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From lawns to meadows: spiders (Arachnida: Araneae) as indicators to measure urban grassland restoration success

Alexander Bach[1] · Jana Jedamski[1] · Benjamin Daniels[1,2] · Martina Roß-Nickoll[1]

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Abstract
In the present study, we investigate how spiders can be used to assess the effectiveness of restoring mesic grasslands on former urban lawns. We compile and analyze a comprehensive dataset, including both past and current data, focusing on the Aachen region. By systematically examining this data, we identify various indicators using different analytical methods. This approach allows us to distinguish distinct species communities, making them useful as diagnostic tools at various stages of habitat development. Additionally, we identify further parameters that are essential for evaluating meadow restoration in urban settings. We highlight the crucial importance of understanding the local species repertoire, as this knowledge is vital for setting realistic benchmarks for restoration projects.

Keywords Spiders · Grassland restoration · Hay meadows · Germany

Introduction

Intensively managed urban lawns are probably the most widespread habitats in European cities (Hedblom et al. 2017). While they may provide recreational space for citizens and improve mental and physical health (de Vries et al. 2003; Nielsen and Hansen 2007; Ma et al. 2019), they are ecologically characterized by a lack of biodiversity (Shwartz et al. 2014; Unterweger et al. 2017; Lerman et al. 2018) and require regular maintenance through mulch mowing which is costly and time-consuming (Chollet et al. 2018; Sturm et al. 2018; Sehrt et al. 2020; Watson et al. 2020). It is important to name the disadvantages of maintaining these lawns precisely and explore alternative land-use type that can provide similar ecosystem services and habitats to promote biodiversity. The most obvious approach in this context is restoration toward an extensive, species-rich grassland (Klaus 2013). However, while biodiversity-rich greenspaces have been shown to have positive effects on human well-being (Taylor and Hochuli 2015; Lai et al. 2019; Fischer et al. 2020), they may not always be suitable for traditional public uses, such as sports and recreation (Nicol and Blake 2000; Peschardt et al. 2012). Balancing between the citizen and environmental needs (Palliwoda et al. 2017; Daniels et al. 2018; Fischer et al. 2020) is crucial to avoid conflicts over urban greenspace use and to highlight the benefits of extensifying lawns in planning and managing these spaces (Campbell 1996; Aronson et al. 2017). But recent findings indicate a high level of public acceptance for the conversion of lawns into extensive species-rich grasslands (Frank et al. 2024).

A simple adjustment to mowing concepts, such as reducing the mowing frequency to ones or twice a year, can often lead to a fast increase in plant biodiversity (Chollet et al. 2018; Sehrt et al. 2020). Of course, reseeding with appropriate seeds also leads to a fast increase of plant species richness (Norton et al. 2019; Daniels et al. 2020). Since extensification of lawns has only recently been recognized as an easy implementation tool to promote urban biodiversity (Chollet et al. 2018; Baldock 2020), knowledge about the effects and developments on arthropod biodiversity here is still scarce and often focusing on pollinating insects (e.g. Burr et al. 2018; Larson et al. 2014; Lerman et al. 2018; Wastian et al. 2016; Wintergerst et al. 2021). A reduction of mowing (and an eventual seeding) and, thus, an increase of flowering resources usually leads to a rapid increase of this highly mobile group, which was shown

✉ Alexander Bach
alexander.bach@bio5.rwth-aachen.de

1 Institute for Environmental Research, RWTH Aachen University, Worringerweg 1, 52074 Aachen, Germany

2 German Environment Agency, Umweltbundesamt (UBA), Wörlitzer Platz 1, 06844 Dessau-Roßlau, Germany

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for example by Hofmann and Renner (2020) on annual flowering strips in Munich. This is also supported by a meta-analysis of Proske et al. (2022), who showed that highly mobile pollinating or phytophagous insect are the most benefitting taxa from a reduced management intensity of urban lawns. Despite a rapid increase of flowering plant and pollinating species it is challenging to determine whether the restored lawns can serve as a permanent habitat for arthropods. While the meadows may provide a valuable food resource, it remains unclear whether they are suitable for reproduction or overwintering of arthropods. However, it is important to have reliable observation and evaluation tools, as these are often required in funding programs like the Federal Program on Biological Diversity ("Bundesprogramm Biologische Vielfalt"), which is intended to implement the goals of the Convention on Biodiversity as part of the National Strategy on Biodiversity in Germany (Flinkerbusch and Nowack 2017).

At this point, epigeic spiders (Arachnida: Araneae), a group that is often neglected in projects dealing with the creation of flowering meadows in urban environments, should be proposed as an additional group, suitable for evaluation. Spiders have the advantage that they can run their complete life cycle in the same habitat (even if preferred microhabitats may differ during life-cycle (Hallander 1970)) and, at least partially, can reach new habitats faster than other wingless predators by spreading with the air plankton via ballooning (Bell et al. 2005). Several studies have already shown that spiders are effective indicators for grassland restoration or extensification efforts (Perner and Malt 2003; Déri et al. 2011; Buchholz et al. 2018; Smith DiCarlo and DeBano 2019; Solascasas et al. 2022) and also in heathland restoration spiders are commonly used as evaluation tools (Cristofoli et al. 2010; Schirmel and Buchholz 2011; Borchard et al. 2014; Hacala et al. 2020).

Since spiders are a widespread trigger of phobias and disgust (Frynta et al. 2021) their use as indicator species in urban environments can also be beneficial from a socio-economic perspective. Studies have shown, that the connection of biodiversity promoting approaches with involving further stakeholders like education and communication partners can lead to a greater acceptance and awareness of arthropods (Garbuzov et al. 2015; New 2018). It was also found, that factual knowledge reduces the level of fear towards animal species (Makashvili et al. 2014; Oražem et al. 2021).

In this case study we investigate which parameters and species of spider communities may be suitable for the evaluation of urban grassland restoration efforts using mesophilic meadows. Since one important aspect in habitat restoration is "What is ecologically feasible?", a good knowledge of regional species pool and species distribution is necessary to define realistic development goals (Bakker et al. 2000; Miller and Hobbs 2007).

Materials and methods

Investigation site

The study area focuses on Aachen, Germany's westernmost city with a size of 160 km^2 and approximate 250.000 residents, which borders on the Netherlands and Belgium and lies in a transitional area between the intensively used agricultural area Jülich-Zülpich Börde in the north and the northern margins of the Eifel mountains in the south and east. Although Aachen is not located near the coast, it has an oceanic climate with comparatively low temperatures in summer, mild winters and an annual precipitation with 908 mm between 1980—2009 (Buttstädt and Schneider 2014).

Dataset

For our study we compiled a regionalized dataset of published and unpublished spider community datasets and classified them along an urbanization gradient, starting with community data from urban ornamental lawns. We are aware that the source-sink model between rural and urban areas is a very simplified approach (Varet et al. 2013) and that habitats influenced by urbanization often form unique communities, differing from their natural and semi-natural equivalents (Sattler et al. 2011) due to different filters (Sattler et al. 2010; Van Nuland and Whitlow 2014). Therefore, we integrated data from urban extensive meadows as a reference point for spider communities in meadows influenced by urbanization. As a habitat that mediates the transition between urban and semi-natural meadows, we used data from species-poor meadows from the agricultural surrounding countryside, since these have the largest proportion of mesophilic grassland in the urban–rural boundary area of Aachen. We assume that species found in these meadows have also a high probability to colonize urban meadows on a short to mid-term time scale. As a reference point for ecologically valuable meadow habitats from a less fragmented and intensively used landscape, we integrated data from extensive used hay meadows, which we use to define target species for mesic grassland restoration in urban areas.

To generate a representative set of study sites, we used the ARAMOB data repository (ARAMOB 2023; Bach et al. 2023) to export all available datasets with spider communities collected with pitfall traps in habitats classified according to EUNIS (Davies et al. 2004) as mesic grassland (E2) in Aachen and the surrounding area and enriched it with further unpublished local project datasets. This allowed us to select a representative sample of mesic grassland communities from different scenarios (see S1

Table 1) that were well-suited for our study. To ensure that the community data was representative collected, all data sets were filtered out that were not collected with at least three pitfall traps and a sixty-day collection timespan within the vegetation period (April—October). After applying our selection criteria, we were left with 38 study sites (S1 Table 2). These plots were divided into four categories: intensively maintained urban ornamental lawns (UI, $n = 13$), urban extensive meadows (UE, $n = 3$), and species-poor agricultural meadows from the surrounding countryside (AM, $n = 7$). The selected urban extensive meadows were the only once available since extensive urban grassland in Aachen was rare. Only in recent years' efforts began to extensify large areas of inner-city ornamental lawns, so the small sample of these type of grasslands and the heterogeneous study design reflects the conditions at the study area to date. We augmented our dataset with spider community data from extensive species rich hay meadows from the neighboring rural Eifel region, with an approximate distance of 50 km from the city center Aachen. These meadows (HM, $n = 15$) served as reference values due to the lower fragmentation of the surrounding landscape matrix and the more semi-natural conditions (Fig. 1).

Sampling took place between 1996—2021 with 51,329 collected individuals from 149 species. Nomenclature was applied according to the World Spider Catalog (2024). Only adult spiders identified to the species level were included in the analyses. All members of species groups that were not split until after the earliest collection year, were named equally in our dataset as long as we could not confirm their identity on all plots (e.g., *Micaria pulicaria* and *Micaria micans* as *Micaria pulicaria* s.l. (Muster and Michalik 2020)).

We standardized the activity density data collected over different time spans and number of pitfall traps by calculating the catch per unit effort based on the approach by Saska et al. (2021). This method essentially measures activity density per trap per day. All calculations were done with this standardized measure of activity density. We will refer to it as "daily activity density" in the following. The term "activity" in this context highlights that the measure is influenced not just by how many spiders are present, but also by their

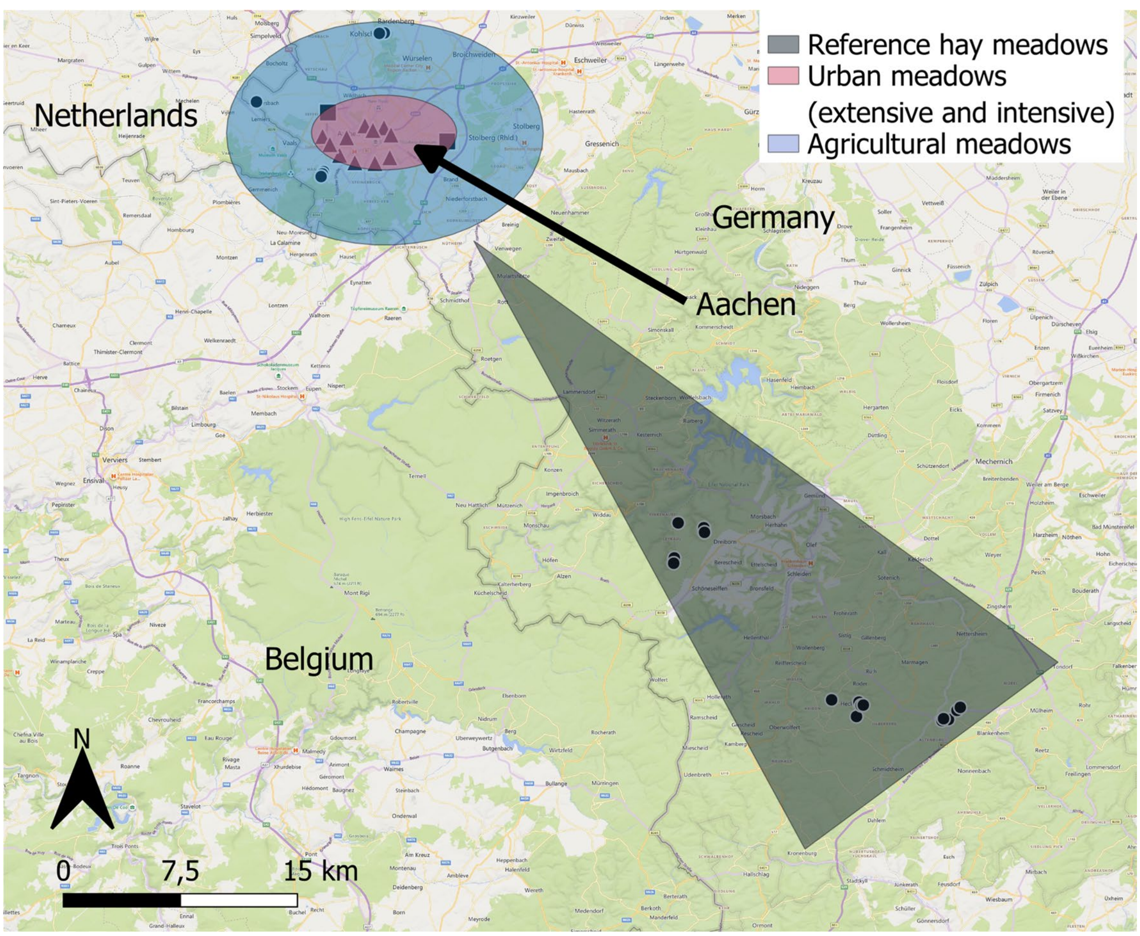

Fig. 1 Sampling sites located in and around Aachen. Black dot indicate exact locations, while colored shapes denote corresponding area categories. In the urban meadows, triangles represent intensive meadows, while squares represent extensive meadows

movement behavior, which affects their likelihood of being captured in pitfall traps (Woodcock 2005).

All spider species were characterized based on traits that are well-documented to reflect responses to urbanization (Buchholz et al. 2018; Lövei et al. 2019; Cabon et al. 2024a, b; Martínez-Núñez et al. 2024). These traits include median (female) body size based on minimum and maximum values (mm) from Nentwig et al. (2023), ballooning ability (Bonte et al. 2003, 2004; Bell et al. 2005; Simonneau et al. 2016), hunting mode (Cardoso et al. 2011), forest affinity as a measure of habitat specificity (Blick et al. 2019; Schneider et al. 2021) and their niche values for moisture and shading demands (Entling et al. 2007). (See also S1 Table 3).

Statistical analyses

All data preparation and analyzing steps were done using R version 4.2.2 with RStudio (2022.07.2 Build 576). We first calculated the Chao1 index to estimate species richness using the vegan package (Oksanen et al. 2018) and compared these estimates with the observed species counts to assess the completeness of the respective sampling effort. Afterwards we performed a Multi-Response Permutation Procedure (MRPP) to confirm the significance of differences in species composition among our predefined site groups (not shown in the "Result" section).

We then compared the daily activity density and species richness in the different site groups. In addition, we calculated the community weighted mean (CWM) trait values using package 'FD' (Laliberte et al. 2014) to find parameters suitable for evaluation efforts. These were tested using a one-way ANOVA to find significant differences ($p \leq 0.05$) in trait characteristics between our groups and Tukeys range test for multiple comparisons (adjusted $p \leq 0.05$). Furthermore, we investigated the size distribution within our four groups by performing a non-parametric density estimation using a Gaussian kernel. Density is weighted using the summed daily activity density data per body size. With the vegan package (Oksanen et al. 2018) we performed a correspondence analysis on the site-species matrix to investigate whether distinct communities emerge in the different groups. We identified species groups for future use to evaluate the restoration success with a three step nested indicator species analysis (ISA) using 'indicpsecies' package (De Cáceres and Legendre 2009). In this approach we did the first ISA with the complete dataset looking for exclusive indicators in all four groups (UI, UE, AM, HM). The calculated indicators ($p \leq 0.05$, Indicator Value ≥ 0.7) were then excluded from the dataset and a second ISA with combined site groups was performed to find indicators separating between urban and less to non-urbanized grasslands (UI + UE vs. AM + HM). Previous step with removing new indicator species was repeated and the third ISA was performed testing all meadows against the lawns to find species which are euryoecious in grassland but missing in lawns (UI vs UE + AM + HM). All indicator species were controlled for their prevalence for mesophilic grasslands using expert knowledge and literature to be considered as ecological meaningful. Only the exclusive indicators of extensive urban grassland were excluded from this process, as we consider these, regardless of their ecology, as species that supplement urban grassland communities through urban filtering and occupying niches that might otherwise remain unoccupied (Fournier et al. 2020).

Results

Species richness estimates, calculated using the Chao1 estimator, varied across the different groups studied (Table 1). The semi-natural hay meadows had the highest Chao1 estimates, suggesting a more comprehensive capture of the spider community. Urban extensive meadows and species-poor agricultural meadows displayed slightly lower Chao1 estimates, indicating fewer unseen species compared to hay meadows. Lawns exhibited the lowest species richness and Chao1 estimates, reflecting a more limited and less diverse spider community. Despite these differences, the relatively high Chao1 estimates across all groups suggest that our sampling captured a substantial portion of the species present.

Figure 2 illustrates that ornamental lawns had lower mean values in both biodiversity parameters than the compared groups. In contrast, extensive meadows in the urban environment showed significantly lower mean daily activity densities compared to meadows in the non-urban

Table 1 Overview of number of species richness, the total number of individuals collected (unstandardized), the estimated species richness (Chao1 Index) with associated standard error (SE), and the sampling completeness percentage across the groups on the urban-intensification gradient

Group	Species collected	Individuals collected (unstandardized)	Chao1 ± SE	Completeness
UI (*n* = 13)	59	3550	67.67 ± 6,41	87.19%
UE (*n* = 3)	64	2438	77.13 ± 9,01	82.98%
AM (*n* = 7)	63	12,598	80.00 ± 10,65	78.75%
HM (*n* = 15)	109	32,743	116.29 ± 4,71	93.73%

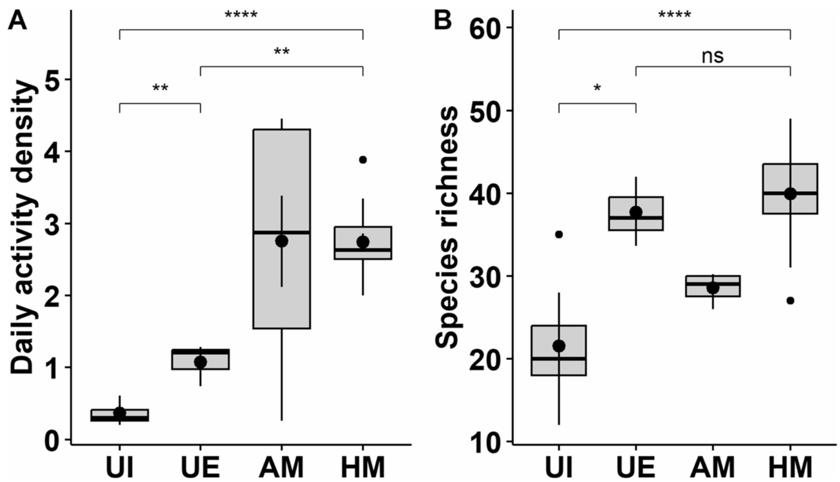

Fig. 2 Daily activity density (**A**) and species richness (**B**) of lawns resp. meadows in different fragmentation and intensity scenarios. Statistical significance was calculated using Kruskal–Wallis, pairwise comparison was done with Wilcoxon. (< 0.0001 = ****, < 0.001 = ***, < 0.01 = **, < 0.05 = *, > 0.05 = ns). UI = urban intensive, UE = urban extensive, AM = agricultural meadows, HM = hay meadows

environment, but no significant differences for species richness compared to the reference group of semi-natural hay meadows. However, the species activity densities of the urban meadows were still significantly higher than on the lawns.

A comparison of the CWM of the different trait characteristics (Table 2) shows that the intensive lawns differ mainly in the structure of the hunting guilds, which is also reflected in the composition of the spider families. Ornamental lawns also have an increased proportion of species not strictly tied to open habitats, as well as a higher proportion of species with lower moisture demands compared to hay meadows. In contrast, urban meadows only had a higher proportion of species with a preference for light forests or forest edges compared to hay meadows, no other significant differences could be found in the values shown here.

Ecologically intact hay meadows show a broadly similar distribution between spiders of 2—8 mm body size, with spiders between 6—7 mm dominating, caused mainly by species of the wolf spider genus *Pardosa* (Fig. 3). After

Table 2 Results of one way ANOVA statistics and subsequent postHoc Tukey HSD tests of different traits and their (significant) characteristics (CWM) and proportions of the most dominant families between the groups on the urban-intensification gradient. Tukey only shows the results against the UI group. A + indicates a significantly ($p < 0.05$) higher value of the characteristic feature,—a significantly ($p < 0.05$) lower value compared to UI. Tests vs. UE are not presented since the only significance was a higher CWM of Forest affinity – forest light compared to HM, all other comparisons were not significant

		ANOVA		Tukey HSD (vs UI)		
		p (F)	F	HM	AM	UE
Body size		0.001	6.565	+	+	n.s
Forest affinity	Open	0.002	6.255	n.s	+	n.s
	Mixed open	< 0.001	9.595	-	-	n.s
	Forest light	0.018	3.863	n.s	n.s	+
Hunting mode	Ambush hunters	0.004	5.440	+	n.s	+
	Ground hunters	< 0.001	16.228	+	+	+
	Orb web hunters	< 0.001	17.624	+	n.s	+
	Other hunters	< 0.001	19.643	-	-	-
	Sheet web hunters	< 0.001	14.306	-	-	n.s
	Space web hunters	0.014	4.094	-	-	n.s
Niche values	Shading	0.011	4.331	n.s	n.s	n.s
	Moisture	0.003	5.801	+	n.s	n.s
Ballooning	Yes	0.029	3.391	n.s	+	n.s
	No	0.029	3.391	n.s	-	n.s
Family proportions	Gnaphosidae	0.034	3.245	+	n.s	n.s
	Hahniidae	0.001	6.645	-	-	n.s
	Linyphiidae	< 0.001	23.194	-	-	-
	Lycosidae	< 0.001	27.435	+	+	+
	Tetragnathidae	< 0.001	17.590	+	n.s	+
	Theridiidae	0.014	4.094	-	-	n.s
	Thomisidae	0.004	5.440	+	n.s	+

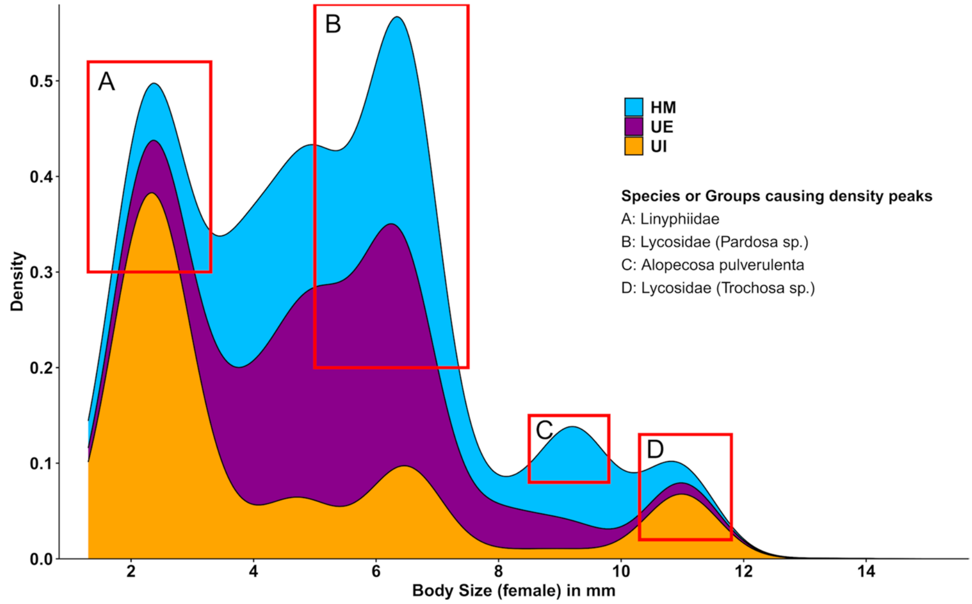

Fig. 3 Density plot showing the distribution of body sizes in spider communities of Group HM, UE and UI (AM has been excluded here for display reasons). UI = urban intensive, UE = urban extensive, HM = hay meadows

that, the proportion of larger spiders drops sharply and only smaller peaks appear, due to the larger lycosids *Alopecosa pulverulenta* and *Trochosa terricola*. The distribution pattern of extensive urban meadows equals that of hay meadows, with weaker or absent (*A. pulverulenta*) wolf spider peaks. The similarity also reflects the results of the analysis of the body size CWM values, which could not find a significant difference. However, lawns are quite different from this pattern; here, the first peak (< 3 mm) is followed by an almost equally severe decline, which does not recover. The wolf spider peaks are almost completely missing, only at the end *Trochosa ruricola* triggers another peak in a similar magnitude compared the other two groups.

The analysis of the spider communities (Fig. 4) shows that especially lawns and meadows in the urban environment and the hay meadows separate from each other and form distinct communities. Only the species-poor meadows from the agricultural surrounding area have a less distinct community and overlap with urban meadows and hay meadows. The calculated indicator species (see also Fig. 5) in the plot show a clear clustering around the hay meadows plots. Apart from exclusive urban lawns and meadows indicators, only *Erigone atra* and *Pardosa amentata* are located more distant.

A total of 17 indicator species were identified (Fig. 5, S1 Table 4), of which 3 indicated for ornamental lawns (curved arrow). Group A includes established meadow species in the urban environment, partially excluding those marked with asterisks, as these are exclusive indicators of urban extensive meadows and not necessarily occurring in mesic grassland but can also include species adapted to conditions in urban environment. Group B represents meadow species from the adjacent agrarian countryside, which in addition with group A are expected on a short to medium time scale on extensified ornamental lawns due to their spatial proximity. In contrast, bold species in Group C represent indicators of semi natural hay meadows and are therefore defined as regional long-term target species.

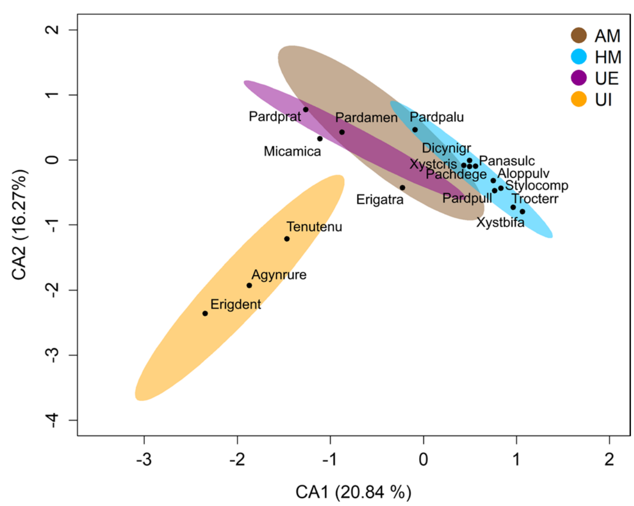

Fig. 4 Correspondence Analysis showing the mesic grassland plots from different urbanization and intensity scenarios. (Variance explained by CA1: 20.84%, CA1 + 2: 37.11%). Ellipses were used as envelopes to encounter all sites. Black dots refer to calculated indicator species. Agynrure = *Agyneta rurestris*, Aloppulv = *Alopecosa pulverulenta*, Dicynigr = *Dicymbium nigrum*, Erigatra = *Erigone atra*, Erigdent = *Erigone dentipalpis*, Micamica = *Micaria micans*, Panasulc = *Panamomops sulcifrons*, Pardamen = *Pardosa amentata*, Pardpalu = *Pardosa palustris*, Pardprat = *Pardosa prativaga*, Pardpull = *Pardosa pullata*, Pachdege = *Pachygnatha degeeri*, Stylcomp = *Styloctetor compar*, Tenutenu = *Tenuiphantes tenuis*, Trocterr = *Trochosa terricola*, Xystbifa = *Xysticus bifasciatus*, Xystcris = *Xysticus cristatus*; UI = urban intensive, UE = urban extensive, AM = agricultural meadows, HM = hay meadows

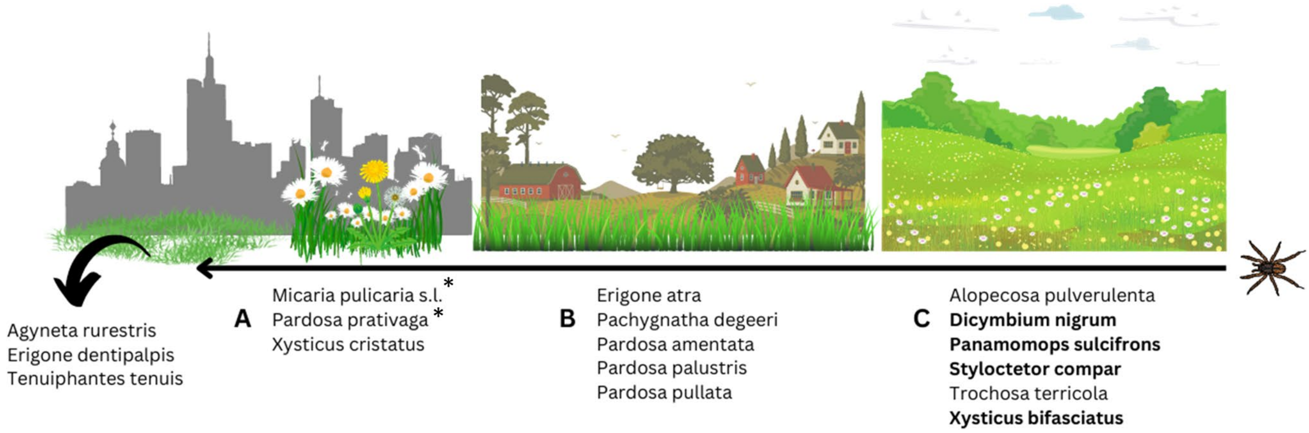

Fig. 5 Result of the nested Indicator species analyses. Species are ordered according to their spatial proximity to urban lawns. Detailed results of nested ISA see Supplement Table 4. Graphic was created with canva.com

Non-bold species in Group C were also exclusive indicators of hay meadows but were not defined as long-term target species due to their ecology and expectability in urban areas.

Discussion

Biodiversity parameters

The results of our study show that urban extensive meadows can have similar parameters regarding species richness and functional diversity compared to semi-natural hay meadows found in less urbanized landscape matrices. Of concern are the low abundance values, as low population sizes may pose an increasing risk of local extinction events (O'Grady et al. 2004). However, other studies found little differences on spider activity densities along urban gradients (Sattler et al. 2011; Philpott et al. 2014; Otoshi et al. 2015), so we attribute this to a combination of local conditions, small sample and a temporal bias in our dataset, as all urban meadows were sampled in the same year, while sampling on sites in all other groups took place in different years, and not to a general pattern. Spider population sizes are known to shift significantly, even between years (Workman 1977; Kobel-Lamparski and Gack 2020).

Species and trait composition

Another striking parameter in the evaluation of restoration or extensification efforts on urban lawns is the species composition of the spider community. While the correspondence analysis supports the hypothesis made at the beginning about agricultural meadows in the adjacent countryside as mediators between urban and semi natural meadows, the ornamental lawns form their own distinct communities. According to the results of Cockfield and Potter (1984), lycosid, thomisid and tetragnathid (here mainly *Pachygnatha degeeri* and *Pachygnatha clercki*) spiders as typical species of intact hay meadows (Nyffeler and Breene 1990) are strongly decreasing on ornamental lawns, also explaining significant differences in hunting guild structure and mean body size. This can of course be linked with the high management intensity and the resulting structural poverty of these habitats (Bell et al. 2001). The urban reference group demonstrates that family compositions (Table 2), equal to hay meadows, are possible in urban environments with an appropriate habitat quality. Especially wolf spiders (Lycosidae) usually known for the highest activity density in grassland compared to other spider families (Standen 2000) may be suitable for evaluation, as, at least an identification up to family level can be done even by less experienced researchers. Furthermore, a monitoring with pitfall traps is cost and time efficient (Work et al. 2002; Hohbein and Conway 2018). While their proportion to the total spider community on the studied lawns was on average around 25%, all other meadows in this study never had wolf spider proportions below 50% (not shown in the "Result" section). Since Lycosidae are known to dominate pitfall catches in grassland habitats (Duffey 1962; Samu et al. 1996; Lang 2000; Weeks Jr and Holtzer 2000; Jocqué and Alderweireldt 2005; Woodcock 2005; Jansen et al. 2013; Burkman and Gardiner 2015) and even urban gardens (Otoshi et al. 2015), a threshold value of a minimum of 50% of the total spider catch should belong to Lycosidae as a parameter for the positive evaluation of the extensification efforts on former lawns.

The spatial proximity, on the other hand, of spider communities on urban meadows compared to reference hay meadows demonstrates that similar communities can develop, but nevertheless form distinct communities probably caused by urban filtering (Fournier et al. 2020) and different disturbance intensities (Sattler et al. 2010). While the influence of different mowing techniques and regimes on spider communities in grassland ecosystems are well studied (Haskins and Shaddy 1986; Nyffeler and Breene 1990; Cizek et al. 2012; Pech et al. 2015; Buri et al. 2016; Berger et al. 2024), there is a lack of knowledge on the influence of low-threshold disturbances on arthropod communities in grasslands which occur daily in an urban context, like littering leading to new microhabitats (Kolenda et al. 2021). Furthermore Buchholz et al. (2021) demonstrated i.a. a negative correlation between spider diversity and a high dog presence resp. activity on urban dry grasslands in Berlin. Wu and Elias (2014) showed how anthropogenic caused vibratory noise limits sensory abilities in prey detection in spiders or Goßmann et al. (2022) who identified spider webs as sinks for microplastics like tire wear particles. Thus, the extent to which communities in urban habitats are or will be disturbed is difficult to predict, nor is the degree of disturbance in communities strictly correlated with urbanization (Niemelä and Kotze 2009; Nagy et al. 2018). However, the regional species pool has the greatest influence on the composition of urban communities (Fournier et al. 2020) and should therefore be considered as an ecological constraint of what is possible in restoration projects (Miller and Hobbs 2007).

Target species

By analyzing the regional species pool, we were able to identify three species groups that can be used to indicate habitat improvements of restored meadows at two different scales (Fig. 5). Group A consists of *Xysticus cristatus*, which indicated for all meadow types except ornamental lawns, and two indicator species exclusive for urban meadows, distinguishing them from less to non-urbanized meadows. Contrasting to *Pardosa prativaga,* which is together with *X. cristatus* associated with hay meadows (Nyffeler and Breene 1990), *Micaria pulicaria* s.l. (which is highly probably *M. micans* since only individuals belonging to this species are known to the authors from urban areas in Aachen) prefers warm and dry habitats (valid for *M. micans* (Muster and Michalik 2020)), appearing to be a species with favored traits for urban environments like thermophilia (Menke et al. 2011; Magura et al. 2013; Meineke et al. 2017; Piano et al. 2020). Apart from this, all three species are nevertheless generalists with a broad ecological amplitude.

This is also true for species in Group B, which are also euryoecious with a focus on mesic grassland ecosystems (Nyffeler and Breene 1990; Martin 2020). Of particular interest here is the separation of *Erigone dentipalpis* and *Erigone atra*. Although, as highly mobile pioneer species and r-strategists (Bell et al. 2001) both belong to the most common spiders on arable fields (Blick et al. 2000), ornamental lawns seem to be a tough place even for survivalists. Presumably, this confirms Wiehle's (1960) observation that *E. atra* has a slightly higher moisture requirement than *E. dentipalpis* since lawns have a constant risk of drying out in summer (Smagin et al. 2006). We expect Group A and B to be potential early colonizers for several reasons: 1) All species are highly mobile (except *M.* cf. *micans*) generalists. 2) All species occur in the city or the adjacent landscape. 3) All species have already been reported from urban environments by other authors (Rozwałka 2006; Keer et al. 2010; Sattler et al. 2011; Buchholz et al. 2018; Braschler et al. 2020). However, it is questionable in which time span a colonization is expectable. Although concrete studies are lacking for this specific question, studies from other urban habitat types concluded that for those generalists the decisive factor is primarily habitat quality and neither time nor habitat connectivity (Vergnes et al. 2012; Varet et al. 2013; Burkman and Gardiner 2015; Vähätalo et al. 2024). Equal results came from orthopteran assemblages where management is more important than landscape parameters (Huchler et al. 2023). Huhta et al. (1979) reported a low spider density in the first year after the creation of artificial soil plots in garden grassland with a rapidly increase in the following years. We expect two years as a rough guide to measure first changes in species composition, whereby this is of course also dependent on factors that are beyond one's control like weather (Shochat et al. 2008).

In contrast to the species just discussed, bold species from Group C are more specialized mesic grassland species even with national conservation concerns (*Styloctetor compar* (Blick et al. 2016)) or considered as rare on a national or regional scale (*Panamomops sulcifrons*, *Dicymbium nigrum* (Buchholz et al. 2010; Blick et al. 2016)) and are identified as valuable target species. Although literature usually describes *Xysticus bifasciatus* as a species of dry grass- and heathlands (Heimer and Nentwig 1991; Roberts 1995; Bee et al. 2017), several studies recorded *X. bifasciatus* in hay meadows (Nyffeler and Benz 1979; Prokopenko 2015; Szmatona-Túri et al. 2017), even co-occurring with *S. compar* (Řezáč and Heneberg 2018; Frenzel et al. 2022). Also Martin (2020) described wet and mesic meadows as the preferred habitat, so we consider the ecological relevance to be given here to name *X. bifasciatus* as a possible target species for mesic grassland restoration in this region. Except for *X. bifasciatus* (which was found by Buchholz et al. (2018) on urban grassland in Berlin) historical records from Aachen are known for these species (Arachnologische Gesellschaft 2023) emphasizing the possibility of a general occurrence of these species in suitable urban habitats. The hygrophilous species (Heimer and Nentwig 1991) *Styloctetor compar* should be highlighted: At the beginning of the twentieth century this species was described as "nicht selten bei Aachen" (not rare near Aachen, Bösenberg 1902). Since then no recent records from Aachen or the adjacent landscape were available, except for an individual specimen from an AM plot in our dataset, what may be linked to the large-scale drainage of wetlands and the canalization of urban streams to reduce malaria causing *Anopheles* sp. populations and to increase general urban hygiene (Kortenhaus 1928).

The two non-bold species are also exclusive indicators of hay meadows, but based on their ecology, occurrence in urban habitats and general frequency, they certainly belong to the groups discussed first. Notable is *Trochosa terricola*, which is not a classic meadow species since it has a higher demand for shading, thus prefers forests, forest edges or hedgerows (Hänggi et al. 1995; Martin 2020) and possibly benefitting from increasing vegetation height in semi-natural hay meadows (Bonte et al. 2000; Dennis et al. 2001). Being one of the largest local species, its amplitude is also clearly seen in the density distribution of the body sizes in the hay meadows (Fig. 4). Surprisingly, the ornamental lawns also peak in this area, caused by its sibling species *Trochosa ruricola* (with significant increased daily abundances compared to hay meadows where *T.ruricola* was nearly absent with singeltons only). This also led to a missing significance in analysis of body size CWM between urban lawns and urban meadows, as *T. ruricola* was the dominant species on some lawns, providing very high variance in this group. It seems contradictory that in a habitat that obviously filters large species, a species belonging to the largest lycosid spiders is one of the most captured (by ornamental lawn standards) species. In contrast to the otherwise diurnal wolf spiders, *T. ruricola* may benefit here from its nocturnal activity (Bayram 1995) to escape the increased predation pressure by birds on urban lawns (Mennechez and Clergeau 2001), to which it would be exposed as a large vagrant species (Gunnarsson 1996; Gunnarsson and Wiklander 2015). On the other hand, a methodological bias would also be conceivable, since a larger body size is associated with increased mobility and can provide a higher trapping probability (Luff 1975; Hancock and Legg 2012). Due to the different ecological demands of the two species, we did not exclude *T. terricola* from the list of indicator species and consider it a possible indicator of improvements in vegetation structure.

Apart from *T. terricola* and *Alopecosa pulverulenta*, which can be regularly detected in urban areas, it is impossible to speculate on when the defined target species will occur (if they ever do). Nevertheless, Bauer et al. (2024) have recently shown that urban grasslands are capable of supporting spider species of conservation concern. Our results therefore can provide important insights, for example, when trying to identify suitable donor grassland sites for translocation of arthropod communities during a restoration process (Helbing et al. 2020).

In summary, as a first step to measure improved habitat quality using epigeic spiders on former ornamental lawns in the short term, generalist grassland spiders should show increasing abundance and species richness. In Central Europe, a large part of the indicators discussed here can probably also be used, but an a priori overview of the regional species pool using publicly available sources like Atlas of the European Arachnids (https://atlas.arages.de) or the data portal of the arachnological society (www.aramob.de) should always be obtained. Research projects with low levels of funding could also measure an increase in wolf spider populations in general, as this family can be easily identified even by less experienced researchers and a monitoring with pitfall traps is cost (Morrill 1975) and time efficient (Hohbein and Conway 2018). This could be useful for research projects with a citizen science approach (Pocock et al. 2014; Zapponi et al. 2017). Nevertheless, species-level determination should always be preferred, as this is the only way to reliably track ecological and functional developments (Derraik et al. 2002). If no plot-specific initial surveys were done, which will presumably mostly be the case for ornamental lawns, a short- to medium-term target value of 50% wolf spider share of total pitfall trap catch can be used here with a sampling duration of at least two months within the vegetation period. On the long term, the focus should be on the detection of the grassland specialist target species as ecological indicators. For this purpose, adapted sampling by synchronizing collection time span with species phenological data or using semi-quantitative rapid assessment methods (e.g. Cardoso et al. (2008)), can take place in later phases to further reduce the workload. Using spiders as flagship species in urban restoration projects combined with public promotion such as area signage, local news coverage, or the creation of educational school materials can increase visibility for this species group. This heightened exposure stimuli, along with increased knowledge, may help reduce fear and disgust among local citizens (Smits et al. 2002; Abado et al. 2020), ultimately lowering the economic costs associated with these fears (DuPont et al. 1996; Pittig et al. 2014).

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Author contributions All authors conceptualized the study and designed the methodology. A.B. and J.J. compiled and curated the dataset. M.R.-N. supervised the project and provided critical revisions. A.B. conducted the formal analysis and wrote the main manuscript text. A.B., J.J. and B.D. prepared the figures and tables. All authors reviewed and approved the final manuscript.

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Data availability The data and the code of the analyses will be made available on GitHub (https://github.com/alexander-bach/lawns_to_meadows) following its publication. Data is also available in the ARAMOB data repository.

Declarations

Competing interests The authors declare no competing interests.

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