soil, as well (Selvi  
228 *et al.*, 2017). Coniferous forests generally provide less diversified herbaceous understory  
229 vegetation than deciduous forests due to different soil conditions and lower light availability  
230 (Barbier *et al.*, 2008). The resulting relatively uniform microhabitat conditions of pine plantations  
231 may result in a uniform spider species composition (Schultz, 1997). Besides habitat structure, leaf  
232 litter also influences the abundance of decomposer organisms, and therefore, potential food  
233 sources for spiders. Springtails (Collembola) provide a large part of the diet of ground-dwelling  
234 spiders in forests (Block & Zettel, 2003; Wise, 2004). Springtails are more abundant in native  
235 forests than in exotic plantations (Kováč *et al.*, 2005; Bolger *et al.*, 2013), offering an easily  
236 accessible food source for ground-dwelling spiders in poplar forests, and may enhance the

237 colonization and increase the abundance of larger species of spider. In the present study, we also  
238 found larger CWM size values in poplar forests.

239 Invasive plants affect species composition of spider assemblages (Bultman & DeWitt,  
240 2008; Mgobozi *et al.*, 2008), and the behavior and density of spider species (Gallé *et al.*, 2015;  
241 Pearson, 2009). Invasive plant species may have a direct effect on spiders, as they affect the  
242 architecture of vegetation (Souza & Martins, 2005; Simao *et al.*, 2010) and therefore, habitat  
243 structure. Included in these changes are a variety of shelters and structural supports for web  
244 building (Litt *et al.*, 2014).

245 Plant invasion may provide herbivore arthropods with novel food resources (Bezemer *et*  
246 *al.*, 2014), thus affecting the potential prey abundance for spiders. In North America, where *A.*  
247 *syriaca* is a native plant, 457 insect species from 8 orders are associated with it, mainly as  
248 pollinators and specialist herbivores (Dailey *et al.*, 1978). The continuously open flowers are a  
249 relatively large and stable food resource for pollinator insects (Dafni & Kevan, 1997). However,  
250 association as herbivores or pollinators may require a common evolutionary history with the  
251 invasive plant (Tallamy *et al.*, 2010). The poisonous cardenolide content of its white latex hinders  
252 top-down control of native generalist herbivores (Zandt & Agrawal, 2018), and specialist native  
253 herbivores are presumably negatively affected by loss of native vegetation due to the invasion of  
254 *A. syriaca* (Litt *et al.*, 2014). Several authors found that herbivore abundance was reduced due to  
255 plant invasion (Simao *et al.*, 2010; Cronin *et al.*, 2015).

256 Plant invasion may also change plant–pollinator relations, either positively or negatively  
257 (Larson *et al.*, 2006; Bartomeus *et al.*, 2008; Fenesi *et al.*, 2015). Furthermore, invasive plant  
258 species can weaken the relationship between native plants and their pollinators (Aizen *et al.*, 2008),  
259 resulting in significant changes in pollinator abundances and assemblage structure. In accordance  
260 with Bezemer *et al.*, (2014), we did not find a significant indirect effect of altered prey availability  
261 of invaded sites on spider species richness and abundance. This was in line with Groot *et al.*,  
262 (2007), who suggested that profiles of predatory arthropods such as spiders were not closely related  
263 to plant species composition, and were less vulnerable to the effects of invasive plants. However,  
264 we found that *A. syriaca* had a negative effect on the functional diversity of spiders, and this effect  
265 was larger in pine plantations than in poplar forests.

266 In pine plantations, the similar species richness and the higher functional diversity (RaoQ  
267 index) of non-invaded sites suggest that traits values are less similar than in invaded sites, and

268 functionally different species are present in the assemblage (Schirmel & Buchholz, 2013). In  
269 contrast, the invaded sites had lower functional diversity, and thus a uniform trait state  
270 composition. Invaded pine forests only favored certain trait state combinations, which implied that  
271 environmental filtering played an important role in species sorting. This presumably precluded the  
272 colonization of several species of the original forest-steppe fauna.

273 In conclusion, plantation type and invasion of *A. syriaca* affected different elements of  
274 spider functional diversity. Spider species composition of exotic forests was different from that of  
275 native forest assemblages, and they were not functionally equivalent. This might also affect  
276 arthropod food web structure (Gratton & Denno, 2006). In exotic plantations, invasion of *A.*  
277 *syriaca* had an effect on the trait composition of spiders, suggesting strong habitat filtering and the  
278 generation of low quality secondary habitats for the original spider fauna. This may have further  
279 top-down effects on the broader invertebrate herbivore and detritivore community~~this may have a~~  
280 ~~top-down effect on invertebrate herbivore and decomposer assemblages~~. The information on the  
281 effect of pine plantations and *A. syriaca* invasion on biodiversity is critical for forestry and  
282 conservation management (Mgobozi *et al.*, 2008).

283

284 Acknowledgement

285

286 This work was supported by the Hungarian National Research, Development and Innovation  
287 Office (Grant Id: NKFIFK-124579) and the "Lendület" program of the Hungarian Academy of  
288 Sciences. KI and HK are supported by Stipendium Hungaricum Scholarship of Tempus Public  
289 foundation. Authors have no conflict of interest.

290

291

292 **References**

- 293 Aizen, M.A., Morales, C.L., & Morales, J.M. (2008) Invasive mutualists erode native pollination  
294 webs. *PLoS Biology*. **6**, 396–403.
- 295 Augusto, L., Ranger, J., Binkley, D., & Rothe, A. (2002) Impact of several common tree species  
296 of European temperate forests on soil fertility. *Annals of Forest Science* **59**, 233–253.
- 297 Balandier, P., Collet, C., Miller, J.H., Reynolds, P.E., & Zedaker, S.M. (2006) Designing forest  
298 vegetation management strategies based on the mechanisms and dynamics of crop tree  
299 competition by neighbouring vegetation. *Forestry*. **79**, 3–27.
- 300 Balogh, L., Dancza, I., & Király, G. (2007) Preliminary report on the grid-based mapping of  
301 invasive plants in Hungary. In : *In Rabitsch, W., F. Essl & F. Klingenstein (Eds.).*  
302 *Biological Invasions – from Ecology to Conservation*. 105–114.
- 303 Barbier, S., Gosselin, F., & Balandier, P. (2008) Influence of tree species on understory  
304 vegetation diversity and mechanisms involved- a critical review for temperate and boreal  
305 forests. *Forest Ecology and Management*. **254**, 1–15.
- 306 Bartomeus, I., Vila, M., & Santamaría, L. (2008) Contrasting effects of invasive plants in plant-  
307 pollinator networks. *Oecologia*. **155**, 761–770.
- 308 Bell, J.R., Bohan, D.A., Shaw, E.M., & Weyman, G.S. (2005) Ballooning dispersal using silk:  
309 world fauna, phylogenies, genetics and models. *Bulletin of Environmental Research*. **95**,  
310 69–114.
- 311 Bezemer, T.M., Harvey, J.A., & Cronin, J.T. (2014) Response of native insect communities to  
312 invasive plants. *Annual Reviews in Entomology* **59**, 119–141.
- 313 Blandenier, G. (2009) Ballooning of spiders (Araneae) in Switzerland: general results from an  
314 eleven-year survey. *Bulletin of British Arachnological Society* **14**, 308–316.
- 315 Block, W., & Zettel, J. (2003) Activity and dormancy in relation to body water and cold  
316 tolerance in a winter-active springtail (Collembola). *European Journal of Entomology*.  
317 **100**, 305–312.
- 318 Bolger, T., Kenny, J., & Arroyo, J. (2013) The Collembola fauna of Irish forests—a comparison  
319 between forest type and microhabitats within the forests. *Soil Organisms*. **85**, 61–67.
- 320 Botta-Dukat, Z., & Czucz, B. (2016) Testing the ability of functional diversity indices to detect  
321 trait convergence and divergence using individual-based simulation. *Methods in Ecology*  
322 *and Evolution*. **7**, 114–126.
- 323 Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., & Sayer, J. V (2008) Plantation forests  
324 and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**, 925–951.
- 325 Buchar, J., & Ruzicka, V. (2002) Catalogue of spiders of the Czech Republic. Peres, Prague.

- 326 Bukovinszky, T., Gols, R., Agrawal, A.A., Roge, C., Bezemer, T.M., Biere, A., & Harvey, J.A.  
327 (2014) Reciprocal interactions between native and introduced populations of common  
328 milkweed, *Asclepias syriaca*, and the specialist aphid, *Aphis nerii*. *Basic and Applied*  
329 *Ecology*. **15**, 444–452.
- 330 Bultman, T.L., & DeWitt, D.J. (2008) Effect of an invasive ground cover plant on the abundance  
331 and diversity of a forest floor spider assemblage. *Biological Invasions*. **10**, 749–756.
- 332 Calviño-cancela, M., Rubido-bará, M., & Etten, E.J.B. Van (2012) Do eucalypt plantations  
333 provide habitat for native forest biodiversity? *Forest Ecology and Management*. **270**,  
334 153–162.
- 335 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,  
336 Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace,  
337 J.B., Larigauderie, A., Srivastava, D., Naeem, S. (2012) Biodiversity loss and its impact  
338 on humanity. *Nature*. **486**, 59–67.
- 339 Cardoso, P., Pekar, S., Jocque, R., & Coddington, J.A. (2011) Global patterns of guild  
340 composition and functional diversity of spiders. *PLoS One*. **6**.
- 341 Carter, E.T., Eads, B.C., Ravesi, M.J., & Kingsbury, B.A. (2015) Exotic invasive plants alter  
342 thermal regimes: implications for management using a case study of a native ectotherm.  
343 *Functional Ecology*. **29**, 683–693.
- 344 Castro, A., & Wise, D.H. (2009) Influence of fine woody debris on spider diversity and  
345 community structure in forest leaf litter. *Biodivers Conserv*. **18**, 3705–3731.
- 346 Chiarucci, A., & De Dominicis, V. (1995) Effects of pine plantations on ultramafic vegetation of  
347 central Italy. *Israel journal of plant sciences*. **43**, 7–20.
- 348 Corcuera, P., Valverde, P.L., Jimenez, M.L., Ponce-Mendoza, A., Rosa, G.D. la, Nieto, G.  
349 (2016) Ground Spider Guilds and Functional Diversity in Native Pine Woodlands and  
350 Eucalyptus Plantations. *Community and Ecosystem Ecology*. **45**, 292–300.
- 351 Cronin, J.T., Bhattarai, G.P., Allen, W.J., & Meyerson, L.A. (2015) Biogeography of a plant  
352 invasion: plant-herbivore interactions. *Ecology*. **96**, 1115–1127.
- 353 Császár, P., Torma, A., Gallé-Szpisjak, N., Tölgyesi, C., & Gallé, R. (2018) Efficiency of pitfall  
354 traps with funnels and/or roofs in capturing ground-dwelling arthropods. *European*  
355 *Journal of Entomology*. **115**, 15–24.
- 356 Csontos, P., Bozsing, E., Cseresnyes, I., & Penksza, K. (2009) Reproductive potential of the  
357 alien species *Asclepias syriaca* (Asclepiadaceae) in the rural landscape. *Polish Journal of*  
358 *Ecology*. **57**, 383–388.
- 359 Dafni, B.A., & Kevan, M.L.P.G. (1997) Spatial flower parameters and insect spatial vision.  
360 *Biological Reviews*. **72**, 239–282.

- 361 Dailey, P.J., Graves, R.C., & Kingsolver, J.M. (1978) Survey of coleoptera collected on the  
362 common milkweed, *Asclepias syriaca*, at one site in Ohio. *The Coleopterists Bulletin*. **32**,  
363 223–229.
- 364 Dalzochio, M.S., Baldin, R., Stenert, C., Maltchik, L. (2016) How does the management of rice  
365 in natural ponds alter aquatic insect community functional structure? *Marine Freshwater*  
366 *Research*. **67**, 1644-1654.
- 367 Dalzochio, M.S., Périco, E., Renner, S., Sahlén, G. (2018). Effect of tree plantations on the  
368 functional composition of Odonata species in the highlands of southern Brazil.  
369 *Hydrobiologia*, **808**, 283-300.
- 370 Ducs, A., Kazi, A., Bilkó, Á., & Altbäcker, V. (2016) Milkweed control by food imprinted  
371 rabbits. *Behavioural Processes*. **130**, 75–80.
- 372 Duftrne, M., & Legendre, P. (1997) Species assemblages and indicator species: the need for a  
373 flexible asymmetrical approach. *Ecological Monographs*. **67**, 345–366.
- 374 Fenesi, A., Vágási, C.I., Beldean, M., Földesi, R., Kolcsár, L., Teresa, J., & Török, E. (2015)  
375 *Solidago canadensis* impacts on native plant and pollinator communities in different-aged  
376 old fields. *Basic and Applied Ecology*. **16**, 335–346.
- 377 Finch, O.-D. (2005) Evaluation of mature conifer plantations as secondary habitat for epigeic  
378 forest arthropods (Coleoptera: Carabidae; Araneae). *Forest Ecology and Management*.  
379 **204**, 21–34.
- 380 Gaertner, E. (1979) The history and use of milkweed (*Asclepias syriaca* L.). *Economic Botany*.  
381 **33**, 119–123.
- 382 Gallé, R., Erdélyi, N., Szpisjak, N., Csaba, T., & Maák, I. (2015) The effect of the invasive  
383 *Asclepias syriaca* on the ground-dwelling arthropod fauna. *Biologia*. **70**, 104–112.
- 384 Gallé, R., Kanizsai, O., Ács, V., & Molnár, B. (2014) Functioning of ecotones – spiders and ants  
385 of edges between native and non-native forest plantations. *Polish Journal of Ecology*,  
386 815–820.
- 387 Gallé, R., Szabó, Á., Császár, P., & Torma, A. (2018) Forest Ecology and Management Spider  
388 assemblage structure and functional diversity patterns of natural forest steppes and exotic  
389 forest plantations. *Forest Ecology and Management*. **411**, 234–239.
- 390 Gomes, M., Carvalho, C., & Gomes, P. (2017) Invasive plants induce the taxonomic and  
391 functional replacement of dune spiders. *Biological Invasions*.
- 392 Gratton, C., & Denno, R. (2006) Arthropod food web restoration following removal of an  
393 invasive wetland plant. *Ecological Applications*. **16**, 622–631.
- 394 Groot, M. De, Kleijn, D., & Jogan, N. (2007) Species groups occupying different trophic levels  
395 respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*.

- 396 *Biological Conservation*. **136**, 612–617.
- 397 Harms, W.R., Whitesell, C.D., & DeBell, D.S. (2000) Growth and development of loblolly pine  
398 in a spacing trial planted in Hawaii. *Forest Ecology and Management*. **126**, 13–24.
- 399 Henneron, L., Aubert, M., Bureau, F., Dumas, Y., Ningre, F., Perret, S., Richter, C., Balandier,  
400 P., & Chauvat, M. (2015) Forest management adaptation to climate change: a Cornelian  
401 dilemma between drought resistance and soil macro-detritivore functional diversity. *J.*  
402 *Appl. Ecol.* **52**, 913–927.
- 403 Kelemen, A., Valk, O., Kroel-Dulay, G., Deak, B., Torok, P., Toth, K., Miglecz, T., &  
404 Tothmeresz, B. (2016) The invasion of common milkweed (*Asclepias syriaca*) in sandy  
405 old-fields – is it a threat to the native flora? *Applied Vegetation Science*. **19**, 218–224.
- 406 Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie,  
407 M.E., Howe, K.M., Reich, P.B., Siemann, E., & Groth, J. (1999) Effects of plant species  
408 richness on invasion dynamics, disease outbreaks, insect abundances and diversity.  
409 *Ecology Letters*. **2**, 286–293.
- 410 Kováč, L.U., Kostúrová, N., & Miklisová, D. (2005) Comparison of collembolan assemblages  
411 (Hexapoda, Collembola) of thermophilous oak woods and *Pinus nigra* plantations in the  
412 Slovak Karst (Slovakia). *Pedobiologia*. **49**, 29–40.
- 413 Kuuluvainen, T., Tahvonen, O., & Aakala, T. (2012) Even-aged and uneven-aged forest  
414 management in Boreal Fennoscandia: a review. *AMBIO*. **41**, 720–737.
- 415 Laliberté, E., Legendre, P., & Shipley, B. (2014) FD: measuring functional diversity from  
416 multiple traits, and other tools for functional ecology. R package version 1.0-12.
- 417 Laliberté, E., Legendre, P. (2010) A distance-based framework for measuring functional  
418 diversity from multiple traits. *Ecology* **91**, 299–305.
- 419 Lange, M., Weisser, W.W., Gossner, M.M., Carlos, J., Fonseca, R., Kowalski, E., & Tu, M.  
420 (2011) The impact of forest management on litter-dwelling invertebrates: a subtropical-  
421 temperate contrast. *Biodiversity and Conservation* **20**, 2133–2147.
- 422 Larson, D.L., Royer, R.A., & Royer, M.R. (2006) Insect visitation and pollen deposition in an  
423 invaded prairie plant community. *Biological Conservation*. **130**, 148–159.
- 424 Lassauce, A., Paillet, Y., Jactel, H. & Bouget C. (2011) Deadwood as a surrogate for forest  
425 biodiversity: meta-analysis of correlations between deadwood volume and species  
426 richness of saproxylic organisms. *Ecological Indicators*. **11**, 1027–1039.
- 427 Litt, A.R., Cord, E.E., Fulbright, T.E., & Schuster, G.L. (2014) Effects of invasive plants on  
428 arthropods. *Conservation Biology*. **28**, 1532–1549.
- 429 Magura, T. (2017) Ignoring functional and phylogenetic features masks the edge influence on  
430 ground beetle diversity across forest-grassland gradient. *Forest Ecology and*



- 431           *Management*. **384**, 371–377.
- 432 Mgobozi, M., Somers, M.J., & Dippenaar-schoeman, A.S. (2008) Spider responses to alien plant  
433 invasion : the effect of short- and long-term *Chromolaena odorata* invasion and  
434 management. *Journal of Applied Ecology*. **45**, 1189–1197.
- 435 Nentwig, W., Blick, T., Gloor, D., Hanggi, A., & Kropf, C. (2017) Spiders of Europe. [online].  
436 Available from: [www.araneae.unibe.ch](http://www.araneae.unibe.ch) [Accessed March 9, 2018].
- 437 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson,  
438 G.L., Solymos, P., Stevens, H.M.H., & Wagner H. (2015) vegan: Community Ecology  
439 Package. R package version 2.3-0.
- 440 Payn, T., Carnus, G., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez,  
441 L., Silva, L., & Wingfield, M. (2015) Changes in planted forests and future global  
442 implications. *Forest Ecology and Management*. **352**, 57–67.
- 443 Pearce, J.L., Venier, L.A., Eccles, G., Pedlar, J., & Mckenney, D. (2004) Influence of habitat and  
444 microhabitat on epigeal spider (Araneae) assemblages in four stand types. *Biodiversity  
445 and Conservation*. **13**, 1305–1334.
- 446 Pearson, D.E. (2009) Invasive plant architecture alters trophic interactions by changing predator  
447 abundance and behavior. *Oecologia*. **159**, 549–558.
- 448 Petchey, O.L., & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward.  
449 *Ecology Letters*. **9**, 741–758.
- 450 Pysek, P., Jarosik, V., Hulme, P., Pergl, J., Hejda, M., Schaffner, U., & Vila, M. (2012) A global  
451 assessment of invasive plant impacts on resident species, communities and ecosystems:  
452 the interaction of impact measures, invading species’ traits and environment. *Global  
453 Change Biology*. **18**, 1725–1737.
- 454 Roberts, D.W., & Roberts, M.D.W. (2016) Package ‘labdsv’. Ordination and Multivariate.
- 455 Rodrigues, E.N.L., & Mendonça Jr, M. de S. (2012) Spider guilds in the tree-shrub strata of  
456 riparian forests in southern Brazil. *The Journal of Arachnology*. **40**, 39–47.
- 457 Schirmel, J., Blindow, I., & Buchholz, S. (2012) Life-history trait and functional diversity  
458 patterns of ground beetles and spiders along a coastal heathland successional gradient.  
459 *Basic and Applied Ecology*. **13**, 606–614.
- 460 Schirmel, J., & Buchholz, S. (2013) Invasive moss alters patterns in life-history traits and  
461 functional diversity of spiders and carabids. *Biological Invasions*. **15**, 1089–1100.
- 462 Schultz, R. (1997) *Loblolly pine- the ecology and culture of Loblolly pine (Pinus taeda L.)*. US  
463 Government printing office.
- 464 Schulze, E. D., Aas, G., Grimm, G. W., Gossner, M. M., Walentowski, H., Ammer, C., & Von

- 465 Gadow, K. (2016) A review on plant diversity and forest management of European beech  
466 forests. *European journal of forest research*. **135**, 51-67.
- 467 Selvi, F., Carrari, E., Colzi, I., Coppi, A., & Gonnelli, C. (2017) Responses of serpentine plants  
468 to pine invasion: vegetation diversity and nickel accumulation in species with contrasting  
469 adaptive strategies. *Science of the Total Environment*. **595**, 72–80.
- 470 Simao, M.C.M., Flory, S.L., & Rudgers, J.A. (2010) Experimental plant invasion reduces  
471 arthropod abundance and richness across multiple trophic levels. *Oikos*. **119**, 1553–1562.
- 472 Somogyi, A.A., Gabor, L., Kovacs, J., & Maak, I.E. (2017) Structure of ant assemblages in  
473 planted poplar (*Populus alba*) forests and the effect of the common milkweed (*Asclepias*  
474 *syriaca*). *Acta Zoologica Academiae Scientiarum Hungaricae*. **63**, 443–457.
- 475 Southwick, E.E. (1983) Nectar biology and nectar feeders of common milkweed , *Asclepias*  
476 *syriaca* L. *Bulletin of the Torrey Botanical Club*. **110**, 324–334.
- 477 Souza, T. De, Martins, P. (2005) Foliage density of branches and distribution of plant-dwelling  
478 spiders. *Biotropica*. **37**, 416–420.
- 479 Spirito, F., Yahdjian, L., Tognetti, P.M., & Chaneton, E.J. (2014) Soil ecosystem function under  
480 native and exotic plant assemblages as alternative states of successional grasslands. *Acta*  
481 *Oecologica*. **54**, 4–12.
- 482 Szitar, K., Kroel-dulay, G., & Torok, K. (2018) Invasive *Asclepias syriaca* can have facilitative  
483 effects on native grass establishment in a water- - stressed ecosystem. *Applied Vegetation*  
484 *Science*. **21**, 607-614.
- 485 Szitár, K., Ónodi, G., Somay, L., Pándi, I., Kucs, P., & Kröel-dulay, G. (2016) Contrasting  
486 effects of land use legacies on grassland restoration in burnt pine plantations. *Biological*  
487 *Conservation*. **201**, 356–362.
- 488 Tallamy, D.W., Ballard, M., & Amico, V.D. (2010) Can alien plants support generalist insect  
489 herbivores? *Biological Invasions*. **12**, 2285–2292.
- 490 Török, K., Halassy, M., & Szabó, R. (2003) Restoration strategy for endemic grasslands in a low  
491 productive region of Hungary. In *Proceedings of the VIIth International Rangelands*  
492 *Congress*. 1132–1138.
- 493 Urcelay, C., Longo, S., Geml, J., Tecco, P.A., & Nouhra, E. (2017) Co-invasive exotic pines and  
494 their ectomycorrhizal symbionts show capabilities for wide distance and altitudinal range  
495 expansion. *Fungal Ecology*. **25**, 50–58.
- 496 Vitousek, P.M., D'Antonio, C.M., Loope, L.L., & Westbrooks, R. (1996) Biological invasions as  
497 global environmental change. *American Scientist*, 218–228.
- 498 Wise, D.H. (2004) Wandering spiders limit densities of a major microbi-detritivore in the forest-  
499 floor food web. *Pedobiologia*. **48**, 181–188.

500 Zandt, P.A. Van, & Agrawal, A.A. (2018) Specificity of induced plant responses to specialist  
501 herbivores of the common milkweed *Asclepias syriaca*. *Oikos*. **104**, 401–409.

502

503 Figure legends

504

505 Figure 1. Effect of forest type and *Asclepias syriaca* invasion on spider functional diversity. Open  
506 circles: non-invaded; black dots: invaded sites. (A) RaoQ index; (B) Community weighted mean  
507 (CWM) of hunting strategy; (C) CWM value of spider body sizes.

508

509 Figure 2. NMDS ordination plot of spider samples (dots), with significant indicator species  
510 (crosses), and community weighted mean values (CWM) also fitted (arrows). ~~NMDS ordination~~  
511 ~~plot of sampling sites (dots), and significant indicator species (crosses), community weighted mean~~  
512 ~~values (CWM) are fitted onto the ordination plot (arrows).~~ Black dots: pine plantations, open  
513 circles: poplar plantations. Species names are abbreviated with the first letter of genus name and  
514 the first three letters of species names, please see Appendix 2. for further details.

515

## Associate Editor Comments to Author:

Associate Editor

Comments to the Author:

Thank you for submitting your revised manuscript. An additional reviewer has looked at your manuscript and has suggested some further minor comments. I have also given a list of small changes below that I would like you to make.

**Answer:** We would like to thank the Editor for the comments, we made the requested changes in the revised manuscript.

L23 Change sentence to "We found a significant effect of *A. syriaca* invasion on spider functional diversity (Rao's quadratentropy), with invaded sites having a lower functional diversity than non-invaded sites".

**Answer:** We corrected.

L27 Split sentence in two, and change second half to "We found no effect of *A. syriaca* invasion on species richness or abundance of spiders."

**Answer:** We changed.

L29 Change to "Species composition of spider assemblages in the two forest types were clearly..."

**Answer:** We changed.

L39 Add 'Araneae' to the key words

**Answer:** We added Araneae to key words

L218 change "PERANOVA" to "PERMANOVA"

**Answer:** We corrected.

L277 Change sentence to "This may have further top-down effects on the broader invertebrate herbivore and detritivore community".

**Answer:** We changed.

L503 Please add "spider" before "functional diversity" in the caption of Figure 1 so that it is clear these data refer to your spider functional diversity.

**Answer:** We corrected the figure legends.

L507 For clarity, please change the caption to Figure 2 to the following: "NMDS ordination plot of spider samples (dots), with significant indicator species (crosses), and community weighted mean values (CWM) also fitted (arrows)..."

**Answer:** We changed.

Reviewer(s)' Comments to Author:

Reviewer: 1

#### Comments to the Author

This study looks at the effects of forest type and milkweed invasion on spider assemblages, using both taxon and functional data. It is clear, straightforward and pretty much ready for publication after the initial review. I just have a few extra comments:

**Answer:** We would like to thank Pedro Cardoso for the overall positive evaluation of our study, we made the requested changes in the manuscript.

Ln 104 – Hypothesis 3 should include a tentative explanatory mechanism, why should the effect be different?

**Answer:** We added to hypothesis (3) “We assumed, that changes in habitat structure by *A. syriaca* in the low quality exotic pine habitat may have a more pronounced deterioration effect on spider communities than in native forests.”

Ln 151 – It is not clear why these were excluded? Please clarify

**Answer:** For clarification, we added to Ln 148-150 “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, as their distribution is determined by other factors.”

Ln 155 – “(the) FEve (index) ...”

**Answer:** We corrected

Ln 218 – PER(M)ANOVA

**Answer:** We corrected

Pedro Cardoso

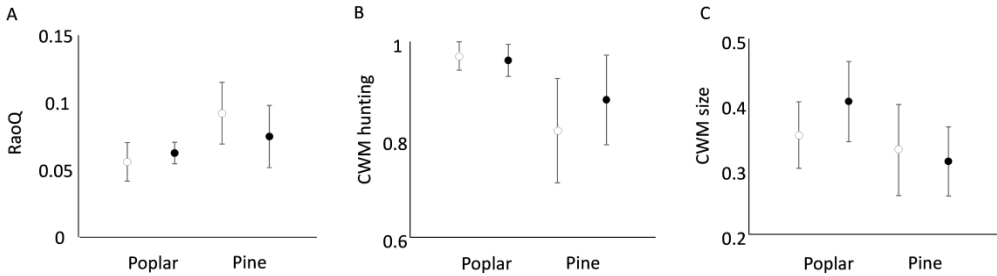


Figure 1. Effect of forest type and *Asclepias syriaca* invasion on functional diversity. Open circles: non-invaded; black dots: invaded sites. (A) RaoQ index; (B) Community weighted mean (CWM) of hunting strategy; (C) CWM value of spider body sizes.

1268x374mm (96 x 96 DPI)

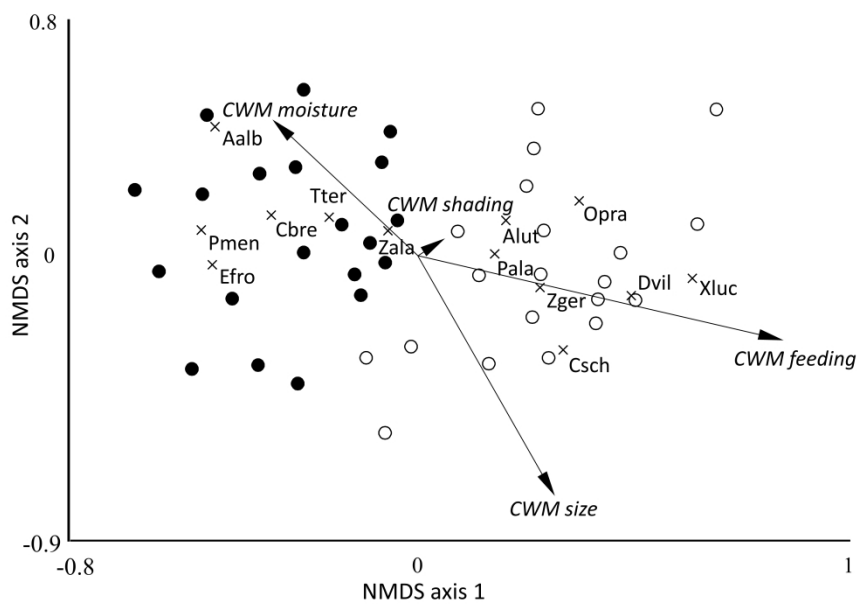


Figure 2. NMDS ordination plot of sampling sites (dots), and significant indicator species (crosses), community weighted mean values (CWM) are fitted onto the ordination plot (arrows). Black dots: pine plantations, open circles: poplar plantations. Species names are abbreviated with the first letter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

1270x762mm (96 x 96 DPI)



1 Table 1. The effect of tree species and *Asclepias syriaca* invasion on species richness, abundance  
 2 and functional diversity measures of spiders according to mixed models, parameter estimates  $\pm$   
 3 95% confidence intervals and (z/t values) are given. Ep: exotic pine; np: native poplar; i:  
 4 invaded; n: non invaded sites.

5

	<b>Tree (np/ep)</b>	<b>Type (n/i)</b>	<b>Tree: Type</b>
Species richness <sup>1</sup>	0.052 $\pm$ 0.256 (0.396)	-0.149 $\pm$ 0.245 (-1.189)	0.140 $\pm$ 0.358 (0.767)
Abundance <sup>2</sup>	-0.143 $\pm$ 0.231 (- 0.121)	-0.171 $\pm$ 0.182 (- 1.800)	1.176 $\pm$ 0.260 (1.320)
FRic	-0.077 $\pm$ 2.254 (-0.06)	-1.305 $\pm$ 1.779 (- 1.437)	2.226 $\pm$ 2.516 (1.733)
FEve	0.042 $\pm$ 0.088 (0.930)	0.040 $\pm$ 0.088 (0.890)	-0.062 $\pm$ 0.125 (- 0.972)
RaoQ <sup>3</sup>	0.012 $\pm$ 0.015 (1.431)	-0.017 $\pm$ 0.013 (-2.223)*	0.023 $\pm$ 0.021 (2.166)*
Shading CWM <sup>3</sup>	-0.015 $\pm$ 0.070 (-0.436)	0.174 $\pm$ 0.039 (0.770)	-0.032 $\pm$ 0.062 (-1.023)
Hunting CWM <sup>3</sup>	-0.080 $\pm$ 0.068 (-2.284)*	0.063 $\pm$ 0.058 (2.037)	-0.072 $\pm$ 0.084 (1.656)
Moisture CWM <sup>3</sup>	0.034 $\pm$ 0.052 (1.288)	-0.028 $\pm$ 0.035 (-1.556)	0.018 $\pm$ 0.029 (0.711)
Size CWM <sup>3</sup>	-0.091 $\pm$ 0.027 (-3.318)**	-0.017 $\pm$ 0.049 (-0.683)	0.069 $\pm$ 0.071 (-1.907)

6 <sup>1</sup> Models were fitted with Poisson distribution

7 <sup>2</sup> Models were fitted with negative binomial distribution

8 <sup>3</sup> Models were fitted with normal distribution

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

10