

Forest type interacts with milkweed invasion to affect spider communities

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

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

3. We found a significant effect of *A. syriaca* invasion on spider functional diversity (Rao's quadratic entropy), with invaded sites having a lower functional diversity than non-invaded sites. A larger effect of invasion with *A. syriaca* on the RaoQ of spiders was observed in pine compared to poplar plantations. Spider species were larger, and web-building spiders were more frequent in poplar forests than in pine plantations. We found no effect of *A. syriaca* invasion on species richness or abundance of spiders.

4. Species composition of spider assemblages in the two forest types was clearly separated according to non-metric multidimensional scaling. We identified seven species associated with pine plantations and six species associated with poplar plantations.

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

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

Introduction

The land cover of commercial tree plantations is increasing worldwide, replacing natural forests. These secondary forests include native and non-native tree plantations. Generally, they have a negative impact on the original native

ecosystems (Vitousek *et al.*, 1996; Gratton & Denno, 2006; Spirito *et al.*, 2014). Although international pressure is increasing to tackle the negative environmental effects of such plantations, tree plantation covers more than 7% of total forest area worldwide (Payn *et al.*, 2015). Plantations may, however, also have a positive impact on local biodiversity by providing secondary habitats for rare and threatened species (Brockhoff *et al.*, 2008).

Pine plantations are common in Europe, where they are generally used for timber production. Pine trees can alter

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

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

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

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

functionally similar species (Cardinale *et al.*, 2012; Dalzochio *et al.*, 2016).

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

In this study, we assessed the effect of *A. syriaca* invasion on species richness, and species composition of spiders in the native and exotic plantation. We also applied the functional diversity concept to link diversity patterns with ecosystem processes and functioning. Hypotheses for this study were as follows: (i) species richness would be higher in native forests compared to exotic forests, and tree species would have an effect on species functional diversity (i.e. functional richness and evenness, Rao's quadratic entropy and community-weighted mean trait values) and composition of spider assemblages; (ii) functional diversity and abundance of spiders would be higher in the forests which were invaded by *A. syriaca* as this plant would attract more pollinators, herbivores and associated predators; and (iii) *A. syriaca* would have a different effect on spider diversity in native and exotic forests. 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.

Materials and methods

Study area

The present study was carried out in the Kiskunság region, in the southern part of the Great Hungarian Plain (Appendix S1). The landscape was dominated by agriculture and semi-natural forest plantations, with small patches of the original forest-steppe habitats (Gallé *et al.*, 2018). The soil was calcareous coarse sand, and the climate was semiarid with mean annual precipitation and temperatures in the ranges 550–600 mm and 10.2–10.8 °C, respectively (Török *et al.*, 2003).

Study design and sampling

We selected five poplar and five pine plantation forests for spider sampling. We surveyed ground-dwelling spiders at four sampling sites in each of the 10 forests, for a total of 40 sampling sites. Sites were selected according to tree species (native poplar forests vs. exotic pine plantations) and common milkweed density (invaded vs. non-invaded

sites) in a full factorial design resulting in 10 replicates per treatment combination. All sampled plantations were mature forests with no recent intensive forestry activity. Sampling sites were located at least 70 m distance from each other, and each sampling site was located more than 100 m from the forest edges. We assessed *A. syriaca* quantity in four 1-m² quadrats at each invaded sampling site; the density of *A. syriaca* stems was 7.33 ± 3.86 stems m⁻² (mean \pm SD), and its cover was $30.31\% \pm 17.05$ (mean \pm SD). We characterised the habitat structure at the sampling sites by the approximate percentage cover of herbaceous plants (excluding *A. syriaca*), the average height of the vegetation and the cover of leaf litter.

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

Data analysis

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

We chose four attributes for functional categorisation of spiders. We classified species according to the following: shading tolerance, ranging from 1 (open) to 4 (shaded); moisture preference, ranging from 1 (very dry) to 5 (very humid habitats); feeding, 0 (active hunter) and 1 (web builder); and size, as a continuous variable in mm (Buchar & Ruzicka, 2002; Bell *et al.*, 2005; Blandenier, 2009; Nentwig *et al.*, 2017). If a species was assigned to more than one category, the values were averaged. Spiders were considered as generalists if they were assigned to more than three categories in the case of shading tolerance and moisture preference. They were also considered generalist species if they were present at both extremes of the given categories, and their score was excluded from further analyses, as their distribution is determined by other factors. We calculated community-weighted mean (CWM) values for each trait at each sampling site: functional richness (FRic), functional evenness (FEve) and Rao's quadratic entropy (RaoQ) to characterise the functional diversity of spider assemblages, using FD package in R (Laliberté *et al.*, 2014). The FRic index describes the dispersion of all species in a trait space without information on relative abundances, and the FEve index combines

distribution of species traits and evenness of species relative abundances (Laliberté & Legendre, 2010). The RaoQ index was useful for detecting assembly rules, habitat filtering (trait convergence) and limiting similarity (trait divergence; Botta-Dukat & Czucz, 2016). We used the Poisson error term for species richness data, negative binomial error term for abundance data to account for over-dispersion of the data and Gaussian error terms for RaoQ and CWM values.

We explored the multivariate response of spider assemblages to tree species and the presence of *A. syriaca* with non-metric multidimensional scaling (NMDS) using Bray–Curtis distance measure. We tested the effect of the above variables on spider assemblage composition with non-metric multivariate analysis of variance (PERMANOVA), using the Bray–Curtis distance measure, 10 000 permutations and the vegan analysis package (Oksanen *et al.*, 2015). Where significant correlation with tree species and *A. syriaca* invasion was found, we used indicator value analysis to detect characteristic spider species (IndVal; Dufrene & Legendre, 1997) with the “labdsv” package (Roberts & Roberts, 2016).

Results

Herbaceous plant cover was higher in non-invaded than in invaded sites ($z = 2.257$, $P = 0.024$). Leaf litter cover, however, was higher in invaded than in non-invaded sites ($z = -2.032$, $P = 0.042$), and it was higher in poplar compared to pine plantations ($z = 2.547$, $P = 0.011$). No difference was found in the height of the vegetation.

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

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

Spider assemblages of the two forest types clearly separated according to the NMDS (Fig. 2). Non-metric multivariate ANOVA indicated a significant difference in composition of spider assemblages from poplar and pines

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

	Tree (np/ep)	Type (n/i)	Tree: Type
Species richness [†]	0.052 \pm 0.256 (0.396)	-0.149 \pm 0.245 (-1.189)	0.140 \pm 0.358 (0.767)
Abundance [‡]	-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 [§]	0.012 \pm 0.015 (1.431)	-0.017 \pm 0.013 (-2.223)*	0.023 \pm 0.021 (2.166)*
Shading CWM [§]	-0.015 \pm 0.070 (-0.436)	0.174 \pm 0.039 (0.770)	-0.032 \pm 0.062 (-1.023)
Hunting CWM [§]	-0.080 \pm 0.068 (-2.284)*	0.063 \pm 0.058 (2.037)	-0.072 \pm 0.084 (1.656)
Moisture CWM [§]	0.034 \pm 0.052 (1.288)	-0.028 \pm 0.035 (-1.556)	0.018 \pm 0.029 (0.711)
Size CWM [§]	-0.091 \pm 0.027 (-3.318)**	-0.017 \pm 0.049 (-0.683)	0.069 \pm 0.071 (-1.907)

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

[†]Models were fitted with Poisson distribution.

[‡]Models were fitted with negative binomial distribution.

[§]Models were fitted with normal distribution.

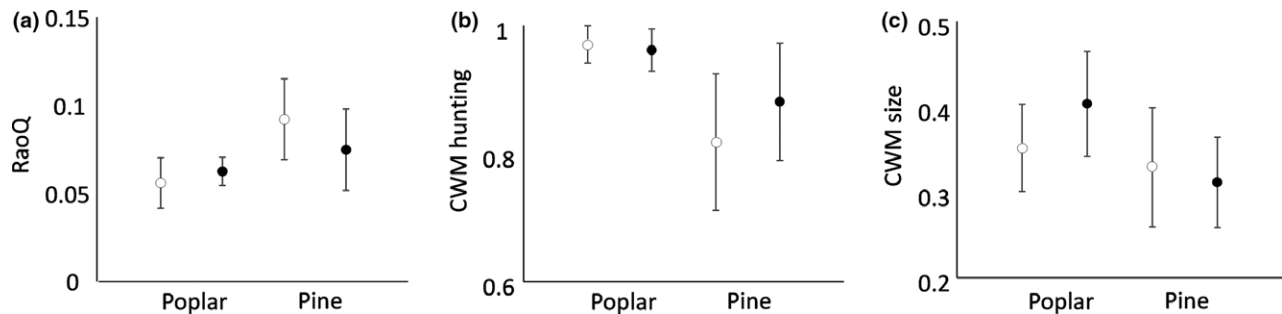


Fig. 1. Effect of forest type and *Asclepias syriaca* invasion on spider functional diversity. Open circles: non-invaded; black dots: invaded sites. (a) RaoQ index; (b) community-weighted mean (CWM) of hunting strategy; (c) CWM value of spider body sizes.

forests ($R^2 = -0.227$, $P < 0.001$). We found seven species associated with pine plantations and six species associated with poplar plantations, according to indicator value analysis (Appendix S2).

Discussion

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

Canopy closure is among the most important determinants of spider species richness and assemblage composition, because it can affect the soil microclimate and understory vegetation development (Finch, 2005; Lange

et al., 2011). Vegetation structure provides various micro-habitats (Rodrigues & Mendonça, 2012), which, in turn, determine the species composition of spider assemblages. In the present study, both poplar and pines forests were commercially mature. Mature plantation forests generally have dense understory vegetation (Calviño-cancela *et al.*, 2012) and well-developed canopies that reduce extreme microclimatic variation (Harms *et al.*, 2000). Herbaceous vegetation structure depends on the light availability at the forest floor. Poplar forests have relatively open canopies and sunlight penetrates to the forest floor, favouring more diverse herbaceous understory vegetation than for pine plantations with their closed canopies (Balandier *et al.*, 2006). The resulting complex vegetation structure might provide numerous potential web attachments for web-building spider species (Schirmel *et al.*, 2012). We found that species composition differed between forest types, as indicated by the significant results of multivariate PERMANOVA and the clear separation by NMDS ordination. The high number of significant indicator species also underpinned the marked differences in spider assemblages of pine and poplar forests, even though we

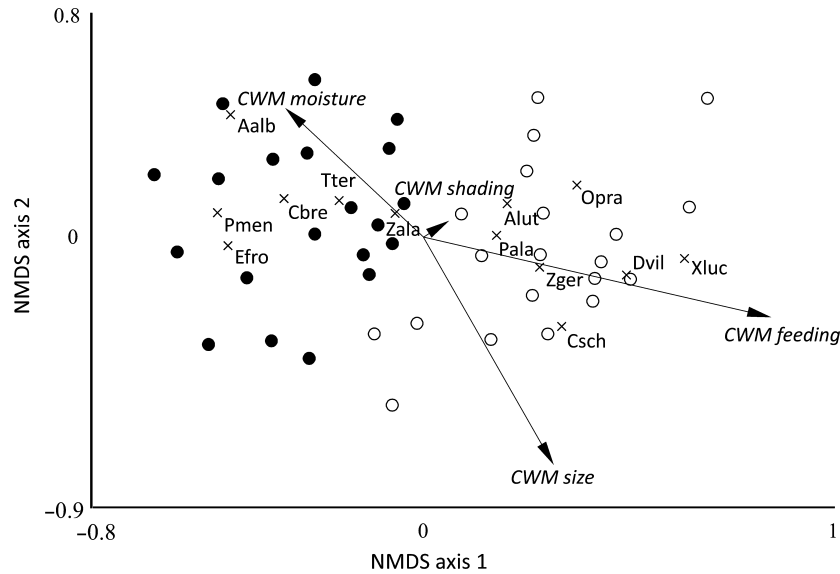


Fig. 2. NMDS ordination plot of spider samples (dots), with significant indicator species (crosses), and community-weighted mean values (CWM) also fitted (arrows). Black dots: pine plantations, open circles: poplar plantations. Species names are abbreviated with the first letter of genus name and the first three letters of species names, please see Appendix S2 for further details.

detected no differences in herbaceous vegetation cover between the plantations types.

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

Invasive plants affect species composition of spider assemblages (Bultman & DeWitt, 2008; Mgobozi *et al.*, 2008), and the behaviour and density of spider species (Pearson, 2009; Gallé *et al.*, 2015). Invasive plant species may have a direct effect on spiders, as they affect the

architecture of vegetation (Souza & Martins, 2005; Simao *et al.*, 2010) and, therefore, habitat structure. Included in these changes are a variety of shelters and structural supports for web building (Litt *et al.*, 2014).

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

Plant invasion may also change plant–pollinator relations, either positively or negatively (Larson *et al.*, 2006; Bartomeus *et al.*, 2008; Fenesi *et al.*, 2015). Furthermore, invasive plant species can weaken the relationship between native plants and their pollinators (Aizen *et al.*, 2008), resulting in significant changes in pollinator abundances and assemblage structure. In accordance with Bezemer *et al.* (2014), we did not find a significant indirect effect of altered prey availability of invaded sites on spider species richness and abundance. This was in line with Groot *et al.*

(2007), who suggested that profiles of predatory arthropods such as spiders were not closely related to plant species composition and were less vulnerable to the effects of invasive plants. We, however, found that *A. syriaca* had a negative effect on the functional diversity of spiders, and this effect was larger in pine plantations than in poplar forests.

In pine plantations, the similar species richness and the higher functional diversity (RaoQ index) of non-invaded sites suggest that traits values are less similar than in invaded sites, and functionally different species are present in the assemblage (Schirmel & Buchholz, 2013). In contrast, the invaded sites had lower functional diversity and thus a uniform trait state composition. Invaded pine forests only favoured certain trait state combinations, which implied that environmental filtering played an important role in species sorting. This presumably precluded the colonisation of several species of the original forest-steppe fauna.

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

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Conflict of interest

Authors have no conflict of interest.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Location of the study area (A) and sampling design (B). Black dot: Study area is, dark grey

squares are invaded plots, grey squares are non-invaded plots.

Appendix S2. List of collected species and indicator values for significant indicator species to its maximum class. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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