Effects of urbanization, management and invasive neophytes on grassland arthropods in Karlsruhe, Germany

by

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Content

Abstract

Urbanization drives environmental change at multiple scales and negatively effects biodiversity in several ways. Nonetheless, urban areas concomitantly offer resources and habitat for an array of different organisms and represent a still mostly unutilized opportunity for biodiversity conversation. On the other hand, cities have been identified as hotspots for alien plant species and facilitator for invasive plants. As a result, many urban habitats are dominated by non-native species.

Green spaces represent the most important habitat analogue for organisms in cities. In this regard, urban grasslands have one of the greatest potential for conservation. With a majority of urban grassland still excessively managed solely for ornamental purposes, recent research demonstrated that extensively managed urban meadows with only one or two cuts per year facilitate a great diversity of arthropods, including species of conservation concern (cc). Nonetheless, the role of urban grassland in the applied conservation of arthropods at the local scale is still little investigated. The first part of the dissertation therefore aimed at disentangling the effects of management, local and landscape parameter on spiders (Araneae) and ground beetles (Carabidae) that occur in urban grassland situated in a large city of Southern Germany (Karlsruhe, Baden-Württemberg). For both taxonomic groups national recording schemes as well as local red lists are available. 27 urban grasslands in two management intensities (1-2 cuts with biomass removal, 3-5 cuts with self-composting) along an urbanization and humidity gradient were sampled with pitfall traps and sweep net. The results demonstrate that local parameters such as humidity and vegetation height had the strongest effects on the abundance of species of cc as well as assemblage composition, while intensive management negatively effected the abundance of both groups. Landscape parameters such as urbanization or isolation had comparatively minor effects on diversity and abundance. Dry and sparsely vegetated urban grassland hosted the largest number of species of cc, while the assemblages of mesic and humid grasslands mostly consisted of common species. In part, species of cc were sampled in high numbers on dry grasslands, indicating flourishing populations. If biodiversity-friendly management is financially or otherwise limited, it should primarily target dry grassland in urban areas.

A further comparison with a large nearby grassland reserve ("Alter Flugplatz") revealed that urban grasslands mostly harboured a subset of the spider diversity already present at the reserve, with only a few species exclusively found in urban grassland. Several specialists of xerothermic conditions remained restricted to the reserve with only a fraction of species of conservation cc recovered from urban grasslands (13 out of 37 species, 4 exclusive to urban grasslands). This comparison demonstrates that small urban grasslands may harbour several species of cc, but also exclude other, potentially area-sensitive specialists.

To further address effects of urbanization and the urban matrix on organisms, we compared urban, suburban and rural populations of a common grasshopper (*Chorthippus biguttulus*) and analysed whether morphological and behavioural differences between them exist. Urban populations showed increased boldness and higher rates of fluctuating asymmetry, which may be explained by higher environmental stress in urban habitats during development and selection for bolder individuals in the urban landscape.

The last part of the project focused on the effects of two invasive plant invaders. American species of goldenrod (*Solidago canadensis* and *S. gigantea*) and Himalayan balsam are common invasive plants in Karlsruhe, however, virtually nothing is known on their effects on vegetation-dwelling predators during flowering season. Spiders and potential prey items sampled from dense stands of both invaders showed contrasting effects on sampled specimens and functional groups in comparison with mixed stands of native plant species, demonstrating that both invaders altered spider abundances in different ways.

Chapter I

Introduction
urbanization, the environment & biodiversity

Tobias Bauer

Urban areas – characteristics and history

How to define urbanization and urban areas?

From which point on should a place where people live together be defined as an urban rather than a rural place? Areas in which people agglomerate are traditionally separated into urban and rural communities by the virtual absence of agricultural activities in inhabitants and the local economy (Firebaugh 1979, Weeks 2010). However, this strict dichotomy of rural and urban areas becomes increasingly difficult to maintain, especially given massive and often uncontrolled urban sprawl all over the world, suburbanization (e.g. Hesse & Siedentop 2018) and fast urbanization of formerly rural regions in the global south (Farell 2016, Hutchings *et al.* 2022). Further modern developments render a strict dichotomy of urban and rural areas through classification of its dominant sector of employment antiquated. For example, commuting long distances between an urban workspace and a rural resident through the usage of modern technology (Giménez-Nadal *et al.* 2022) or increasing rates of remote work in rural residents working in urban economies (Paul 2022, Zenkteler *et al.* 2022) intermix the primary income sector of urban and rural areas or make it possible to work from any place in the world.

Weeks (2010) proposed the following modern framework for urban areas:

"urban" is a place-based characteristic that incorporates elements of population density, social and economic organization, and the transformation of the natural environment into a built environment

Urban areas are therefore built-up environments in which natural structures have been mostly replaced with artificial ones such as buildings, streets and below-ground infrastructure to increase population density, economic output and social interactions.

Figure I: Hong Kong Harbour area and skyline, from Victoria Peak in June 2019, CC BY-SA 4.0, Author: Benh Lieu Song

Hence, the probably most important indicator of urbanization is the transformation of the natural environment by built-up structures, with artificial impervious surface cover as the most crucial proxy (Weeks 2010). However, impervious surface cover may vary greatly between cities. The historic centres of cities or borough cities in Germany, which often have been inhabited since Roman or early medieval times, may have an impervious soil coverage of over 90% (Environmental Atlas Berlin 2021). Large and considerably younger grid square cities in the United States may exhibit a total impervious surface cover of over 60% (e.g. New York), with others, such as Nashville with only around 18% experienced less soil sealing (Nowak & Greenfield 2012). Hong Kong (Fig. I), limited by steep mountain ranges and the sea is one of the regions with the highest population density in the world (e.g. Yeh 2011) and one of the highest developed free-market economies. In the past, the city had one of the fastest urbanization rates and experienced one of the highest rates of soil sealing in the world, with today up to nearly 95% in some business areas (Wong *et al.* 2017). These parts of Hong Kong act as a striking example of a fully urbanized area with a virtually complete transformation of the natural surface into an artificial, built-up environment optimized for economical purposes. Impervious surface cover has been frequently linked to the abovementioned framework that Weeks (2010) used to define urbaness, e.g. factors such as (daytime) population density, tax capacity, municipal revenues as well as infrastructure proxies like road density (Behnisch *et al.* 2016, Stankowski 1972, Zang *et al.* 2021).

The often observed succession in impervious surface from a rural area to the center of a city is frequently described as the rural-urban gradient (Batáry *et al.* 2018, Weeks 2010), with suburban areas as a transition zone between consolidated urban areas and rural areas. Suburban areas are defined as essentially residential areas in commuting distance of a large city or metropolitan area (Garreau 1992). The amount of soil sealing is often relatively low compared to the centre of the city (Salvati 2014). Suburban areas are usually described as a main component of urban sprawl (Jaret *et al.* 2009) and often depicted as a non-sustainable urban outgrowth, e.g. due to very high land consumption rates per inhabitant and dependence on automobiles and subsequent high carbon emissions (Leonard 2023). However, considerable differences exist between the character of suburban areas on different continents, e.g. in their economic profile, history and consolidation (e.g. Hesse & Siedentop 2018, Kowarik 2008, Salvati 2014), which impede a simple characterization of suburban areas. For example, areas potentially described as the suburban transition zone in German cities are often older than the city centre itself and frequently exhibit very high local soil sealing rates, at least locally. This is often related to inhabitation and subsequent urban consolidation of historic districts since ancient or medieval times (Environmental Atlas Berlin 2021, Hesse & Siedentop 2018).

In conclusion, urban areas cannot be strictly separated from rural areas. Moreover, “urbaness” and “ruralness” represent extremes of a continuum and not a dichotomy, and might vary strongly on the local scale. Fully urbanized areas are therefore characterized by the virtual replacement of the natural environment by built-up structures (Weeks 2010) and are often, but not always, delimited from the rural landscape by suburban areas with an intermediate degree of urbanization.

A brief history of urbanization

Urbanization and urban agglomeration are not a modern phenomenon. In ancient times, cities such as Rome, Babylon or Qiyi already accommodated between 100 000 and 1 million people (Modelski 2003), possessed a finely-tuned administration and used legal systems equally applied to nearly all inhabitants. However, until the 18th century (Fig. IIA), a millennia-old equilibrium between the urban and rural population existed. The vast majority of people lived in rural areas with a minor agricultural surplus production enabling only a small urban population that did not actively participate in working the land. With the onset of the British agricultural and industrial revolution in the 18th century (Allen 2009) and the invention of the Haber-process (Smil 1999) this relationship quickly dissolved and a large proportion of rural workers where now available for working in quickly emerging industrial centres. As a result of the massively increased agricultural production (Smil 1999) by only a part of the former labour force, especially since 1950, and strongly decreasing infant mortality due to improved sanitation and medical care (e.g. Lee 2007), an unparalleled global population growth followed that is still unbroken today and will likely not weaken until 2040 or 2050 and probably reverse in 2100 (Fig. IIB).

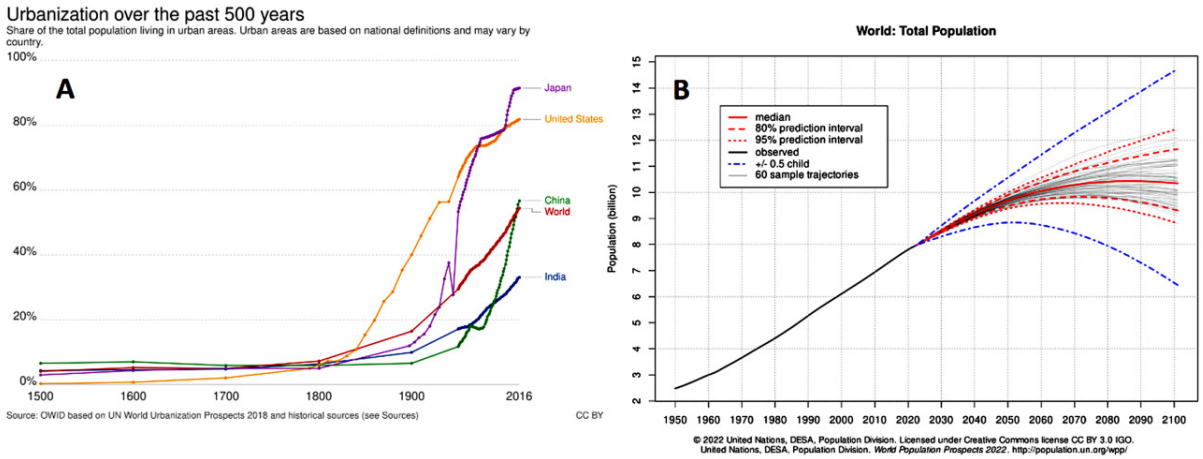

Figure II: Global urbanization over the past 500 years (A) and global population development since 1950 (B)

Stimulated by the replacement of manual labour in agriculture by machines, the massive increase in population and the necessity of workers as well as experts living close to industrial centres, large urban areas of never-seen size developed in the Western World at the beginning of the 19th century. These were followed some decades later by developing countries such as China and India (Fig. IIa). Lately, the year 2007 marked the year in which 50% of the world population (PRB 2007) lived in urban areas. This trend will further increase in the future and by 2050 only one third of the global population will probably live in rural areas (Cohen 2015).
Currently, only around 4-5% of the population in the European Union and around one quarter on a global scale (Roser 2023) is employed in the agricultural sector, which will further decrease in the future (Eurostats 2025) due to urbanization and further mechanization of agriculture in developing

countries. Today, Large urban areas with over one million inhabitants are not equally distributed across the globe but are primarily localized in coastal and lowland regions (Fig. III). In contrast to previous times, the majority of people will now be born, raised and work in urban areas and experience nature on a daily basis only as tiny fragments in a built-up environment.

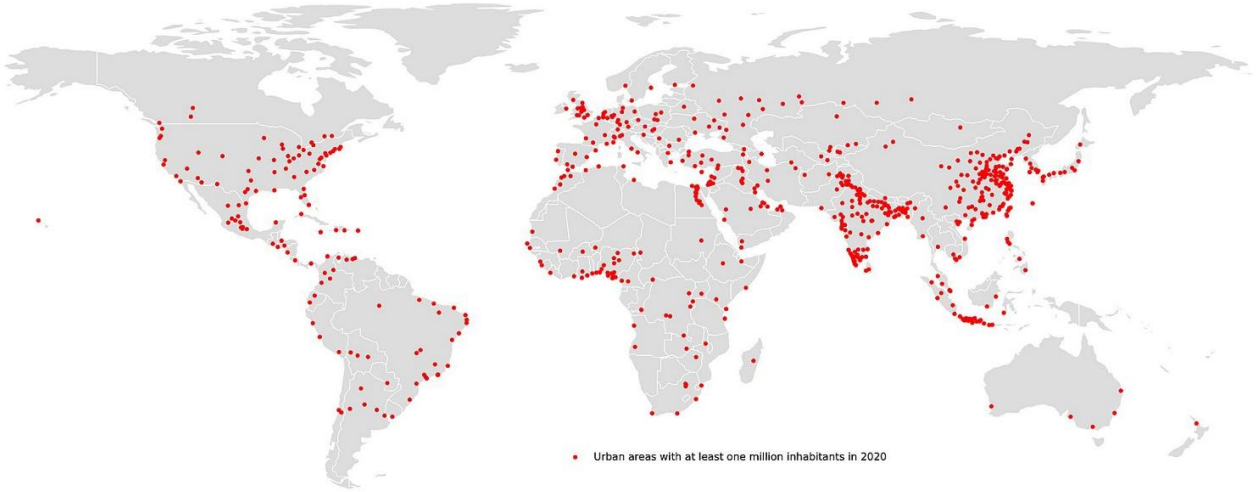

Figure III: Global Cities with over one million inhabitants. Petnog, CC BY 4.0 <https://creativecommons.org/licenses/by/4.0>, via Wikimedia Commons

Urban areas, green spaces and the natural environment

"But escape from nature assumed an infinite cornucopia." Gleeson & Low 2000:1

Urban areas and their effects on the natural environment

Although cities only cover around 2% of the world surface, they consume around 75% of resources and produce over 60-80% of all greenhouse gases as well as 50% of all waste (CBD 2007, IUCN 2023, United Nations 2020). With ongoing urbanization and population growth, especially in developing countries, these rates will very likely increase over the next years. The majority of environmental conditions in urban areas are anthropogenically altered to cater to human or economic needs. In hostile environments such as the United Arabian Emirates this may create urban environments in which most human activities take place inside fully air-conditioned buildings and transport systems (e.g. Alrahma *et al.* 2023). Cities strictly depend on the import of energy as well as agricultural and industrial products for their function and stability, thereby driving

environmental change at multiple scales (Grimm *et al.* 2008) and acting as consumers of their environment (Gleeson & Low 2000). On the other hand, cities produce and export huge amounts of waste products that affect even remote environments (Lu *et al.* 2024, Zeller *et al.* 2019). As established above, the natural vegetation in cities has been extensively replaced with built-up structures and a large fraction of soil surface has been covered up by artificial impervious surfaces and buildings. Urban areas have often been built in biodiversity hotspots along rivers and coasts resulting in an array of negative impacts reaching from river regulations with subsequent loss of river dynamics over artificial coastal fortifications destroying habitat for coastal organisms to excessive water pollution by local industry (Bruns 2014, Knoll *et al.* 2017, Wang *et al.* 2012). Extensive soil sealing in cities alters climate regulation and changes the natural water cycle by increasing runoff and reducing evaporation, ultimately leading to a shift in the urban heat balance (Wessolek 2008). The higher temperature of city environments, especially in summer, compared to their rural counterparts is known as the urban heat island effect (Fig. IV) (Deilami *et al.* 2018) and negatively affects the health of citizens as well as urban biodiversity. The urban heat island effect has been reinforced in many cities by climate change and further consolidation (e.g. Cai *et al.* 2023, Yang *et al.* 2016). Rapid and unplanned urbanization, especially in developing countries, also triggers severe social distortions and multiple health issues, for example stress or diseases caused by air, water, light and noise pollution (Salter *et al.* 2015, Walker *et al.* 2020, Zhang *et al.* 2022). Unplanned urbanization also often leads to higher cost of living in cities, high unemployment rates, high criminality and grave wage inequality (Zhang 2016). Nevertheless, recent research emphasizes many possibilities and already deployed plans of sustainable developments within cities (Niemets *et al.* 2021, Riffat *et al.* 2016), with an increasing focus on carbon neutrality and adaptions to climate change (Mi *et al.* 2019, Reckien *et al.* 2018). The challenges towards becoming environmentally and socially sustainable are, however, overwhelming for most cities, especially in developing countries. Nonetheless, green spaces play a crucial role in mitigating the manifold negative effects of urbanization on the environment at the local scale. Especially large green spaces with a size of over 10 ha considerably reduce the urban heat island effect and act as cool islands ("cool island effect") within the urban matrix (Aram *et al.* 2019, Du *et al.* 2017). Similarly, shading by urban trees mitigate the urban heat island effect during the day (Bowler *et al.* 2010, Yu *et al.* 2020). Urban green spaces also provide multiple water-related ecosystem services, for example rainfall interception, reduction of urban runoff and overall water regulation (Yao *et al.* 2015, Zhang *et al.* 2012). Urban vegetation is also frequently discussed as a buffer against air, noise and even light pollution (Diener & Mudu 2021, Dzhambov & Dimitrova 2014, Straka *et al.* 2021). Because of their positive effects and overall importance, the administration of many cities tend to view urban green spaces as a universal recipe or quick fix for an array of differently scaled environmental problems caused by urbanization (e.g. Holgersen & Malm 2015). Many environmental issues, however, are inherently linked to the state and sheer existence of cities, for example fossil energy consumption, waste production and land consumption. Their solution requires not only technical progress, but maybe also a different attitude towards economy, standard of living and consumption in general. Nonetheless, the globally increasing efforts toward carbon neutrality, limitation of urban sprawl as well as greening of cities to reduce the urban heat island effect (e.g. the million tree initiative, Pincetl 2013) benefit local city

residents concomitantly at different scales by creating jobs, reducing pollution in general and conserving of soil and water resources for future generations.

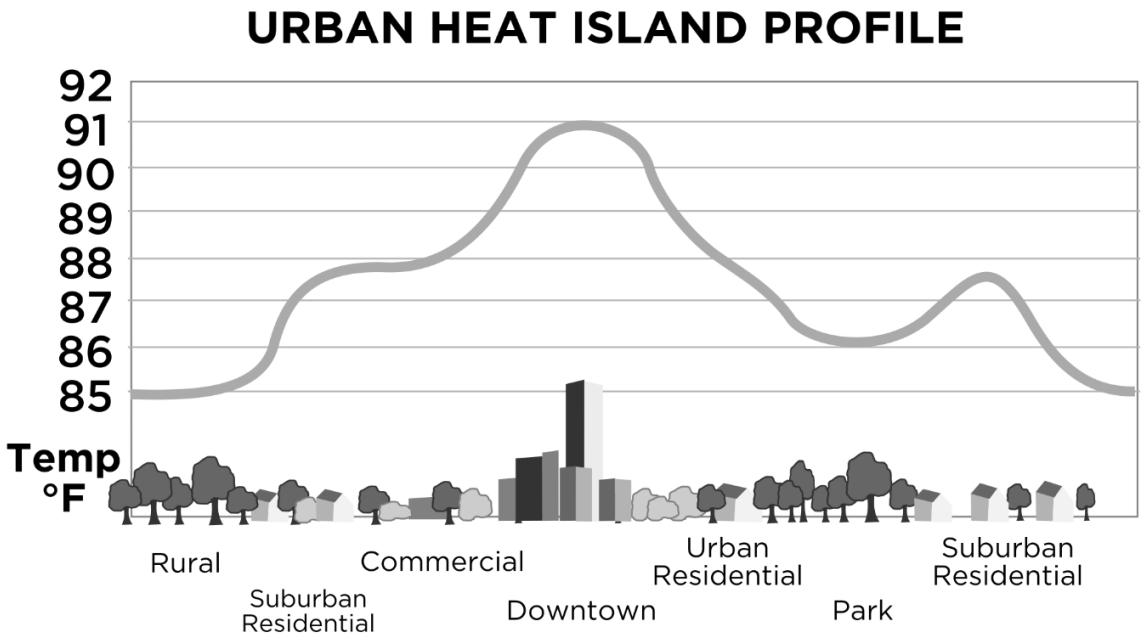

Figure IV: Urban heat island profile over the rural-urban gradient. Please note temperature scale in Fahrenheit, for conversion to Celsius: x °F ≡ (x − 32) × 5/9 °C. Image: public domain

Urban green as a part of urban history and identity

Basically, urban green spaces (all urban land covered by vegetation of any kind; *sensu* WHO 2017) represent rural or wilderness elements (e.g. trees, bushes, flowers) selectively planted and/or tolerated within city limits for predominantly non-agricultural, e.g. ornamental and/or functional, reasons. An exception is unmanaged urban wasteland wilderness which usually develops naturally on abandoned post-industrial sites or any other type of abandoned urban area. Managed urban green places already appear very early in the history of urbanization. During the roman time, Emperor Augustus (63 BC – 14 AD) and other aristocrats transformed many areas in the city of Rome into recreational parks while simultaneously creating flourishing private gardens with imported exotic plants, for example parts of Campus Martius (Jacobs & Conlin 2014) or the famous gardens of Villa Arianna (Langgut 2022). Stemming from an early appreciation of the function of trees in soil and water conservation by classical Chinese authors, intensive urban tree planting organized by an administrative structure is documented for the city of Chang'an during the Tang-Dynasty (618 to 907) and many other historic cities in China (Zhang 2024). In official documents of the Chang'an administration, even the exact species of trees that had to be planted along city roads were established (Zhang 2024). In Medieval times as well as the Renaissance, flourishing urban parks and gardens were found in urban settlements all over the globe, ranging from urban sacral places

in Mesoamerican cultures to gardens in large cities of the Qing-Dynasty in China (Stark 2014). Cities and green spaces such as parks, gardens and alley trees always developed in close companionship and in relation to cultural and environmental needs and vary greatly today in their availability to local population, ranging from 2% urban green in Dubai to over 45% in Moscow and Singapore (Lawler 2018). However, urban green was and is present in cities all around the globe, independent of the cultural background. Today, many modern cities invest large amounts of personal, financial and intellectual resources in the maintenance, development and conservation of urban green (e.g. Choi & Kim 2022, Litman 2020, Loughran 2020). Nonetheless, urban green is increasingly under a multitude of threats, ranging from global warming (Sánchez *et al.* 2018, Tubby & Webber 2010) over urban consolidation (Lin 2010) to alien pest species (Branco *et al.* 2019, Paap *et al.* 2017). In addition, with incremental negative changes in green space management in combination with a shifting baseline on how green spaces look (Colding *et al.* 2020), urban green in many cities faces an uncertain future. Although often seen by city planners as an accessory rather than an elemental need, green spaces and their availability considerable affect the emotional state, health and other proxies of well-being in local residents and has even been linked to lower crime rates (Coppel & Wüstemann 2017, Kondo *et al.* 2018, Weijs-Perrée *et al.* 2020). Increased green space supply also fosters community attachment in urban residents (Arnberger & Eder 2012). Hence, destruction of public urban green, e.g. cutting down of old trees or concreting park areas for further urban development can trigger grave and bitter protests, as happened for example in Stuttgart (Germany) 2010 (Baumgarten & Rucht 2013) or Istanbul (Turkey) 2013 (Fig. V) (Gezer & Popp 2013). Given the multidimensional interest of citizens (including local scientists like the author of this dissertation) in urban green spaces, it is not surprising that the involvement of local residents in realizing, conserving and managing public green spaces drastically increased in the past decades (Mattijssen *et al.* 2018). Hence, there is a large body of evidence that urban green is deeply engraved in the daily routines and identity of urban residents. The importance of urban green spaces in cities from a cultural and medical aspect cannot be overestimated. From a city planner's perspective, urban green finally needs to be understood as a crucial part of urban history and personal identity, connecting urban citizens emotionally to their residential area as well as positively influencing their health, socioeconomic existence and overall well-being.

Figure V: Green space destruction can trigger violent escalations among local citizens. Besiktas football team supporter club Carşı members hijacked a bulldozer and chased police vehicles during Gezi park protests. (Gezginrocker, CC BY-SA 3.0 <https://creativecommons.org/licenses/by-sa/3.0>, via Wikimedia Commons)

Urbanization and biodiversity

Urban ecology as an emerging field of research

As established above, urbanization is a complex process involving population density, economic output and social organization. Its main characteristic is the transformation of the natural environment into built-up structures such as buildings and streets, with impervious surface cover as its most important proxy. Nonetheless, urban green and green spaces such as parks are an inseparable part of cities. Maybe due to their inherent high artificiality and ostensible lack of wildlife, cities and their effects on biodiversity have been heavily neglected by ecologists until quite recently (Botkin & Beveridge 1997, Grimm *et al.* 2008, Rega-Brodsky *et al.* 2022, Sukkopp & Wittig 1998). However, over the last three decades, urban ecology has established as a research field of transdisciplinary importance, comprising elements of urban planning, species conservation, invasion science, health management and urban environments as drivers of evolution (e.g. Aerts *et al.* 2018, Des Roches *et al.* 2021, Merckx *et al.* 2018). An overview of current research questions and hypotheses is given in Lokatis *et al.* (2023, Tab. 1).

Species diversity in urban habitats and the role of urban grasslands

No other species modifies and dominates its habitat to such an extent as the *Homo sapiens*. Cities have been built to accommodate extremely high levels of human population and to meet the needs and demands of its human inhabitants. In other words, humans drastically altered the majority of natural parameters in cities and thereby created their preferred ecological niche within a potentially hostile environment. Naturally, one would consider urban areas as depleted of wildlife. Indeed, higher levels of urbanization usually have a negative impact on native biodiversity and are considered as one of the major drivers of species loss worldwide due to direct effects such as replacement of natural vegetation by artificial structures, fragmentation and isolation of habitats (Fenoglio *et al.* 2020, McKinney 2008, Sol *et al.* 2020), disruption of biotic interactions (e.g. Straka *et al.* 2025) and increased human disturbance (Batten 1972). However, indirect effects of urbanization may be detrimental to native species as well, for example increased introduction and establishment of competing exotic species via anthropogenic assistance (Kowarik 2011), both advertent and inadvertent (e.g. Genovesi 2005, Wauters *et al.* 2023), increased mortality caused by artificial structures (Boal & Dykstra 2018) as well as overhunting in the vicinity of cities due to an unsustainable demand for bush meat in expanding urban communities (Nguyen & Jones 2022). In addition, cities are discussed as main drivers of biotic homogenization by re-structuring vegetation and local resources in a way that only offers habitat to a certain set of mostly eurytopic and widespread species (Lokatis & Jeschke 2022).

Despite the undeniable negative effects of urbanization on native biodiversity, recent research demonstrated that cities may also represent an opportunity for species conservation. Cities as a whole are undeniably - and maybe unexpectedly - rich in species (Kovarik 2011, Kühn *et al.* 2004, Rogers *et al.* 2023). Suburban residential areas harbour a large variety of different organisms, ranging from insects to large birds of prey such as the black vulture (*Coragyps atratus*) (Boal & Dykstra 2018, Leveau *et al.* 2022, Rogers *et al.* 2023,). Urban wastelands are valuable habitat analogues for dry grassland arthropods (e.g. Eckert *et al.* 2017, Small *et al.* 2002, Twerd *et al.* 2019) and old urban trees are home to a large variety of saprophytic beetles (Hórak 2018). Cities also have been promoted as sanctuaries and last resorts for some endangered species (e.g. Lepczyk *et al.* 2023, Soanes & Lentini 2019). Nonetheless, the urban matrix is increasingly recognized as a filter for some functional groups (Buchholz *et al.* 2020, Piquet *et al.* 2024) with some of them usually absent from or strongly depleted in urban habitats despite an apparent habitat suitability on the local scale. The causality behind such filter processes are manifold and usually unknown. Urban habitats are prone to high disturbance rates and pollution, for example by urban noise or contamination by heavy metals from industrial processes. In addition, they often offer different food sources, e.g. invasive alien plants instead of native species. Animals living in urban areas therefore often express an array of physiological, morphological and behavioural differences, such as increased boldness (Baxter-Gilbert *et al.* 2019), reduced responses to stressors (Partecke *et al.* 2006) or fluctuating asymmetry in body parts, which is often attributed to developmental instability caused by environmental stress (De Coster *et al.* 2013, Lazić *et al.* 2013). However, species responses to urban habitats are not always related to decreased fitness or survival levels. Some species, for example some birds of prey, exhibit higher survival and fitness rates in urban habitats due to e.g. an increased availability of prey or nesting possibilities (Boal & Dykstra 2018).

Figure VI: Various aspects of urban grasslands in Karlsruhe (Baden-Württemberg, Germany) (Images by Tobias Bauer, Daniela Warzecha & Hubert Höfer)

For the majority of species, green structures are the most important habitat analogue in cities, with urban green spaces and private gardens as the spatially most common (e.g., Aronson *et al.* 2017). However, the diversity of organisms, especially of arthropods, in urban grasslands (Fig. VI) and gardens is strongly influenced by the intensity of the management (Smith *et al.* 2015, Aronson al. 2017). In Europe, semi-natural grassland of rural areas is known as one of the species-richest habitats, but is currently in severe crisis due to agricultural intensification as well as abandonment of management (Shipley *et al.* 2024). Similar to intensively managed rural meadows that experience a high mowing frequency, lawn-like turf grass (ornamental lawn; Fig. VII) is usually depleted of arthropods (Fekete *et al.* 2024, Smith *et al.* 2015, Unterweger *et al.* 2017). However, turf grass is the dominant urban green in many cities around the world and its maintenance often

includes intensive fertilization as well as input of herbicide and other pesticides (Paudel & States 2023, Smith *et al.* 2015). Over the last decades, many cities, especially in Europe, have started to diversify their mowing regimes, partly to foster local arthropod diversity but also to simply reduce costs by limiting the number of cuts on urban grasslands that are not used for recreational activities (Helmut Kern, pers. comm., Paudel & States 2023). These extensively managed and often benignly neglected urban grasslands (Fig. VI) have recently been identified as a suitable habitat analogue for a vast array of arthropod species, e.g. wild bees (Buchholz *et al.* 2020), spiders and carabids (Buchholz *et al.* 2018, Venn *et al.* 2013, Venn & Kotze 2014) or true bugs (Unterweger *et al.* 2017). In addition, they also provide a number of often neglected cultural services, among them the usage as outdoor classrooms or stress reduction related to experience of nature (Paudel & States 2023). Given the ongoing and unprecedented global arthropod crisis (Hallmann *et al.* 2017, Harvey *et al.* 2020, Wagner *et al.* 2021), extensively managed urban grasslands and their restoration may therefore represent one of the most promising opportunities for species conservation in urban areas (Klaus 2013, Venn *et al.* 2013). Nonetheless, a well-founded scientific basis for pressing questions, especially on the local scale, is still lacking (Klaus 2013). Consequently, many urban grasslands are managed or restored without a goal specified *a priori*. This often results in a very vague idea of arthropod-friendly management. Typical examples observed in Karlsruhe, Ettlingen and Stuttgart (Baden-Württemberg, Germany) by the author include reductions in cutting frequencies of randomly selected grassland plots without further knowledge on their potential for species conservation, e.g., on the basis of vegetation, soil humidity or isolation. Further observations were reductions of cutting frequencies in very small (<400 m^2), nutrient-rich grassland fragments mainly consisting of grass and one time partial-mowing in summer with subsequent mechanical mulching of fallow stripes in fall/winter. The Latter may potentially create an ecological trap for overwintering arthropods and other organisms. Research that aims at disentangling local and landscape effects on arthropod species diversity, abundance as well as species of conservation concern is therefore urgently needed. Such a framework can guide local administrations in decisions on which grassland has the greatest potential for biodiversity conservation as well as how and when to mow.

Figure VII: Urban lawn (turf grass) in Whakatane, New Zealand, with invasive common Myna (*Acridotheres tristis*), December 2019 (© Tobias Bauer). Turf grass is virtually the only type of grassland present in many cities of New Zealand and still managed not only by cutting, but also input of herbicides and fertilizer.

Linking applied arthropod conservation and urban grassland science

From an applied conservation perspective, the role of extensively managed urban grassland in the conservation of arthropods is very little investigated. Applied conservation, i.e. the monitoring of species occurrences, the development and execution of measures to preserve biodiversity with special attention on endangered and iconic species, naturally focused on areas reserved for species conservation such as nature reserves and national parks. This has slightly changed over the last years due to the global arthropod crisis and the identification of landscape level drivers (Hallmann *et al.* 2017, Seibold *et al.* 2019, Wagner *et al.* 2021). In hindsight, conservation efforts focusing on only a few protected areas have been shown to be insufficient to maintain arthropod biodiversity and abundance on the regional as well as the landscape level (Blick *et al.* 2016, Seibold *et al.* 2019). However, recent studies demonstrated that urban grassland can host a wide variety of species of conservation concern (cc) as well as flourishing arthropod populations, ranging from spiders over ground beetles to wild bees (Buchholz *et al.* 2018, Grossmann *et al.* 2022, Venn *et al.* 2013). Nevertheless, in some studies focusing on urban grassland species of cc were virtually absent, and although assemblages were species-rich, they consisted mainly of common species (e.g. Bach *et*

al. 2025). The occurrence of many arthropods of conservation cc, for example in spiders, are linked to habitats with extreme conditions (Entling *et al.* 2007). These are unevenly distributed over the landscape due to relief, climate and geology. Typical examples are sandy, nutrient-poor grassland, xerothermic slopes, wetlands or swamp forests (Blick *et al.* 2016). Cities in regions that are either naturally poor in such structures or have been virtually depleted of them by human activities in the past (e.g. by melioration for agriculture) may exhibit a different *a priori* potential to host species of cc than cities that feature fragments of such habitats. The area of Berlin, known for its low precipitation rate, is rich in dry grassland fragments that host a plethora of nationally endangered spider species (Möller *et al.* 2019). In contrast, urban grasslands and artificially created wildflower meadows in Aachen, built in a region with average precipitation on the national scale and comparatively good soils, seem to host rich spider assemblages, but only of common species typical for mesic or humid conditions (Bach *et al.* 2025). In this regard, comparing arthropod assemblages in urban grasslands to already known results from nearby protected areas could demonstrate the potential of urban grasslands for applied conservation on the scale of an urbanized landscape well as effects of the urban matrix as a filter for, e.g., species of conservation cc. However, inventories approaching completeness of species-rich groups such as spiders are rarely available, even in regions rich in ecologists. The urban nature reserve "Alter Flugplatz" in Karlsruhe, Germany is one of only a few in Central Europe for which the vast majority of occurring spider species are known, including several endangered species (Hemm *et al.* 2012). According to the species-area relationship, such large habitat patches harbour more species than smaller patches and may facilitate species sensitive to patch size (Rosenzweig 1995). However, a large number of small habitat patches might also harbour a large variety of different species due to varying environmental conditions on the local scale (Beninde *et al.* 2015). A comparison with results from nearby urban grassland fragments in the city area should therefore shed some light on the role of nature reserves and urban grassland fragments in conserving spider species in an urbanized landscape and emphasize the importance of large high-quality habitat fragments in conserving species of cc.

The role of plant invaders as habitat analogue in urbanized regions

On various scales, plant invasions have detrimental effects on ecosystems, biodiversity, economy and health worldwide, reaching from local displacement of native plant species over loss of food sources for specialized arthropod herbivores over serious medical implications for allergic persons due to highly-allergic pollen (Dostál *et al.* 2013, Mazza *et al.* 2014, Nentwig *et al.* 2018, Schirmel *et al.* 2016). Although comparatively rarely documented, plant invasions may even drive species (close) to extinction (Gilbert & Levine 2013), with *Hogna ingens*, the world's largest wolf spider and endemic to a single island off Madeira, as the maybe most prominent, however little-known, example (Crespo *et al.* 2014).

Urban areas are very rich in alien plant species, and some habitats are completely dominated by invaders, with some of them performing even better in their introduced compared to their native range (e.g. Ebeling *et al.* 2008, Kowarik 2008). Many city habitats frequently experience disturbance, e.g. through soil movement, soil alteration and soil sealing, trampling, removal of vegetation, noise/vibrations or permanent presence of humans. It is widely accepted that this high

rate of anthropogenic disturbance is the main driver of alien (nonnative) plant establishment in cities (Godefroid & Ricotta 2018, Kowarik 2008, Pyšek 1998). Many of those alien plant species have been introduced inadvertently to areas outside their native distribution, e.g. through stowaway seed and shoot transport in the international trade (Hulme 2021) or through tourism (Van Wilgen *et al.* 2017). However, some of the most invasive plant species worldwide have been actively introduced, many of them solely for ornamental purposes in urban areas (Niemiera & Holle 2009, Richardson & Rejmánek 2011). Nonetheless, alien plant species are used by many native species as a food resource and habitat analogue (Grutters *et al.* 2015, Padovani *et al.* 2020, Rodriguez 2006). In novel habitats, which are especially common in urbanized areas, native organisms may even depend on nonnative plants as a habitat for their survival (Packer *et al.* 2016) or use them more often as a food source than native plants (Hanley *et al.* 2014). Green spaces in Karlsruhe are, like many urban habitats (Kowarik 2008), rich in alien plants. One of the most dominant in urban grassland and open fringe areas are American goldenrod species (*Solidago canadensis/gigantea*) and Himalayan Balsam (*Impatiens glandulifera*). Both species flower late in summer and create a potential habitat analogue for plant-dwelling spiders that lurk on pollinators or build their web between high forbs. Comparing spider assemblages made from dense stands of both invaders with those from nearby stands of native plants should yield insights into the usage of invasive plants by native predators as well as functional differences between assemblages inhabiting both habitats.

Locality

All research was conducted in and around Karlsruhe (Baden-Württemberg, Germany), currently the third-largest city in Baden-Württemberg (Statistisches Landesamt BW 2025). Founded in 1715 as a planned city in the shape of a fan ("Fächerstadt Karlsruhe"), major parts of the city did not grow organically. Large areas of the Hardtwald, a forest on sandy and nutrient-poor soils, have been cut down over the years to allow further urban expansion (Blum 2004). From a European perspective, Karlsruhe is a rather young city and one of the few planned cities in Germany. The average rate of soil sealing in the city area is estimated to be around 54% (GDV 2023). For further data on climate and soil, please see chapter II and V.

Karlsruhe has a long-standing tradition in biodiversity-friendly green space management (Fig. VIII; see also chapter II). Besides extensively managed grasslands, local administration conserves old oak trees as habitat for the great Capricorn beetle (*Cerambyx cerdo*) and the stag beetle (*Lucanus cervus*) (Stadtwiki Karlsruhe 2025), and consider the effects of planted tree species on biodiversity, especially pollinators (Gartenbaumt, pers. comm.). City administration also actively promotes biodiversity-friendly management of private gardens and the restoration of gravel gardens. However, Karlsruhe is a growing city and many urban green spaces compete with further urban development and are under immediate threat due to consolidation efforts. As a result, as least one grassland area surveyed in chapter II (WGS 84 coordinates: 48.9999, 8.3433) has already been lost, which demonstrates the high pressure urban grassland currently faces in the city.

Like other German cities, Karlsruhe is very rich in alien plant species. For example, dense stands of the American goldenrod species (*Solidago canadensis*, *S. gigantea*) are present along the railways and roads and the invasive tree *Prunus serotina* is frequently found in forested areas (e.g.

Schäfer *et al.* 2023). The Latter represents a severe threat to open, sandy areas due to quick afforestation when not strictly managed (Zimmermann 2011). However, little is known on the ecosystem services and disservices these plants provide in the city area. Overwhelmingly, they are perceived as disservice providers by the public and administration (e.g. Zimmermann 2011), while potential positive effects, e.g. food sources for pollinators, have not been investigated so far.

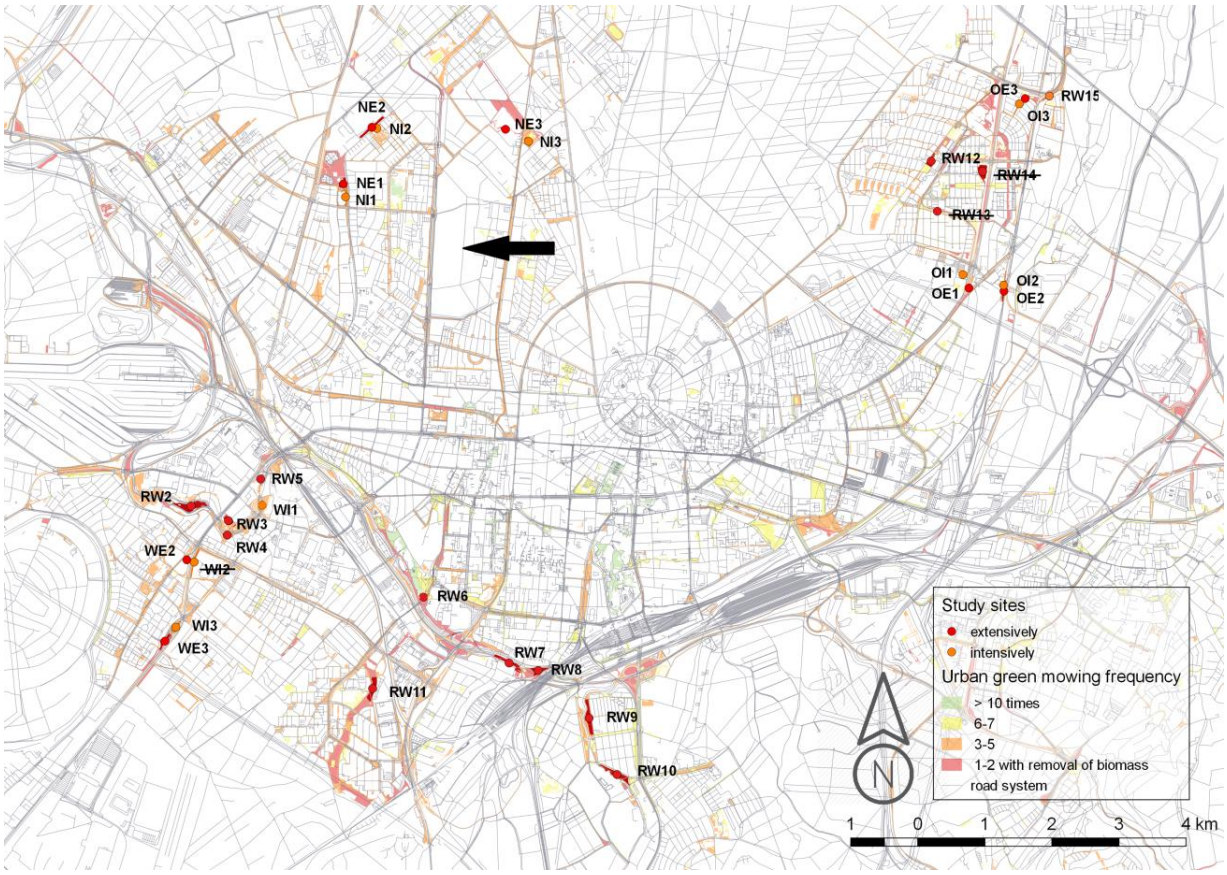

Figure VIII: Localisation of surveyed urban grasslands (Chapter II) in Karlsruhe, Germany. Arrow marks nature reserve "Alter Flugplatz". Localities ultimately not surveyed due to vandalism of traps or flooding in strikethrough text. (© created by Daniela Warzecha, edited by Tobias Bauer).

Research questions

Chapter II (a): Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritized for biodiversity-friendly mowing regimes

Although localized in a heavily modified environment, urban grasslands can host a large number of arthropod species and specimens when experiencing extensive, i.e. low-intensity, management (Fekete *et al.* 2024). Nevertheless, their potential for arthropod species of conservation concern

(cc) is largely unexplored. However, in most cities, various financial constraints, personal resources and acceptance by the public will limit the area of urban grassland that can be managed in a way that benefits local biodiversity. Determining which patch of urban grassland may be the most promising for species conservation by facilitating the most species of cc as well as overall diversity and abundance is therefore of crucial importance for local stakeholders. The city of Karlsruhe (Germany) has a long-standing tradition in extensive management of urban grassland, with some managed very extensively for over 30 years. In addition, a great variety of local parameters allows for the selection of sparsely vegetated dry, dense and high-growing mesic and comparatively humid grasslands, which allows entangling the effects of soil humidity and vegetation height on local arthropod communities.

1) ***Which landscape and local factors characterize urban grasslands that host rich arthropod assemblages as well as arthropods of conservation concern?***

Species of conservation concern such as the amount of locally threatened species usually indicate a high conservation value of a given area, but their presence may not be related or may even be contradictory to higher species numbers.

2) ***How does management of urban grassland influence arthropod abundance and diversity?***

Management intensity has been identified as a strong, if not the strongest, influence on local arthropod biodiversity and abundance in urban grassland (Fekete *et al.* 2024). However, little is known of effects on species of cc and when various important environmental factors such as soil humidity or vegetation height progressively change throughout a given selection of urban grasslands. The city of Karlsruhe manages dry, mesic and relatively humid urban grasslands, which is partly due to the special geology of the area, with some parts of the city built on sandy soils. It is therefore the perfect setting for disentangling effects of management and environmental factors such as soil humidity.

Chapter II (b): Spider assemblages (Arachnida: Araneae) in urban grassland patches in Karlsruhe (Baden-Württemberg, Germany)

Datasets of spider assemblages made during ecological projects contain valuable information for conservation issues, biogeography and further ecological questions deviating from the primary hypothesis. However, often they remained unpublished or, when published as an appendix, lack important metadata (Bach *et al.* 2024). In the worst cases, such datasets have been lost due to loss of digital storage facilities or the death of the researcher. This makes it impossible to reproduce published results and seriously impedes good scientific practice (Whitlock *et al.* 2010). The project ARAMOB (https://aramob.de) has been created to gather, mobilize and archive such datasets and to make them available through various data portals (GBIF, the German spider record scheme, portal of ARAMOB). For this, datasets may be submitted to the journal Arachnologische Mitteilungen (Arachnology letters) as a data publication (Fig. IX). A data publication does not present results derived from analyses of the data in the first place, but remains restricted to a detailed description of the data, which contain additional metadata following the template and manual for data publications (Bach *et al.* 2023). As spiders are still little sampled in urban environments and even basic questions remain unanswered, the assemblages made for investigating

questions in chapter II(a) have been enriched with all necessary metadata (e.g. sex, exact collection date, collection method) and published as a data paper in the mentioned journal.

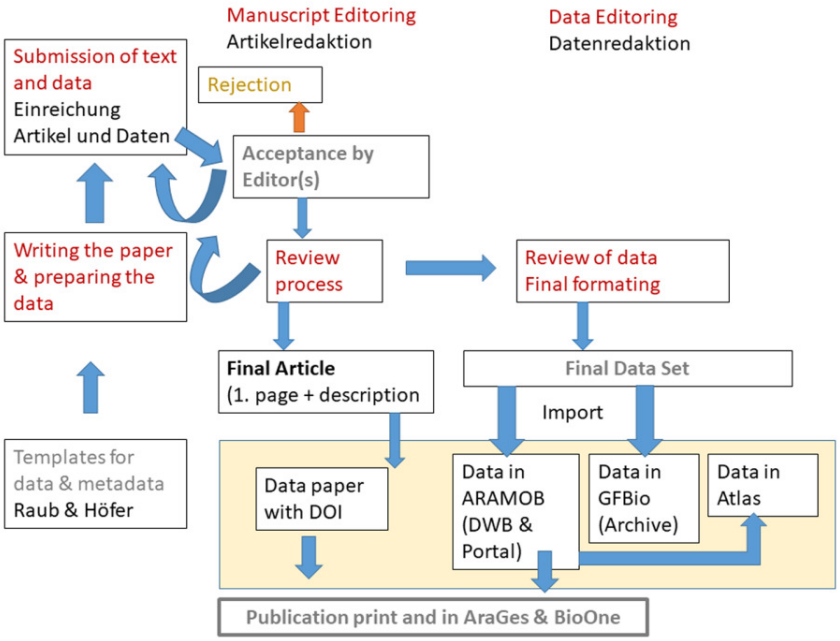

Figure IX: Data paper publishing procedure and long-term research data archiving in the scientific journal "Arachnology letters" (Image by Hubert Höfer & Florian Raub, with permission)

Chapter III: A Large urban reserve and many small urban grassland fragments together effectively preserve local grassland spider diversity in a city

Do urban grasslands feature a similar diversity and spider assemblages as a single large grassland reserve?

Depending on the landscape, climate and geology, cities may feature fragments of habitats that have a higher potential of harbouring arthropod species of cc. In the northern part of Karlsruhe, the nature reserve "Alter Flugplatz" is, despite its localization within the city, known to be inhabited by several endangered species. Most of them are specialists of xerothermic grassland (Hemm *et al.* 2012). A comparison of assemblages described in chapter II made on urban grasslands in Karlsruhe and those made in the nature reserve by Hemm *et al.* (2012) should demonstrate the potential of urban grasslands for applied arthropod conservation on the local scale and the role of the urban matrix as a filter for species of cc.

Chapter IV: Urbanization increases fluctuating asymmetry and affects behavioral traits of a common grasshopper

Does urbanization influence the behavior and morphology of a common grasshopper flourishing on urban grassland?

Urban areas are characterized by high environmental stress due to human disturbance and various types of pollution. Environmental stress is known to affect organisms in many ways and can lead to morphological aberrations, altered behavior (e.g. risk response, boldness or activity pattern) and various physiological responses. The research investigated effects of environmental stress on the morphology and behavior on urban and rural populations of a *Chorthippus biguttulus*, a common grasshopper flourishing in disturbed habitats.

Chapter V: Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season

How do dense urban stands of two plant invaders (American Solidago sp., Impatiens glandulifera) influence the diversity and composition of vegetation-dwelling spiders compared to stands composed of native plant species?

Nonnative plants often dominate urban habitats. Nonetheless, they may represent a habitat analogue for native arthropod species, especially vegetation-dwelling predators, which do not depend on native plant species as a food source. During their late summer flowering season in Central Europe (August, September), invasive American *Solidago* sp. and *Impatiens glandulifera* are visited by a many polylectic pollinator species and often represent the only substantial pollen and nectar source in urban areas at this time of the year. However, it is unknown to which extent flowering stands of these invaders are also inhabited by predators that may prey on pollinators. The research therefore aimed at comparing assemblages of spiders, the numerically most common pollinator predator in the vegetation, and potential prey items dwelling on flowering plant invader stands with those found on mixed stands of native plant species.

References

Please see chapter VII

Chapter II (a)

Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritized for biodiversity-friendly mowing regimes

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Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes

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Abstract

1. Although urbanisation is one of the greatest threats to biodiversity, its effect on particular invertebrate groups remains ambiguous on local and landscape scales.
2. We aimed to analyse the effect of urban grassland management on spiders (Araneae) and carabids (Coleoptera: Carabidae), as well as other local and landscape parameters. We investigated 27 grasslands of two different management intensities ('extensive': one to two late cuts with removal of biomass [$n = 18$]; 'intensive': three to five mulching cuts [$n = 9$]) in the city of Karlsruhe, Germany. Pitfall trapping and sweep netting were performed to sample carabids and spiders.
3. Results indicate that urban grasslands in Karlsruhe are inhabited by species-rich assemblages, including several species of conservation concern (cc). Latter remain mostly restricted to dry grassland. The number of total specimens and of those belonging to species of cc were negatively affected by intensive management. The number of specimens of species of cc further decreased with increasing humidity and in spiders, additionally, by vegetation height. Landscape factors had limited effects, and only isolation of meadows negatively influenced the species richness of carabids (total and of species of cc).
4. Our results demonstrate that conservation of dry grasslands in urban areas is crucial for sustaining local arthropod communities. Dry urban grassland may also act as a refugium for species of cc and mitigate the global insect crisis on a local and regional scale. In conclusion, biodiversity-friendly mowing regimes should be applied on a broader scale in urban areas and target especially dry grassland plots. In addition, increasing connectivity and permeability of the urban matrix assist the colonisation by species of cc.

KEYWORDS
Araneae, Carabidae, central Europe, ground beetles, rare species, Red List, species conservation, spiders, urban matrix, urbanisation

INTRODUCTION

The spread of urbanised areas represents a major threat to global biodiversity due to the alteration of natural and cultural landscapes (Fenoglio et al., 2020; Hou et al., 2023; McKinney, 2008; Sushinsky et al., 2013). On the other hand, cities can concurrently harbour species-rich communities (Sattler et al., 2011) and contribute to the conservation of many threatened or declining taxa (e.g., Boal & Dykstra, 2018; Buchholz et al., 2018; Ives et al., 2016; Spotswood et al., 2021). For example, old trees in parks or forest fragments within cities can serve as habitat for endangered bats or the great capricorn beetle *Cerambyx cerdo* (Linnaeus, 1758) (Dietz et al., 2020; Evelyn et al. 2004; Kadej et al., 2017) and artificial structures such as buildings are used as habitat analogues by predatory birds such as the locally endangered peregrine falcon (Boal & Dykstra, 2018).

Urban green spaces can also represent valuable refugia for grassland arthropods, which are threatened by intensive agricultural practices in rural landscapes. Examples are wild bees foraging in gardens or grasshoppers and carabids flourishing in industrial wastelands (Buchholz & Egerer, 2020; Eckert et al., 2017; Eyre et al., 2003; Fischer et al., 2016; Hall et al., 2017, Threlfall et al., 2015). The management of urban green spaces, such as urban grassland, thereby presents a major factor influencing urban arthropod diversity (e.g., Aronson et al., 2017; Buchholz et al., 2018; Delgado de la Flor et al., 2020; Lepczyk et al., 2017; Threlfall et al., 2015). Frequently mown grassland represents the most common type of green space in European cities, but is, at the same time, heavily understudied regarding its potential for harbouring species of conservation concern (cc), as well as sustaining local arthropod diversity in general (Buchholz et al., 2018). Because semi-natural grasslands are among the most species-rich habitats in central Europe (Habel et al., 2013), it is pivotal to understand how management and urbanisation influence arthropod communities in this widespread type of urban green space.

Previous research provides evidence that increased mowing frequency negatively affect urban biodiversity (Watson et al., 2020). However, only little is known about impacts of grassland mowing regimes in combination with landscape and local environmental variables, such as patch area or soil humidity, in an urban context (Beninde et al., 2015). Similarly, the effect of urban green-space management on rare or endangered arthropod species is understudied, which is often linked to a limited availability of baseline distribution data and endangerment classifications for many taxa. However, the resources for biodiversity-friendly mowing regimes, especially in cities, are often financially limited or underfunded, and prioritisation of localities with high potential for rare species should be pursued.

Dating back to the 1980, Karlsruhe was one of the first German cities that established extensive mowing regimes for some of its urban green spaces to benefit local biodiversity (Gartenbauamt Karlsruhe, pers. comm.). This practice includes a reduction of the mowing frequency to one or two cuts per year with hay removal (to avoid accumulation of nitrogen in the soil) resulting in the establishment of forb-rich meadows within the city area. At the same time, large amounts of urban green spaces in Karlsruhe are still managed more intensively and mulched three to five times per year. This is also done because mechanical mulching of urban meadows is less costly and does not require special machinery and time for hay removal (Gartenbauamt Karlsruhe, pers. comm.).

Spiders (Araneae) and carabids (Coleoptera: Carabidae) are species-rich groups known to be sensitive to disturbance and anthropogenic habitat alteration and inhabit a wide range of terrestrial habitats, while at the same time individual species usually show differentiated niche positions along environmental gradients and react to changes in the structural complexity of their habitats (e.g., Buchholz, 2016; Buchholz et al., 2018; Entling et al., 2007; Rainio & Niemelä, 2003; Schirmel et al., 2015). In addition, an online-available and constantly updated record scheme for spiders with over 2 million records (Arachnologische Gesellschaft, 2023) and a record scheme of carabids (Trautner et al., 2014) provide valuable data on current local species distributions in Germany. In combination with the available Red Lists with the assessment of the status of endangerment (Nährig et al., 2003; Trautner, 2005), both spiders and carabids are highly suitable indicators for the investigation of differently managed urban meadows.

We conducted a comprehensive investigation of urban meadows across the city of Karlsruhe by sampling spiders and carabids and by incorporating important urban environmental gradients at the landscape (isolation, impervious surface) and local level (soil humidity, vegetation). Investigated urban meadows differed in management intensity and were either mown extensively (one to two cuts per year) or intensively (three to five cuts per year). We hypothesised that (i) intensive management negatively influences the species richness and number of individuals of spiders and carabids, as well as the presence of species of cc (Buchholz et al., 2018; Proske et al., 2022), (ii) increasing isolation and urbanisation reduce spider and carabid species richness and number of individuals (Buchholz et al., 2018; Mader et al., 1990; Rainio & Niemelä, 2003) and (iii) local habitat parameters (soil humidity, vegetation; Entling et al., 2007; Schirmel et al., 2015) are further important determinants for spider and carabid diversity and species composition.

The disentangling of (interacting) local and landscape parameters should aid local agencies in their decision-making by emphasising which factors have the largest impact on biodiversity and species of cc in urban meadows.

MATERIALS AND METHODS

Study area and sites

The study was conducted in the urban area of Karlsruhe, Baden-Württemberg, Germany. Karlsruhe is located in the Upper Rhine Valley, with a major part of the city situated on Pleistocene sand and gravel and brown earth along watercourses (Regierungspräsidium Karlsruhe, 1999). In 2019, Karlsruhe had ca. 312,000 residents and extends to ca. 173 km^2 (Statistisches Bundesamt, 2019). Karlsruhe is among the German cities with the highest mean annual temperature

(ca 11°C) and receives approximately 870 mm of precipitation per year (DWD, 2023).

For various reasons, such as promoting biodiversity, recreational use or cost considerations, urban meadows in Karlsruhe are managed at different intensities. At the time of the investigation, about a quarter of the urban meadows in Karlsruhe were cut only one (to two) times per year (one cut in late June/July, with a potential second cut in late autumn), allowing the establishment of flowering forbs and tall grasses. Hay is removed after mowing (=extensive management). Approximately half of the meadows were mechanically mulched three to five times per year (=intensive management), with cut biomass remaining on the ground for self-composting The remaining areas (around 25%) were mown up to 12 times per year.

We selected 27 meadows (9 intensive, 18 extensive; Figure 1) for our investigation, which had been managed in the same way for at least 10 years. Study sites were evenly distributed over the city area and included comparatively humid meadows partly shaded by trees and hedges (8), meadows of mesic conditions (11) as well as exposed, dry meadows on sandy soils (8).

Spiders and carabids

Per site, four pitfall traps (white plastic cups; opening diameter: 6.5 cm) were installed along a transect with approximately 7 m distance between traps. Capture fluid was propylene glycol with a drop

FIGURE 1 Urban meadows in Karlsruhe. (a) Intensively managed meadow (three to five cuts) in May 2018, some days after the first cut. (b) Extensively managed meadow (one to two late cuts) in May 2018. (c) Extensively managed, dry grassland in July 2018.

of odourless dish liquid as a detergent. The first sampling period was from end of April to the first half of June in 2018. Traps were usually emptied every 2 weeks, with a longer captive period of about 3 weeks until the beginning of mowing in extensively managed meadows around 20th June. This was done to minimise vegetation damage by trampling to avoid influences on the sampling efficiency, especially in meadows with tall forbs and grasses. Traps were again installed for 14 days in late August to beginning of September 2018. Due to destruction of traps at two sites, the late sampling phase had to be repeated from mid to late September 2018 at these sites. Overall, sampling time per site added up to 48 days each. Sweep netting (30 blind sweeps over a linear transect) was performed on every plot on 30 May 2018 to target spiders sitting in the vegetation. The whole sweep net sample was directly transferred to ethanol in the field.

Spiders and carabids were stored in 75% ethanol and deposited at the study material collection of the State Museum of Natural History Karlsruhe (SMNK-STUD). Spiders were determined by using Nentwig et al. (2021) and additional literature (Grimm, 1985, 1986; Jantscher, 2001; Logunov, 2001; Roberts, 1987; Tongiorgi, 1966) as well as comparative material from the collection of the SMNK, partly from the same area (e.g. Hemm et al., 2012). Carabids were determined by using Müller-Motzfeld (2004). *Harpalus subcylindricus* Dejean, 1829 and *H. anxius* (Duftschmid, 1812) were determined using Marggi et al. (2010); in males, the penis was additionally removed for species delineation. Nomenclature of spiders follows the World Spider Catalog (2023) and nomenclature of carabids follows Trautner et al. (2014).

The status of endangerment was assessed using Blick et al. (2016), Nährig et al. (2003), Schmidt et al. (2016) and Trautner (2005). A species was denominated to be of cc when it is listed on the endangerment categories (III-I or G), on the so-called 'Vorwarnliste' (i.e., near-threatened) or as 'data deficient'. Species that are listed as 'data deficient' may not be directly threatened by human activities but are often rare and locally distributed in Germany. Therefore, these populations are of overall importance for the species and records indicating populations are of cc.

To gain further insight into the contribution of urban habitats to the regional fauna—independently of the sometimes partly subjective Red Lists—we used the number of known occupied grid records of each species from Trautner et al. (2014) (presence in TK 100 = TK = topographical map, i.e., grid with a resolution of 1: 100 000) for carabids and the German spider record scheme (Arachnologische Gesellschaft, 2021; presence in TK 25 = grid with a resolution of 1: 25 000). For each site, the number of occupied grid records of all sampled species of the site was summed and divided by the number of observed species of the site. The resulting index indicates the commonness of the assemblage ('commonness-index'). A high index value is achieved by an aggregated presence of common species, whereas a low value is the result of a high number of rare species. Species rarity is recognised as a reliable measure for the conservation value of habitats but is often generated from findings within the dataset (e.g., Samu et al., 2008). Our approach, in contrast, aims at using an external source of species rarity (i.e., record schemes), to generate a more general conservation value of assemblages. As pitfall trapping only measures the activity density, and not abundances, we did not include the number of specimens caught in this calculation.

Vegetation

The vegetation at was assessed in 2018 by the first author and again in 2019 by a local expert (Andreas Kleinsteuber). Each site was visited at least three times during the early vegetation period (April to June), and all occurring plant species were recorded (plant richness). Based on the list of plant species generated, the average Ellenberg indicator value for humidity was calculated for each site (BOKU, 2021; Ellenberg et al., 1991; Mettre, 2024). Dry meadows were characterised by the occurrence of typical indicator species for xerothermic conditions, for example, *Centaurea stoebe* L., *Sedum sexangulare* L., *Trifolium arvense* L. or *Dianthus deltoides* L. Humid meadows contained typical indicators for those conditions, such as *Phalaris arundinacea* L., *Ranunculus repens* L. or *Angelica sylvestris* L. However, as most open green spaces in cities, the vegetation showed great variability over time and within plots. Spiders, especially web-building spiders (e.g. Birkhofer et al., 2007), and carabids are known to react to small-scale changes in vegetation and shading (see Entling et al., 2007; Schirmel et al., 2011); therefore vegetation height was assessed at the end of May by measuring plant height at five random spots in a maximal distance of 10 m to the pitfall trap transects and taking the arithmetic mean.

Urban matrix

To determine the impact of the surrounding urban matrix on spider and carabid assemblages (see, e.g., Buchholz et al., 2018), the amount of urbanised and wooded land in a 500 m buffer area was assessed. For this, online-available land-use maps were taken from OpenStreetMaps and blended with shapefiles of green spaces provided by the Gartenbauamt Karlsruhe that contained mowing frequencies and polygons for urban green spaces in Karlsruhe. The analysis was made in QGIS Desktop Version 2.18.3. Residential and industrial area, buildings and paved parking lots were defined as 'urbanised area'. Shrubs, bushland and forests were defined as 'wooded area'. In addition, isolation was assessed following Fischer et al. (2016) based on distances to the pitfall trap transects in aerial images, as well as field observations and assessments of the adjacent vegetation at each site at the time of pitfall trap exposition. The value ranges from 0 to 12, where 0 describes no isolation of a locality at all and 12 denominates very highly isolated plots. This parameter assesses the permeability of adjacent structures and density of vegetation, which is especially important for flying insects, such as wild bees and most carabids (Fischer et al., 2016). Furthermore, the nearest neighbour distance was calculated as the closest linear distance between the edge of a site and the edge of the next meadow. Finally, the area (size) of each site was defined by delimitations by forest, bushland, streets or buildings. Narrow, gravelled footpaths were not counted as barriers.

Statistical analysis

Statistical analyses were mostly conducted in the R environment (R Core Team, 2022). In single cases, one of the four traps of one plot was destroyed but the other three remained intact. We then extrapolated the missing value by adding the average number of specimens per species caught in the other three pitfall traps during this sampling period.

Environmental variables (Table 1) were related to the dependent variables using generalised linear models. In addition to the variables, the interaction between management and humidity were included in every model. For count data, Poisson distributions were used. When overdispersion was detected, models were corrected using a negative-binomial distribution (function 'glm.nb', Package 'MASS', Ripley et al., 2020). For models including the commonness-indicator, a metric number, the Gaussian distribution was used. Collinearity of independent parameters was measured by calculating the variance inflation factor (function 'VIF' from R package 'regclass'; Petrie, 2020). The limit for considerable collinearity was set to a VIF of 5, which was never reached by any model/parameters. Model selection was done by using the Akaike information criterion implemented in the stepwise algorithm of the function 'stepAIC' in R package 'MASS' (Ripley et al., 2020). In one case, severe underdispersion of data forced us to use a Conway–Maxwell Poisson generalised linear model (function 'glm.cmp', R Package 'mpcmp', Fung, 2020). In this case, model decision was based on a manual backward elimination, that is, removal of statistical insignificant variables.

Assemblage structure was analysed using nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis distance with the function 'metaMDS' in the R Package 'vegan' (Oksanen et al., 2020). To reduce the influence of dominant species, we used a Hellinger transformation of the dataset before calculating the community matrix. Environmental parameters were fitted on the ordination using the function 'envfit' (R package 'vegan') and tested for significance using a permutation test (9999 permutations).

Global rarefaction analysis was conducted in the R-based online version of iNEXT (iNEXT, 2023) based on the number of sampled individuals. This was done to see if longer trapping over the vegetation period (i.e., a higher number of sampled specimens, not a higher number of traps) would drastically increase the number of sampled species, indicated usually by a high number of singletons and doubletons in the assemblage.

RESULTS

Overall, 10,704 (8973 adults, 1731 juveniles) spider specimens and 2660 carabids were collected (Tables S1–S3). The spiders belong to 21 families, with Lycosidae (5365 ind.), Tetragnathidae (1119 ind.), Gnaphosidae (974 ind.), Linyphiidae (616 ind.) and Thomisidae (439 ind.) representing the five dominant families. With 86 species (Table S2), the number of spider species was higher than that of carabids (55; Table S1). In contrast, the amount of species of cc and specimens belonging to these taxa was similar. Seven spider species recorded are of cc in Germany, 18 in the federal state of Baden-Württemberg; 17 carabid species are of cc in Baden-Württemberg, 9 in Germany (Tables S1–S4). Some species of cc were sampled in high numbers (Table S4). The global rarefaction analyses (Figure 2) based on the number of individuals sampled for both groups showed a clear flattening of the curves before extrapolation sets in, indicating that only a small proportion of the species have not been sampled.

TABLE 1 Environmental and landscape variables used as predictor variables.

Independent variable	Type	Range	Explanation
Management	Factor	Extensive versus intensive	Mowing regime; one to two cuts (with removal) versus three to five cuts (without removal)/year
Landscape parameters			
Urbanised area	Continuous	24–72	% area of buildings, streets, residential areas, industrial areas and paved parking lots in 500 m radius
Wooded area	Continuous	0.5–17	% area of bushland and forest in 500 m radius
Isolation	Factor (0–12)	3–10	See Fischer et al. (2016); 0 = no isolation, 12 = highest isolation
Nearest neighbour	Continuous	5–230	Linear distance to next meadow (edge to edge) [in metres]
Local parameters			
Height of vegetation	Continuous	20–140	Average height of vegetation at end of May 2018 [in centimetres]
Area (patch size)	Continuous	1200–26,000	Area of the meadow outlined by streets or buildings [in square metres]
Plant richness	Continuous	30–99	Number of plant species
Humidity	Continuous	3.74–5.54	Σ of Ellenberg humidity values of plant species/number plant species per plot

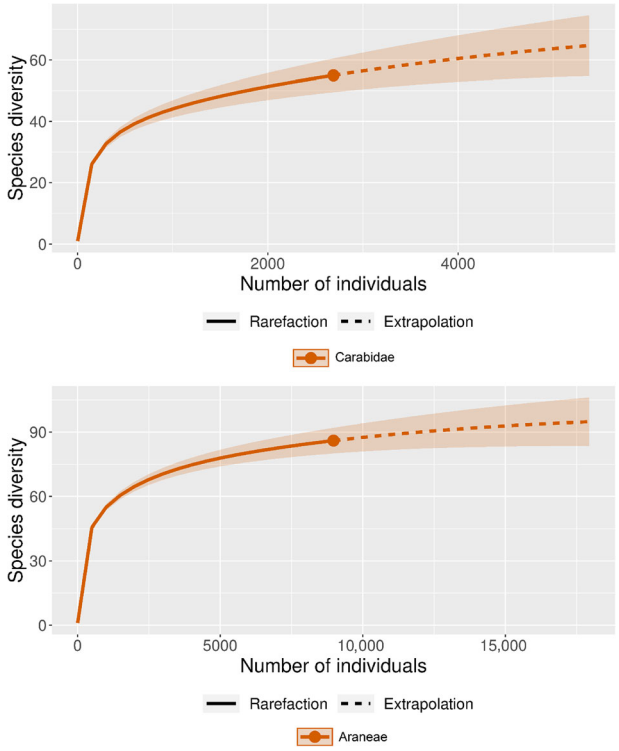

FIGURE 2 Global rarefaction analyses of species diversity based on the number of observed specimens per group (Araneae, Carabidae) from 27 green spaces in Karlsruhe.

Responses to environmental variables

Spiders

The spider species number was not significantly affected by any of the environmental variables (Table 2). Intensive management had a strong negative effect on the number of spider specimens with on average twice as much species sampled from extensively managed meadows (Figure 3g), whereas on larger meadows, significantly more spider specimens were captured (Figure 3a). The number of spider species of cc were only affected by humidity (Figure 3b), that is, dryer habitats harboured significantly more species of cc. The amount of specimens belonging to such species further responded negatively to increasing humidity, intensive management and higher vegetation (Figure 3c,d,h). The commonness-index of the spider assemblages was positively correlated with increasing humidity and the distance to the next meadows (nearest neighbour), indicating more common species in less connected and more humid meadows (Figure 3e,f).

Carabids

The carabid species number was negatively influenced by local isolation, but responded positively to a larger distance to the next meadow (nearest neighbour) (Table 2 and Figure 4a,b). The number of carabid specimens was significantly reduced by intensive management (Table 2, Figure 4g). The diversity of carabid species of cc was negatively affected by humidity and isolation (Table 2 and Figure 4c,d). Similar to spiders, intensive management (Figure 4i) and higher humidity had a strong negative effect (Figure 4e) on the number of carabid specimens belonging to species of cc. When *Harpalus subcylindricus* (the dominant species of cc) was removed from the dataset, a higher vegetation cover had a negative effect on this group as well, whereas humidity did not (Table 2). The commonness-index in carabids significantly increased with intensive management and with higher plant species richness (Figure 4f,h).

Community analyses

The NMDS ordination (Figure 5 and Table 3) showed no significant influence of the management or landscape parameters on the assemblage structure in both groups. Spider and carabid assemblages were rather significantly influenced by the local habitat parameters vegetation height and humidity.

DISCUSSION

Urban meadows in Karlsruhe host species-rich spider and carabid assemblages that consist of common as well as rarely recorded species, several of them of cc (Tables S1–S7). In line with our first and third hypothesis, carabid and spider communities were mainly shaped by local factors. Most importantly, extensive management increased the number of spider and carabid specimens and benefitted species of cc. Moreover, species of cc were negatively affected by humidity and were, therefore, mainly restricted to dry meadows. For carabids, increasing isolation had additional negative effects on the overall diversity as well as the diversity of species of cc. In contrast to our third hypothesis, urbanisation did not influence the diversity and number of carabids and spiders, but we found a negative effect of isolation on carabid species number and species of cc.

Conservation value of urban grassland for spiders and carabids

Our results show that urban grasslands in Karlsruhe sustain diverse spider and carabid communities (Tables S5 and S6), despite the fact that all sites were frequently managed and mown at least once a year (cf. Buchholz et al., 2018). The records of 86 spider and 55 carabid species correspond to nearly 9% of the spider and about 10% of the carabid species known as established in Germany (Blick et al., 2016; Nentwig et al., 2023; Schmidt et al., 2016). These results are similar to other surveys of spiders and carabids in agricultural as well as urban areas, which typical yielded between 6% and 12% of the known species in Germany (e.g., Bailey et al., 2010; Buchholz et al., 2018; Rischen et al., 2022; Wersebeckmann et al., 2021).

The comparatively high number of species of cc can be explained by the presence of dry and sparsely vegetated sandy grasslands in Karlsruhe as well as in our setting, which is an important habitat for

TABLE 2 Impact of environmental variables and management on spiders (Araneae) and carabids in urban meadows of Karlsruhe.

Dependent variable	Predictor variable	Estimate	Standard error	*z* value	*p* value
Spiders (Araneae)					
Sampled specimens	(Intercept)	5.664	0.153	36.956	
	Management	−0.515	0.177	−2.916	**0.004**
	Area	<0.001	<0.001	2.534	**0.013**
Species number	~				
Species of CC	(Intercept)	5.147	1.344	3.830	
	Wooded area	3.758	2.059	1.825	0.076
	Humidity	−0.902	0.302	−2.988	**0.002**
Specimens CC	(Intercept)	12.814	2.762	4.639	
	Management	−1.961	0.557	−3.518	**0.001**
	Humidity	−1.530	0.648	−2.363	**0.013**
	Vegetation height	−0.025	0.007	−3.442	**0.003**
Commonness[a]	(Intercept)	18.626	1.675	11.121	
	Nearest neighbour	0.007	0.003	2.675	**0.007**
	Humidity	1.246	0.368	3.389	**<0.001**
	Wooded area	−4.590	3.197	−1.436	0.151
Carabids (Carabidae)					
Sampled specimens	(Intercept)	4.746	0.140	33.841	
	Management	−0.519	0.244	−2.124	**0.039**
Species number	(Intercept)	3.947	0.707	5.584	
	Nearest neighbour	0.002	0.001	2.051	**0.047**
	Humidity	−0.227	0.155	−1.468	0.139
	Isolation	−0.067	0.027	−2.427	**0.015**
Species of CC	(X intercept)	12.713	3.994	3.183	
	(S intercept)	1.178	0.275	4.285	
	Nearest neighbour	0.322	0.166	1.943	0.052
	Isolation	−0.255	0.107	−2.393	**0.017**
	Humidity	−1.516	0.601	−2.524	**0.012**
Specimens CC	(Intercept)	7.829	1.7353	4.511	
	Management	−1.114	0.2941	−3.786	**<0.001**
	Humidity	−0.800	0.3857	−2.074	**0.018**
Specimens CC[b]	(Intercept)	4.024	0.457	8.812	
	Management	−0.845	0.366	−2.309	**0.024**
	Vegetation height	−0.010	0.005	−2.114	**0.044**
Commonness	(Intercept)	118.466	8.783	13.488	
	Management	10.037	4.336	2.315	**0.021**
	Plant species	0.3493	0.13	2.694	**0.007**

Note: Selection of variables in final model following calculation of Akaike's information criterion. Bold indicates $p < 0.05$.
Abbreviation: CC, conservation concern.
[a]Square root transformed for model.
[b]*Harpalus subcylindricus* removed from carabid dataset.

endangered xerothermic spiders and carabids (Blick et al., 2016; Hemm et al., 2012; Trautner et al., 2014). Many spider species of cc in Germany inhabit habitats positioned at both extremes along the humidity gradient, that is, either prefer very dry or very wet habitats (Entling et al., 2007; Hänggi et al., 1995; Martin, 1991). Here, nearly all species of cc are adapted to dry or moderately dry habitats (Hänggi et al., 1995) with some occurring in high numbers on some dry meadows, for example, the ground spiders *Drassyllus praeficus* or *Zelotes longipes* (Tables S2 and S4). This indicates that these habitats are not only stepping-stones but also host stable populations

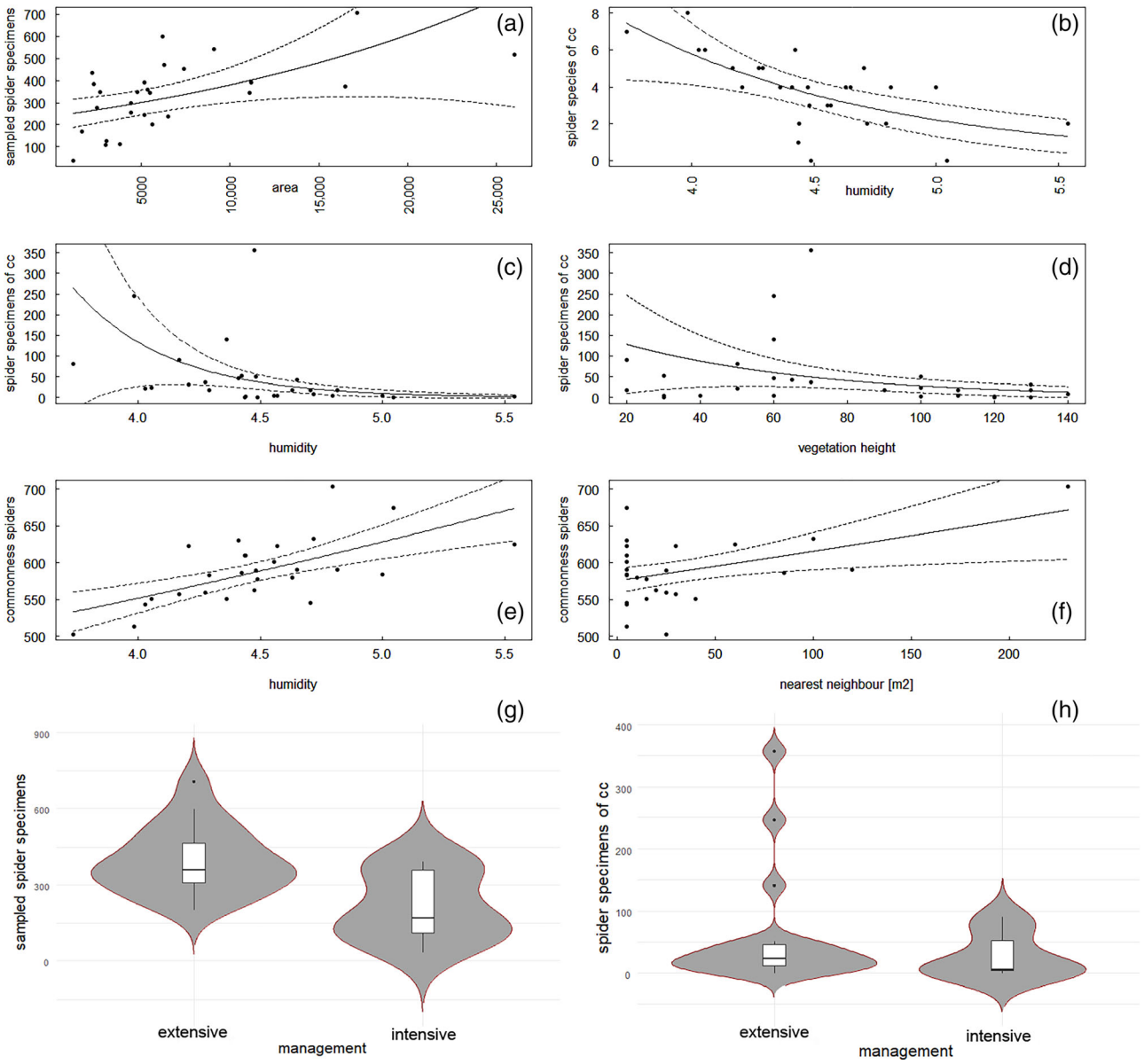

FIGURE 3 Significant interactions between diversity proxies of spiders (Araneae) and environmental factors in urban meadows of Karlsruhe, Germany. (a–f) Relationships between diversity proxies and environmental factors; (g and h) relationships between diversity proxies and management. For results see Table 2.

embedded into the local matrix. Dry grassland areas in cities can thus harbour a considerable number of xerophilic species of cc (cf. Fattorini, 2011; Venn et al., 2013), which may be additionally facilitated by the urban heat island effect (Banaszak-Cibicka, 2014; Kaiser et al., 2016). Species records like the spiders *Pardosa wagleri* (Hahn, 1822) (Table S2), a species usually inhabiting frequently disturbed gravel banks with sparse vegetation along rivers (Tongiorgi, 1966) and occasionally occurring in similar habitats away from water (Blick, pers. comm; Bauer, pers. obs.), *Cheiracanthium campestre* Lohmander, 1944, a rarely recorded species of central and eastern Europe (Blick et al., 2016; Nentwig et al., 2023; Próchniewicz, 1991) or the carabid *Masoreus wetterhalli* (Gyllenhal, 1813), a stenotopic species of sandy areas relatively rarely found inland and strongly endangered in Baden-Württemberg (GBIF, 2023; Trautner, 2005), also illustrate the potential of urban grassland for surprising records of rare species.

Moreover, no spider species of cc usually restricted to humid conditions were found during our investigation, although some of our sites along the river Alb and along the Heidesee, a small quarry pond in the North of Karlsruhe, are characterised by quite humid conditions, which is supported by the finding of several common spider species usually found only in humid conditions, for example, *Arctosa leopardus* (Sundevall, 1833) or *Piratula uliginosa* (Thorell, 1856). *Agyneta mollis* (O. Pickard-Cambridge, 1871), a small linyphiid species and near-threatened according to Nährig et al. (2003), is mentioned frequently as a species living in humid conditions (e.g. in Heimer & Nentwig, 1991) but was found by us in dry, mesic and humid grasslands,

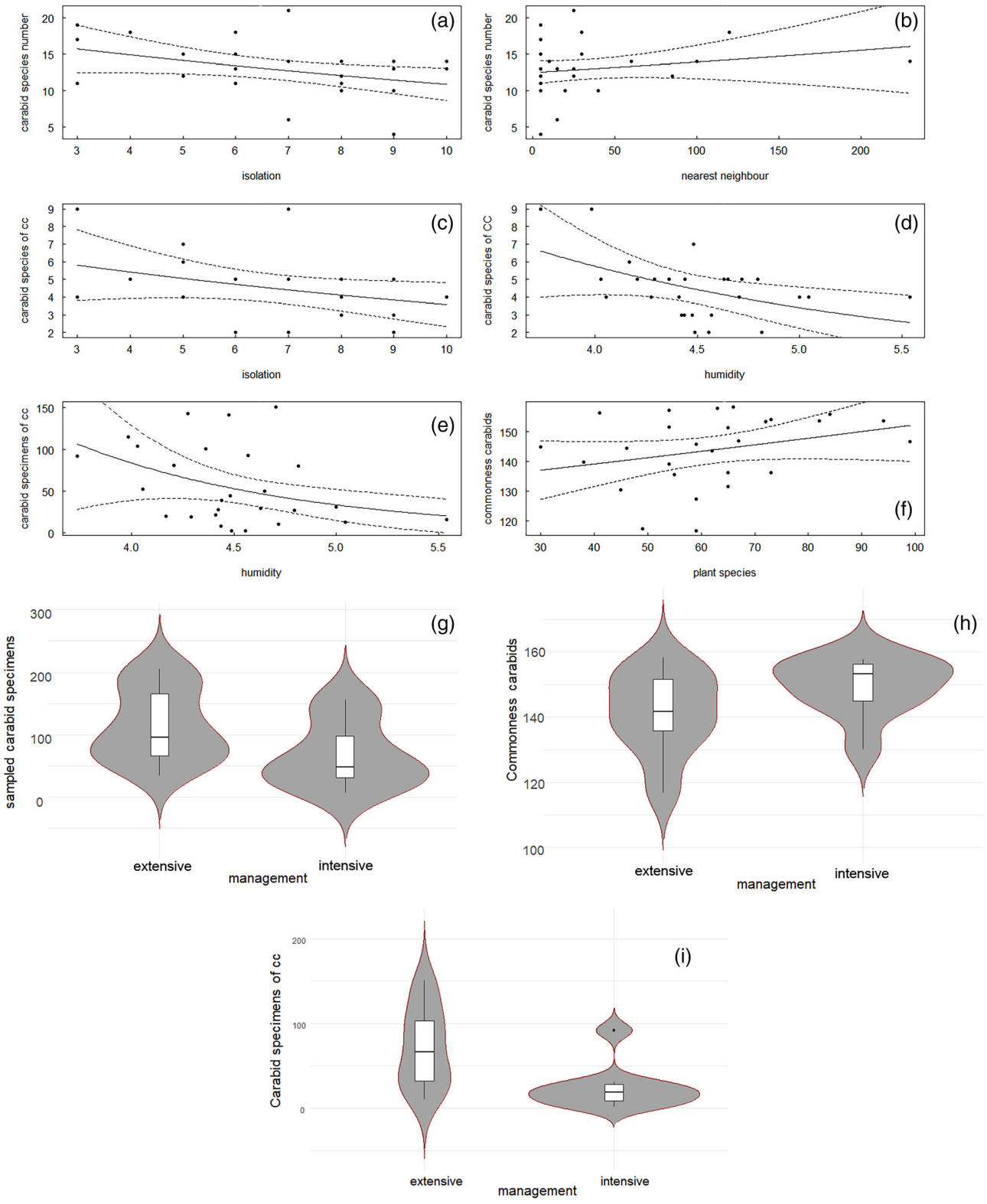

FIGURE 4 Significant interactions between diversity proxies of carabid beetles (Coleoptera: Carabidae) and environmental factors and management. in urban meadows of Karlsruhe, Germany. (a–f) relationships between diversity proxies and environmental factors; (g–i) relationships between diversity proxies and management. For results see Table 2.

paralleling the findings of Thaler (1983) that came from habitats with varying humidity as well, including urban parks in Vienna. The assemblages of the humid meadows were rather dominated by common species, for example, *Pardosa palustris* (Linnaeus, 1758), *Trochosa ruricola* (De Geer, 1778) or *Pachygnatha degeeri* (Sundevall, 1830), widely resistant to disturbances and often also found on cropland in central

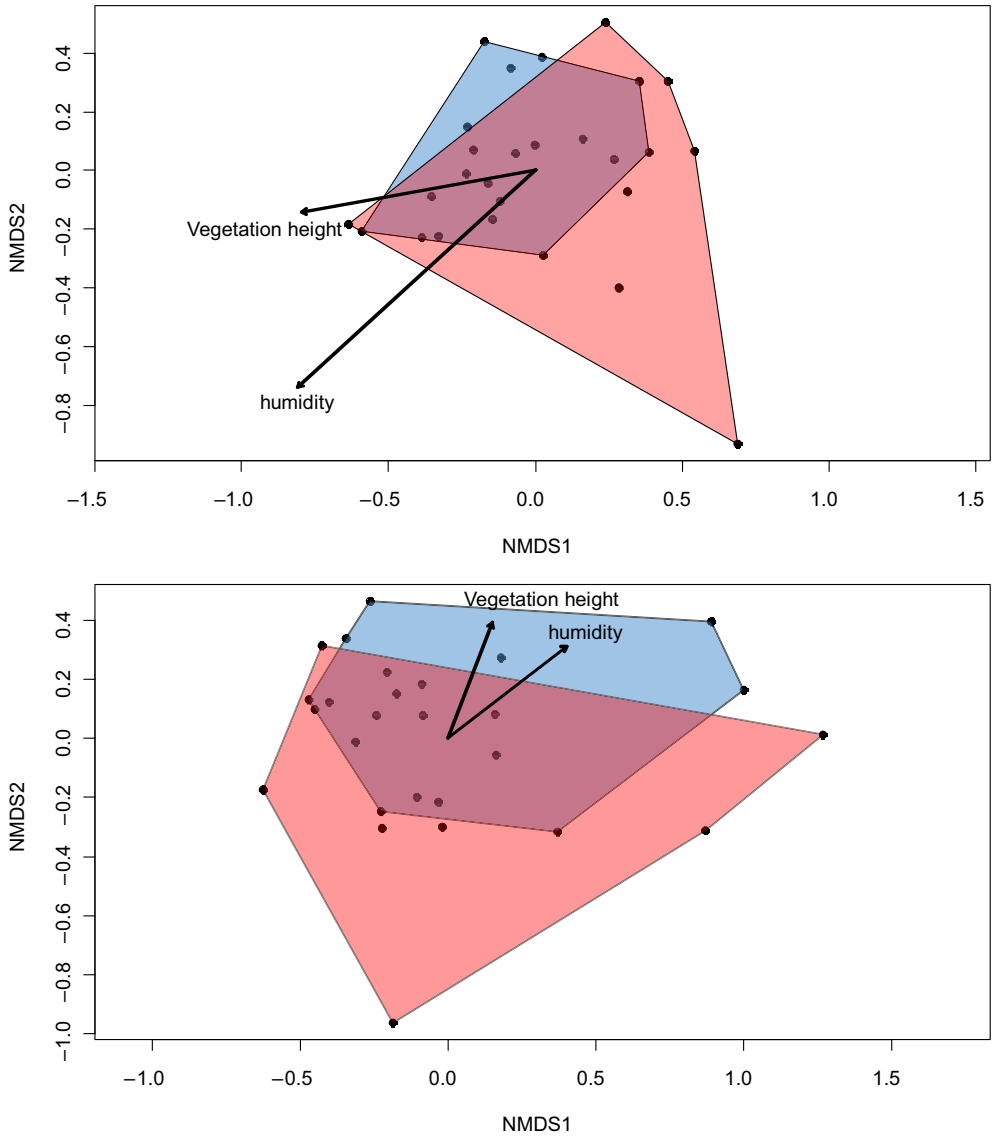

FIGURE 5 Nonmetric multidimensional scaling (NMDS) ordination of spider (top) and ground beetle (bottom) assemblages. Stress value = 0.13/0.14 (3 dimensions). Only significant variables (vegetation height, humidity) and axes 1 & 2 shown, see Table 3. Red polygon = intensively managed sites, blue polygon = extensively managed sites.

Europe (e.g., Blick et al., 2000, cf. Table S2). For spiders, this is in accordance with the results of Tajthi et al. (2017), who investigated floodplain forest along an urban gradient in Hungary and found the lowest number of hygrophilous and disturbance-sensitive spider species in the urbanised area. The reasons for an absence of such species of cc at our localities might be related to the urban heat island effect and a strong negative effect of drought periods on such humid habitat patches. Probably, hygrophilous species are also more sensitive towards the applied grassland management, where frequent mowing in summer results in open and low vegetation with a (temporarily) rather dry and hot microclimate.

In carabids, one of the dominant species in the dataset present at 26 of the 27 locations was *H. subcylindricus*, a locally endangered species according to Trautner (2005). This assessment was preliminary according to Wolf-Schwenninger (2003) given the insufficiently known distribution of this species. We show that this species is quite common in Karlsruhe and might be more widespread than previously thought.

Drivers of spiders and carabid numbers in urban grassland

For both spiders and carabids, extensive grassland management had positive effects on the number of specimens, but not on the species diversity per se. In general, management intensity shapes spider assemblages (Sattler et al., 2010), among others by direct mortality and abrupt loss of habitat by reduction of structural complexity. Hence, reduced mowing intensity generally benefits arthropod abundance in urban meadows (Proske et al., 2022; von Berg et al., 2023)

TABLE 3 Influences of fitted management and environmental variables on spider (Araneae) and carabid beetle (Carabidae) assemblages in nonmetric multidimensional scaling (NMDS) ordination, *p*-values calculated by permutation test (9999 iterations).

	NMDS1	NMDS2	NMDS3	r^2	*p value*
Araneae					
Isolation	0.912	−0.310	0.269	0.010	0.970
Area	−0.897	0.267	−0.354	0.235	0.098
Nearest neighbour	−0.403	−0.207	−0.891	0.197	0.151
Urbanisation	−0.896	−0.130	0.424	0.182	0.194
Wooded area	0.315	0.313	−0.896	0.247	0.088
Humidity	−0.724	−0.662	−0.195	0.594	**<0.001**
Plant species number	−0.031	0.987	−0.156	0.140	0.327
Vegetation height	−0.855	−0.153	0.496	0.413	**0.005**
Management (extensive)	0.086	0.046	−0.011	0.077	0.102
Management (intensive)	0.172	−0.093	0.021		
Carabidae					
Isolation	0.234	0.774	−0.588	0.164	0.233
Area	0.462	0.872	0.165	0.210	0.142
Nearest neighbour	0.926	0.156	−0.344	0.068	0.621
Urbanisation	0.981	−0.051	0.187	0.113	0.414
Wooded area	−0.459	−0.511	0.727	0.091	0.519
Humidity	0.751	0.580	−0.316	0.576	**<0.001**
Plant species number	−0.286	−0.610	0.739	0.192	0.176
Vegetation height	0.354	0.912	0.207	0.365	**0.011**
Management (extensive)	−0.005	0.102	0.069	0.078	0.108
Management (intensive)	0.011	−0.203	−0.139		

Note: Bold indicates $p < 0.05$.

and decreases the exposition to predators like birds (e.g., Lafage & Pétillon, 2014). Our results are also partly in line with Buchholz et al. (2018), who also found negative effects of increased management on spiders, however, not on the number of individuals but rather on the species. This might be due to different scales of management: Buchholz et al. (2018) sampled from infrequently and very extensively (one cut per year) managed meadows, whereas we sampled from meadows that were cut one to two times and three to five times per year. It seems possible that infrequent management of grasslands may additionally allow the presence of disturbance-sensitive species that are absent from meadows cut every year. This is indicated by a large number of linyphiid species typical for more shaded and less disturbed habitats in the dataset of Buchholz et al. (2018). Our results further indicate that extensive management was especially beneficial for spider and carabid species of cc. For carabids, rare species also benefitted from extensive management as indicated by the commonness-index. It is known that higher disturbance often favours more opportunistic and widespread species in carabids (e.g., Niemelä & Kotze, 2009). Intensive grassland management might therefore reinforce their 'rarity' and increase the risk of regional extinction of single species over time (Fattorini, 2011).

Humidity had a strong effect on the occurrence of species of cc in both groups. With increasing soil humidity, species of cc gradually declined and were replaced by common and widely distributed species (Arachnologische Gesellschaft, 2023; Blick et al., 2016; Hänggi et al., 1995). This is also reflected by the impact of humidity on the commonness-index of spider assemblages, which is especially high when several common and usually non-threatened species were found at a site. By contrast, humidity had no impact on the commonness-index of carabid assemblages. Probably, other factors, for example, management, mask or counteract the effect of humidity on the commonness-index of carabids, by facilitating common, eurytopic species resistant to disturbances in dry grassland.

Interestingly, the number of plant species per site was positively related with the commonness of the carabid assemblage. One explanation could be that frequent disturbances on a small scale, that is, local, small-scale digging for roadside construction or trampling by passengers, on these meadows added additional disturbance-tolerant plant species (Sousa, 1984), and the disturbance itself facilitated common carabid species. This would be supported by the increased presence of annual species typical for disturbed habitats, like *Chenopodium album* L., *Artemisia vulgaris* L., *Diplotaxis tenuifolia* L. (DC.) or *Mercurialis annua* L. at the locality ('Loreal_Ex', see Table S7) with the highest plant diversity, which is also one of the most frequented locality by dog walkers. However, this hypothesis needs further investigations,

as local, temporarily restricted disturbances are very common in nearly all urban habitats, but not easy to document over time.

Landscape factors showed only limited effects on spider and carabid communities in urban meadows of Karlsruhe. For spiders, the patch size increased the number of specimens. Patch size is recognised being a pivotal factor for preventing biodiversity loss in cities (Beninde et al., 2015). Isolation had a negative effect on spider diversity in an investigation of urban meadows in Berlin, Germany (Buchholz et al., 2018), but not in our study. However, most spiders, due to their ability to balloon (Bell et al., 2005), are known to be successful colonisers of isolated areas, for example, islands (Carvalho & Cardoso, 2014) and have the ability to overcome migration barriers over time. This fits to our finding that increased distance to the next patch increased the commonness of the spider assemblage, as eurytopic species inhabiting disturbed and isolated patches engage more often in ballooning than specialists, which are, in addition, often poor dispersers (Bonte et al., 2003).

Besides, the urban area of Karlsruhe is significantly smaller than Berlin, and its green spaces might benefit more from occasional immigration of spider species living in the rural surroundings of the city. The latter might also have counteracted a possible effect of urbanisation on the assemblages. However, isolation still had a negative effect on carabid species number, probably best explained by the group's generally weaker dispersal capabilities, with some species even (e.g. members of the genus *Carabus*) being flightless. The weak positive effect of an increased distance to the next meadow (nearest neighbour) on the carabid species number might be best explained by a slightly higher diversity of neighbouring habitats (roadsides, gardens, hedges) in more segregated plots that lead to a higher species number by immigration of additional species into these meadows, while local isolation acts as a migration barrier.

The question whether local isolation affects grassland patches in larger cities stronger is of great interest for future research, as patch isolation usually increases with further urbanisation of areas. In carabids, local isolation clearly negatively affected the overall species number as well as the number of species of cc. Many stenotopic carabids are known to be affected by fragmentation and isolation (Niemelä, 2001) and even paved roads can act as movement barriers (Mader et al., 1990). Promoting extensively managed grassland corridors in cities seems therefore crucial to avoid species-loss of carabids and especially of species of cc.

Drivers of assemblage structure

Humidity and vegetation height determined the spider assemblages. This is in accordance with Entling et al. (2007), who identified shading and humidity as the two most important environmental variables for the composition of spider assemblages by analysing the dataset compiled by Hänggi et al. (1995). Buchholz et al. (2018), Otoshi et al. (2015), Delgado de la Flor et al. (2020) and Sattler et al. (2010) also showed that spider assemblages in urban areas are often shaped by local factors rather than landscape characteristics. In contrast, management intensity had no impact on the spider community. This is probably not only due to the presence of several eurytopic species at nearly all locations but also due to the presence of some stenotopic species, like *Xerolycosa miniata*, at drier locations independently of management intensities (Blick et al., 2000; Entling et al., 2007).

Similar to spiders, the carabid assemblages were shaped by humidity and vegetation height, but not by management. It may be possible that the differences between our management types were too small to generate visible effects on the assemblage structure. Venn and Kotze (2014) found only relatively small differences in the carabid assemblages of three types of very different mowing regimes in an urban setting of southern Finland, similar to Buchholz et al. (2018) who investigated infrequently and extensively mown meadows in Berlin. Overall, it seems that the rather strong differences in local factors like humidity and vegetation height overlay effects of management and urbanisation on our assemblages (Philpott et al., 2014).

CONCLUSION

Our results demonstrate that dry grassland in urban areas of central Europe can harbour a significant number of arthropod species of cc, whereas mesic and humid conditions and increased management mostly facilitate generalists in our setting. For biodiversity conservation in cities, dry grassland is therefore pivotal and can be a refugium for a certain number of species of cc. We urge the local and regional administration and conservation agencies to prioritise dry urban grassland for extensive management whenever possible to avoid depletion of local populations and to mitigate effects of the ongoing global insect crisis (Forister et al., 2019). Increasing connectivity and the creation of fallow stripes (Buchholz et al., 2018) could further benefit species diversity and assist in the colonisation of grassland sites by species of cc.

AUTHOR CONTRIBUTIONS

Tobias Bauer: Conceptualization; methodology; investigation; funding acquisition; writing – original draft; writing – review and editing; data curation; formal analysis; software; visualization; project administration. **Hubert Höfer:** Conceptualization; methodology; investigation; writing – review and editing; resources. **Jens Schirmel:** Conceptualization; methodology; formal analysis; software; writing – review and editing; validation; investigation; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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REFERENCES

Arachnologische Gesellschaft. (2021) Atlas der Spinnentiere Europas. Available at: https://atlas.arages.de [Accessed 15th January 2021].

Arachnologische Gesellschaft. (2023) Atlas der Spinnentiere Europas. Available at: https://atlas.arages.de [Accessed 3th June 2023].

Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S. et al. (2017) Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15, 189–196.

Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U. et al. (2010) Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology*, 47, 1003–1013.

Banaszak-Cibicka, W. (2014) Are urban areas suitable for thermophilic and xerothermic bee species (Hymenoptera: Apoidea: Apiformes)? *Apidologie*, 45, 145–155.

Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, 95, 69–114.

Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18, 581–592.

Birkhofer, K., Scheu, S. & Wise, D.H. (2007) Small-scale spatial pattern of web-building spiders (Araneae) in alfalfa: relationship to disturbance from cutting, prey availability, and intraguild interactions. *Environmental Entomology*, 36, 801–810.

Blick, T., Finch, O.-D., Harms, K.H., Kiechle, J., Kielhorn, K.-H., Kreuels, M. et al. (2016) Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae) Deutschlands. 3. Fassung, Stand April 2008, einzelne Änderungen und Nachträge bis August 2015. *Naturschutz Und Biologische Vielfalt*, 70, 383–510.

Blick, T., Pfiffner, L. & Luka, H. (2000) Epigäische Spinnen auf Äckern der Nordwest-Schweiz im mitteleuropäischen Vergleich (Arachnida: Araneae). *Mitteilungen der Deutschen Gesellschaft für allgemeine angewandte Entomologie*, 12, 267–276.

Boal, C.W. & Dykstra, C.R. (2018) *Urban raptors: ecology and conservation of birds of prey in cities*. Washington, USA: Island Press.

BOKU. (2021) Universität für Bodenkultur Wien. Available at: https://statedv.boku.ac.at/zeigerwerte [Accessed 5th June 2021].

Bonte, D., Vandenbroecke, N., Lens, L. & Maelfait, J.P. (2003) Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 270, 1601–1607.

Buchholz, S. (2016) Natural peat bog remnants promote distinct spider assemblages and habitat specific traits. *Ecological Indicators*, 60, 774–780.

Buchholz, S. & Egerer, M.H. (2020) Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. *Biodiversity and Conservation*, 29, 2779–2801.

Buchholz, S., Hannig, K., Möller, M. & Schirmel, J. (2018) Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. *Urban Ecosystems*, 21, 1139–1149.

Carvalho, J.C. & Cardoso, P. (2014) Drivers of beta diversity in Macaronesian spiders in relation to dispersal ability. *Journal of Biogeography*, 41, 1859–1870.

Delgado de la Flor, Y.A., Perry, K.I., Turo, K.J., Parker, D.M., Thompson, J.L. & Gardiner, M.M. (2020) Local and landscape-scale environmental filters drive the functional diversity and taxonomic composition of spiders across urban greenspaces. *Journal of Applied Ecology*, 57, 1570–1580.

Dietz, M., Bögelsack, K., Krannich, A. & Simon, O. (2020) Woodland fragments in urban landscapes are important bat areas: an example of the endangered Bechstein's bat *Myotis bechsteinii*. *Urban Ecosystems*, 23, 1359–1370.

DWD. (2023) Deutscher Wetterdienst. Available at: https://dwd.de/DE/leistungen/klimadatendeutschland/mittelwerte/temp_8110_fest_html.html?view=nasPublication&nn=16102 [Accessed 4th May 2023].

Eckert, S., Möller, M. & Buchholz, S. (2017) Grasshopper diversity of urban wastelands is primarily boosted by habitat factors. *Insect Conservation and Diversity*, 10, 248–257.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991) *Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica*, 18, 9–166.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2007) Niche properties of central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, 16, 440–448.

Evelyn, M. J., Stiles, D. A. & Young, R. A. (2004) Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biological Conservation*, 115, 463–473.

Eyre, M.D., Luff, M.L. & Woodward, J.C. (2003) Beetles (Coleoptera) on brownfield sites in England: an important conservation resource? *Journal of Insect Conservation*, 7, 223–231.

Fattorini, S. (2011) Insect rarity, extinction and conservation in urban Rome (Italy): a 120-year-long study of tenebrionid beetles. *Insect Conservation and Diversity*, 4, 307–315.

Fenoglio, M.S., Rossetti, M.R. & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. *Global Ecology and Biogeography*, 29, 1412–1429.

Fischer, L.K., Eichfeld, J., Kowarik, I. & Buchholz, S. (2016) Disentangling urban habitat and matrix effects on wild bee species. *PeerJ*, 4, e2729.

Forister, M.L., Pelton, E.M. & Black, S.H. (2019) Declines in insect abundance and diversity: we know enough to act now. *Conservation Science and Practice*, 1, e80.

Fung, T. (2020) mpcmp: mean-parametrized Conway-Maxwell Poisson (COM-Poisson) regression. Available at: https://rdrr.io/cran/mpcmp. [Accessed 4th June 2020].

GBIF. (2023) *Masoreus wetterhallii* (Gyllenhal, 1813). Available at: https://www.gbif.org/species/4471202 [Accessed 23th December 2023].

Grimm, U. (1985) Die Gnaphosidae Mitteleuropas (Arachnida, Araneae). *Abhandlungen Des Naturwissenschaftlichen Vereins in Hamburg (NF)*, 26, 1–318.

Grimm, U. (1986) Die Clubionidae Mitteleuropas: Corinninae und Liocraninae (Arachnida, Araneae). *Abhandlungen Des Naturwissenschaftlichen Vereins in Hamburg (NF)*, 27, 1–91.

Habel, J.C., Dengler, J., Janišová, M., Török, P., Wellstein, C. & Wiezik, M. (2013) European grassland ecosystems: threatened hotspots of biodiversity. *Biodiversity and Conservation*, 22, 2131–2138.

Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M. et al. (2017) The city as a refuge for insect pollinators. *Conservation Biology*, 31, 24–29.

Hänggi, A., Stöckli, E. & Nentwig, W. (1995) Lebensräume mitteleuropäischer Spinnen: Charakterisierung der Lebensräume der häufigsten Spinnenarten Mitteleuropas und der mit diesen vergesellschafteten Arten. *Miscellanea Faunistica Helvetiae*, 4, 1–459.

Heimer, S. & Nentwig, W. (1991) *Spinnen Mitteleuropas: Ein Bestimmungsbuch*. Berlin: Paul Parey.

Hemm, V., Meyer, F. & Höfer, H. (2012) Die epigäische Spinnenfauna (Arachnida, Araneae) in Sandrasen, Borstgrasrasen und Ruderalfluren im Naturschutzgebiet "Alter Flugplatz Karlsruhe". *Arachnologische Mitteilungen*, 44, 20–40.

Hou, Y., Li, J., Li, G. & Qi, W. (2023) Negative effects of urbanization on plants: a global meta-analysis. *Ecology and Evolution*, 13, e9894.

iNEXT. (2023) *iNEXT*. Available at: https://chao.shinyapps.io/iNEXTOnline [Accessed 15th March 2023].

Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G.E. et al. (2016) Cities are hotspots for threatened species. *Global Ecology and Biogeography*, 25, 117–126.

Jantscher, E. (2001) Revision der Krabbenspinnengattung *Xysticus* C.L. Koch, 1835 (Araneae, Thomisidae) in Zentraleuropa. Dissertation, Universität Graz, AT.

Kadej, M., Zając, K., Smolis, A., Tarnawski, D., Tyszecka, K., Malkiewicz, A. et al. (2017) The great capricorn beetle *Cerambyx cerdo* L. in southwestern Poland—the current state and perspectives of conservation in one of the recent distribution centres in central Europe. *Nature Conservation*, 19, 111–134.

Kaiser, A., Merckx, T. & Van Dyck, H. (2016) The urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. *Ecology and Evolution*, 6, 4129–4140.

Lafage, D. & Pétillon, J. (2014) Impact of cutting date on carabids and spiders in a wet meadow. *Agriculture, Ecosystems & Environment*, 185, 1–8.

Lepczyk, C.A., Aronson, M.F., Evans, K.L., Goddard, M.A., Lerman, S.B. & MacIvor, J.S. (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *Bioscience*, 67, 799–807.

Logunov, D.V. (2001) A redefinition of the genera *Bianor* Peckham & Peckham, 1885 and *Harmochirus* Simon, 1885, with the establishment of a new genus *Sibianor* gen. n. (Aranei: Salticidae). *Arthropoda Selecta*, 9, 221–286.

Mader, H.J., Schell, C. & Kornacker, P. (1990) Linear barriers to arthropod movements in the landscape. *Biological Conservation*, 54, 209–222.

Marggi, W., Luka, H., Huber, C., Wrase, D.W. & Durrer, H. (2010) *Harpalus* (s. str.) *subcylindricus* Dejean, 1829 (Coleoptera, Carabidae) auch in der Schweiz und im Elsass (F). *Entomologische Blätter*, 106, 195–202.

Martin, D. (1991) Zur Autökologie der Spinnen (Arachnida: Araneae) I. Charakteristik der Habitatausstattung und Präferenzverhalten epigäischer Spinnenarten. *Arachnologische Mitteilungen*, 1, 5–26.

McKinney, M.L. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, 11, 161–176.

Mettre. (2024) Ellenbergsche Zeigerwerte. Available at: http://botanik.mettre.de/alpha_liste.shtml [Accessed 5th August, 2021]

Müller-Motzfeld, G. (2004) Bd. 2 Adephaga 1: Carabidae (Laufkäfer). In: Freude, H., Harde, K.W., Lohse, G.A. & Klausnitzer, B. (Eds.) *Die Käfer Mitteleuropas*, 2nd edition. Heidelberg/Berlin: Spektrum verlag.

Nährig, D., Kiechle, J. & Harms, K.H. (2003) *Rote Liste der Webspinnen (Araneae) Baden-Württembergs*. Karlsruhe (Landesanstalt für Umweltschutz Baden-Württemberg). Fachdienst Naturschutz. Naturschutz-Praxis: Artenschutz 7, pp. 7–162.

Nentwig, W., Blick, T., Bosmans, R., Gloor, D., Hänggi, A. & Kropf, C. (2021) Spiders of Europe. Version 1. Available at: https://www.araneae.nmbe.ch [Accessed 10th April 2021].

Nentwig, W., Blick, T., Bosmans, R., Gloor, D., Hänggi, A. & Kropf, C. (2023) Spiders of Europe. Version 7. Available at: https://www.araneae.nmbe.ch [Accessed 27th July 2023].

Niemelä, J. & Kotze, D.J. (2009) Carabid beetle assemblages along urban to rural gradients: a review. *Landscape and Urban Planning*, 92, 65–71.

Niemelä, J.A.R.I. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology*, 98, 127–132.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, R., Minchin, P.R. et al. (2020) vegan: Community ecology package. Version. 2.5. Available at: https://cran.r-project.org/web/packages/vegan/index.html [Accessed 3th July 2020].

Otoshi, M.D., Bichier, P. & Philpott, S.M. (2015) Local and landscape correlates of spider activity density and species richness in urban gardens. *Environmental Entomology*, 44, 1043–1051.

Petrie, A. (2020) regclass: tools for an introductory class in regression and modeling. Available at: https://cran.r-project.org/web/packages/regclass/index.html [Accessed 12th June 2020].

Philpott, S.M., Cotton, J., Bichier, P., Friedrich, R.L., Moorhead, L.C., Uno, S. et al. (2014) Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. *Urban Ecosystems*, 17, 513–532.

Próchniewicz, M. (1991) *Cheiracanthium campestre* Lohmander (1944) eine Seltene Clubionidae (Araneae). *Bulletin of the Polish Academy of Science, Biological Sciences*, 39, 175–179.

Proske, A., Lokatis, S. & Rolff, J. (2022) Impact of mowing frequency on arthropod abundance and diversity in urban habitats: a meta-analysis. *Urban Forestry & Urban Greening*, 76, 127714.

R Core Team. (2022) *R: A language and environment for statistical computing*. Vienna, Austria. Available at: https://www.r-project.org [Accessed 5th May 2022].

Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, 12, 487–506.

Regierungspräsidium Karlsruhe. (1999) *Landschaften und Böden im Regierungsbezirk Karlsruhe*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A. & Firth, D. (2020) MASS: support functions and datasets for venables and Ripley's MASS. Available at: https://cran.r-project.org/web/packages/MASS/index.html [Accessed 12th June 2020].

Rischen, T., Geisbüsch, K., Ruppert, D. & Fischer, K. (2022) Farmland biodiversity: wildflower-sown islands within arable fields and grassy field margins both promote spider diversity. *Journal of Insect Conservation*, 26, 415–424.

Roberts, M.J. (1987) *The spiders of Great Britain and Ireland: Linyphiidae and check list, volume 2*. Colchester: Harley Books.

Samu, F., Csontos, P. & Szinetár, C. (2008) From multi-criteria approach to simple protocol: assessing habitat patches for conservation value using species rarity. *Biological Conservation*, 141, 1310–1320.

Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M.K. et al. (2010) Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology*, 91, 3343–3353.

Sattler, T., Obrist, M.K., Duelli, P. & Moretti, M. (2011) Urban arthropod communities: added value or just a blend of surrounding biodiversity? *Landscape and Urban Planning*, 103, 347–361.

Schirmel, J., Mantilla-Contreras, J., Gauger, D. & Blindow, I. (2015) Carabid beetles as indicators for shrub encroachment in dry grasslands. *Ecological Indicators*, 49, 76–82.

Schirmel, J., Timler, L. & Buchholz, S. (2011) Impact of the invasive moss *Campylopus introflexus* on carabid beetles (Coleoptera: Carabidae) and spiders (Araneae) in acidic coastal dunes at the southern Baltic Sea. *Biological Invasions*, 13, 605–620.

Schmidt, J., Trautner, J. & Müller-Motzfeld, G. (2016) Rote Liste und Gesamtartenliste der Laufkäfer (Coleoptera: Carabidae) Deutschlands. *Naturschutz Und Biologische Vielfalt*, 70, 139–204.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15, 353–391.

Spotswood, E.N., Beller, E.E., Grossinger, R., Grenier, J.L., Heller, N.E. & Aronson, M.F. (2021) The biological deserts fallacy: cities in their landscapes contribute more than we think to regional biodiversity. *Bioscience*, 71, 148–160.

Statistisches Bundesamt. (2019) National accounts, domestic product. Available at: https://www.destatis.de/DE/Home/_inhalt.html [Accessed 27th July 2023]

Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., Gill, T.K. & Fuller, R.A. (2013) How should we grow cities to minimize their biodiversity impacts? *Global Change Biology*, 19, 401–410.

Tajthi, B., Horváth, R., Mizser, S., Nagy, D.D. & Tóthmérész, B. (2017) Spider assemblages in floodplain forests along an urbanization gradient. *Community Ecology*, 18, 311–318.

Thaler, K. (1983) Bemerkenswerte Spinnenfunde in Nordtirol (Österreich) und Nachbarländern: Deckennetzspinnen, Linyphiidae (Arachnida: Aranei). *Veröffentlichungen Des Museum Ferdinandeum in Innsbruck*, 63, 135–167.

Threlfall, C.G., Walker, K., Williams, N.S., Hahs, A.K., Mata, L., Stork, N. et al. (2015) The conservation value of urban green space habitats for Australian native bee communities. *Biological Conservation*, 187, 240–248.

Tongiorgi, P. (1966) Italian wolf spiders of the genus *Pardosa* (Araneae: Lycosidae). *Bulletin of the Museum of Comparative Zoology*, 134, 275–334.

Trautner, J. (2005) *Rote Liste und Artenverzeichnis der Laufkäfer Baden-Württembergs*, vol. 9. Karlsruhe: Landesanstalt für Umweltschutz Baden-Württemberg. Naturschutz-Praxis.

Trautner, J., Fritze, M.A., Hannig, K. & Kaiser, M. (2014) *Verbreitungsatlas der Laufkäfer Deutschlands*. Norderstedt: Books on demand.

Venn, S. & Kotze, D.J. (2014) Benign neglect enhances urban habitat heterogeneity: responses of vegetation and carabid beetles (Coleoptera: Carabidae) to the cessation of mowing of park lawns. *European Journal of Entomology*, 111, 703–714.

Venn, S.J., Kotze, D.J., Lassila, T. & Niemelä, J.K. (2013) Urban dry meadows provide valuable habitat for granivorous and xerophylic carabid beetles. *Journal of Insect Conservation*, 17, 747–764.

von Berg, L., Frank, J., Sann, M., Betz, O., Steidle, J.L. & Böttinger, S. (2023) Insect-and spider-friendly mowing technology in grassland—overview and evaluation. *Landtechnik*, 78, 80–96.

Watson, C.J., Carignan-Guillemette, L., Turcotte, C., Maire, V. & Proulx, R. (2020) Ecological and economic benefits of low-intensity urban lawn management. *Journal of Applied Ecology*, 57, 436–446.

Wersebeckmann, V., Kolb, S., Entling, M.H. & Leyer, I. (2021) Maintaining steep slope viticulture for spider diversity. *Global Ecology and Conservation*, 29, e01727.

Wolf-Schwenninger, K. (2003) Zur Verbreitung von *Harpalus subcylindricus* (Dejean, 1829) in Baden-Württemberg (Coleoptera: Carabidae). *Mitteilungen des Entomologischen Vereins Stuttgart*, 38, 23–26.

World Spider Catalog. (2023) World spider catalog. Version 24. Natural History Museum Bern. Available at: http://wsc.nmbe.ch [Accessed 27th July 2023].

SUPPORTING INFORMATION

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

Table S1. Species of carabid beetles sampled from urban grassland in Karlsruhe, Germany (NE = not endangered, BW = Baden-Württemberg, G = Germany).

Table S2. Species of spiders (Araneae) sampled from urban grassland in Karlsruhe, Germany (NE = not endangered, BW = Baden-Württemberg, G = Germany).

Table S3. Further data on species numbers and sampled specimens. Ex = extensively managed ($n = 18$, one to two cuts), int = intensively managed ($n = 9$, three to five cuts). CC = conservation concern according to Red Lists of Baden-Württemberg and Germany (in ())

Table S4. Selected species of conservation concern sampled from urban grassland in Karlsruhe. ex = extensively managed ($n = 18$, one to two cuts), int = intensively managed ($n = 9$, three to five cuts). Category = assessment in the Red Lists of Baden-Württemberg.

Table S5. Spider data and environmental and landscape variables.

Table S6. Carabid data and environmental and landscape variables.

Table S7. Grassland localities in the urban area of Karlsruhe, Germany.

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Table S1: Species of Carabid beetles sampled from urban grasland in Karlsruhe, Germany (NE = not endangered, BW = Baden-Württemberg, G = Germany)

Species	individuals	Red List BW	Red List G
Amara aenea	177	NE	NE
Amara communis	7	NE	NE
Amara convexior	27	NE	NE
Amara familiaris	9	NE	NE
Amara kulti	45	NE	NE
Amara lucida	1	**2**	**V**
Amara lunicollis	81	NE	NE
Amara municipalis	1	**3**	NE
Amara plebeja	1	NE	NE
Amara similata	4	NE	NE
Amara tricuspidata	20	**D**	**V**
Anchomenus dorsalis	1	NE	NE
Anisodactylus binotatus	36	NE	NE
Anisodactylus nemorivagus	1	**3**	**2**
Badister bullatus	20	NE	NE
Bembidion guttula	1	**3**	NE
Brachinus crepitans	1	NE	**V**
Brachinus explodens	11	NE	**V**
Calathus cinctus	12	NE	NE
Calathus fuscipes	15	NE	NE
Calathus melanocephalus	37	NE	NE
Calathus micropterus	1	**3**	NE
Carabus auratus	12	NE	NE
Carabus coriaceus	1	NE	NE
Cicindela campestris	1	NE	NE
Diachromus germanus	4	NE	NE
Harpalus affinis	57	NE	NE
Harpalus anxius	10	**V**	NE
Harpalus attenuatus	3	NE	NE
Harpalus dimidiatus	252	**V**	**3**
Harpalus distinguendus	2	NE	NE
Harpalus latus	13	NE	NE
Harpalus luteicornis	21	**V**	NE
Harpalus pumilus	27	**V**	NE
Harpalus rubripes	188	NE	NE
Harpalus rufipes	24	NE	NE
Harpalus serripes	24	**3**	**3**
Harpalus signaticornis	4	NE	NE
Harpalus smaragdinus	83	**V**	NE
Harpalus subcylindricus	942	**2**	**G**
Harpalus tardus	142	NE	NE
Masoreus wetterhallii	2	**1**	NE
Microlestes minutulus	5	NE	NE
Nebria brevicollis	1	NE	NE
Ophonus azureus	13	NE	NE
Ophonus puncticeps	2	NE	NE
Ophonus schaubergerianus	1	NE	**V**
Panagaeus bipustulatus	4	**V**	NE
Parophonus maculicornis	102	**V**	NE
Poecilus cupreus	1	NE	NE
Poecilus lepidus	5	**3**	NE
Poecilus versicolor	137	NE	NE
Pterostichus melanarius	57	NE	NE
Syntomus foveatus	2	NE	NE
Syntomus truncatellus	9	NE	NE

Table S2: Species of spiders (Araneae) sampled from urban grasland in Karlsruhe, Germany (NE = not endangered, BW = Baden-Württemberg, G = Germany)

Species	Family	Individuals	Red List BW	Red List G
Agyneta affinis	Linyphiidae	185	NE	NE
Agyneta fuscipalpa	Linyphiidae	1	**D**	NE
Agyneta mollis	Linyphiidae	31	**V**	NE
Agyneta rurestris	Linyphiidae	61	NE	NE
Alopecosa cuneata	Lycosidae	424	NE	NE
Arctosa leopardus	Lycosidae	29	NE	NE
Arctosa lutetiana	Lycosidae	47	NE	NE
Argenna subnigra	Dictynidae	40	**V**	NE
Asagena phalerata	Theridiidae	131	NE	NE
Atypus piceus	Atypidae	1	**V**	**V**
Aulonia albimana	Lycosidae	200	NE	NE
Bathyphantes gracilis	Linyphiidae	4	NE	NE
Centromerita bicolor	Linyphiidae	2	NE	NE
Centromerita concinna	Linyphiidae	1	**D**	NE
Cheiracanthium campestre	Cheiracanthiidae	4	**2**	**G**
Clubiona neglecta	Clubionidae	5	NE	NE
Dicymbium nigrum brevisetosum	Linyphiidae	6	NE	NE
Diplostyla concolor	Linyphiidae	5	NE	NE
Drassyllus praeficus	Gnaphosidae	285	**V**	NE
Drassyllus pusillus	Gnaphosidae	136	NE	NE
Dysdera crocata	Dysderidae	5	NE	NE
Enoplognatha thoracica	Theridiidae	11	NE	NE
Erigone atra	Linyphiidae	1	NE	NE
Erigone dentipalpis	Linyphiidae	55	NE	NE
Erigonella hiemalis	Linyphiidae	1	NE	NE
Ero aphana	Mimetidae	1	NE	NE
Euophrys frontalis	Salticidae	21	NE	NE
Hahnia nava	Hahniidae	48	NE	NE
Haplodrassus dalmatensis	Gnaphosidae	5	**2**	**V**
Haplodrassus signifer	Gnaphosidae	386	NE	NE
Heliophanus flavipes	Salticidae	4	NE	NE
Hypsosinga pygmaea	Araneidae	2	**2**	**3**
Mangora acalypha	Araneidae	39	NE	NE
Mermessus trilobatus	Linyphiidae	28	NE	NE
*Micaria micans**	Gnaphosidae	10	**not_listed**	**not_listed**
Micrargus subaequalis	Linyphiidae	18	NE	NE
Microlinyphia pusilla	Linyphiidae	2	NE	NE
Neon reticulatus	Salticidae	1	NE	NE
Neottiura bimaculata	Theridiidae	4	NE	NE
Oedothorax retusus	Linyphiidae	21	NE	NE
Ozyptila claveata	Thomisidae	41	NE	NE
Ozyptila simplex	Thomisidae	135	NE	NE
Pachygnatha degeeri	Tetragnathidae	1110	NE	NE
Palliduphantes pallidus	Linyphiidae	1	NE	NE
Pardosa agrestis	Lycosidae	6	NE	NE
Pardosa hortensis	Lycosidae	78	NE	NE
Pardosa lugubris s.l.	Lycosidae	2	NE	NE
Pardosa monticola	Lycosidae	6	**V**	NE
Pardosa palustris	Lycosidae	2063	NE	NE
Pardosa prativaga	Lycosidae	437	NE	NE
Pardosa pullata	Lycosidae	735	NE	NE
Pardosa wagleri	Lycosidae	2	**3**	**3**
Pelecopsis parallela	Linyphiidae	115	NE	NE
Phlegra fasciata	Salticidae	31	NE	NE
Phrurolithus festivus	Phrurolithidae	22	NE	NE
Phrurolithus minimus	Phrurolithidae	1	NE	NE
Phylloneta impressa	Theridiidae	8	NE	NE
Piratula hygrophila	Lycosidae	2	NE	NE
Piratula latitans	Lycosidae	43	NE	NE
Piratula uliginosa	Lycosidae	4	NE	NE
Pisaura mirabilis	Pisauridae	5	NE	NE
Scotina celans	Locranidae	1	**V**	NE
*Sibianor cf. tantulus**	Salticidae	1	**not_listed**	**R**
Talavera aequipes	Salticidae	5	NE	NE

Tenuiphantes flavipes	Linyphiidae	1	NE	NE
Tenuiphantes tenuis	Linyphiidae	56	NE	NE
Tenuiphantes zimmermanni	Linyphiidae	1	NE	NE
Tetragnatha pinicola	Tetragnathidae	9	NE	NE
Tibellus oblongus	Philodromidae	3	NE	NE
Tiso vagans	Linyphiidae	15	NE	NE
Trachyzelotes pedestris	Gnaphosidae	21	NE	NE
Trichopterna cito	Linyphiidae	2	**3**	**3**
Trochosa ruricola	Lycosidae	530	NE	NE
Trochosa terricola	Lycosidae	9	NE	NE
Walckenaeria antica	Linyphiidae	3	NE	NE
Xerolycosa miniata	Lycosidae	748	**V**	NE
Xysticus acerbus	Thomisidae	18	**V**	NE
Xysticus cristatus	Thomisidae	67	NE	NE
Xysticus kochi	Thomisidae	177	NE	NE
Xysticus ulmi	Thomisidae	1	NE	NE
Zelotes electus	Gnaphosidae	76	**3**	NE
Zelotes latreillei	Gnaphosidae	10	NE	NE
Zelotes longipes	Gnaphosidae	32	**3**	NE
Zelotes petrensis	Gnaphosidae	13	NE	NE
Zodarion italicum	Zodariidae	63	NE	NE
Zora spinimana	Miturgidae	3	NE	NE

**Micaria micans* recognized as disctinct species byMuster & Michalik (2020); common species in Germany/BW

***Sibianor aurocinctus* recognized as group of species by Logunov (2001), not cited by Nährig et al. (2003). Single male specimen are sometimes not determinable to species level (Logunov, pers. comm). All species of the group in BW are rare and restricted to endangered habitats, therefore all records/species are of conservation concern

Table S3: Further data on species numbers and sampled specimens. Ex = extensively managed (n=18, 1-2 cuts), int = intensively managed (n=9, 3-5 cuts). CC = conservation concern according to Red Lists of Baden-Württemberg and Germany (in ())

Indicator group	total species number	sampled specimens	species of CC	CC specimens
spiders (Araneae)	86	8973	18 (7)	1256
carabid beetles (Carabidae)	55	2660	17 (9)	1497

spiders	1-2 cuts per year	3-5 cuts per year
species number	28.7±3.3	25.6±5.8
caught adult specimens	392±127	213±126
species of CC	3.6±5.8	4.1±1.28
CC specimens	56±84	27±34
Carabids		
species number	13.3±2.7	12.2±5.3
caught adult specimens	113±54	68±50
species of CC	4.7±1.5	4.2±2.2
CC specimens	71±44	24±26

Table S4: Selected species of conservation concern sampled from urban grassland in Karlsruhe. ex = extensively managed (n=18, 1-2 cuts), int = intensively managed (n=9, 3-5 cuts). Category = assessment in the red list of Baden-Württemberg

Araneae	**ex**	**int**	**total capture**	**category**
Xerolycosa miniata	657	91	748	V
Drassyllus praeficus	184	101	285	V
Zelotes electus	52	24	76	3
Argenna subnigra	33	7	40	V
Zelotes longipes	23	9	32	3
Xysticus acerbus	17	1	18	V
Carabidae				
Harpalus subcylindricus	862	80	942	2
Harpalus dimidiatus	226	26	252	V
Parophonus maculicornis	72	30	102	V
Harpalus smaragdinus	61	22	83	V
Harpalus pumilus	14	13	27	V
Harpalus serripes	17	7	24	3
Harpalus luteicornis	16	5	21	V

Chapter II (b)

Spider assemblages (Arachnida: Araneae) in urban grassland patches in Karlsruhe (Baden-Württemberg, Germany)

Tobias Bauer, Hubert Höfer & Jens Schirmel

Data Paper

Spider assemblages (Arachnida: Araneae) in urban grassland patches in Karlsruhe (Baden-Württemberg, Germany)

Tobias Bauer, Hubert Höfer & Jens Schirmel

doi: 10.30963/aramit6801

Abstract. Grassland patches embedded in an urban matrix can harbour a significant number of spider taxa, including rare and endangered species. To further benefit urban biodiversity, Karlsruhe was one of the first cities in Central Europe that adopted biodiversity friendly mowing regimes. The aim of this study was to investigate the effects of two mowing regimes (1–2 cuts and 3–5 cuts per year) and environmental parameters such as urbanization and soil humidity on arthropod assemblages inhabiting such grassland patches in Karlsruhe, Germany. For this, 27 urban grassland plots (18 with 1–2 cuts, 9 with 3–5 cuts) were selected. Four pitfall traps per site were operated for a total of 48 days in May, June and August/September of 2018. Sweep netting was performed one time in May 2018. In total, 10704 (8973 adult, 1731 juvenile) specimens in 86 species were sampled. Seven species are either endangered or otherwise of conservation concern (cc) in Germany, 18 regionally endangered or otherwise of cc in the federal state of Baden-Württemberg. The majority of species of cc prefers xerothermic conditions. This corresponds to some of the investigated grassland plots that are characterized by sandy soils and vegetation typical for dry conditions. Exceptional records of cross-regional importance are *Pardosa wagleri* (Hahn, 1822) at one plot and *Cheiracanthium campestre* (Lohmander, 1944) at three plots. The record of *P. wagleri* is the northernmost known locality for the species, the records of *Cheiracanthium campestre* are situated at the western distribution limit for this rare species.

Keywords: diversity, dry grassland, endangered species, management, urban habitats

The complete data sets and metadata corresponding to abstracts of a Data Paper are published electronically as Supporting Information in the online version of the article and through the ARAMOB data repository at https://aramob.de/en/data/data-exploitation/ - Filter for Project ARAMIT_Bauer2024.

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Academic editor: Alexander Bach
Data editor: Florian Raub

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Data Paper

Spider assemblages (Arachnida, Araneae) in urban grassland patches in Karlsruhe (Baden-Württemberg, Germany)

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Introduction

The original study was initiated to investigate the arthropod diversity and effects of management intensities, urbanization and local environmental parameters on urban grassland patches in the city of Karlsruhe, Germany. Grassland patches embedded in an urban matrix can harbour a significant number of spider taxa, including rare and endangered species. Karlsruhe was one of the first cities in Central Europe that adopted biodiversity friendly mowing regimes to benefit urban biodiversity. The city manages over 850 hectare of green spaces in various intensities and has a long-standing, nearly 50-year-old tradition in extensive grassland management. Many of those extensively managed grassland patches within the city border are known to harbour comparably extensive pollinator diversity (Rennwald et al. 2002, Warzecha et al. in prep.). However, data on epigeic arthropod diversity and species inhabiting the herb layer were lacking so far. In addition, different management intensities and their effect on local arthropod diversity were never directly compared. Spiders were sampled in 27 grassland plots (18 with 1-2 cuts, 9 with 3-5 cuts with four pitfall traps per plot, approximately 7 m apart, operated for a total of 48 days in May/June and August/September 2018. Traps were filled with propylene glycol with a drop of odourless dish detergent and protected by white plastic roofs. Sweep netting was performed once in May 2018. Spiders were determined by using Nentwig et al. (2024) and additional literature (Grimm 1985, 1986; Jantscher 2001; Logunov 2001; Roberts 1987; Tongiorgi 1966) as well as comparative material from the collection of the SMNK, mainly sampled in a study by Hemm et al. (2012). The dataset includes 8973 adult spiders of 86 species in 21 families.

Keywords: diversity, dry grassland, endangered species, management, urban habitats

METADATA

Data set identity. Data on spider assemblages (Arachnida, Araneae) in public urban grassland managed with two different intensities (1-2 cuts or 3-5 cuts per year) in Karlsruhe, Germany

Overall project description

Objectives of original study. 1. Study the effects of urbanization, local environmental variables and management on arthropod assemblages in an urban setting; 2. Revealing local species occurrences and overall diversity in the city of Karlsruhe

Principal Investigator(s)/Verantwortlicher Wissenschaftler: Tobias Bauer

Involved persons/Beteiligte Personen: Jens Schirmel, Hubert Höfer, Andreas Kleinsteuber, Daniela Warzecha

Source of funding/Geldgeber: Friedrich-Ebert Stiftung e.V.

Data Source Institution/Datenliefernde Institution: Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, 76133 Karlsruhe

Period of study or time extent/Zeitraum der Untersuchung: April to June 2018 (48 days) and August to September 2018 (14 days)

Survey design

Site description. All grassland plots (Tab. 1) were located in the city area of Karlsruhe, Germany, and represented public greenspaces managed by the Gartenbauamt Karlsruhe. Nine sites (*) were intensively managed (3-5 mulch cuts), 18 were extensively managed (1-2 cuts, biomass removed). Conditions and aspects ranged from humid and dense meadows along the river Alb to dry, sandy sites with low and sparse vegetation. See also Bauer et al. (2024) for further local variables.

Table 1: Studied grassland plots in the city of Karlsruhe, Germany (coordinates in decimal degrees, WGS 84, *intensively managed site)

location	latitude	longitude	EUNIS
ERW6	48.9964	8.3751	E2
EWI1*	49.0050	8.3538	E3
NE1	49.0326	8.3643	E2
NE2	49.0376	8.3678	E2
NE3	49.0376	8.3860	E5
NI1*	49.0315	8.3647	E2
NI2*	49.0375	8.3683	E2
NI3*	49.0365	8.3892	E2.64
OE1	49.0235	8.4484	E2
OE2	49.0239	8.4529	E2
OE3	49.0403	8.4556	E1
OI1*	49.0248	8.4473	E1
OI2*	49.0240	8.4527	E2.64
RW10	48.9812	8.4006	E3
RW11	48.9892	8.3684	E1
RW12	49.0346	8.4431	E1
RW15*	49.0410	8.4603	E2.64
RW2	49.0045	8.3440	E3
RW3	49.0033	8.3488	E2
RW4*	49.0020	8.3487	E3
RW5	49.0070	8.3532	E1
RW7	48.9914	8.3848	E2
RW8	48.9901	8.3902	E2
RW9	48.9850	8.3974	E3
WE2	48.9999	8.3433	E1
WE3	48.9929	8.3405	E2
WI3*	48.9938	8.3417	E1

Methods of data collection. 4 pitfall traps per location (white plastic cups with 6.5 cm diameter in pre-installed tubing) with a distance of approximately 7 m in a linear transect. Traps were protected against rain with white plastic lids mounted on a nail of 20 cm length. Traps were active from end of April until June, 20 2018. In May, they were usually emptied every 2 weeks. In the third period until the beginning of mowing operations, traps were active for 20 days. Traps were active for a fourth period of 2 weeks from end of August into September 2018. Sweep netting was performed on May, 30 2018 (30 blind sweeps over a linear transect). At

three locations (NI3, RW7, WE2) a single trap was destroyed during one sample period, probably due to crows removing the cups.

Methods of sample processing, storage and identification. Samples were transferred into 75 % ethanol in the field and sorted in the laboratory. Spiders were determined by T. Bauer using Nentwig et al. (2024) and additional literature (Grimm 1985, 1986; Jantscher 2001; Logunov 2001; Roberts 1987; Tongiorgi 1966). Nomenclature follows World Spider Catalog (2024).

Vouchers/Material deposited. Voucher specimens are deposited in the collections SMNK-ARA and SMNK-STUD of the State Museum of Natural History Karlsruhe.

Significance of data set. Bauer et al. (2024) published main results of the study. The dataset contains records on 86 spider species (8973 adult specimens). 1731 sampled juvenile specimens are not part of the dataset, because they cannot be determined to species level. Given the frequent disturbances on many plots, including mowing operations, and the limited capture period, the species number is surprisingly high. In addition, the dataset contains records of several species of conservation concern despite the localization of all plots in a highly urbanized region. Seven species are either endangered or otherwise of conservation concern (cc) in Germany, 18 species are regionally endangered or otherwise of cc in the federal state of Baden-Württemberg. The majority of species of cc prefer xerothermic conditions. This corresponds to grassland plots that are characterized by sandy soils and vegetation typical for dry conditions (for more details see Bauer et al. 2024). Two females of *Pardosa wagleri* (Hahn, 1822) were sampled at one location, marking the northernmost record of this species in Germany (Arachnologische Gesellschaft 2024). This species of gravelly river banks might spread along railroads due to the subgrade and ballast material used for construction, which is close to the natural habitat of the species. Railroads were in immediate proximity of the location. Two females and two males of *Cheiracanthium campestre* Lohmander, 1944, a European species with an insufficiently known distribution, were sampled at three locations. These records are located at the western border of its known distribution (Nentwig et al. 2024). Several records of species that were not expected to occur in urban grassland plots are remarkable: *Arctosa lutetiana* (Simon, 1876), a red-listed species in some other federal states of Germany and inhabitant of warm open habitats, was recorded at eight locations and sampled in high numbers at one. *Ozyptila claveata* (Walckenaer, 1837), a species with large record gaps in Germany and frequently associated with extensively managed dry grassland in lowland areas (Arachnologische Gesellschaft 2024) was found at several locations throughout the city. *Aulonia albimana* (Walckenaer, 1805), the only member of the lycosid subfamily Venoniinae in Central Europe, was recorded from nearly every location in partly very high numbers, demonstrating that this species copes well with urbanization and disturbance.

DATA SET STATUS AND ACCESSIBILITY

Status

Data submitted: 2024-09-30, **Data accepted:** 2024-10-14

Academic editor: Alexander Bach

Data editor: Florian Raub

Latest data update: October 2024

Latest metadata update: October 2024

Accessibility

Storage location and medium. Metadata and data files are stored by Arachnologische Gesellschaft, data are included in the ARAMOB database using the database framework Diversity Workbench (https://diversityworkbench.net/), data are accessible via https://aramob.de/en/data/data-exploitation/ Filter: Project ARAMIT_Bauer2024

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DATA STRUCTURAL DESCRIPTORS

Data Set Files

Bauer2024_obsdata.csv, 593 KB, spider abundance data set
Bauer2024_plotdata.csv, 6 KB, locations of the sampling sites (decimal coordinates, WGS84)

Authentication procedures

MD5 hash checksums generated by WinHash v.1.6.6787:
Bauer2024_obsdata.csv: D01ED152590ABB9F15CCA9A23F351E3F
Bauer2024_plotdata.csv: 682B6B19B5DBA83E524410CC79B3981C

SUPPLEMENTAL DESCRIPTORS

Publications using the data set: Bauer T, Höfer H & Schirmel J 2024 Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes. Insect Conservation and Diversity 1-15, https://doi.org/10.1111/icad.12746

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References

Arachnologische Gesellschaft 2024 Atlas der Spinnentiere Europas. Internet: https://atlas.arages.de (13. Oct. 2024)

Bauer T, Höfer H & Schirmel J 2024 Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes. – Insect Conservation and Diversity. – doi: 10.1111/icad.12746

Grimm U 1985 Die Gnaphosidae Mitteleuropas (Arachnida, Araneae). – Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 26: 1-318

Grimm U 1986 Die Clubionidae Mitteleuropas: Corinninae und Liocraninae (Arachnida, Araneae). – Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 27: 1-91

Hemm V, Meyer F & Höfer H 2012 Die epigäische Spinnenfauna (Arachnida, Araneae) in Sandrasen, Borstgrasrasen und Ruderalfluren im Naturschutzgebiet „Alter Flugplatz Karlsruhe “. – Arachnologische Mitteilungen, 44: 20-40

Jantscher E 2001 Revision der Krabbenspinnengattung *Xysticus* C.L. Koch, 1835 (Araneae, Thomisidae) in Zentraleuropa. Dissertation, Universität Graz, 328 pp.

Logunov DV 2001 A redefinition of the genera *Bianor* Peckham & Peckham, 1885 and *Harmochirus* Simon, 1885, with the establishment of a new genus *Sibianor* gen. n. (Aranei: Salticidae). – Arthropoda Selecta 9: 221-286

Nentwig W, Blick T, Bosmans R, Gloor D, Hänggi A, Kropf C (2024) Spinnen Europas. Version 9.2024. Internet: https://www.araneae.nmbe.ch (14. Sep. 2024)

Rennwald E, Rennwald K & Doczkal D 2002 Ergebnisse von faunistischen Stichprobenerhebungen als Basis für eine zoologisch-fachliche Bewertung verschiedener seit zehn und mehr Jahren extensiv gemähter Wiesenbereiche in Grünanlagen der Stadt Karlsruhe (Tagfalter, tagaktive Nachtfalter,

Heuschrecken und Grillen, Wildbienen, Wespen, Schwebfliegen und andere Insekten). Gutachten im Auftrag der Stadt Karlsruhe, Gartenbauamt (unpublished)

Roberts MJ 1987 The spiders of Great Britain and Ireland, Volume 2: Linyphiidae and check list. Harley Books Colchester, England. 204 pp.

Tongiorgi P 1966 Italian wolf spiders of the genus *Pardosa* (Araneae: Lycosidae). – Bulletin of the Museum of Comparative Zoology 134: 275-334

World Spider Catalog 2024 World Spider Catalog. Version 25.5. Natural History Museum Bern. Internet: http://wsc.nmbe.ch (10. Oct. 2024). – doi: 10.24436/2

Chapter III

A large urban reserve and many small urban grassland fragments together effectively preserve local grassland spider diversity in a city

Tobias Bauer, Hubert Höfer & Jens Schirmel

A large urban reserve and many small urban grassland fragments together effectively preserve local grassland spider diversity in a city

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Abstract

Urban grassland in temperate regions ise known to harbour rich spider assemblages, often including some species of local conservation concern (cc). However, its role in species conservation in connection with nearby nature reserves is little investigated. In this work we used two datasets, one from an exhaustively sampled urban grassland reserve (Alter Flugplatz, AF) and the other from 27 intensively sampled urban grassland fragments (UGF), in the city of Karlsruhe (Germany). We aimed at determining which grassland spider species occur exclusively in the city area and which in the nature reserve and whether AF influences spider diversity in its direct surroundings. While species assemblages of single UGF represented mostly species subsets of the spider community of AF, we did not find a significant influence of the linear distance of AF on the spider diversity on UGF. Most species found in UGF were already known from AF, however, a small percentage of species was exclusively found in UG. Species diversity was significantly higher in AF than in UGF. Species diversity in UGF acted independently of UGF patch size and distance to AF. Species exclusive to AF were significantly rarer recorded in Germany than species sampled from AF.. Exclusive species of cc were significantly rarer in Germany as well. Cursorial hunters exclusive to AF showed significantly lower humidity preferences, while no differences were found in a comparison of species of cc. Body size did not differ between both datasets, but species of cc exclusive to AF showed larger variations concerning minimal and maximum species size. Effective grassland spider conservation in cities therefore depend on large, high-quality areas that preserve the majority of species and small patches in the surroundings with variations in local conditions such as humidity.

Keywords: Araneae, beta diversity, red lists, species inventory, protected areas, traits

Introduction

According to the species-area relationship, larger areas usually host more species than small areas, and with decreasing size, area-sensitive, and often endangered, species disappear first (Rosenzweig 1995). This holds true for urban areas as well, where patch size has been identified as one of the most crucial factors for maintaining high biodiversity levels at the local level (Beninde *et al.* 2015, Nielsen *et al.* 2014). However, green space in cities competes with other land uses in urban area and is limited especially for large habitat patches or nature reserves (Knapp *et al.* 2008). For most organisms, the majority of suitable habitat patches in cities tend to be small, isolated and fragmented, surrounded by impervious surfaces, which leads to very complex interactions between organisms and landscape and a heterogeneous mixture of planted and natural vegetation types (Norton *et al.* 2016). Further, green spaces in cities are also strongly affected by management decisions of local administration (e.g. mowing, planting of exotic species and fertilization) (Aronson *et al.* 2017). However, even small patches can support diverse species assemblages (Rösch *et al.* 2015), and several small fragments together often contain more species than a single large patch of comparable size (Fahrig 2020). Cities with their many small patches are indeed areas relatively rich in species (e.g. Buchholz *et al.* 2018, Kühn *et al.* 2004), which, however, strongly depends on taxonomic group and environmental conditions (Beninde *et al.* 2015, Fenoglio *et al.* 2020).

Given their abundance, high species richness, and sensitivity to environmental stress as well as narrow ecological niche of many species, spiders (Araneae) are a frequently studied group of terrestrial arthropods when it comes to effects of urbanization, effectiveness of protected areas and variations in local environmental parameters (Bauer *et al.* 2024, Buchholz *et al.* 2018, Hemm & Höfer 2012, Piano *et al.* 2020, Sattler *et al.* 2010b). Although sensitive to urbanization and fragmentation at the local scale (e.g. Piano *et al.* 2020), spiders maintain high levels of overall biodiversity in urbanized landscapes when, for example, patches of valuable habitat remain intact, a variety of different habitats is present and when some remaining patches are of large size (Bach *et al.* 2025, Möller *et al.* 2019, Hemm *et al.* 2012, Van Keer *et al.* 2010).

Nevertheless, our knowledge about the sensitivity of rare and endangered spider species to urbanization is still limited. While spiders of conservation concern (species of cc) may colonize secondary habitats in urban areas, such as extensively managed dry grasslands, wastelands, and green roofs (e.g. Bauer *et al.* 2024, Brenneisen & Hänggi 2006, Kadas 2006, Kielhorn 2024), they may also be absent from suitable habitats, such as recently created urban wildflower meadows with mesic conditions (Bach *et al.* 2025). In fact, the urban matrix is often described to act as a strong filter for many organisms (e.g. Aronson *et al.* 2017, Buchholz *et al.* 2020, Gathof *et al.* 2022). Habitats in the urban matrix are often characterized by impoverished assemblages when compared to potential source areas of high value for biodiversity (Fenoglio *et al.* 2020, Melo *et al.* 2022). In addition, urban areas often show trends towards biotic homogenization (Kühn & Klotz 2006, Lokatis & Jeschke 2022). However, these effects strongly depend on the focal taxonomic group and study area (Fenoglio *et al.* 2020, Lane & Burgin 2008), but also habitat specialization (Lizée *et al.* 2011) and biological traits of single species or functional groups (Buchholz *et al.* 2020, Leveau 2013, Piquet *et al.* 2024). Nonetheless, for many locally rare and endangered spider species in Central Europe it remains unknown whether they can, if present in nearby, larger habitat patches or protected areas, penetrate the urban matrix and colonize small fragments of suitable habitat, for example grassland fragments.

In order to investigate this question, we used a unique dataset of spider species from one of the largest Central European nature reserves fully located in an urbanized area, namely the 'Alter Flugplatz' (AF; size = 69 ha) in the city of Karlsruhe, Germany (Hemm *et al.* 2012). The nature reserve is characterized by partly very dry and little-disturbed semi-natural grassland, including mattgrass and sandy, sparsely vegetated grassland on very poor soils. Its spider fauna was exhaustively sampled in the recent years, indicating the presence of a high percentage of comparably large species as well as species of cc, many of them narrow-niched species thriving under xerothermic conditions (Hemm *et al.* 2012). We compared the spider species from AF to assemblages of 27 urban grassland fragments (UGF; summed area = 18 ha) within Karlsruhe, which were studied in 2018 (Bauer *et al.* 2024). Although some UGF consisted of dry, sandy grassland, the soil of these grasslands is generally richer in nutrients and its vegetation is denser and higher due to eutrophication. Nonetheless, Bauer *et al.* (2024) found that UGF are not depleted of species of cc, but, in contrast, harbour several endangered or rare species, many of them preferring open xerothermic habitats, as well as a relatively high overall spider diversity. This additionally raises questions concerning the effectiveness of AF for spider species conservation and the function of UGF in preserving large spider species, species of cc and specialists of xerothermic grasslands.

The following hypotheses were tested:

1) According to the species-area-relationship, the species richness of spiders is higher in the large nature reserve AF than in the total area of all UGF.
2) Individual UGF mostly represent subsets of the AF spider assemblage.
3) Because AF acts as a source of species, diversity and similarity decrease with increasing distance from AF. Large UGF are expected to be more similar to AF than small UGF.
4) Large UGF harbour several species not present in smaller UGF.
5) Exclusive spiders of AF are rarer in Germany and of higher conservation value (rare species = potentially area-sensitive), rare species in UGF remain restricted to a small number of plots
6) Large species (cf. Merckx *et al.* 2018) as well as species preferring distinct xerothermic conditions remain restricted to AF

Material and methods

Localities and datasets

For our analyses, we used two dataset of spiders from the city of Karlsruhe. The dataset of Hemm *et al.* (2012) contained the spider fauna of the nature reserve "Alter Flugplatz" (AF) (Fig. 1) and the one published by Bauer *et al.* (2024) contained data on spiders of 27 urban grassland fragments (UGF), which are managed by local city administration (Gartenbaumt Karlsruhe). AF extends to about 69 hectares (690 000 m^2) in the northwestern part of Karlsruhe. With an exception at the northern side, AF is completely enclosed by ongoing urban development. A major part of the vegetation consists of completely flat, very dry sandy grassland with many small non-vegetated areas (today mainly caused by a large rabbit population) and areas with matgrass (*Nardus stricta*) (for further details, see Hemm *et al.* 2012). It is managed by a combination of grazing (sandy grassland) and extensive cutting (matgrass areas). In addition, the management of the vegetation of some fringe areas was benignly neglected in the past and now consists of a mosaic of infrequently managed grassland patches, single trees (mainly Scots pine (*Pinus silvestris*) and silver birch (*Betula pendula*)) as well as small bushes. Overall, this part exhibits comparably humid conditions for grassland spiders. At the beginning of the 19th century, the remaining forest was cut down and the area was used for military activities and later as an anchor area for airships. After the Second World War, part of the area was again used by the American forces as a military area. After return to local administration, parts of the original area were converted into housing and commercial areas. The majority of the remaining area was designated as a reserve in 2010 (Zimmermann 2011). The area and its habitats were repeatedly sampled over several years by various authors, culminating in the extensive species list given in Hemm *et al.* (2012). In addition, the first author further collected spiders in the Alter Flugplatz reserve from 2018-2020, which resulted only in one additional grassland species record (*Phylloneta impressa*). During this time, several species of cc were encountered again. Given this extensive survey of the area, it can be assumed that the vast majority of (grassland) species that has been present at the reserve is now known.

Bauer *et al.* (2024) intensively sampled 27 remnant grassland plots in the urban matrix of Karlsruhe in 2018 by pitfall trapping and sweep netting. The size of single UGF varied between 1 200 and 26 000 m^2 ($\sum$27 UGF = 181 000 m^2; Bauer *et al.* 2024), ranging from relatively humid meadows with scattered trees and hedges to dry and sandy grasslands comparable to the ruderalized area of AF. Additional sweep netting to cover species that may have been missed in 2018 was carried out again in early May 2023 on the same plots (similar to Bauer *et al.* 2024, but only half the sweeps), with one exception, as one grassland was used for construction. However, this resulted only in two new records for UGP, both common species (*Evarcha arcuata*, *Pardosa amentata*) previously known from AF.

Figure 1: various aspects of the nature reserve "Alter Flugplatz" in Karlsruhe**. A:** Sandy Grassland in spring; **B:** Sandy grassland in summer: **C:** benignly neglected fringe areas; **D:** Matgrass area in summer

Dataset preparation

Since we wanted to analyse and compare the composition of grassland spider species in both species lists, we removed singletons of species usually occurring in other habitats and may have wandered into pitfall traps from nearby areas (e.g. species inhabiting bushes, trees; Arachnologische Gesellschaft 2024; Hänggi *et al.* 1995) and typical forest and forest edge species that were sampled from the ruderalized area of AF (Dorow *et al.* 2019). We also removed *Diplocephalus cristatus*, *Araeoncus humilis* and *Porrhomma microphtalmum,* three typical aeronaut species and indicators of disturbance (Blick *et al.* 2000), as they were only sampled on AF in very low numbers or singletons (Hemm *et al.* 2012) and are probably linked to local soil disturbance by rabbits. Material determined as *Cheiracanthium virescens* in Hemm *et al.* (2012) were re-examined by the first author and turned out to be *C. campestre*, a species also found in UGF. We only used presence-absence data, as the species list of AF consists of an accumulated mixture of different species lists from a set of assemblages made over several years by various authors (Hemm *et al.* 2012). To gain further insights into the biodiversity of both localities, we compared two overlapping periods of pitfall trapping of one year (May, June) from the investigations in Bauer et al. (2024) and Hemm et al. (2012). For this, results (total species

diversity, species of cc) from single traps (standardized to two week-periods per trap) were compared. This resulted in 311 pitfall trap periods for UGF and 233 for AF.

Spiders were classified as species of conservation concern (cc) according to Nährig *et al.* (2003). Any native spider species listed as threatened, vulnerable, regionally restricted or data deficient was considered as of conservation concern. Humidity preferences were extracted from Entling *et al.* (2007; 1 = lowest humidity preference, 0 = highest humidity preference), and the medium body size (of the female) from Nentwig *et al.* (2024). For size comparisons, linyphiid spiders were excluded from the analysis as grassland linyphiids are constrained in their body size (usually < 3 mm), which would result in a skewed comparison given the large number of eurytopic linyphiid species present in both datasets. As proxy for the frequency of species in Germany, we downloaded grid cell records (1:25 000) from the German spider record scheme, which contains records of every spider species found in Germany (Arachnologische Gesellschaft 2024). For further details, see Bauer *et al.* (2024).

Statistical analyses

All analyses were carried out in the R environment (R Core Team 2022). Continuous species and grid cell count data (dependent variables) were analyzed by using a negative binomial distribution, as they showed non-normal distribution (function glm.nb, "MASS; Venables & Ripley 2002) and subsequent testing with function "Anova" (Package "car"; Fox & Weisberg (2019). Models including continuous data that fall between 0 and 1 (dissimilarity data) were analyzed with function glmmTMB and a beta-distribution (Brooks *et al.* 2017). For pairwise comparisons, all of them with non-normal distribution, the wilcoxon rank sum test with continuity correction was used function ("wilcox.test"), as distributions were unknown. For calculation of correlations, Pearson correlation coefficient and subsequent testing (function "cor.test") was used. Grouped data on the patch size were analyzed with the Kruskal–Wallis test on global differences in the dataset. For comparison of patch sizes and species dissimilarity to AF (Jaccard 1902), UGF were divided in three groups (n=9) according to their size. To demonstrate the contribution of large fragments to the total number of recorded species in UGF (cf. Rösch *et al.* 2015) we additionally accumulated all species along the UGF patch size from smallest to largest fragment. Species accumulation of pitfall trap results was done with the function "speccacum" in vegan (100 randomisations, Oksanen et al. 2013).

Results

Species composition and diversity

Of the 121 species associated with grassland in the full AF dataset, 72 (59%) were also found on UGF (Fig. 2A), with 10 species recorded exclusively in UGF and 49 species (40%) found only on AF. In standardized comparisons of pitfall trapping results (Fig. 3A), species accumulated more quickly and single pitfall traps contained significantly more species on AF (Fig. 3C).
The dissimilarity of the species compositions between individual UGF and the AF was generally very high and constant (Jaccard index ranging, with one exception, from 0.75-0.8), with 15 out of

27 UGF having exactly zero exclusive species and only one plot having 3 exclusive species. Exclusive species occurred numerically more often in plots with higher humidity (Fig. 2C).
Out of the 37 species of conservation concern (cc) present in the dataset of AF (Fig. 2B), 13 were recovered from UGF. Only 4 species of cc were exclusively collected on UGF. The proportion of species of cc was higher in AF (31%) than in UGF (20%). In the exclusive AF species that were not found on UGF, the proportion of species of cc was even 47%. In standardized comparisons of pitfall trapping results, species of cc accumulated more quickly (Fig. 3B) and single pitfall traps contained significantly more species on AF (Fig. 3D).

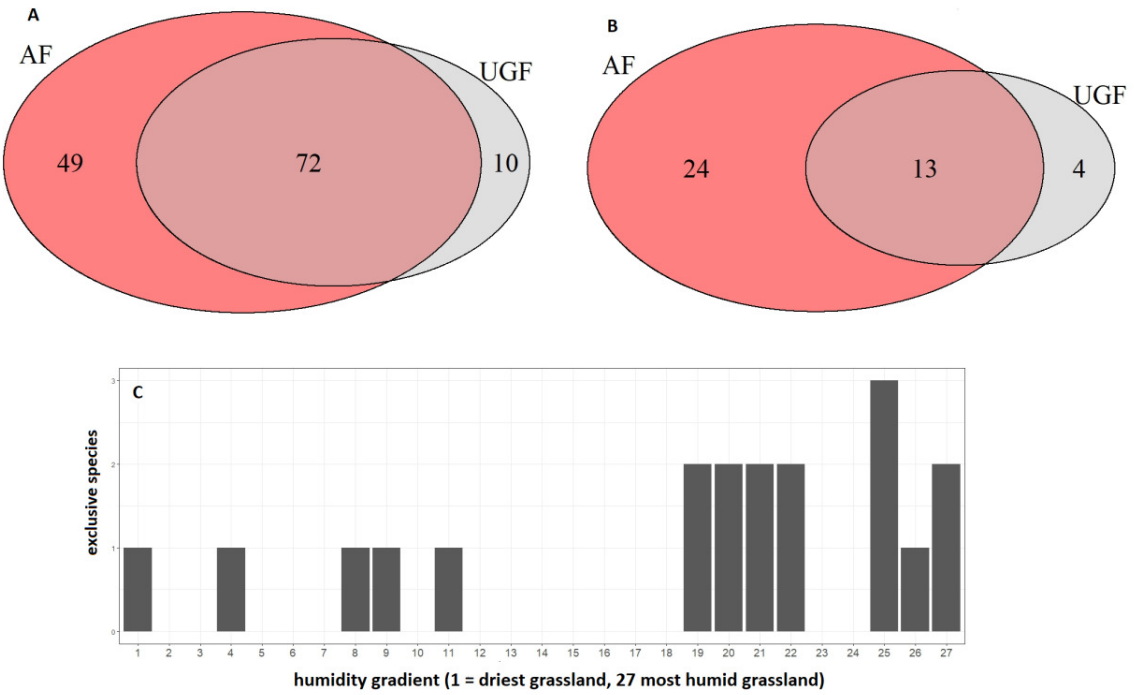

Figure 2: A: Shared and exclusive spider species of the nature reserve Alter Flugplatz (AF) and urban grassland fragments (UGF) in Karlsruhe, Germany; **B:** Shared and exclusive spider species of conservation concern of the nature reserve Alter Flugplatz (AF) and urban grassland fragments (UGF) in Karlsruhe, Germany **C:** Number of exclusive species of UGF along the humidity gradient.

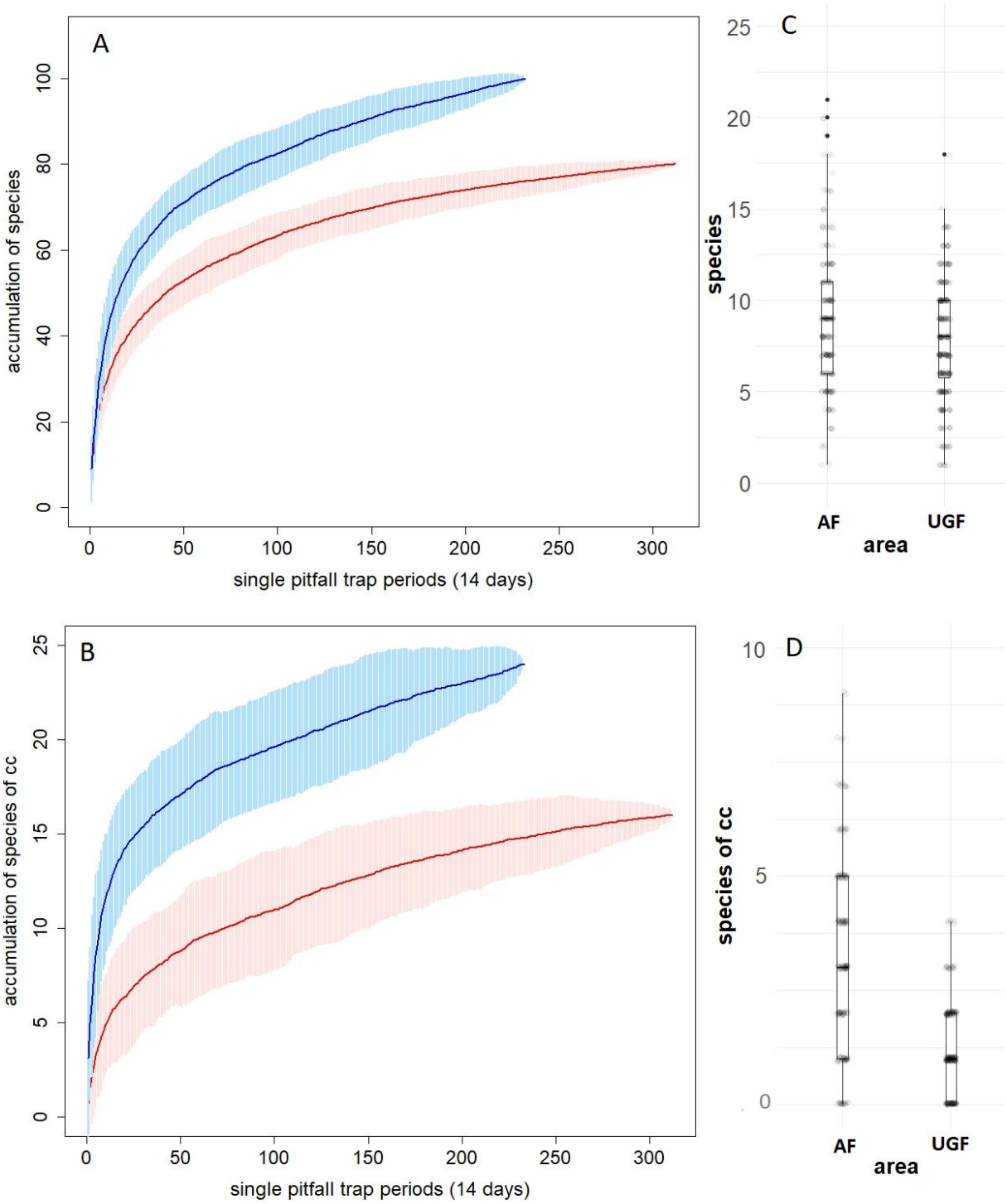

Figure 3: A-B: Accumulation of spider species (A = all species, B = all species) over 233 (Alter Flugplatz; AF) and 311 two-week pitfall trap periods (Urban grassland fragments in Karlsruhe = UG) in May/June (100 randomisations). (Blue = AF, red = UGF). C-D, Comparison of the number of spider species in 233 (AF) and 311 (UGF) pitfall trap periods (two weeks) on nature reserve

Alter Flugplatz (AF) and urban grassland fragments (UGF) in Karlsruhe, Germany (C = all species; W = 42198, p = < 0.001, D = species of cc; W= 56840, p = < 0.001).

Influences of distance to AF and fragment area on diversity and similarity

The distance to AF had no significant effect on the total species number (z = 0.0904, p = 0.365) and the number of species of cc (z = 1.64, p = 0. 094) (Fig. 4A, B). Similarly, the dissimilarity of UGF to AF was not significantly influenced by distance to AF (z = -1.071, p = 0.284) (Fig. 4C). The species composition of larger UGF (Fig. 4D) were also not significantly more similar to AF than those from smaller UGF (Kruskall-Wallis chi-squared = 18.537, p = 0.61). Overall, dissimilarity varied for the most plots between 0.75 and 0.85.

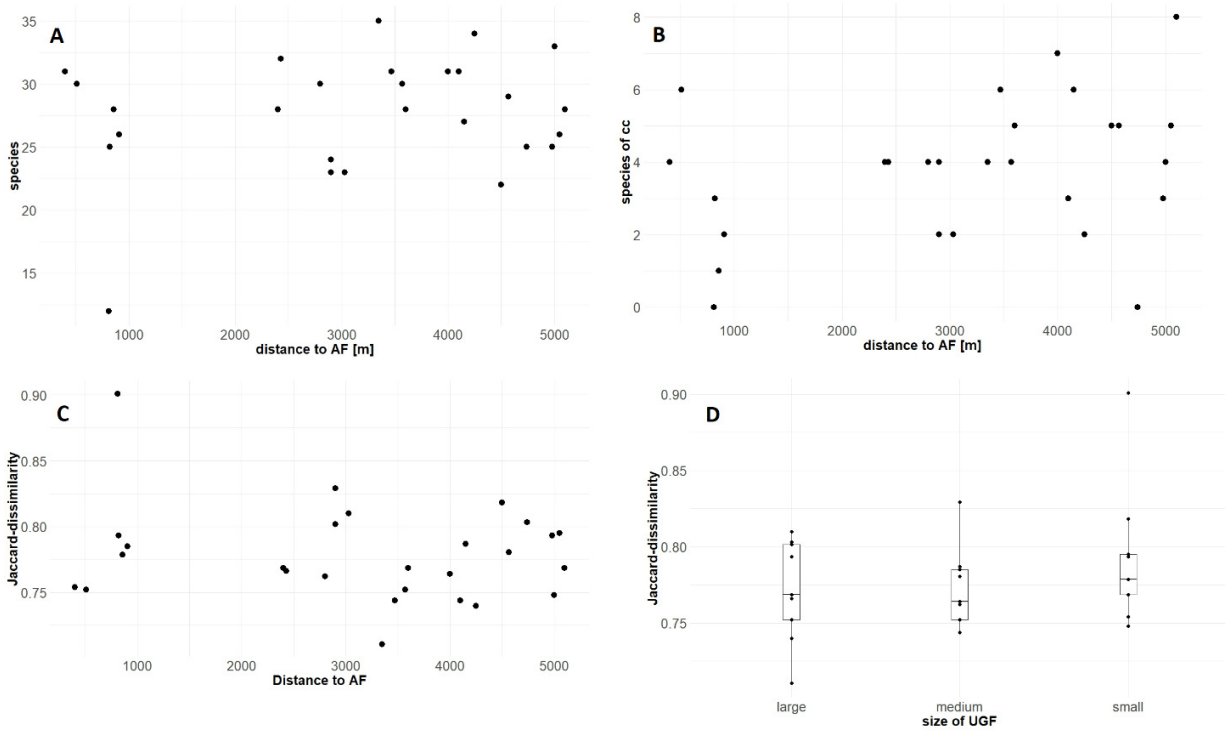

Figure 4: Distance and dissimilarity-analyses of UGF to AF. **A:** Relationship between distance to AF and species number of UGF (z = 0.0904, p = 0.365). **B:** Relationship between distance to AF and number of species of cc in UGF (z = 1.64, p = 0. 094). **C**: Jaccard-dissimilarity of UGF in relation to area to UF (z = 1.071, p = 0.284); **B:** Jaccard**-**dissimilarity of large, medium and small UGF to AF (n= 9 per category) (Kruskall-Wallis-test, chi-squared = 18.537, p = 0.61).

Species accumulation rate over area on UGF

When all UGF were sorted by area (starting with the smallest fragment, Fig. 5) and the addition of new species per plot is visualized, 80 species were already present in the first 17 UGF. The largest ten plots only added two further species. When species of cc were accumulated, 16 out of 17 species were present in the first 17 UGF, the largest ten UGF only added one further species of cc.

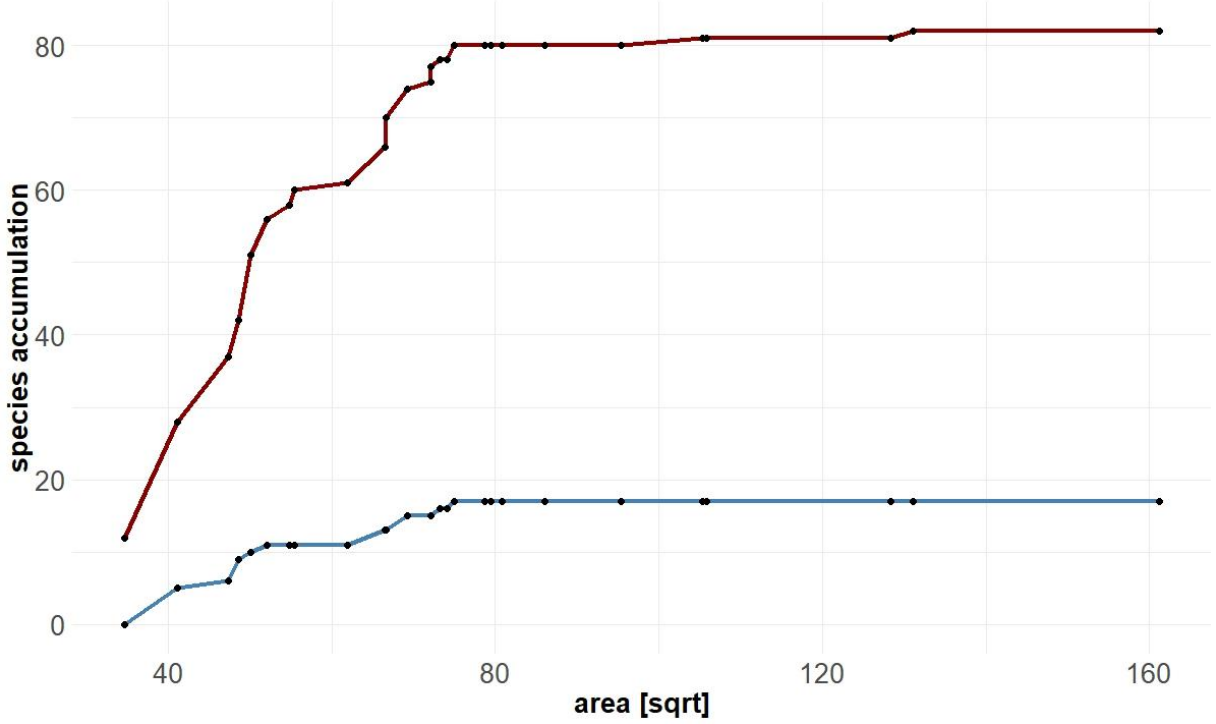

Figure 5: species accumulation from smallest to largest UGF (red line = all species, blue line = species of cc). area = [sqrt] m^2

Sampling frequency of species recorded at AF and UGF

species exclusively sampled from AF showed highly significant differences concerning their national grid record number ($W = 896.5$, $p = <0.0001$) (Fig. 6A). Species of cc exclusively sampled from AF were also known from significantly less grid records in Germany than species of cc (re)sampled from UGF ($w = 115$, $p = 0.0192$) (Fig. 6B). This points towards a trend of generally increased rareness and a higher average conservation value of species that were only present on AF, while species sampled from UGF tend to be more common and widespread.
The rediscovery rate (number of records in all 27 UGF localities) of species (Fig. 6C) was significantly related to the number of grid cell records in Germany ($Est = 0.02$, $\sigma = 0.009$, $z = 2.344$, $p = 0.019$), demonstrating that species which are rarely recorded in Germany tend to be only sampled in a small number of UGF in Karlsruhe, while commonly sampled species are present in a higher number of plots.

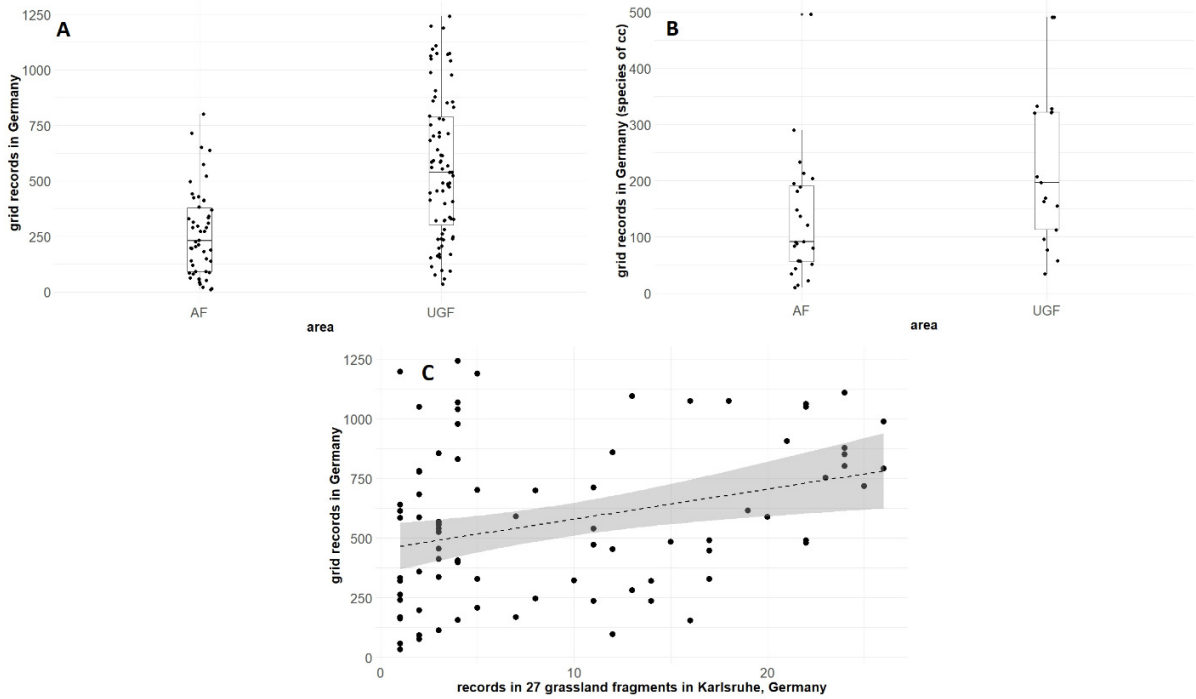

Figure 6: Comparison of grid cell records (Arages.atlas.de) in Germany of spider species exclusive to the nature reserve "Alter Flugplatz (AF) and (re)sampled on urban grassland fragments (UGF) in Karlsruhe. **A:** all species (W = 896.5, p = <0.0001); **B:** species of cc (w = 115, p = 0.0192). C: relation of records of rediscovered species in all 27 UGF to national grid cell record number. Single data points slightly spread for better visibility. (Est = 0.02, σ = 0.009, z = 2.344, p = 0.019). Grey area = Confidence interval (95%)

Differences in humidity preferences and size composition

On average, spider species sampled exclusively from AF did not show significantly different humidity preferences compared to those from UGF, although a clear trend towards drier niches in AF species was visible (W = 2432, p-value = 0.054) (Fig 7A). No significant differences were observed for the humidity preferences of exclusive species of cc when compared to those known from UGP (W = 240.5, p = 0.34; Fig. 7B). However, when large and species-rich cursorial families (Salticidae, Lycosidae, Gnaphosidae, Thomisidae) were considered together (Fig. 7C), a group where niche differences in individual species along the humidity gradient are particularly pronounced, species exclusive to AF showed a significantly greater preference for drier habitats than those (re)sampled from UGF (w = 542.5, p = 0.001) (Fig. 6C).

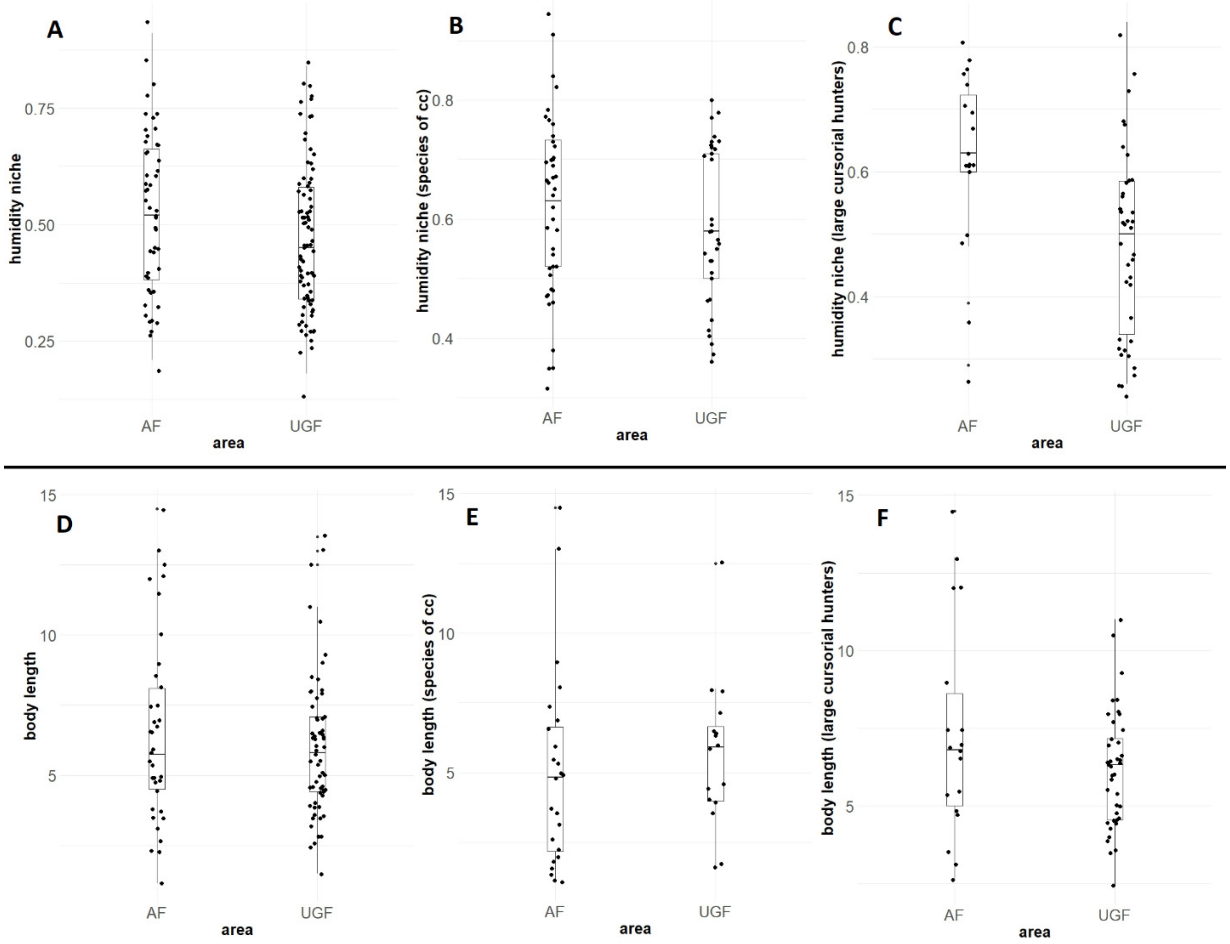

Figure 7: Comparison of the humidity niche (A-C) (Entling *et al.* 2007) and body length in mm (D-F) of spider species exclusive to the nature reserve "Alter Flugplatz") and species (re)sampled from urban grassland plots (UGP) in Karlsruhe, Germany. **A:** all species except Linyphiidae (W = 2432, p-value = 0.054). **B:** species of cc (W = 240.5, p = 0.34). **C:** large cursorial hunters (Salticidae, Gnaphosidae, Lycosidae). w = 542.5, **p = 0.001**. **D:** Species (Linyphiidae excluded) ((W = 1217.5, p-value = 0.6126); **E:** spider species of conservation concern (w = 157.5, p = 0.35); **F:** large cursorial hunters (W = 423.5, p-value = 0.2895). Single data points slightly spread for better visibility.

Body size did not differ significantly between spider species (excluding Linyphiidae) exclusive to AF and species sampled from UGF (W = 1217.5, p-value = 0.6126) (Fig. 7D). When only the size of all species of cc (Fig. 6E) exclusive to cc and sampled from UGF are considered, result remain insignificant (w = 157.5, p = 0.35). however, species of cc exclusive to AF show a much variance in comparison (12.47 vs. 7.05), pointing towards an increased presence of large and very small species of cc on AF. No differences were found in the body size of large cursorial hunters (Fig. 7F) as well (W = 423.5, p-value = 0.2895).

Correlations between overall sampling frequency and body length and humidity preferences

Overall German grid record frequencies of species recorded from AF show a negative correlation with the humidity values given in Entling *et al.* (2007) ($r^2 = 0.22$, $p = < 0.001$) (i.e. species with low humidity preferences have less grid records in Germany), demonstrating that the trend in the shift of the humidity niche of species exclusively collected on AF is likely related to the accumulated presence of common species sampled in UGF. Correlations between sampling frequency and body length were insignificant ($r^2 = 0.001$, $p=0.68$)

Discussion

Species composition

In line with hypothesis 1 and 2, species richness was higher at AF, in direct comparison of pitfall trapping results as well as overall species counts recorded from the areas, and spider assemblages of UGF were mainly subsets of species already known from the large nature reserve, with over 50% of all UGF plots containing no exclusive species. However, nearly 60% of all species present on AF and 13 out of 37 (35%) species of cc were recovered from the 27 comparatively small UGF within the city, including 10 species never before collected on AF. The total area of all sampled UGF comprised approximately ¼ of AF. Although the single patch assemblages lacked distinctness compared with the species known from AF and only a fraction of species of cc is recovered (cf. hypothesis 2; Bauer *et al.* 2024), the results concerning the summarized diversity of all UGF can still be considered surprising. All grassland fragments are unprotected public urban greenspaces managed in two different intensities. Nonetheless, among others variations in soil humidity (Bauer *et al.* 2024) UGF seem to have facilitated the presence of some species (of cc) outside of the protected area (Fig. 2C). 5 out of 10 species exclusive to UGF, such as *Arctosa leopardus* or *Piratula hygrophila*, are common species of humid habitats (Hänggi *et al.* 1995), and were found on mesic or humid UGF (Bauer *et al.* 2024). Although several of such species were also present at AF, e.g. *Drassyllus lutetianus* or *Pardosa amentata* (Roberts 1995), it seems AF did, despite its size and immense variation in habitat, not exhibit enough niches for some species with higher humidity preferences. Another 4 exclusive species of UGF were of cc, among them *Atypus piceus*, a member of the only genus of mygalomorph spiders in Germany and therefore of high phylogenetic conservation value in the city area. The absence of *A. piceus* from AF is best explained by its geology. AF consists mainly of loose, sandy and highly decalcified soils, while the species usually inhabits agglutinate calcareous soils (Řezáč *et al.* 2007). The only record of *A. piceus* in UGF was sampled on grassland next to the railroad line, for which soil exchange and fixation was necessary during construction, which probably lead to more favorable conditions for *A. piceus*. A small colony was found in 2020 approximately 70 m away from the sampled transect on the same UGF (Bauer, pers. observ.). This is a striking example on how species of cc might be naturally excluded from a nature reserve by their ecological preferences, but can be present in nearby unprotected and disturbed habitats. Then again, UGF lacked nearly all “classic” endangered

red list species of xerothermic grassland in the endangerment categories 1, 2 and 3 that have been collected from AF (Bauer *et al.* 2024, Nährig *et al.* 2003, Hemm *et al.* 2012). Typical examples are *Attulus saltator* (Salticidae), *Alopecosa striatipes* (Lycosidae), *Drassyllus villicus* (Gnaphosidae) or *Spiracme striatipes* (Thomisidae). All of these species suffered severe declines in the past due to the loss of xerothermic grassland in Germany (Blick *et al.* 2016). It seems likely that despite the presence of other xerothermic species of cc on UGF, a large amount of similar species in higher endangerment categories were not able to colonize small grassland fragments in the urban matrix from nearby AF, at least in detectable numbers. However, the presence of species of higher endangerment categories in urban grasslands was documented in Buchholz *et al.* (2018) for Berlin. Interestingly, this is mainly due to methodological differences. The coverage between the UGF dataset and that of Buchholz *et al.* (2018) is high, and shares many species (of cc) *(*5 out of 17/13*; Haplodrassus dalmatensis, Argenna subnigra, Drassyllus praeficus* and *Aulonia albimana*). However, Buchholz *et al.* (2018) used the local red list of Berlin (Platen & von Broen 2005), we used Nährig *et al.* (2003), the red list of Baden-Württemberg. This leads to differences in the categorical assessment as the same species are listed in different categories.

Influence of distance and area on diversity and assemblage similarity

Bauer *et al.* (2024) demonstrated that the spider diversity (total species number) of UGF is not influenced by any local or landscape parameter, including management, recorded in their dataset. As AF harboured a species-rich spider community including a large number of rare species, we hypothesized that this stochasticity in species numbers may be caused by AF being a species-source for nearby patches. However, our results show that there was no significant influence of AF on either total species number and recorded species of cc, rejecting this part of hypothesis 3. Moreover, a weak tendency for a positive influence of distance on the amount of recorded spider species of cc became visible. This is most likely caused by the localization of some dry grassland patches (cf. Bauer *et al.* 2024) at the city fringes, farer away from AF than some of the more humid or mesic patches that harboured less species of cc. In addition, neither patch size nor distance to AF influenced the assemblage similarity of UGF, rejecting the second part of hypothesis 3. Several studies (e.g. Buchholz *et al.* 2018, Otoshi *et al.* 2015, Sattler *et al.* 2010a) have shown that spiders react rather weakly to landscape factors in urban areas and assemblages are shaped by local factors (such as management or humidity), which is in line with our results concerning the distance of UGF to AF and the models including factors of the urban matrix in Bauer *et al.* (2024). UGF seem to be inhabited by species assemblages that act rather independently to AF, which does not seem to play a role as permanent species source for these smaller grasslands within the urban matrix. Also, Bauer *et al.* (2024) showed that many species, including species of cc, occurred in high numbers in UGF during mating season (e.g. early summer), which further supports the hypothesis that UGF did not depend on AF as a constant species donor.

Species accumulation curves

Recorded species of UGF accumulated very fast and 80 out of 82 species were present in the 17 smallest UGF. The results from the largest 10 UGF only added 2 further species. The rate of accumulation was very similar for species of cc, with 16 out of 17 species present in the 17 smallest UGF. In addition, rarer species were mostly present in only a few plots, while common species tended to be present in the majority of plots. It seems that despite their varying area with plots of

considerable size (e.g. the largest with 26 000 m^2), the relatively high diversity of spiders in UGF is, on the other hand, constrained on the upper end by other factors than only patch size (rejecting hypothesis 4). Large UGF patches seem not to facilitate a greater number of exclusive, area-sensitive species that are not present in smaller patches. In direct comparison of pitfall trapping results, AF accumulated species very quickly and on a higher rate than UGF, despite a lower amount of pitfall trapping periods in the analysis. While the accumulation curve of UGF considerably flattened after 200 periods, the AF curves were not saturated. Accumulation results for species of cc were similar. This might be related to the function of the urban matrix as a filter for some organisms, especially specialized species and certain functional groups (Buchholz *et al.* 2020, Gathof *et al.* 2022, Piquet *et al.* 2024). In addition, All UGF were at least mown completely once per year during this time, without exception. In contrast, the AF experienced a very different management regime, ranging from extensively mowed over grazed to benignly neglected parts. Hemm & Höfer (2012) have shown that factors related to vegetation structure, and ultimately management, are responsible for the composition of rich and distinct spider assemblages at grazed, mowed and ruderalized sites of AF. Buchholz *et al.* (2018) showed that irregular managed and extensively mown urban grasslands in Berlin strongly differ in their assemblage composition. Based on this, it seems likely that the rather uniform mowing of UGF in combination with other, unknown factors present in the urban matrix are responsible for the quickly saturated number of species present in UGF, with patch size being only one of them. In addition, all UGF in Karlsruhe are relatively well connected due to the high amount of green spaces present in the city (over 40 % of the city area) and in all cases UGF were not completely isolated by impervious surfaces, but bordered forest structures, other greenspaces or gardens. This probably helped in species exchange between larger and smaller fragments and might further mask the potential impact of small patch size on species abundance (but cf. Bauer *et al.* 2024 for results of patch size on spider abundance).

National sampling frequency of species recorded at AF and UGP

Following the IUCN, a protected area is a “clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services (ESs) and cultural values” (IUCN)”. However, in general, the effectiveness of protected areas for biodiversity conservation in Germany is difficult to assess as many species also occur in nearby areas of the cultural landscape (Pflüger *et al.* 2024) and data for arthropods occurring in protected areas, especially spiders, are relatively scarce (Arachnologische Gesellschaft 2024). Our approach aimed at comparing a large protected grassland area of potentially high value for rare species with several small, isolated and disturbed grassland fragments. We demonstrate that not only several species of cc were not found in our extensive survey of UGF, but also that the species exclusive to AF are less frequently recorded in Germany on average, independent of their red list status. These results are in accordance with hypothesis 5, impressively demonstrate the high value of AF as a refugia for rare species (several of them of cc) and represent a direct indicator for the effectiveness of AF for species conservation (Chape *et al.* 2005), at least for the focal group. Additionally, the assemblage sampled from UGF contains mostly species that are widespread in Germany, with the majority (63 out of 82) having 250 grid records or more (Arachnologische Gesellschaft 2024). Such frequently sampled, usually wide-niched species are among the 300 most commonly found spider species in Germany (out of around 1000 established species) (Arachnologische Gesellschaft 2024). A high abundance of

common, opportunistic generalists with relatively low habitat specialization is typical and well-known for urban landscapes with its various stress factors such as fragmentation, disturbance and nutrient pollution (Kowarik 2011, Piquet *et al.* 2024, Werner 2011). Despite this, rare species were not completely absent from the assemblage of UGF, with 12 species having under 200 grid records in Germany, which are considered rare or having a locally limited distribution. This includes all four species of cc exclusive to UGF (Nährig *et al.* 2003) and demonstrates that rare species may not be absent from small and disturbed habitat fragments in urbanized landscapes, which are often overlooked in nature conservation. Moreover, spider species of cc may be absent from nature reserves, but present in nearby, non-protected habitats.

Differences in humidity preferences and size composition

The humidity differences between all species exclusive to AF and those sampled from UGF show a trend towards species with lower humidity preferences in AF and is in accordance with this part of hypothesis 6. This trend increases to highly significant values when only large cursorial spider families are taken into account and decreases into insignificance when species of cc are compared. This shows that the presence of a species in UGF in comparison with the known species of UGF is not a stochastic event and linked to the species' habitat preferences. The sandy grassland of AF is extremely dry and nutrient-poor and, in addition, very little disturbed. This is in stark contrast to UGF plots, where especially dry grasslands with low vegetation are frequently trampled or used for dog walking as well as mown completely once per year, while AF is managed by mowing, grazing and also benign neglect of fringe areas (Hemm & Höfer 2012). Specialists of sandy areas are also known for a low propensity for aerial dispersal (Ballooning) (Bell *et al.* 2005, Bonte *et al.* 2003), which might reinforce their absence from UGF as local extinction events are not compensated as quickly as in euryotopic species. As the number of national grid records of species from AF are negatively correlated to the humidity values in Entling *et al.* (2007) (see results), it seems that the higher humidity preferences of species from AF are linked to the results of sampling frequency, i.e. the majority of species sampled in UGF are common and widespread, relatively wide-niched and stress-tolerant generalists with intermediate humidity presences. However, we discovered no differences in the humidity preferences of species of cc between exclusive species of AF and those sampled from UGF. Not all species of cc recorded in both assemblages are narrow-niched xerothermic species according to Entling *et al.* (2007) (e.g. *Argenna subnigra, Thanatus striatus* or *Xysticus acerbus*), but also occur in other more humid settings, e.g. heath or open bogs (Arachnologische Gesellschaft 2024, Hänggi *et al.* 1995). Their occurrence on AF is rather linked to the larger area, management and vegetation structure of the reserve instead of its mainly xerothermic conditions. In addition, not only AF, but also UGF contained typical xerothermic species of cc with low humidity preferences, e.g. *Trichopterna cito* or *Zelotes electus.* This explains why no differences in this group were found.

Merckx *et al.* (2018) demonstrated that increasing urbanization shifts the body length of spider communities towards smaller species, both epigeic and web-building. Despite the absence of certain large and very small species on UGF, no clear differences in body size composition were found, in contrast to our assumption in hypothesis 6. However, we found a much greater variation in body size of species of cc exclusively present on AF in comparison with those from UGF. Very small and very large species of cc were nearly exclusively present on AF, while on UGF species of cc were mostly of medium size between 4 and 8 mm. The accumulated absence of small,

thermophile linyphiid species of cc from UGF such as *Typhochrestus digitatus* or *Tapinocyba praecox* might be related to local competition with very high numbers of medium-sized euryotopic and disturbance-tolerant spider species, such as the wolf spider *Pardosa palustris*, present on nearly every UGF (cf. sampling results in Bauer *et al.* 2024 and Hemm *et al.* 2012), heterogenic climatic conditions due to local disturbance or sensitivity towards latter. The absence of certain large species of cc (e.g. *Alopecosa striatipes, Trochosa robusta* or *Alopecosa farinosa*), despite the presence of medium sized species of cc with similar climatic preferences (e.g. *Xerolycosa miniata* or *Zelotes electus*), is best explained by the small patch size of most UGF. Many sandy grassland specialists in general are very sensitive towards decreasing patch sizes even in rural landscapes, as demonstrated by a 9-year study in Hungary (Horváth *et al.* 2013), and in combination with the surrounding urbanization (cf. Merckx *et al.* 2018) and the general increased disturbance in urban areas (e.g. trampling, dog walking, mowing), large sandy grassland specialists such as *A. striatipes* seem not to be able to cope with the conditions on UGF in Karlsruhe.

Conclusion

Our results demonstrate that urban grassland fragments in Karlsruhe (UGF) harbour a considerable diversity of grassland spiders, however, they do not compensate for the loss of large, well-preserved habitat patches such as the nature reserve Alter Flugplatz (AF), which harbour significantly more species. In addition to total patch area, we assume that a lack of diversity in vegetation structure and other, unknown factors constrain the total number of spider species in UGF compared to AF, as patch size did not significantly influence the similarity of patches to AF or their diversity, nor did larger patches add a substantial amount of species not already present in much smaller patches.

A large fraction of species, especially specialists of very dry grassland, were only found in AF despite the presence of sandy grassland plots in the setting of UGF. On the other hand, a fraction of mostly medium sized species of cc was able to colonize urban grasslands and persisted outside the protected area. Species exclusive to AF were less frequently recorded in Germany on average and exhibited lower humidity preferences. This suggests that patch size, management and surrounding urbanization act as a filter for rare species with distinct xerothermic preferences and, on the other hand, favour generalists, which were found in higher frequencies in UGF than rare species. Still, 10 species were only found outside the reserve, including 4 species of cc. Differences in average body size were not detected, however, several very large and very small species of cc remained restricted to AF. Effective conservation of spider species of cc in urban areas therefore depends on a combination of large, well-preserved patches (e.g. nature reserves) and a high number of small, well-connected patches in the surrounding area (cf. Rösch *et al.* 2015), in the best case with biodiversity-friendly, diversified mowing regimes and benign, limited neglect of some parts to increase vegetation complexity and spider diversity.

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References

Arachnologische Gesellschaft (2024) Atlas der Spinnentiere Europas. Retrieved from https://atlas.arages.de (12.12.2024)

Aronson, M. F., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., *et al.* (2017) Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15: 189-196

Bach, A., Jedamski, J., Daniels, B., & Roß-Nickoll, M. (2025) From lawns to meadows: spiders (Arachnida: Araneae) as indicators to measure urban grassland restoration success. Urban Ecosystems 28: 1-14

Bauer, T., Höfer, H., & Schirmel, J. (2024) Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes. Insect Conservation and Diversity, 17(5), 811-825

Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bulletin of entomological research 95: 69-114

Beninde, J., Veith, M., & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecology letters 18: 581-592

Blick, T., Finch, O.-D., Harms, K. H., Kiechle, J., Kielhorn, K.-H., Kreuels, M., Malten, A., *et al.* (2016) Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae) Deutschlands. 3. Fassung, Stand April 2008, einzelne Änderungen und Nachträge bis August 2015. Naturschutz und Biologische Vielfalt 70: 383-510

Blick, T., Pfiffner, L., & Luka, H. (2000) Epigäische Spinnen auf Äckern der Nordwest-Schweiz im mitteleuropäischen Vergleich (Arachnida: Araneae). Mitteilungen der Deutsche Gesellschaft allgemeine angewandte Entomologie, 12 267-276

Brenneisen, S., & Hänggi, A. (2006) Begrünte Dächer–ökofaunistische Charakterisierung eines neuen Habitattyps in Siedlungsgebieten anhand eines Vergleichs der Spinnenfauna von Dachbegrünungen mit naturschutzrelevanten Bahnarealen in Basel (Schweiz). Mitteilungen der Naturforschenden Gesellschaften beider Basel 9: 99-12.

Bonte, D., Vandenbroecke, N., Lens, L., & Maelfait, J. P. (2003) Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. Proceedings of the Royal Society of London. Series B: Biological Sciences, 270: 1601-1607

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9: 378–400

Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018) Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. Urban Ecosystems, 21: 1139-1149

Buchholz, S., Gathof, A. K., Grossmann, A. J., Kowarik, I., & Fischer, L. K. (2020) Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. Landscape and Urban Planning 196: 103731

Chape, S., Harrison, J., Spalding, M., & Lysenko, I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society B: Biological Sciences 360: 443-455

Entling, W., Schmidt, M. H., Bacher, S., Brandl, R., & Nentwig, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Global ecology and biogeography 16: 440-448

Fahrig, L. (2020) Why do several small patches hold more species than few large patches? Global ecology and biogeography, 29: 615-628

Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. Global Ecology and Biogeography 29: 1412-1429

Fox J, Weisberg S (2019) An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. https://www.john-fox.ca/Companion/

Dorow, W. H., Blick, T., Pauls, S. U., & Schneider, A. (2019) Waldbindung ausgewählter Tiergruppen Deutschlands. BfN-Skripten 544: 1-388

Gathof, A. K., Grossmann, A. J., Herrmann, J., & Buchholz, S. (2022) Who can pass the urban filter? A multi-taxon approach to disentangle pollinator trait–environmental relationships. Oecologia 199: 165-179

Hänggi, A., Stöckli, E. & Nentwig, W. (1995) Lebensräume mitteleuropäischer Spinnen: Charakterisierung der Lebensräume der häufigsten Spinnenarten Mitteleuropas und der mit diesen vergesellschafteten Arten. Miscellanea Faunistica Helvetiae 4: 1–459

Hemm, V., & Höfer, H. (2012) Effects of grazing and habitat structure on the epigeic spider fauna in an open xerothermic area in southern Germany. Arachnology 15: 260-268

Hemm, V., Meyer, F., & Höfer, H. (2012) Die epigäische Spinnenfauna (Arachnida, Araneae) in Sandrasen, Borstgrasrasen und Ruderalfluren im Naturschutzgebiet „Alter Flugplatz Karlsruhe “. Arachnologische Mitteilungen 44: 20-40

Horváth, R., Magura, T., Szinetár, C., Eichardt, J., & Tóthmérész, B. (2013) Large and least isolated fragments preserve habitat specialist spiders best in dry sandy grasslands in Hungary. Biodiversity and conservation 22: 2139-2150

Jaccard, P. (1902) Distribution comparée de la flore alpine dans quelques régions des Alpes occidentales et orientales. Bulletin de la Murithienne 31: 81-92

Kadas, G. (2006) Rare invertebrates colonizing green roofs in London. Urban habitats 4: 66-86

Kielhorn, K-H. (2024) Spinnen und Weberknechte auf Bahnbrachen im Stadtgebiet von Erfurt (Arachnida: Araneae, Opiliones). Thüringer Faunistische Abhandlungen 28: 275–297

Knapp, S., Kühn, I., Mosbrugger, V., & Klotz, S. (2008) Do protected areas in urban and rural landscapes differ in species diversity? Biodiversity and conservation 17: 1595-1612

Kowarik, I. (2011) Novel urban ecosystems, biodiversity, and conservation. Environmental pollution, 159: 1974-1983

Kühn, I., & Klotz, S. (2006) Urbanization and homogenization–comparing the floras of urban and rural areas in Germany. Biological conservation 127: 292-300

Kühn, I., Brandl, R., & Klotz, S. (2004) The flora of German cities is naturally species rich. Evolutionary ecology research 6: 749-764

Lane, A., & Burgin, S. (2008) Comparison of frog assemblages between urban and non-urban habitats in the upper Blue Mountains of Australia. Freshwater Biology, 53: 2484-2493

Leveau, L. M. (2013) Bird traits in urban–rural gradients: how many functional groups are there?. Journal of Ornithology 154: 655-662

Lokatis, S., & Jeschke, J. M. (2022) Urban biotic homogenization: Approaches and knowledge gaps. Ecological Applications 32: e2703

Melo, M. A., Sanches, P. M., Silva Filho, D. F., & Piratelli, A. J. (2022) Influence of habitat type and distance from source area on bird taxonomic and functional diversity in a Neotropical megacity. Urban Ecosystems 25: 545-560

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., *et al.* (2018) Body-size shifts in aquatic and terrestrial urban communities. Nature 558: 113-116

Möller, M., Blick, T., & Buchholz, S. (2019) Spinnen der Trockenrasen in und um Berlin–Vielfalt, Verbreitung und Gefährdung. Arachnologische Mitteilungen: Arachnology Letters 58: 52-61

Nährig, D., Kiechle, J. & Harms, K.H. (2003) Rote Liste der Webspinnen (Araneae) Baden-Württembergs. Karlsruhe (Landesanstalt für Umweltschutz Baden-Württemberg). Fachdienst Naturschutz. Naturschutz-Praxis: Artenschutz 7: 7–162

Nentwig W, Blick T, Bosmans R, Hänggi A, Kropf C, Stäubli A (2025) Spinnen Europas. Version 12.2024. retrieved from www.araneae.nmbe.ch (01.12.2024)

Nielsen, A. B., Van Den Bosch, M., Maruthaveeran, S., & van den Bosch, C. K. (2014) Species richness in urban parks and its drivers: A review of empirical evidence. Urban ecosystems 17: 305-327

Norton, B. A., Evans, K. L., & Warren, P. H. (2016) Urban biodiversity and landscape ecology: patterns, processes and planning. Current Landscape Ecology Reports 1: 178-192

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., et al. (2013) Package 'vegan'. Community ecology package, version 2: 1-295.

Otoshi, M. D., Bichier, P., & Philpott, S. M. (2015) Local and landscape correlates of spider activity density and species richness in urban gardens. Environmental Entomology 44: 1043-1051

Pflüger, F. J., Frank, C., Busch, M., Wahl, J., Dröschmeister, R., Sudfeldt, C., & Kamp, J. (2024) Semi-structured citizen science data reveal mixed effectiveness of EU Special Protection Areas (SPA) in Germany. Biological Conservation 299: 110801

Piano, E., Giuliano, D., & Isaia, M. (2020) Islands in cities: Urbanization and fragmentation drive taxonomic and functional variation in ground arthropods. Basic and Applied Ecology 43: 86-98

Piquet, A., Piano, E., Tolve, M., & Isaia, M. (2024) City as a filter: urban density affects taxonomic and functional diversity of foliage dwelling spiders. Landscape Ecology 40: 3

Platen, R., & von Broen, B. (2005) Gesamtartenliste und Rote Liste der Webspinnen und Weberknechte (Arachnida: Araneae, Opiliones) des Landes Berlin. Der Landesbeauftragte für Naturschutz und Landschaftspflege/Senatsverwaltung für Stadtentwicklung (Hrsg.) Rote Listen der gefährdeten Pflanzen und Tiere von Berlin.

R Core Team (2022) R: A Language and Environment for Statistical Computing (Version 4.2.0). Vienna.

Řezáč, M., Řezáčová, V., & Pekár, S. (2007) The distribution of purse-web Atypus spiders (Araneae: Mygalomorphae) in central Europe is constrained by microclimatic continentality and soil compactness. Journal of Biogeography 34: 1016-1027

Roberts, M. J. (1995) Collins Field Guide: Spiders of Britain & Northern Europe. HarperCollins London, 383 pp.

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia 179: 209-222

Rosenzweig, M. L. (1995) Species diversity in space and time. Cambridge University Press

Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. K., & Moretti, M. (2010a) Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology 91: 3343-3353

Sattler, T., Duelli, P., Obrist, M. K., Arlettaz, R., & Moretti, M. (2010b) Response of arthropod species richness and functional groups to urban habitat structure and management. Landscape ecology 25: 941-954

Van Keer, K., Vanuytven, H., De Koninck, H., & Van Keer, J. (2010) More than one third of the Belgian spider fauna (Araneae) found within the city of Antwerp: faunistics and some reflections on urban ecology. Nieuwsbrief van de Belgische Arachnologische Vereniging 25:160-180

Venables, W.N. & Ripley, B.D. (2002) Modern Applied Statistics with S, Fourth edition. Springer, New York

Werner, P. (2011) The ecology of urban areas and their functions for species diversity. Landscape and Ecological Engineering 7: 231-240

Zimmermann, P. (2011) Der „Alte Flugplatz Karlsruhe “: ein neues Naturschutzgebiet. Carolinea 69: 139-163

Chapter IV

Urbanization increases fluctuating asymmetry and affects behavioral traits of a common grasshopper

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Urbanization increases fluctuating asymmetry and affects behavioral traits of a common grasshopper

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Abstract

Urbanization has a major impact on biodiversity. For many organisms, the urbanization process means environmental stress caused by fragmentation and increased temperatures in cities and atmospheric, soil, light, and noise pollution. Such environmental stress can influence both the morphology and behavior of animals. Hence, individuals might be selected for survival-facilitating traits under high pressures in urban areas. The specific impact of urbanization on insect behavior is still largely unexplored. We studied the impact of urbanization on one of the most common grasshopper species in Germany, *Chorthippus biguttulus*, by comparing morphological and behavioral traits of individuals sampled from grasslands with low, medium, and high urbanization levels. We first investigated whether urbanization as a stressor affected body size and fluctuating asymmetry in the locomotor organs. Next, we examined whether urbanization induced changes in the individuals' boldness and activity. Our results showed that fluctuating asymmetry of grasshoppers' locomotory organs increased more than twofold with urbanization level. Further, individuals' boldness and walking activity increased from areas with low to high urbanization levels. Our results indicate strong responses of grasshoppers in terms of morphology and behavior to the urban environment. To compensate for urbanization effects on arthropod populations, management strategies need to be developed that maintain ecological processes and reduce environmental stress in urban areas.

KEYWORDS
activity, behavior, boldness, *Chorthippus biguttulus*, environmental stress, Orthoptera

TAXONOMY CLASSIFICATION
Urban ecology

1 | INTRODUCTION

Urbanization is a globally increasing phenomenon (Gaston, 2010) and one of the significant causes of land use change worldwide (Grimm et al., 2000). The accompanying increase in sealed impervious surfaces strongly alters local ecosystem conditions and material flows (Alberti, 2005; Hasan et al., 2020; Hutyra et al., 2014; McKinney, 2002; Tannier et al., 2016). A major concern related to urbanization are changes in biodiversity due to alterations in habitat connectivity (Beninde et al., 2015). Urbanization has been shown to

negatively affect species richness and abundance for aquatic, limnoterrestrial, and terrestrial invertebrates (Fattorini, 2011; Fenoglio et al., 2020; Piano et al., 2019; Schirmel, 2021) and is thus regarded as one of the greatest threats to global biodiversity (Seto et al., 2012). Besides its negative effects on many taxa, urbanization exposes species to environmental stress through environmental changes such as increased temperatures (urban heat island effect = heat accumulation in urban areas due to urban constructions), atmospheric and soil pollution, anthropogenic noise, and light pollution (Grimm et al., 2008). Conversely, urban areas can also contribute to the conservation of biodiversity and provide important habitats for birds of prey (Boal & Dykstra, 2018), insect pollinators (Derby Lewis et al., 2019; Hall et al., 2017), and arthropods (Buchholz et al., 2018).

Environmental stress can affect organisms in various ways, which include altered predation pressure, novel species interactions, and changes in food resource availability (Lowry et al., 2013). Moreover, environmental stress can increase phenotypic and genotypic variability of organisms (Hoffman & Parsons, 1991; Holloway et al., 1990; Pimpinelli & Piacentini, 2019). A widespread characteristic of this is the development of fluctuating asymmetry of bilateral traits. Fluctuating asymmetry is a measure of developmental stability, and the level of expression can be used as an indicator for different types of environmental stress (Clarke, 1995; Parsons, 1992). Fluctuating asymmetry has also been used in relation to urbanization for different animal groups such as mammals or insects (Beasley et al., 2013; Coda et al., 2017).

Further, environmental stress can induce intraspecific differences in physiological, ecological, and behavioral traits (Gunn et al., 2021; Gutiérrez et al., 2020; Kassahn et al., 2009; Koolhaas et al., 2011; Scherber et al., 2013). Thus, individuals from urban habitats may be characterized by physiological or behavioral traits that distinguish them from individuals inhabiting rural habitats. For example, individuals in anthropogenically modified environments are often flexible in behavior (phenotypic plasticity) (Lapiedra et al., 2016; Miranda et al., 2013) or show more bold and risk-taking behavior toward enemies (Lowry et al., 2013; Schuett et al., 2010). Stress-related behavior patterns prove to be good indicators of individual variation in behavior because they are applicable across species (Dingemanse et al., 2010). For example, individual differences in behavior can be very important in explaining variation in survival (Moiron et al., 2019). Typical behavioral patterns studied in animals include boldness and activity (Réale et al., 2007). Boldness describes an individual's response to a risky situation in a non-novel environment, including reaction to predators and humans. Activity describes the general activity of an individual (Réale et al., 2007).

Selection may affect both sexes differently and can therefore cause sex-specific differences in traits (Slatkin, 1984). Growing literature indicates that females and males differ in the mean levels of behavioral expression (Schuett et al., 2010) and repeatability of behavioral traits (Bell et al., 2009). Although a meta-analysis has already shown that personality and traits are not sex-dependent in most of the animals (Harrison et al., 2021), there may be sex-specific differences with respect to certain traits in some species (e.g., sex-specific dispersal, Han & Dingemanse, 2017; Li & Kokko, 2019; Trochet et al., 2016; exploration and aggression, Kralj-Fišer et al., 2019, 2021; activity and risk-taking behavior, Mezőfi et al., 2022), leading to the evolution of sex-specific genetic architecture behind such traits (Lande, 1980). In addition, responses to environmental stress may be sex-dependent. For example, males and females of the butterfly *Melitaea cinxia* responded differently to larval food stress and warm-night temperatures (Rosa & Saastamoinen, 2017, 2021) and the nonbiting midge *Chironomus riparius* showed sex-specific responses to pesticide exposition (Roodt et al., 2022).

Behavioral differences between rural and urban individuals of a species are widespread across bird species, underscoring a substantial ecological influence of urbanization on animal behavior (Miranda et al., 2013). Urbanization has also been shown to be a stress to insects, including grasshoppers. For instance, urban individuals of the grasshopper *Chorthippus brunneus* showed higher levels of mobility-related morphology traits than those from the rural populations (San Martin y Gomez & Van Dyck, 2011). However, the empirical evidence of the impact of urbanization on insect morphological and behavioral traits is still very limited (Diamond et al., 2015).

Here, we studied the impact of urbanization on morphological (fluctuating asymmetries and length of the femora and tegmina) and behavioral traits (boldness, activity) of one of the most common European grasshopper species, *Chorthippus biguttulus*. We sampled individuals in the field from grassland sites differing in their urbanization levels (low, medium, and high) and investigated fluctuating asymmetry of the forewings and the femora, boldness, and activity patterns. We hypothesized that (i) urbanization increases the expression of fluctuating asymmetry in locomotor organs of *C. biguttulus* and that individuals inhabiting more built-up areas are (ii) bolder and (iii) more active than counterparts from the less urbanized areas. We further investigated whether the effect of urbanization on traits was sex-dependent.

2 | MATERIALS AND METHODS

2.1 | Study species and sampling sites

Chorthippus biguttulus is one of the most common grasshoppers in Central Europe (Bellmann et al., 2019). In Germany, *C. biguttulus* is widely distributed in various grassland habitats with a preference for dry-warm conditions and sandy substrates (Detzel, 1998). The species is herbivorous and feeds on leaves of different plant families (Zahid et al., 2017).

Grasshoppers were collected from 15 sites in the greater Karlsruhe area (Baden-Wuerttemberg, Germany; Appendix S1). The sites consisted of extensively managed meadows in urban green spaces that serve as suitable habitats for the target species. Sampling sites were selected according to their surrounding urbanization level. For this purpose, a buffer of a 500 m radius was set around each site, and the total amount of buildings, residential and industrial area was determined using digital land-use maps from

OpenStreetMaps (OSM), supplemented with land-use maps of green spaces provided by the greenspace administration of Karlsruhe (Gartenbauamt Karlsruhe) using QGIS Desktop 2.18.3 (QGIS Development Team, 2017). Public parks, graveyards and greenspaces, meadows, cropland, forest- and scrubland, railroads and allotments were not considered as urbanized area.

The sites were then classified into three categories: "low" with a proportion of <10%, "medium" with 30%–50%, and "high" with >60% of urbanization in the 500 m buffer. For each of the categories, five sites were sampled. Sampling with a sweep net was conducted in August 2020 for a total of 6 days during dry weather conditions. When walking the sample sites the sweep net was swung twice per step and examined for individuals of *C. biguttulus*. We aimed to sample 10 individuals per site, and finally, 149 individuals (92 females and 57 males) were collected for the experiments.

2.2 | Rearing of the individuals in the laboratory

After sampling in the field, individuals were individually caged in round microcosms (radius: 5.9 cm, volume: 870 ml) in Landau, Germany. Each animal received an unique encrypted code to make the sample area and its degree of urbanization unrecognizable during the experiments to avoid experimenter bias (Martin & Bateson, 1993). The microcosms contained sand as a soil layer and were stored in a climate-controlled chamber under standard conditions (day = 25°C, night = 20°C, RH = ~65%, L:D = 15:9) to provide optimal living conditions for grasshoppers. The animals were fed fresh grass (Poaceae) every 2 days. To simulate near-natural humidity conditions like dew and precipitation, each microcosm was humidified every 2 days with three sprays of water. Each animal was kept under the conditions described above for at least 24 h before being prepared for the first experiment. Between experimental runs, the caging time was also at least 24 h. After the experiments, the animals were stored in 70% 1,2-propanediol until morphological measurements were taken to determine fluctuating asymmetries.

2.3 | Fluctuating asymmetry

Two different metric parameters were examined and measured for fluctuating asymmetry in the target species. Because paired traits that are as large as possible are needed for the statistical evaluation of fluctuating asymmetry, the length of the forewings (tegmina), and the femora of the jumping legs were measured (Van Dongen et al., 2008). All measurements were made by the same person using a digital electronic caliper (Preciva) with a measurement accuracy of 0.01 mm, under a stereo microscope. The measurements of femora and tegmina were conducted three times and the mean was used to determine the asymmetries. In preparation for the measurements, the hind legs were removed from the body using forceps. Then the femora were separated from the adjacent tibia and coxa. The femora were attached to white cardboard with transparent adhesive tape to avoid slipping of the body parts during the measurement procedure. The most distant points of the outer edge of the upper, larger lobe of the notched base, and the outer edge of the upper of the two genicular lobes at the apex were chosen as measurement points of the femur. In preparation for the measurements of the tegmina, first, the entire wing apparatus under the pronotum was removed. Subsequently, the forewings were separated. For the measurement, the forewings were smoothed with a microscope slide and then attached to white cardboard using transparent adhesive tape. For the measurements of the tegmina, the measurement points were the starting point of the marginal membrane at the base of the forewing and the rounded apex of the forewing.

2.4 | Boldness

In risky situations, such as the appearance of predators or humans, the expression of boldness in grasshoppers can be observed (Niemelä et al., 2011; Nishino & Sakai, 1996). Because birds and other animals often grab grasshoppers, they defend themselves by using tonic immobility and this defensive response to a predator can be interpreted as boldness (Ruxton, 2006). This tonic immobility can be simulated and used to interpret the boldness or risk-taking of individual grasshoppers. Hence, to measure boldness of the animals, the tonic immobility of each individual was quantified. The animal was grabbed by both jumping legs at the tibia and held in the air about 1.50 m above the ground. After an acclimation period of 10 s, the time was stopped within 30 s to see how long the grasshopper remained in a rigid position. The shorter the individual used tonic immobility, the more pronounced its boldness. The experiment was performed three times on each individual (with pauses of 5 min between trials) to evaluate the mean and reduce outlier values and extreme deviations.

2.5 | Activity

For the measurement of activity, an open field test was performed (Appendix S2). This test is generally used to observe the activity and exploration of animals (Réale et al., 2007). The basic assumption in performing the test is that the animals used are exposed to an unknown open area that offers them no possibility of retreat. Thus, the activity of the animals can be observed, which depends on various factors such as fear behavior, readiness to flee, and exploration. For the open field test, a suitable arena was prepared. A transparent Plexiglas foil was cut to size and glued together in a cylindrical shape (diameter: 50 cm). The grasshoppers have a pronounced hiding behavior and seek retreats in danger (Hassenstein & Rustert, 1999). The arena, hence, was designed round in order not to offer the animals shelters in corners that could influence their behavior. The floor of the arena was fitted with white cardboard to provide better video footage for analysis. The arena was covered with a glass plate to prevent the animals from escaping. Outside the arena, a tripod with

a video camera (Panasonic 4 K Ultra HD-Camcorder HC-VXF990; Panasonic Corporation) was set up to record the activity of the animals (Appendix S3). The video camera was placed at a 180° angle to film the entire arena from above. Each animal was filmed for a total of 10 min and 20 s. The recording was started, then the animal was deployed in the center of the arena, and the glass plate was placed on top of the arena as a lid. During the trials, we left the room to reduce the stress factor (Mestre et al., 2020). For the analysis of activity, the first 20 s were discarded so that exactly 10 min of video footage was analyzed for each animal.

To analyze the activity, we used EthoVision XT12 (Noldus Information Technology), which allows the automation of behavioral observations (Noldus et al., 2001). The parameters studied were distance traveled, mobility, and movement. Distance traveled describes the total distance traveled from the center of the marked animal body in 10 min. Mobility describes the percentage of changed pixels of the detected object on average. Mobility is defined as the degree of movement of the animal's body independent of the spatial displacement of the center of the body (Noldus et al., 2001). Therefore, note that an animal may have high mobility and yet, at the same time, a low movement. Measurement of mobility is often used to demonstrate inferences about immobility in fear-related behavior (Pham et al., 2009). Movement determines the periods of time during which the center of the marked body of the animal is in motion or not in motion. The status is characterized by the values "in motion" and "not in motion". In order to measure these values correctly and avoid measurement errors, measurement limits were defined. The status "in motion" is applied from the time when the average speed of the center of the marked body exceeds a defined starting speed. The state "not in motion" occurred as soon as the average velocity of the marked body center fell below a defined stop velocity. The measurement limit selected for the start velocity was 0.1 cm/s and for the stop velocity was 0.05 cm/s.

2.6 | Statistical analysis

In total, 149 (92 females and 57 males) individuals were used for the measurements of fluctuating asymmetry, 132 (83 females and 49 males) individuals were tested for boldness behavior, and 111 individuals (67 females, 44 males) for activity. The number of individuals used for the different experiments decreased because some grasshoppers died over the rearing period.

To test the correlation between fluctuating asymmetries, Spearman-correlation was applied. For all data, linear mixed-effects models were created in R 4.0.5 (R Core Team, 2021) using the command "lmer" from the R package "lme4" (Bates et al., 2015). The urbanization level (factor with three levels: low, medium, and high), grasshoppers' sex (factor with two levels: male and female) and interaction of both (urbanization level × sex) were included in the models as fixed factors. To account for the presence of multiple individuals collected from the same sample plots, plot IDs (factor with 15 levels) were included as random effects in the models. Subsequently, the significance of the explanatory variables was calculated using type-II analysis-of-variance-tables based on Wald Chi^2 tests using the "ANOVA" command from the R package "car" (Fox & Weisberg, 2019).

3 | RESULTS

3.1 | Fluctuating asymmetry

Urbanization had no impact on femur and tegmina length (Table 1). With increasing levels of urbanization, fluctuating asymmetries occurred significantly more frequently in both the tegmina and femora of *Chorthippus biguttulus*. Thereby, individuals showed an increase of 242% for the tegmina and 276% for the femora fluctuating asymmetry from the lowest to the highest urbanization level (Figure 1a,b). The fluctuating asymmetries correlated positively with each other (Spearman-r = .51). Sex and the interaction between urbanization and sex did not significantly affect the fluctuating asymmetry of tegmina and femora (Table 1).

3.2 | Boldness

Boldness of individuals significantly increased with the level of urbanization (Table 1; Figure 2). Individuals from highly urbanized sites showed, on average, a 12% shorter tonic immobility than animals from sites with a low degree of urbanization. Both female and male individuals exhibited a similar level of boldness irrespective of urbanization level (urbanization level × sex; Table 1).

3.3 | Activity

Grasshoppers' mobility and movement significantly increased with urbanization level. Individuals from areas with high urbanization were 30% more mobile and had a longer movement time than counterparts from areas with medium and low urbanization levels (Table 1, Figure 3a,b). Individuals from areas with high, medium, and low levels of urbanization moved similar distances during our experiments (Table 1). Further, both sexes showed similar rates of all activity parameters irrespective of urbanization levels (urbanization level × sex; Table 1).

4 | DISCUSSION

Our results indicate that urban individuals experienced higher environmental stress throughout their development, expressed by the higher levels of asymmetry. As hypothesized, the fluctuating asymmetry in the studied body parts, namely tegmina and femora, of *Chorthippus biguttulus* steadily increased with an increasing degree of urbanization. Both fluctuating asymmetries are strongly

TABLE 1 Results of linear mixed effect models testing the relations of morphological and behavioral traits of *Chorthippus biguttulus* to urbanization, sex, and their interaction (fixed effects).

Trait variable	Explaining variables	χ^2	*p*
Femur length	Urbanization	3.710	.156
	Sex	1411.65	**<.001**
	Urbanization × Sex	0.457	.796
Tegmina length	Urbanization	4.254	.1192
	Sex	886.013	**<.001**
	Urbanization × Sex	1.913	.3842
Fluctuating asymmetry tegmina	Urbanization	38.872	**<.001**
	Sex	3.195	.074
	Urbanization × Sex	4.871	.088
Fluctuating asymmetry femur	Urbanization	34.964	**<.001**
	Sex	0.011	.917
	Urbanization × Sex	0.547	.761
Boldness	Urbanization	13.407	**.001**
	Sex	0.002	.967
	Urbanization × Sex	0.424	.809
Traveled distance	Urbanization	2.940	.223
	Sex	0.807	.369
	Urbanization × Sex	1.105	.576
Mobility	Urbanization	10.079	**.007**
	Sex	0.010	.919
	Urbanization × Sex	0.590	.745
Movement	Urbanization	17.821	**<.001**
	Sex	2.995	.084
	Urbanization × Sex	1.928	.381

Note: To account for the presence of multiple individuals collected from the same sample plots, plot IDs were included as random effects in the models. The significance of the explanatory variables was calculated based on Chi^2 statistics, and significant results ($p < .05$) are shown in bold.

correlated, which indicates that when an individual exhibits fluctuating asymmetry, it occurs in both body parts. Fluctuating asymmetry is a reliable biomarker of environmental stress impacting individuals (Beasley et al., 2013; Leung et al., 2000), which has previously been shown for other stressors besides urbanization, such as, for example, agrochemical pollution (Jentzsch et al., 2003), natural disasters (Gerard et al., 2018), and parasitism (Uetz et al., 2009). However, it is challenging to answer which urban stress factor is crucial in affecting fluctuating asymmetry. Presumable stressors would be artificial light at night, noise pollution, a higher number of stressful encounters with people (and their dogs), increased experience of local drought periods, temperature changes, or chemical pollution (Beasley et al., 2013). The effects of urbanization on *C. biguttulus* can affect the performance of individuals in several ways. Femora have a stronger function than tegmina for the movement pattern of *C. biguttulus* since individuals of this species move more by running and jumping than by flying; moreover, the tegmina only play a minor role in active flying and are more important for song production since the hindwings are the main flying organs in grasshoppers (Detzel, 1998). We observed a slightly less pronounced fluctuating asymmetry with increasing urbanization in the femora than in the tegmina. This supports the assumption that body parts whose symmetry is more important for certain functions are more resistant and less susceptible to fluctuating asymmetry. Body parts that do not strongly influence the individual fitness of the target organism, such as tegmina in *C. biguttulus*, have a lower buffering capacity for fluctuating asymmetry and tend to develop fluctuating asymmetry more strongly (Clarke, 1995; Markow, 1995). Asymmetry in the locomotor extremities (here mainly the femora) is considered detrimental because it causes locomotor limitations (Møller, 1993). For this reason, among others, the presence of fluctuating asymmetry might negatively affect the individual fitness of animals (Beasley et al., 2013). For *C. biguttulus* and grasshoppers in general, restricted movement means restricted escape behavior from predators and an increased risk of being preyed upon.

We tested the boldness behavior of *C. biguttulus* in the form of a simulated attack situation. This evoked tonic immobility in the animals, representing a defensive response to predation and thus can be interpreted as bold behavior. Thereby, boldness is a behavioral pattern that is often related to the individual activity (Réale et al., 2007). As hypothesized, we found that *C. biguttulus* individuals from highly urbanized habitats were bolder (= lower tonic immobility) and thus

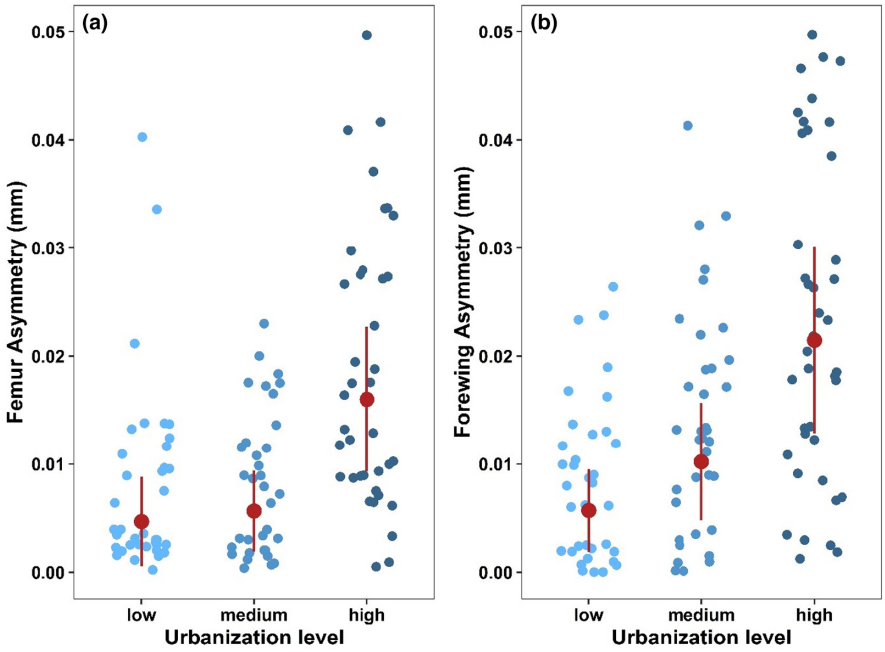

FIGURE 1 Effects of urbanization (low, medium, and high) on fluctuating asymmetry (mm) in (a) the femora and (b) the tegmina of *Chorthippus biguttulus*. Plots include raw data points, mean, and standard deviation.

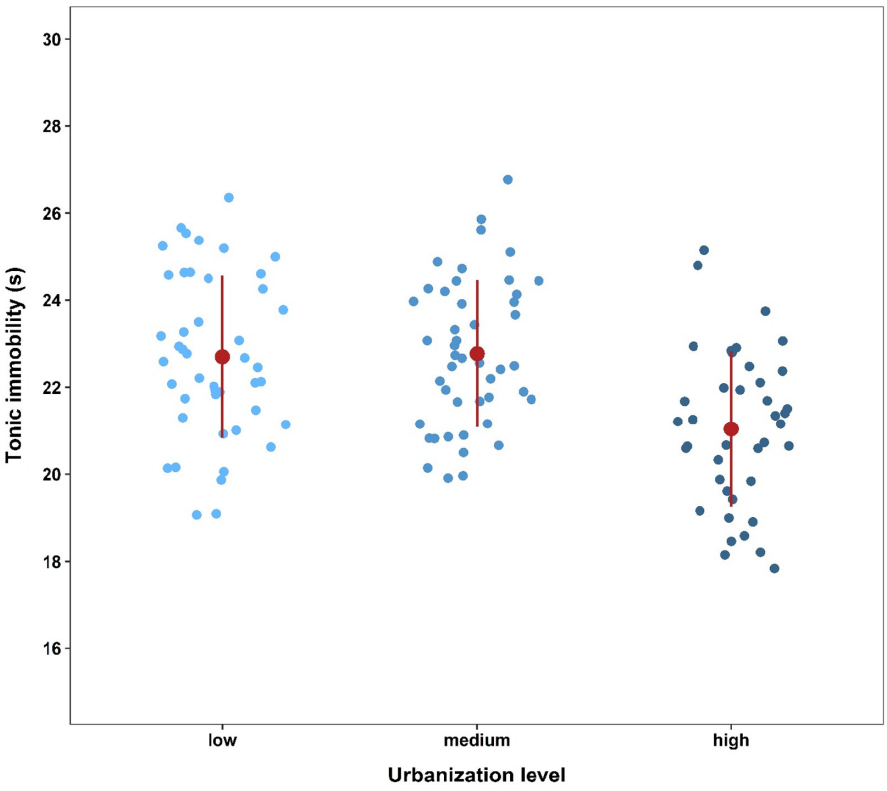

FIGURE 2 Effects of urbanization (low, medium, and high) on boldness (tonic immobility; s) of *Chorthippus biguttulus*. Plots include raw data points, mean, and standard deviation.

expressed more risk-taking behavior than individuals from less urbanized habitats. This is an often-observed behavioral pattern in many animal species colonizing urban habitats including birds (Atwel et al., 2012; Scales et al., 2011), lizards (Baxter-Gilbert et al., 2019), and insects, as has been shown for example for carabid beetles (Magura et al., 2021; Schuett et al., 2018). A meta-analysis of different animal groups found that, on average, bolder individuals have higher reproductive success and show versatile trade-offs in the factors of survival and fitness (Smith & Blumstein, 2008). However, it remains to be investigated whether lower tonic immobility of *C. biguttulus* provides advantages in a natural predator–prey situation, and thus whether individuals from more urbanized habitats have higher survival and a fitness advantage over individuals from less urbanized habitats.

In support of our hypothesis, *C. biguttulus* individuals from highly urbanized habitats were more active in terms of mobility (i.e., degree of movement of the animal's body independent of the spatial displacement) and movement (i.e., time of the animal in

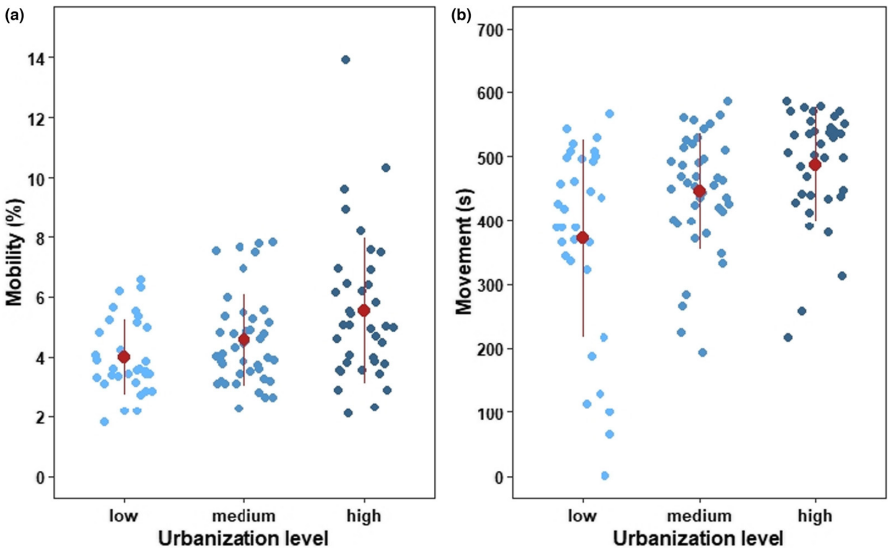

FIGURE 3 Effects of urbanization (low, medium, and high) on (a) mobility and (b) movement of *Chorthippus biguttulus*. Plots include raw data points, mean, and standard deviation.

motion) than those from less urbanized habitats. We used an open field test, where animals were exposed to an unknown open area that offered them no possibility of retreat. The observed activity patterns could therefore be related to the exploration behavior of animals, including fear behavior and readiness to flee (Réale et al., 2007). One of the main factors determining an animal's activity is the amount of time it spends moving (Noldus et al., 2001). The time spent in movement *by C. biguttulus* was found to be increased by one quarter for individuals from highly urbanized compared to those of lowly urbanized habitats. Mobility is regarded as an important factor in escape behavior. It can be assumed that animals that show higher general mobility have higher chances of a successful escape attempt in risky predator–prey situations. In general, grasshoppers tend to avoid risky situations by hiding and showing distinct escape behaviors (Ingrisch & Köhler, 1998). The success of the latter depends on the speed of the individuals and the mobility of their extremities (Hassenstein & Rustert, 1999). The observed higher mobility of individuals from highly urbanized habitats might therefore be an adaption to high predation pressure in cities and evidence for trait variability caused by urbanization (Alberti, 2014; Bolnick et al., 2011). However, activity is a behavior in which fitness tradeoffs are made (Réale et al., 2007). Higher activity of individuals positively affects fitness because it allows for better escape behavior. At the same time, increasing activity enhances the probability of risky situations. Therefore, it should be investigated whether a higher activity of individuals in urban areas indeed provides a fitness advantage.

Although sex may influence the expression of traits, our results on *C. biguttulus* show that boldness and activity are sex independent in this common grasshopper. Further, no differences in asymmetry could be observed between the sexes. Intersexual differences would suggest that particular sex responds more or less strongly to the stressor of urbanization. Also, a difference in boldness behavior between sexes was not observed, indicating that boldness is a sex-independent behavioral pattern in *C. biguttulus*. Although different sexes may exhibit different activity patterns in grasshopper species (Forsman & Appelqvist, 1999), these could not be detected in *C. biguttulus*.

5 | CONCLUSION

Our study shows that urbanization acts as environmental stress, affecting fluctuating asymmetry in locomotor organs in a common grasshopper species. Furthermore, selection for individuals with higher activity rates and boldness in highly urbanized areas indicates the fitness-facilitating character of these behavioral traits in *C. biguttulus*. In the wake of current global change, management strategies need to be intensified to mitigate increasing environmental stress in urban areas and hence contribute to better conservation strategies for urban arthropod communities worldwide.

AUTHOR CONTRIBUTIONS

Florian Rech: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); project administration (lead); resources (equal); software (lead); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Nijat Narimanov:** Conceptualization (supporting); data curation (supporting); formal analysis (equal); investigation (supporting); methodology (equal); project administration (supporting); resources (equal); software (lead); supervision (supporting); validation (equal); visualization (lead); writing – original draft (supporting); writing – review and editing (equal). **Tobias Bauer:** Conceptualization (supporting); formal analysis (equal); investigation (supporting); methodology (equal); supervision (supporting); validation (supporting); writing – original draft (supporting); writing – review and editing (equal). **Jens Schirmel:** Conceptualization (lead); data curation (supporting); formal analysis (equal); investigation (supporting); methodology (supporting); project administration (supporting); resources (equal); software (supporting); supervision (lead); validation (equal); visualization (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Generated and analyzed data during this study are available from Figshare: https://doi.org/10.6084/m9.figshare.19944374.

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REFERENCES

Alberti, M. (2005). The effects of urban patterns on ecosystem function. *International Regional Science Review*, *28*, 168–192. https://doi.org/10.1177/0160017605275160

Alberti, M. (2014). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology & Evolution*, *30*(2), 114–126. https://doi.org/10.1016/j.tree.2014.11.007

Atwel, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., & Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, *23*(5), 960–969. https://doi.org/10.1093/beheco/ars059

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Baxter-Gilbert, J., Riley, J. L., & Whiting, M. J. (2019). Bold New World: Urbanization promotes an innate behavioral trait in a lizard. *Behavioral Ecology and Sociobiology*, *73*(8), 1–10. https://doi.org/10.1007/s00265-019-2713-9

Beasley, D., Andrea, B., & Timothy, A. (2013). The use of fluctuating asymmetry as a measure of environmentally induced developmental instability: A meta-analysis. *Ecological Indicators*, *30*, 218–226. https://doi.org/10.1016/j.ecolind.2013.02.024

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bellmann, H., Rutschmann, F., Roesti, C., & Hochkirch, A. (2019). *Der Kosmos Heuschreckenführer*. Franckh Kosmos Verlag.

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs a space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, *18*, 581–592. https://doi.org/10.1111/ele.12427

Boal, C. W., & Dykstra, C. R. (Eds.). (2018). *Urban raptors: Ecology and conservation of birds of prey in cities*. Island Press. https://doi.org/10.5822/978-1-61091-841-1

Bolnick, D., Amarasekare, P., Araújo, M., Bürger, R., Levine, J., Novak, M., Rudolf, V., Schreiber, S., Urban, M., & Vasseur, D. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*, 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018). Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. *Urban Ecosystem*, *21*(6), 1139–1149. https://doi.org/10.1007/s11252-018-0786-2

Clarke, G. M. (1995). The genetic basis of developmental stability. II. Asymmetry of extreme phenotypes revisited. *The American Naturalist*, *146*, 708–725. https://doi.org/10.1086/285821

Coda, J., Martinez, J., Steinmann, A., Priotto, J., & Gomez, M. (2017). Fluctuating asymmetry as an indicator of environmental stress in small mammals. *Mastozoologia Neotropical*, *24*, 313–321.

Derby Lewis, A., Bouman, M. J., Winter, A. M., Hasle, E. A., Stotz, D. F., Johnston, M. K., Klinger, K. R., Rosenthal, A., & Czarnecki, C. A. (2019). Does nature need cities? Pollinators reveal a role for cities in wildlife conservation. *Frontiers in Ecology and Evolution*, *7*, 220. https://doi.org/10.3389/fevo.2019.00220

Detzel, P. (1998). *Die Heuschrecken Baden-Württembergs*. Ulmer.

Diamond, S. E., Dunn, R. R., Frank, S. D., Haddad, N. M., & Martin, R. A. (2015). Shared and unique responses of insects to the interaction of urbanization and background climate. *Current Opinion in Insect Science*, *11*, 71–77. https://doi.org/10.1016/j.cois.2015.180.001

Dingemanse, N., Kazem, A., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Fattorini, S. (2011). Insect extinction by urbanization: A long term study in Rome. *Biological Conservation*, *144*(1), 370–375. https://doi.org/10.1016/j.biocon.2010.09.014

Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, *29*(8), 1412–1429. https://doi.org/10.1111/geb.13107

Forsman, A., & Appelqvist, S. (1999). Experimental manipulation reveals differential effects of colour pattern on survival in male and female pygmy grasshoppers. *Journal of Evolutionary Biology*, *12*, 391–401.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Gaston, K. (2010). *Urban ecology* (Vol. *2010*). Cambridge University Press. https://doi.org/10.1017/CBO9780511778483

Gerard, M., Michez, D., Debat, V., Fullgrabe, L., Meeus, I., Piot, N., Sculfort, O., Vastrade, M., Smagghe, G., & VanderpGlanck, M. (2018). Stressful conditions reveal decrease in size, modification of shape but relatively stable asymmetry in bumblebee wings. *Scientific Reports*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-33429-4

Grimm, N. B., Foster, D., Groffman, P., Grove, J. M., Hopkinson, C. S., Nadelhoffer, K. J., Pataki, D. E., & Peters, D. P. C. (2008). The changing landscape: Ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment*, *6*(5), 264–272. https://doi.org/10.1890/070147

Grimm, N. B., Grove, J. M., Pickett, S. T. A., & Redman, C. L. (2000). Integrated approaches to long-term studies of urban ecological systems. *Bioscience*, *50*(7), 571–584. https://doi.org/10.1641/0006-3568(2000)050[0571:IATLTO]2.0.CO;2

Gunn, R., Hartley, I., Algar, A., Niemelä, P., & Keith, S. (2021). Understanding behavioural responses to human-induced rapid environmental change: A meta-analysis. *Oikos*, *2022*(4), e08366. https://doi.org/10.1111/oik.08366

Gutiérrez, Y., Fresch, M., Ott, D., Brockmeyer, J., & Scherber, C. (2020). Diet composition and social environment determine food

consumption, phenotype and fecundity in an omnivorous insect. *Royal Society Open Science*, *7*(4), 200100. https://doi.org/10.1098/rsos.200100

Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J. S., Baldock, K. C. R., Fowler, F., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M. E., Jackson, J. I., Langellotto, G., Lowenstein, D., Minor, E. S., Philpott, S. M., Potts, S. G., … Threlfall, C. G. (2017). The city as a refuge for insect pollinators. *Conservation Biology*, *31*(1), 24–29. https://doi.org/10.1111/cobi.12840

Han, C. S., & Dingemanse, N. J. (2017). Sex-dependent expression of behavioural genetic architectures and the evolution of sexual dimorphism. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171658. https://doi.org/10.1098/rspb.2017.1658

Harrison, L. M., Noble, D. W. A., & Jennions, M. D. (2021). A meta-analysis of sex differences in animal personality: no evidence for the greater male variability hypothesis. *Biological Reviews Cambridge Philosophical Society*, *97*(2), 679–707. https://doi.org/10.1111/brv.12818

Hasan, S. S., Zhen, L., Miah, M., Ahamed, T., & Samie, A. (2020). Impact of land use change on ecosystem services: A review. *Environmental Development*, *34*, 100527. https://doi.org/10.1016/j.envdev.2020.100527

Hassenstein, B., & Rustert, L. (1999). Hiding responses of locusts to approaching objects. *Journal of Experimental Biology*, *202*(12), 1701–1710. https://doi.org/10.1242/jeb.202.12.1701

Hoffman, A. A., & Parsons, P. A. (1991). *Evolutionary genetics and environmental stress*. Oxford University Press. https://doi.org/10.1046/j.1420-9101.1994.7050634.x

Holloway, G. J., Povey, S. R., & Sibly, R. M. (1990). The effect of new environment on adapted genetic architecture. *Heredity*, *64*, 323–330. https://doi.org/10.1038/hdy.1990.40

Hutyra, L. R., Duren, R., Gurney, K., Grimm, N. B., Kort, E., Larson, E., & Shrestha, G. (2014). Urbanization and the carbon cycle: Current capabilities and future outlook on observing and modeling urban carbon flows. *Earth's Future*, *2*(10), 473–495. https://doi.org/10.1002/2014EF000255

Ingrisch, S., & Köhler, G. (1998). *Die Heuschrecken Mitteleuropas*. Westarp Wissenschaften.

Jentzsch, A., Köhler, G., & Schumacher, J. (2003). Environmental stress and fluctuating asymmetry in the grasshopper *Chorthippus parallelus* (Acrididae: Gomphocerinae). *Zoology*, *106*(2), 117–125. https://doi.org/10.1078/0944-2006-00106

Kassahn, K. S., Crozier, R. H., Pörtner, H. O., & Caley, M. J. (2009). Animal performance and stress: Responses and tolerance limits at different levels of biological organisation. *Biological Reviews*, *84*(2), 277–292. https://doi.org/10.1111/j.1469-185X.2008.00073.x

Koolhaas, J. M., Bartolomucci, A., Buwalda, B., De Boer, S. F., Flügge, G., Korte, S. M., Meerloa, P., Murisong, R., Olivieri, B., Palanzak, P., Richter-Levine, G., Sgoifok, A., Steimerj, T., Stiedlf, O., Van Dijkh, G., Wöhrd, M., & Fuchsb, E. (2011). Stress revisited: A critical evaluation of the stress concept. *Neuroscience & Biobehavioral Reviews*, *35*(5), 1291–1301. https://doi.org/10.1016/j.neubiorev.2011.02.003

Kralj-Fišer, S., Laskowski, K. L., & Garcia-Gonzalez, F. (2019). Sex differences in the genetic architecture of aggressiveness in a sexually dimorphic spider. *Ecology and Evolution*, *9*(18), 10758–10766. https://doi.org/10.1002/ece3.5595

Kralj-Fišer, S., Schneider, J. M., Kuntner, M., Laskowski, K., & Garcia-Gonzalez, F. (2021). The genetic architecture of behavioral traits in a spider. *Ecology and Evolution*, *11*(10), 5381–5392. https://doi.org/10.1002/ece3.7430

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, *34*, 292–305. https://doi.org/10.1111/j.1558-5646.1980.tb04817.x

Lapiedra, O., Chejanovski, Z., & Kolbe, J. (2016). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, *23*(2), 592–603. https://doi.org/10.1111/gcb.13395

Leung, B., Forbes, M., & Houle, D. (2000). Fluctuating asymmetry as a bioindicator of stress: Comparing efficacy of analyses involving multiple traits. *The American Naturalist*, *155*(1), 101–115. https://doi.org/10.1086/303298

Li, X.-Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews*, *94*(2), 721–736. https://doi.org/10.1111/brv.12475

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Magura, T., Mizser, S., Horváth, R., Nagy, D. D., Tóth, M., Csicsek, R., & Lövei, G. L. (2021). Are there personality differences between rural vs. Urban-living individuals of a specialist ground beetle, *Carabus convexus*? *Insects*, *12*(7), 646. https://doi.org/10.3390/insects12070646

Markow, T. A. (1995). Evolutionary ecology and developmental instability. *Annual Review of Entomology*, *40*, 105–120. https://doi.org/10.1146/annurev.en.40.010195.000541

Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide* (2nd ed.). Cambridge University Press. https://doi.org/10.1017/CBO9781139168342

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *Bioscience*, *52*(10), 883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

Mestre, L., Narimanov, N., Menzel, F., & Entling, M. (2020). Non-consumptive effects between predators depend on the foraging mode of intraguild prey. *Journal of Animal Ecology*, *89*(7), 1690–1700. https://doi.org/10.1111/1365-2656.13224

Mezőfi, L., Markó, M., Taranyi, D. A., & Markó, G. (2022). Sex-specific life-history strategies among immature jumping spiders: Differences in body parameters and behavior. *Current Zoology*, zoac069. https://doi.org/10.1093/cz/zoac069

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: A result of microevolution or phenotypic plasticity? *Global Change Biology*, *19*(9), 2634–2644. https://doi.org/10.1111/gcb.12258

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2019). Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecological Letters*, *23*(2), 399–408. https://doi.org/10.1111/ele.13438

Møller, A. (1993). Developmental stability, sexual selection and speciation. *Journal of Evolutionary Biology*, *6*(4), 493–509. https://doi.org/10.1046/j.1420-9101.1993.6040493.x

Niemelä, P., Vainikka, A., Hedrick, A., & Kortet, R. (2011). Integrating behaviour with life history: Boldness of the field cricket, Gryllus integer, during ontogeny. *Functional Ecology*, *26*(2), 450–456. https://doi.org/10.1111/j.1365-2435.2011.01939.x

Nishino, H., & Sakai, M. (1996). Behaviorally significant immobile state of so-called thanatosis in the cricket Gryllus bimaculatus DeGeer: Its characterization, sensory mechanism and function. *Journal of Comparative Physiology*, *179*(5), 613–624. https://doi.org/10.1007/BF00216126

Noldus, L. P. J. J., Spink, A. J., & Tegelenbosch, R. A. J. (2001). EthoVision: A versatile video tracking system for automation of behavioral experiments. *Behavior Research Methods, Instruments, & Computers*, *33*, 398–414. https://doi.org/10.3758/BF03195394

Parsons, P. (1992). Fluctuating asymmetry: A biological monitor of environmental and genomic stress. *Heredity*, *68*, 361–364. https://doi.org/10.1038/hdy.1992.51

Pham, J., Cabrera, S., Sanchis-Segura, C., & Wood, M. A. (2009). Automated scoring of fear-related behavior using EthoVision software. *Journal of Neuroscience Methods*, *178*(2), 323–326. https://doi.org/10.1016/j.jneumeth.2008.12.021

Piano, E., Souffreau, C., Merckx, T., Baardsen, L., Backeljau, T., Bonte, D., Brans, K., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J., Fontaneto, D., Gianuca, A., Govaert, L., Hanashiro, F., Higuti, J., Lens, L., & Hendrickx, F. (2019).

Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, *26*(3), 1196–1211. https://doi.org/10.1111/gcb.14934

Pimpinelli, S., & Piacentini, L. (2019). Environmental change and the evolution of genomes: Transposable elements (TEs) as translators of phenotypic plasticity into genotypic variability. *Functional Ecology*, *34*, 428–441. https://doi.org/10.1111/1365-2435.13497

QGIS Development Team. (2017). *QGIS geographic information system V 2.18.3*. Open Source Geospatial Foundation.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Roodt, A. P., Röder, N., Pietz, S., Kolbenschlag, S., Manfrin, A., Schwenk, K., Bundschuh, M., & Schulz, R. (2022). Emerging midges transport pesticides from aquatic to terrestrial ecosystems: Importance of compound- and organism-specific parameters. *Environmental Science & Technology*, *56*(9), 5478–5488. https://doi.org/10.1021/acs.est.1c08079

Rosa, E., & Saastamoinen, M. (2017). Sex-dependent effects of larval food stress on adult performance under semi-natural conditions: only a matter of size? *Oecologia*, *184*, 633–642. https://doi.org/10.1007/s00442-017-3903-7

Rosa, E., & Saastamoinen, M. (2021). Warm-night temperature alters paternal allocation strategy in a north temperate-zone butterfly. *Ecology and Evolution*, *11*(23), 16514–16523. https://doi.org/10.1002/ece3.8120

Ruxton, G. (2006). Grasshoppers don't play possum. *Nature*, *440*, 880. https://doi.org/10.1038/440880a

San Martin y Gomez, G., & Van Dyck, H. (2011). Ecotypic differentiation between urban and rural populations of the grasshopper *Chorthippus brunneus* relative to climate and habitat fragmentation. *Oecologia*, *169*, 125–133. https://doi.org/10.1007/s00442-011-2189-4

Scales, J., Hyman, J., & Hughes, M. (2011). Behavioral syndromes break down in urban song sparrow populations. *Ethology*, *117*(10), 887–895. https://doi.org/10.1111/j.1439-0310.2011.01943.x

Scherber, C., Gladbach, D. J., Stevnbak, K., Karsten, R. J., Schmidt, I. K., Michelsen, A., Rost, K., Klaus, A. L., Teis, S., Mikkelsen, N., Beier, C., & Christensen, S. (2013). Multi-factor climate change effects on insect herbivore performance. *Ecology and Evolution*, *3*(6), 1449–1460. https://doi.org/10.1002/ece3.564

Schirmel, J. (2021). COVID-19 pandemic turns life-science students into "citizen scientists": Data indicate multiple negative effects of urbanization on biota. *Sustainability*, *13*(5), 2992. https://doi.org/10.3390/su13052992

Schuett, W., Delfs, B., Haller, R., Kruber, S., Roolfs, S., Timm, D., Willmann, M., & Drees, C. (2018). Ground beetles in city forests: Does urbanization predict a personality trait? *PeerJ*, *6*, e4360. https://doi.org/10.7717/peerj.4360

Schuett, W., Tregenza, T., & Dall, S. R. (2010). Sexual selection and animal personality. *Biological Reviews*, *85*(2), 217–246. https://doi.org/10.1111/j.1469-185X.2009.00101.x

Seto, K., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, *109*(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109

Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution*, *38*(3), 622–630. https://doi.org/10.1111/j.1558-5646.1984.tb00327.x

Smith, B., & Blumstein, D. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Tannier, C., Bourgeois, M., Houot, H., & Foltête, J. (2016). Impact of urban developments on the functional connectivity of forested habitats: A joint contribution of advanced urban models and landscape graphs. *Land Use Policy*, *52*, 76–91. https://doi.org/10.1016/j.landusepol.2015.12.002

Trochet, A., Courtois, E. A., Stevens, V. M., Baguette, M., Chaine, A., Schmeller, D. S., & Clobert, J. (2016). Evolution of sex-biased dispersal. *The Quarterly Review of Biology*, *91*(3), 297–320. https://doi.org/10.1086/688097

Uetz, G. W., Roberts, J. A., Wrinn, K. M., Polak, M., & Cameron, G. N. (2009). Impact of a catastrophic natural disturbance on fluctuating asymmetry (FA) in a wolf spider. *Ecoscience*, *16*(3), 379–386. https://doi.org/10.2980/16-3-3261

Van Dongen, S., Molenberghs, G., & Matthysen, E. (2008). The statistical analysis of fluctuating asymmetry: REML estimation of a mixed regression model. *Journal of Evolutionary Biology*, *12*(1), 94–102. https://doi.org/10.1046/j.1420-9101.1999.00012.x

Zahid, S., Panhwar, W., Sultana, R., Mehmood, A., & Wagan, M. S. (2017). Study on food selection in two grasshopper species, *Calliptamus barbarus* (costa, 1836) and *Chorthippus biguttulus* (Linnaeus, 1758) from Pakistan. *Journal of Entomology and Zoology Studies*, *5*(2), 13–15.

SUPPORTING INFORMATION

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

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Chapter V

Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season

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ORIGINAL PAPER

Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season

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Abstract Plant invasions can have major impacts on ecosystems and influence global species diversity. In Central Europe, Himalayan balsam (*Impatiens glandulifera*) and American goldenrods (*Solidago canadensis* and *S. gigantea*) are important invaders often establishing dense and homogeneous stands, especially in urban and other disturbed habitats. We investigated their impacts on plant-dwelling spiders (abundance, family structure, guild structure) and potential spider prey items during flowering season within an urbanized landscape using a paired design comparing invaded and native reference vegetation plots. In general, flowering American goldenrods and Himalayan balsam had no significant impacts on the spider family composition. Invasion of American goldenrods further had no effect on total spider abundance and potential prey item abundance. In contrast, goldenrods showed a significantly increased crab spider (Thomisidae) abundance while being less inhabited by web builders. Himalayan balsam negatively influenced free hunters and running crab spider (Philodromidae) abundance, while we found no effects on other groups and total spider abundance. For Himalayan balsam, potential prey item abundance was higher than in native vegetation stands. Notwithstanding that our results only represent a snapshot of the system, they suggest that large-scale removal of urban goldenrod stands during flowering season might negatively influence local spider abundance, especially of crab spiders. Management efforts should therefore be accompanied by compensation measures to avoid disruptive effects on local plant-dwelling spider communities.

Keywords *Impatiens glandulifera* · Novel ecosystems · Philodromidae · *Solidago canadensis* · *Solidago gigantea* · Thomisidae · Urban management

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Introduction

Biological invasions can have tremendous ecological and socio-economic consequences (Sala et al. 2000; Nentwig et al. 2018). Invasive alien plant species are

one of the major drivers of current global biodiversity erosion (Bellard et al. 2016; Simberloff et al. 2013), yet their eradication can result in enormous costs (Hoffmann and Broadhurst 2016; Pimentel et al. 2005).

In general, invasive plants have negative effects on animal diversity, fitness and abundance (Schirmel et al. 2016). However, the consequences and severity of invasions can vary over time and among different spatial scales, ecosystems and taxa (Dostál et al. 2013; Hulme et al. 2013; Schirmel et al. 2016). Herbivore communities are often directly affected by alien plant invasions due to loss of indigenous vegetation (Gerber et al. 2008; Procheş et al. 2008) and respond with a significant reduction of biomass and species diversity (Schirmel et al. 2016). Invasive plants can also negatively affect predator communities by altering habitat conditions (e.g., Balkenhol et al. 2018; Gerber et al. 2008) and might lower foraging success of some predators (Maerz et al. 2005).

On the other hand, there are well-known examples where invasive plants can facilitate some native species (Rodriguez 2006). Invasive plants may offer suitable resources and habitat requisites for native animals, such as web attachments for spiders (Pearson 2009), habitat analogues for small mammals (Packer et al. 2016) or pollen and nectar supplies for pollinators (Davis et al. 2018; Russo et al. 2016). Especially in landscapes with large proportions of urban and novel habitats, alien plant species are abundant (Kowarik 1995) and can contribute to local biodiversity conservation by facilitation of native animal species (Buchholz et al. 2015; Hausmann et al. 2016; Packer et al. 2016; Rodriguez 2006). Urban greenspaces, gardens, wasteland and parks might even be important habitat analogues for rare or endangered arthropod species (e.g., Buchholz et al. 2018; Eckert et al. 2017) as well as apex predators like birds of prey (Boal and Dykstra 2018).

In Europe, both Himalayan balsam (*Impatiens glandulifera* Royle) and American goldenrods (*Solidago canadensis* L., *Solidago gigantea* Ait.) have been actively introduced during the last few centuries as ornamental and nectar plants (Beerling and Perrins 1993; Weber 2000); nowadays, these species are very widespread and common in a wide variety of habitats in many regions of Germany (Nehring et al. 2013). Himalayan balsam is a tall, annual herb with a height of up to 2.5 m that flowers in late summer and reacts with fast dieback after initial frost events in autumn (Beerling and Perrins 1993). Its relatively large seeds are released by ballistochory and are able to germinate synchronously in spring. Today, the conspicuous purple or pink flowers are a typical aspect of many riparian and forest edge habitats in Central Europe. In the European Union, Himalayan balsam is considered an invasive plant species (Reg. 1143/2014; European Union 2014). However, reported effects of Himalayan balsam on local plant diversity are partly contradictory. While Hulme and Bremner (2006) showed a reduction in local plant diversity due to the replacement of widespread, but native ruderal species by Himalayan balsam, no significant effects on plant diversity were found by Hejda and Pyšek (2006) and Čuda et al. (2017). American goldenrods are rhizomatous perennial plants with a shoot height of up to 2 m, typically invading disturbed sites where they form dense stands with rich, yellow flowers in late summer and autumn (Weber 2000). American goldenrod species are considered invasive in Central Europe (Nehring et al. 2013) due to their known negative effects on local plant diversity (Hejda et al. 2009; Weber 2000).

Impacts of both Himalayan balsam and American goldenrods on native animal diversity are still not fully understood, and past research mainly focused on their effects on pollinators and ground-dwelling arthropods. Himalayan balsam offers extensive floral resources for pollinators and can facilitate native pollinators to some extent (Davis et al. 2018; Lopezaraiza-Mikel et al. 2007). On the other hand, Tanner et al. (2013) demonstrated strong negative effects on foliage-dwelling arthropod diversity and abundance. The invasion of American goldenrods can negatively affect pollinator communities in protected areas and in abandoned arable fields due to its dense stands, competitive advantage and subsequent simplification of floral resources (Fenesi et al. 2015; Morón et al. 2009). In contrast, it was shown that a relatively high number of native pollinator insects, such as wild bees (Weber 2000; Westrich 2019), visit flowering American goldenrods. However, there is a clear research gap in analyzing the impact of these major plant invaders on higher trophic levels (White et al. 2006), such as plant-dwelling predatory arthropods like spiders (Araneae). Especially during flowering season, invasion by Himalayan balsam and goldenrods may

affect spiders via influences on phytophagous and flower-visiting insect prey items.

Crab spiders (Thomisidae) are particularly well known ambush hunters, as they lurk on flowers for visiting pollinators. Because both plant invaders produce very conspicuous flowers or inflorescences, they provide potential hunting grounds especially for crab spiders. Many spiders are habitat specialists with a fast reaction to environmental changes and stress (Hänggi et al. 1995; Buchholz et al. 2015, 2018; Entling et al. 2007). Additionally, spider diversity is usually not related to plant species numbers (Buchholz 2010; Buchholz et al. 2018; Harry et al. 2019), but rather to the structure and microclimate of the habitat (Clausen 1986). There is also evidence that spiders can react to higher prey availability with increased production of offspring (Wise 1979) and survival rates (Bradley 1993), which makes them excellent indicator species for a comparison of (indirect) local effects caused by plant invasions.

In this study, we aimed to analyze the effect of Himalayan balsam and American goldenrods on the abundance, family composition and guild structure of plant-dwelling spiders during the flowering season. We collected spiders and potential prey organisms with sweeping nets and used a paired design (for both Himalayan balsam and American goldenrods) by comparing invaded and uninvaded plots within the city of Karlsruhe in southwest Germany.

We hypothesized that flowering Himalayan balsam and American goldenrods with their rich and simultaneously developed floral presence in late summer (i) positively affect the abundance of potential spider prey organisms (insects), and (ii) affect total abundance, guild structure and family composition of plant-dwelling spiders, whereby flower-dwelling crab spiders (Thomisidae) show higher abundances in invaded plots compared to native vegetation because of a higher presence of floral resources.

Material and methods

Study area and site selection

The study was conducted within the city of Karlsruhe (Baden-Württemberg, Germany; Fig. 1a). In Karlsruhe, Himalayan balsam (*Impatiens glandulifera* Royle; Balsaminaceae) as well as two American goldenrod species (*Solidago canadensis* L., *S. gigantea* Ait.; Asteraceae) are widespread in numerous disturbed urban habitats such as parks, areas along artificial channels and in abandoned industrial wastelands. Major areas of Karlsruhe are located in the Upper Rhine valley on Pleistocene sand and gravel (Karlsruhe 1999). The urban vegetation in open green spaces of Karlsruhe is characterized by a mosaic of extensively managed meadows with 1–2 cuts and intensively managed lawns (from 3–5 up to 12 cuts per year). An establishment of goldenrod and Himalayan balsam on these sites is prevented by a first cut in spring (intensively managed lawns) or summer (June/July; extensively managed meadows). Goldenrod and Himalayan balsam stands are therefore restricted to ruderalized areas with no regular management, like anthropogenic riparian habitats, irregular managed waysides, urban scrub understory or wastelands. During our collection period, patches of ruderalized herbaceous vegetation were the only type of higher and flowering herbaceous vegetation in Karlsruhe due to the cutting of the surrounding lawns and meadows.

We selected 18 American goldenrod and 20 Himalayan balsam plots as "invaded" sites (Fig. 1b, c). All of these plant stands developed spontaneously and were not planted. All plots represented dense, clearly confined and flowering stands with at least 20 single invader plant stems with a very high dominance ($> 80\%$ cover) embedded in a mosaic of various small-scale land use unities like urban forest and scrub, meadows and impervious surface. We avoided sampling very small and highly isolated plots with a size of < 3 m^2 (e.g., isolated by mowing of adjacent vegetation).

In direct vicinity to each invaded plot (about 10 to 20 m) a corresponding reference plot ("native") of similar size with comparable vegetation structure (height and cover) and similar adjacent habitats was selected ($N_{total} = 76$ plots; see Fig. 1). The native plots are characterized by common and tall, native ruderal plant species such as *Urtica dioica L.*, *Cirsium* sp., *Artemisia vulgaris* L., *Lythrum salicaria* L. and, *Lapsana communis* L. (see supplementary material Table 1). Native plots further contained several (dry) grasses such as *Dactylis glomerata* L. and other common species of Poaceae. In some native plots, single alien *Erigeron annuus* (L.) Pers. plants were present, but never in high numbers. Total vegetation

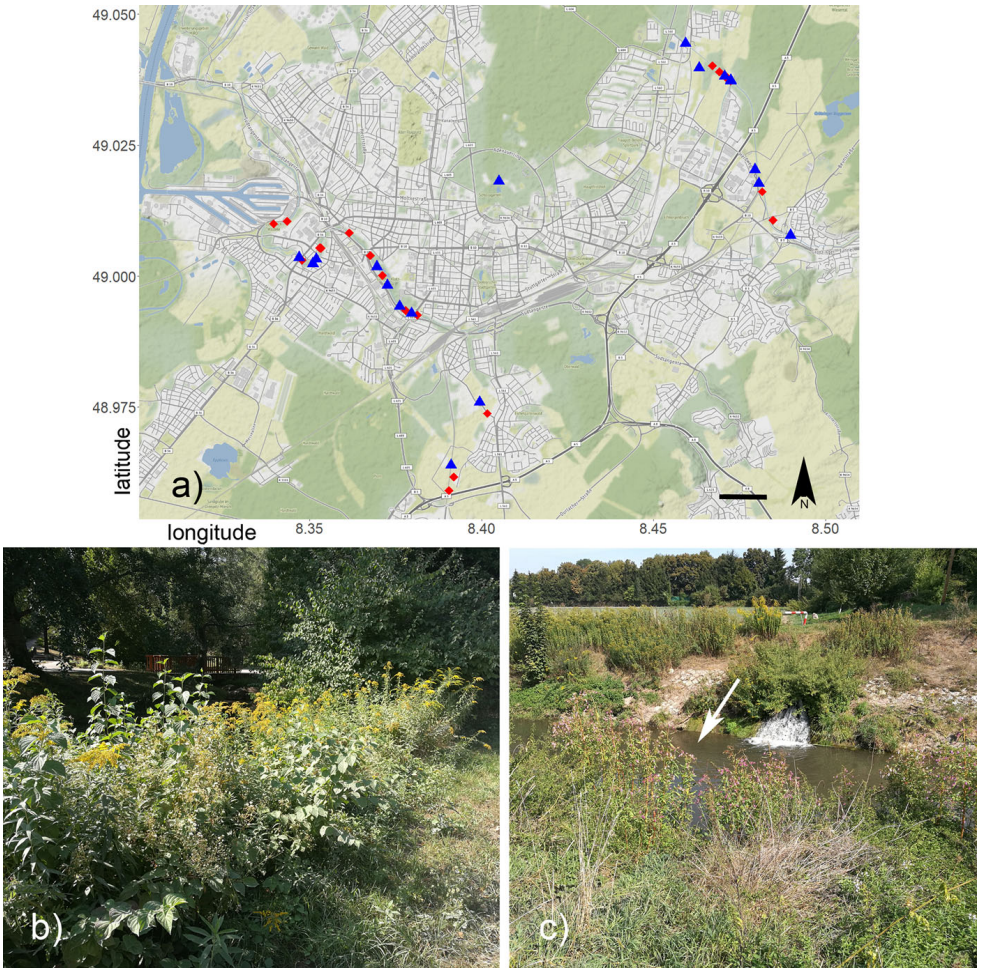

Fig. 1 Sampling localities in and around the city of Karlsruhe, Germany. **a** Map of all sampling plots for Himalayan balsam *Impatiens glandulifera* (red rhombs) and American goldenrods *Solidago gigantea/canadensis* (blue triangles). Native reference plots (not shown) were located in direct vicinity of the invaded plots (Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap,under ODbL). **b** Example of an invaded site by American goldenrod. **c** Example of a disturbed riparian habitat invaded by Himalayan balsam (white arrow). Scale bar = 1 km

cover was over > 90% in each plot (native and invaded).

Data collection

We collected plant-dwelling spiders and potential prey organisms once per plot with a sweeping net in late August/beginning of September 2018 on clear, sunny and windless days. Per plot, twenty sweeps in the upper part of the vegetation were conducted by a single collector (FK), each sweep targeting different plants of the plot. In invaded plots, only plant individuals of the invasive species (either goldenrods or Himalayan balsam) were sampled. In order to avoid killing protected species (by German law) such as wild bees, sweeping net content was emptied onto a large white sheet in the field, and spiders were transferred to 80% ethanol with tweezers. To prevent spiders and prey organisms from escaping, a second person watched the margin of the white sheet for fleeing individuals. Additionally, this collection method allows for instant preservation of juvenile (and often very fragile) spiders, which are sometimes damaged beyond identification or morphospecification (e.g., loss of all legs or abdomen) when transferred together with larger and more sclerotized insects (true bugs, beetles) and plant parts directly into a killing agent and transported to the laboratory. Because most caught specimens were juveniles (as typical for this time of the year; Nentwig et al. 2019) all specimens were identified only to family level with the help of the online determination key of Nentwig et al. (2019) by

DAB and FK. TB verified the identification of the specimens. Numbers of prey items were counted up to 5 individuals, and then further assessed by intervals of five (until 20 individuals) and 10 (> 20 individuals), since counting in the field was done on living and moving prey items of variable size and form, which prevented an exact count.

Spider nomenclature follows the World Spider Catalog (2019). To analyze the functional diversity of spider guilds, all specimens were classified into "web builders" (spiders that use a silken web to subdue and/or sense prey; e.g., Araneidae and Theridiidae) and "free hunters" (spiders that hunt prey without a web; e.g., Salticidae and Thomisidae) based on the determination to the family level, following the "No web" classification of families/subfamilies in Cardoso et al. (2011; supplementary material table S1). The family Cheiracanthiidae, which was part of Miturgidae until recently (World Spider Catalog 2019) was classified by us as "free hunters" ("no web", like Miturgidae in Cardoso et al. 2011). For the classification into guilds, the Linyphiidae were determined to subfamily level (Erigoninae/Linyphiinae/Micronetinae; see Tanasevitch 2020). All material is deposited at the State Museum of Natural History Karlsruhe (SMNK).

Statistical analysis

All analyses were carried out in the R environment (R Core Team 2019). We applied separate models for each plant invader because both plant invaders are dominant in different habitat types in and around the city of Karlsruhe.

The total abundance of prey organisms, total spider abundance, abundance of guild types (web builders, free hunters) and the abundance of the two most dominant spider families (Philodromidae and Thomisidae) were correlated to plant stand type (factor: invaded vs. native) by using generalized linear mixed models (GLMM's) with a Poisson distribution for count data (R package 'lme4'; Bates et al. 2019). (Paired) locations were used as random factor. The *p*-values are based on subsequent ANOVA (chisquare)-testing (R package 'car'; Fox and Weisberg 2011). In the case of overdispersion, a negative binomial distribution was applied; in case of underdispersion, a Conway-Maxwell-Poisson (Lynch et al. 2014) distribution was used to fit the model (Magnusson et al. 2019). In cases of slight overdispersion in poisson models (sum of squared Pearson residuals/residual degrees of freedom between 1.0 and 1.2) we used a function (Overdisp_fun) provided by Ben Bolker on the GLMM FAQ (Bolker 2020) for testing of overdispersion impact, but no significant impacts were found. This is also in accordance with Payne et al. (2018), who determined a general threshold of SSQP residuals/rdf of 1.2 under which a Poisson GLMM usually still performs well. We also tested for potential zero-inflation with 'testZeroInflation' in package DHARMa (Hartig 2020), which compares the number of zeros present in the dataset against the distribution of expected zeros in the model.

Spider family composition was related to plant stand type by using partial redundancy analysis (RDA) using the R package 'vegan' (Oksanen et al. 2017). To emphasize the influence of dominant families, a Hellinger transformation was performed. Because of our paired study design, we used partial RDA where we removed this effect (using the term Condition (pair) in the formula). The significance of the effect of plant stand type was tested using an ANOVA-like permutation test based on 999 permutations.

The map (Fig. 1) was created with package 'ggmap' (Kahle et al. 2019) and the 'terrain'-map of maps.stamen.com.

Results

Effect of American goldenrods and Himalayan balsam on potential spider prey items

American goldenrods had no significant effect on the number of potential spider prey item individuals (Table 1, Fig. 2a). In contrast, the presence of Himalayan balsam significantly affected the number of prey organisms (Table 1), which was on average almost two times higher in invaded than in native plots (Fig. 2b).

American goldenrods

We sampled 409 spider specimens from 12 spider families (supplementary material Table 2). We recorded 194 specimens from 10 families in plots invaded by American goldenrods and 215 specimens from 12 families in native plots. Only singletons represented exclusive families in native plots. The

Table 1 Effect of Himalayan balsam (*Impatiens glandulifera*) and American goldenrods (*Solidago canadensis*/*gigantea*) on the individual number of prey items, total spider abundance, abundance of the two most dominant spider families and of web builders and free hunters

Dependent variable	Predictor	Estimate	SE	z	p	GLMM family
Prey items	American goldenrod	− 0.281	0.208	− 1.352	0.176	n. binom
	Himalayan balsam	0.636	0.171	3.713	**< 0.001**	n. binom
Spider abundance	American goldenrod	− 0.056	0.173	− 0.322	0.748	n. binom
	Himalayan balsam	− 0.286	0.218	− 1.308	0.191	n. binom
Thomisidae abundance	American goldenrod	0.350	0.139	2.523	**0.012**	poisson
	Himalayan balsam	− 0.238	0.26	− 0.916	0.356	compois
Philodromidae abundance	American goldenrod	0.032	0.252	0.126	0.900	poisson
	Himalayan balsam	− 0.623	0.264	− 2.356	**0.018**	poisson
Web builders	American goldenrod	− 0.962	0.151	− 6.384	**< 0.001**	compois
	Himalayan balsam	− 0.289	0.300	− 0.964	0.335	n. binom
Free hunters	American goldenrod	0.250	0.214	1.169	0.242	n. binom
	Himalayan balsam	− 0.334	0.163	− 2.047	**0.041**	poisson

Effects were tested with generalized linear mixed models (n.binom = negative binomial distribution) and subsequent ANOVA (chisquare)-testing. Significant effects are shown in bold

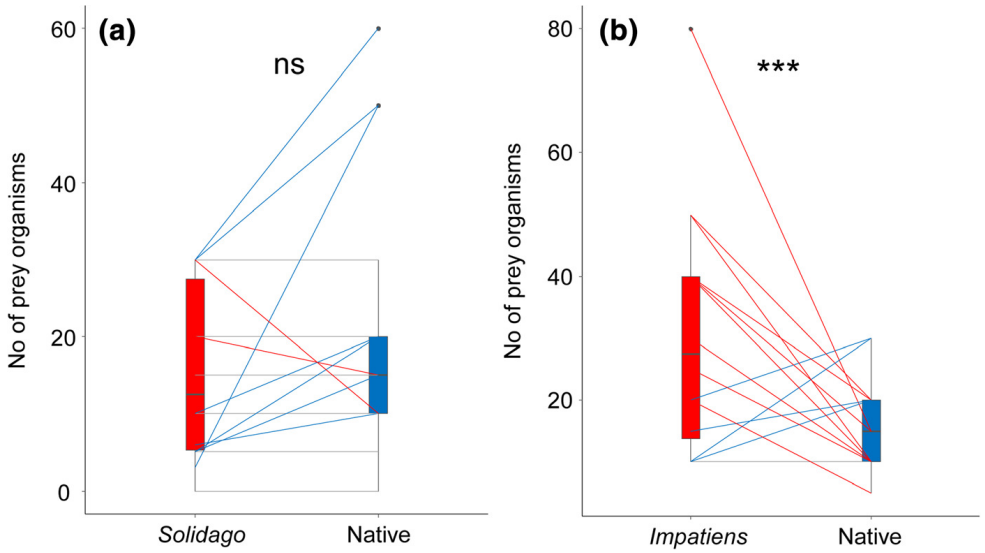

Fig. 2 Paired comparisons of the number of potential spider prey organism individuals between **a** American goldenrods ("*Solidago*") and native vegetation and **b** Himalayan balsam ("*Impatiens*") and native vegetation. Lines connect paired locations, whereby red lines indicate higher individual numbers in the invaded plots, blue lines indicate higher individual numbers in the native plots and grey lines indicate similar individual numbers. Stars illustrate significant differences with ***$p < 0.001$ (*ns* not significant). For statistics see Table 1

most abundant spider family were the crab spiders (Thomisidae; n = 208).

The total number of spider individuals showed no significant difference and little variation between American goldenrod and native plots (Table 1, Fig. 3a). On the family scale, the abundance of crab spiders (Thomisidae) was significantly higher in plots invaded by American goldenrods than in native plots (Table 1, Fig. 3c). On the other hand, for the second most abundant spider family, the running crab spiders (Philodromidae), no significant effect on the abundance was found (Table 1, Fig. 3e). American

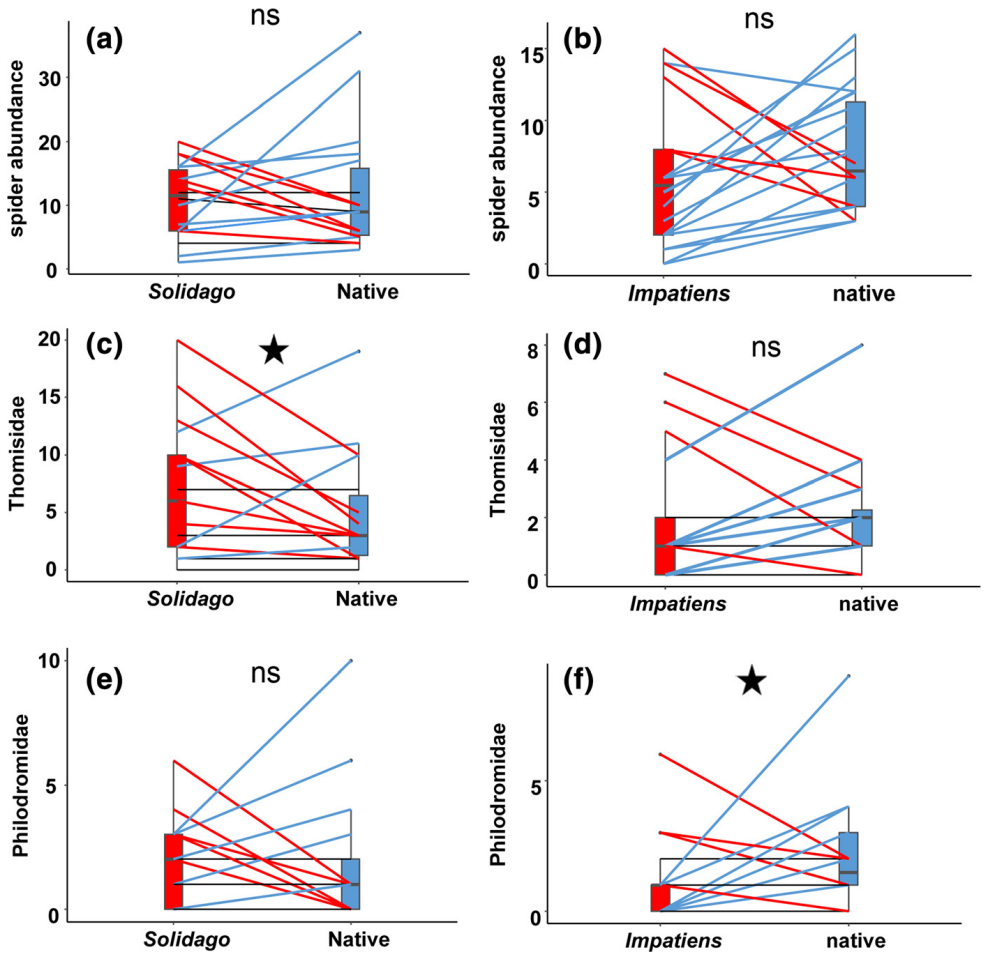

Fig. 3 Paired comparisons of abundances of total spiders **a**,**b**, Thomisidae **c**,**d** and Philodromidae **e**,**f** between American goldenrod (*Solidago gigantea/canadensis*) (left) and Himalayan balsam (*Impatiens glandulifera*) (right) with native vegetation. Lines connect paired locations, whereby red lines indicate higher individual numbers in the invaded plots, blue lines indicate higher individual numbers in the native plots and grey lines indicate equal individual numbers. Stars illustrate significant differences with $*p < 0.05$ (*ns* not significant). For statistics see Table 1

goldenrod had a significantly negative influence on the abundance of web builders, while, in contrast free hunters were not affected (Fig. 4a, b, Table 1).

Although we found more exclusive spider families occurring in native stands (see Venn diagrams in Fig. 5a), the family composition was highly similar between goldenrod and native vegetation stands. Compositions between both plant stand types showed large overlaps and did not differ significantly (F = 1.076, P = 0.347; Fig. 5a).

Himalayan balsam

We sampled 275 spider individuals from 12 families (supplementary material Table 2). 118 spider specimens were caught in plots invaded by Himalayan balsam and 157 specimens in native plots. Invaded and native plots were inhabited by members of 11 spider families (10 shared), respectively. The most dominant spider families were the Thomisidae (n = 72) and Philodromidae (n = 63).

The total spider abundance was not significantly affected by plant stand type (Table 1, Fig. 3b). The two most dominant spider families showed different responses (Table 1, Fig. 3d, f). While abundances of Thomisidae showed high variability and were not significantly affected by plant stand type, Philodromidae abundances were significantly lower in invaded plots (Table 1). The abundance of free hunters was also significantly fewer in invaded plots, while web builders were not affected by the presence of Himalayan balsam (Fig. 4c, d, Table 1).

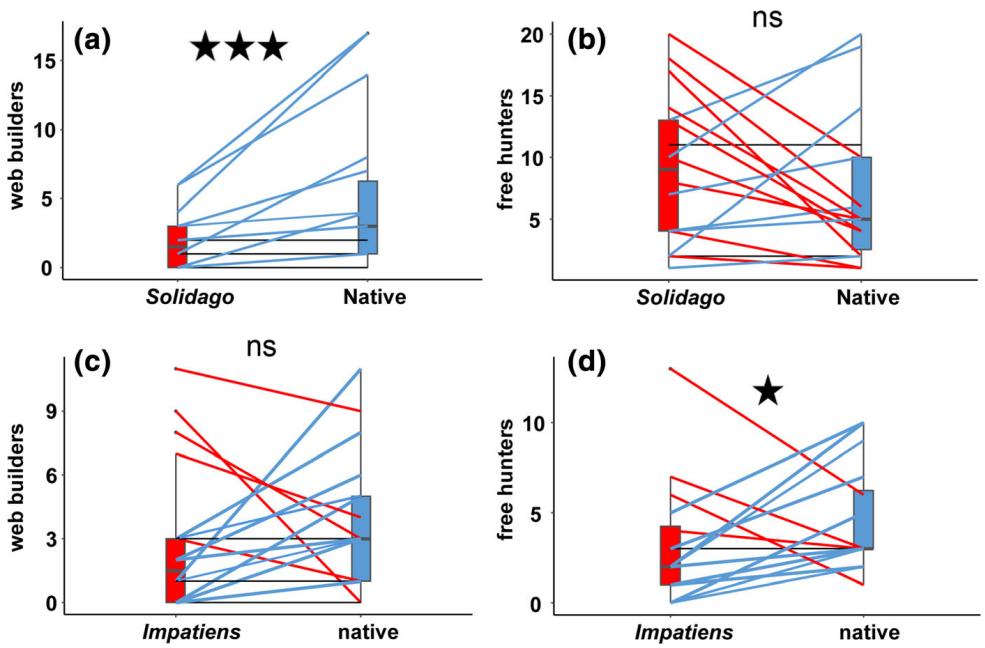

Fig. 4 Paired comparisons of the abundance of free hunters **b**,**d** and web builders **a**,**c** between American goldenrod (*Solidago gigantea/canadensis*) (top) and Himalayan balsam (*Impatiens glandulifera*) (bottom) with native vegetation. Lines connect paired locations, whereby red lines indicate higher individual numbers in the invaded plots, blue lines indicate higher individual numbers in the native plots and grey lines indicate equal individual numbers. Stars illustrate significant differences with $*p < 0.05$ and $***p < 0.001$ (*ns* not significant). For statistics see Table 1

The spider family composition was not significantly affected by the plant stand type (F = 1.4, P = 0.2; Fig. 5b). This is also reflected by the high number of families shared in both stand types (see Venn diagram in Fig. 5b).

Discussion

In general, flowering plant stands of alien American goldenrods and Himalayan balsam had only minor and statistically insignificant impacts on total spider abundances and family compositions. However, we could show that both plant invaders can affect abundances of the two dominant spider families as well as web builders and free hunters in contrasting ways. Even though we did not determine spiders to species level, all found effects affect mostly native spider species, since only very few alien spider species (and no alien thomisids or philodromids) occur in outdoor habitats in Germany (Blick et al. 2016, Nentwig et al. 2019).

American goldenrod

In American goldenrod stands, significantly fewer web builders and more crab spiders were found than in native vegetation stands. This contrasts findings of Dudek et al. (2016), who showed that, in spring, dry stems of goldenrod stands are a preferred habitat of web-building araneids compared with native grass stands, probably due to the availability of more structures for orb-web building (Lubin 1978). The native plots in our study consisted of a dense mixture of grass and herbaceous plants, which may facilitate web building in contrast to the more homogeneous upper part of American goldenrod stands. The significant increased abundance of crab spiders on goldenrods might be explained by their preference for flowers as places to hide while preying on pollinating insects. Several crab spider genera from all continents are known to wait for prey directly on or beneath flowers, where they often catch pollinators larger than their own body size (Foelix 2011; Heiling et al. 2004; Huseynov 2007b; Morse 1983; Romero and Vasconcellos-Neto 2004a, b). Hence, the dense stands and the massive blooms of American goldenrod in late summer very likely attract crab spiders irrespectively

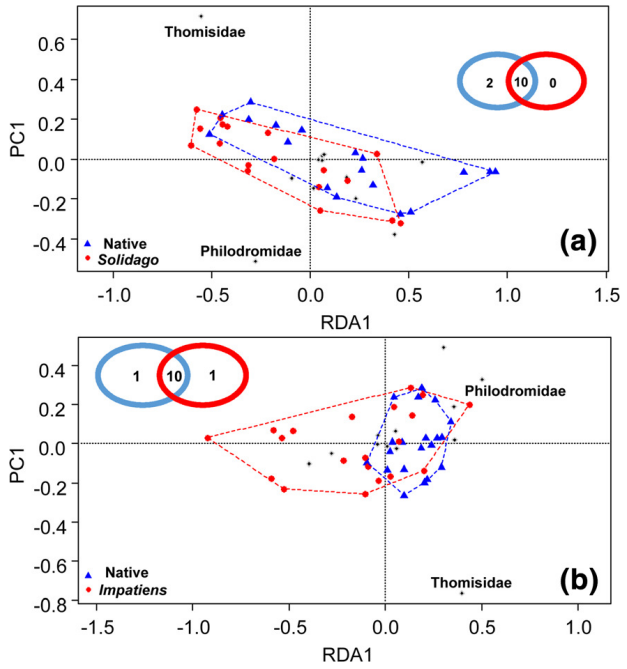

Fig. 5 RDA-ordination showing family composition in American goldenrod ("*Solidago*") and native vegetation stands **a** and in Himalayan balsam ("*Impatiens*") and native vegetation stands **b**. Inlets of Venn diagrams indicate the number of exclusive and shared spider families (red = plots invaded by *Solidago/Impatiens*, blue = plots consisting of native vegetation). Dots represent the spider families (Thomisidae and Philodromidae are additionally labelled with text). For statistics see text

of the plants' non-native origin, but may also reduce the habitat of web-building spiders at the same time. The value of goldenrods for crab spiders is also reflected by *Misumena vatia* (Clerck, 1757), a species with a Holarctic distribution (World Spider Catalog 2019) which is sometimes called "goldenrod crab spider" in North America (Bradley 2013). North American specimens of this species are known for their preference of goldenrod flowers when given the choice between green parts and blooms of goldenrod plants in the laboratory (Morse 2000). However, many European crab spiders also prey on leaves and grassy vegetation (Gawryszewski et al. 2017), hence, the observed effect of American goldenrod on crab spiders might also be related to other, unknown factors.

Interestingly, there was no effect of goldenrod on potential prey items. It is known that alien goldenrod stands can be inhabited by a large number of polyphagous heteropterans, while specialized species are mostly absent (Roháčová and Drozd 2009). Although specialized herbivores might be missing, alien goldenrod still provides habitat for polyphagous insect species, which in turn serve as potential prey for spiders, as most species are opportunistic predators with a wide food niche (e.g., Foelix 2011; Huseynov 2007a, b, 2008; Nentwig 1986).

Himalayan balsam

In contrast to American goldenrods, flowering Himalayan balsam had no positive effects, but a negative effect on philodromid spiders as well as free hunters. In contrast to our hypothesis, no effects on crab spiders and web builders were found.

Himalayan balsam stands, when compared to native vegetation and American goldenrods (Weber 2000), promote erosion along riverbanks due to fast and synchronized diebacks after frost followed by a subsequent lack of vegetation cover and exposure of the underlying bare ground (Greenwood and Kuhn 2014). Bare ground is generally a less preferred overwintering habitat for spiders (Mestre et al. 2018) and possibly leads to a reduced abundance of certain spiders in dense stands of Himalayan balsam. In riparian habitats, this invader also negatively influences epigeic arthropod diversity and abundance in general, with heavily invaded regions differing from less-invaded sites (Seeney et al. 2019). Another reason for the reduced spider abundance, despite increased numbers of prey items, may be trophobiosis between ants and aphids on Himalayan balsam, which was incidentally observed in several plots during the study (FK and DAB pers. obs. during the field survey). Although some opportunistic spiders (including crab spiders) feed on ants (e.g., Huseynov 2007a, b), ants are known to be a difficult prey with some specialized spiders showing a very sophisticated predatory behavior (Heller 1976; Pekár 2004; Pekár et al. 2008). However, some spiders might avoid feeding on ants (e.g., the philodromid *Tibellus macellus* Simon, 1875; Huseynov 2008) and the abundance of web-building spiders can be reduced by these insects (Sanders and Platner 2007). Ants are known to protect aphids and act aggressively against potential aphid predators (Novgorodova and Gavryliuk 2012). A high ant density may therefore suppress the presence of some spiders which might especially be true for little-sclerotized species such as many members of Philodromidae, of which a significantly lower abundance was found on Himalayan balsam. Ant-spider

interactions, including non-consumptive effects (Mestre et al. 2020), should therefore be targeted by future research.

That we found no differences in total spider abundance between Himalayan balsam and native reference vegetation might be related to the one-time sampling in late summer, in which a large number of juvenile spiders is present. Negative effects are potentially more pronounced when sampled over the complete vegetation period, as demonstrated for spiders in general by Tanner et al (2013). In addition, it has to be kept in mind that our results only present a "snapshot" of the system due to the limited sampling period. The damaging impact of the sweep net on flowering plants prevented a second as well as an earlier sampling (especially for the fragile Himalayan balsam stands).

Conclusions

In our studied urban environments, we found contrasting impacts of flowering American goldenrods and Himalayan balsam on plant-dwelling spiders. While both invasive plants had only minor impacts on total spider abundances and family compositions, they influenced the two most common families as well as the guild structure. Himalayan balsam negatively affected numbers of Philodromidae and free hunting spiders, with no positive effects on other groups. Removal of Himalayan balsam might therefore restore native spider communities (see also Tanner et al. 2013), but might also eliminate an important food resource for some pollinators in late summer (Davis et al. 2018).

Presence of American goldenrods had a positive influence on crab spider abundance, but a negative impact on web-builder abundance. Furthermore, total spider abundance was not negatively affected by this plant invader in our study. For American goldenrods, we therefore corroborate the hypothesis that some animal groups (in this case crab spiders) use non-native plant species as a habitat analogue and might be facilitated by the presence of the alien plant to some extent (Davis et al. 2018; Rodriguez 2006; Russo et al. 2016). Based on our results, conservationists and administration should consider that a large-scale removal of invasive American goldenrod stands (Fenesi et al. 2015; Morón et al. 2009) during flowering season could negatively influence local spider abundances due to habitat loss. Additionally, mechanical mulching of goldenrod stands probably increases mortality of juvenile crab spiders dwelling on this plant invader. Compensation measures like sowing of native wildflower seeds with regional origin near the focal area or exclusion of ruderalized native vegetation from management activities like mowing might help to maintain local resources for those groups during and after the removal of this invasive plant invader.

It has to be kept in mind that our results are limited due to the single sampling event, and, more importantly, the impact of both invaders might strongly vary depending on the "novelty" of the ecosystem and the extent of habitat domination (see also Packer et al. 2016). For example, if American goldenrod species or Himalayan balsam invade protected conservation areas and replace diverse and structurally rich native plant communities, negative effects on insects and other arthropods can be assumed (Fenesi et al. 2015; Moroń et al. 2009).

In conclusion, we call for an integrated approach in the management of non-native plant invaders that keeps in mind the potential of plant invaders to facilitate some native arthropod groups, especially in urban and other novel habitats.

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Author contributions All authors contributed to the study conception and design. Material preparation, field work and data preparation were performed by Daria A. Bäte, Fabian Kempfer and Tobias Bauer. Analysis of data was performed by Tobias Bauer and Jens Schirmel. The manuscript was written by Tobias Bauer and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Code availability Standard R-codes from open access-sources described in the "Material and Methods" section were used.

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval Non-applicable.

Consent to participate Non-applicable.

Consent for publication All authors have consented to publish the revised version of the manuscript as it was submitted.

References

Balkenhol B, Gebauer P, Lehmitz R (2018) Steeplebushes conquer the countryside: influence of invasive plant species on spider communities (Araneae) in former wet meadows. Biodivers Conserv 27:2257–2274. https://doi.org/10.1007/s10531-018-1536-8

Bates D, Maechler M, Bolker B et al. (2019) Package'lme4'. Version 1.1–21

Beerling DJ, Perrins JM (1993) *Impatiens Glandulifera* Royle (Impatiens Roylei Walp.). J Ecol 81:367–382

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biol Lett 12:20150623. https://doi.org/10.1098/rsbl.2015.0623

Blick T, Finch O-D, Harms KH, Kiechle J, Kielhorn et al (2016) Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae)Deutschlands. 3. Fassung, Stand April 2008, einzelne Änderungen und Nachträge bis August 2015. Naturschutz und Biologische Vielfalt 70(4):383-510

Boal CW, Dykstra CR (2018) Urban raptors: ecology and conservation of birds of prey in cities. Island Press, Washington, D.C.

Bolker B (2020): Function overdisp_fun. https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html

Bradley R (1993) The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). J Arachnol 21:91–106

Bradley RA (2013) Common spiders of North America. University of California Press, Berkeley

Buchholz S (2010) Ground spider assemblages as indicators for habitat structure in inland sand ecosystems. Biodivers Conserv 19:2565–2595

Buchholz S, Tietze H, Kowarik I, Schirmel J (2015) Effects of a major tree invader on urban woodland arthropods. PLoS ONE 10(9):e0137723. https://doi.org/10.1371/journal.pone.0137723

Buchholz S, Hannig K, Möller M, Schirmel J (2018) Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. Urban Ecosyst 21:1139–1149. https://doi.org/10.1007/s11252-018-0786-2

Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. PLoS ONE 6(6):e21710

Clausen IHS (1986) The use of spiders as ecological indicators. Bull Br Arachnol Soc 7(3):83–86

Čuda J, Vítková M, Albrechtová M et al (2017) Invasive herb *Impatiens glandulifera* has minimal impact on multiple components of temperate forest ecosystem function. Biol Invasions 19:3051–3066. https://doi.org/10.1007/s10530-017-1508-z

Davis ES, Kelly R, Maggs CA, Stout JC (2018) Contrasting impacts of highly invasive plant species on flower-visiting insect communities. Biodivers Conserv 27:2069–2085. https://doi.org/10.1007/s10531-018-1525-y

Dostál P, Müllerová J, Pyšek P et al (2013) The impact of an invasive plant changes over time. Ecol Lett 16:1277–1284. https://doi.org/10.1111/ele.12166

Dudek K, Michlewicz M, Dudek M, Tryjanowski P (2016) Invasive Canadian goldenrod (*Solidago canadensis* L.) as a preferred foraging habitat for spiders. Arthropod Plant Interact 10:377–381. https://doi.org/10.1007/s11829-016-9455-7

Eckert S, Möller M, Buchholz S (2017) Grasshopper diversity of urban wastelands is primarily boosted by habitat factors. Insect Conserv Diver 10(3):248–257

Entling W, Schmidt MH, Bacher S et al (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Glob Ecol Biogeogr 16:440–448

European Union (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A32014R1143

Fenesi A, Vágási CI, Beldean M et al (2015) *Solidago canadensis* impacts on native plant and pollinator communities in different-aged old fields. Basic Appl Ecol 16:335–346. https://doi.org/10.1016/j.baae.2015.03.003

Foelix RF (2011) Biology of spiders. Oxford University Press, New York

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks CA

Gawryszewski FM, Calero-Torralbo MA, Gillespie RG et al (2017) Correlated evolution between coloration and ambush site in predators with visual prey lures. Evolution 71(8):2010–2021

Gerber E, Krebs C, Murrell C, Moretti M, Rocklin R, Schaffner U (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biol Conserv 141(3):646–654

Greenwood P, Kuhn NJ (2014) Does the invasive plant, *Impatiens glandulifera*, promote soil erosion along the riparian zone? An investigation on a small watercourse in northwest Switzerland. J Soils Sediments 14:637–650. https://doi.org/10.1007/s11368-013-0825-9

Hänggi A, Stöckli E, Nentwig W (1995) Lebensräume Mitteleuropäischer Spinnen. Charakterisierung der Lebensräume der häufigsten Spinnenarten Mitteleuropas und der mit diesen vergesellschafteten Arten. Centre suisse de cartographie de la fauna (CSCF).

Harry I, Höfer H, Schielzeth H, Assmann T (2019) Protected habitats of natura 2000 do not coincide with important diversity hotspots of arthropods in mountain grasslands. Insect Conserv Divers 12:329–338

Hartig F (2020) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.3.0. http://florianhartig.github.io/DHARMa

Hausmann SL, Petermann JS, Rolff J (2016) Wild bees as pollinators of city trees. Insect Conserv Divers 9:97–107

Heiling AM, Cheng K, Herberstein ME (2004) Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). Behav Ecol 15:321–326

Hejda M, Pyšek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biol Conserv 132:143–152. https://doi.org/10.1016/j.biocon.2006.03.025

Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97(3):393–403

Heller G (1976) Zum Beutefangverhalten der ameisenfressenden Spinne *Callilepis nocturna* (Arachnida: Araneae: Drassodidae). Entomol Ger 3:100–103

Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. NeoBiota 31:1–18. https://doi.org/10.3897/neobiota.31.6960

Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J Appl Ecol 43:43–50. https://doi.org/10.1111/j.1365-2664.2005.01102.x

Hulme PE, Pyšek P, Jarošík V et al (2013) Bias and error in understanding plant invasion impacts. Trends Ecol Evol 28:212–218. https://doi.org/10.1016/j.tree.2012.10.010

Huseynov EF (2007a) Natural prey of the lynx spider *Oxyopes lineatus* (Araneae: Oxyopidae). Entomol Fenn 18:144–148

Huseynov EF (2007b) Natural prey of the crab spider *Thomisus onustus* (Araneae: Thomisidae), an extremely powerful predator of insects. J Nat Hist 41:2341–2349

Huseynov EF (2008) Natural prey of the spider *Tibellus macellus* (Araneae Philodromidae). Arachnology 14(4):206–208. https://doi.org/10.13156/100.014.0403

Kahle D, Wickham H, Kahle MD (2019). Package 'ggmap'. https://cran.r-project.org/web/packages/ggmap/ggmap.pdf

Karlsruhe R (1999) Landschaften und Böden im Regierungsbezirk Karlsruhe. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart

Kowarik I (1995) On the role of alien species in urban flora and vegetation. In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam, pp 85–103

Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. Ecol Lett 10:539–550. https://doi.org/10.1111/j.1461-0248.2007.01055.x

Lubin YD (1978) Seasonal abundance and diversity of web-building spiders in relation to habitat structure on Barro Colorado Island, Panama. J Arachnol 6:31–51

Lynch HJ, Thorson JT, Shelton AO (2014) Dealing with under- and over-dispersed count data in life history, spatial, and community ecology. Ecology 95:3173–3180. https://doi.org/10.1890/13-1912.1

Maerz JC, Blossey B, Nuzzo V (2005) Green frogs show reduced foraging success in habitats invaded by Japanese knotweed. Biodiv Conserv 14(12):2901–3291

Magnusson A, Skaug H, Nielsen A et al (2019) Package 'glmmTMB'. R Package Version 0.2.3

Mestre L, Schirmel J, Hetz J et al (2018) Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. Agric Ecosyst Environ 267:141–146. https://doi.org/10.1016/j.agee.2018.08.018

Mestre L, Narimanov N, Menzel F, Entling MH (2020) Non-consumptive effects between predators depend on the foraging mode of intraguild prey. J Anim Ecol. https://doi.org/10.1111/1365-2656.13224

Moroń D, Lenda M, Skórka P et al (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. Biol Conserv 142:1322–1332. https://doi.org/10.1016/j.biocon.2008.12.036

Morse DH (1983) Foraging patterns and time budgets of the crab spiders *Xysticus emertoni* Keyserling and *Misumena vatia* (Clerck) (Araneae: Thomisidae) on flowers. J Arachnol 11:87–94

Morse DH (2000) Flower choice by naive young crab spiders and the effect of subsequent experience. Anim Behav 59:943–951

Nehring S, Kowarik I, Rabitsch W, Essl F (2013) Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde Gefäßpflanzen. BfN-Skripten 352:1–202

Nentwig W (1986) Non-webbuilding spiders: prey specialists or generalists? Oecologia 69(4):571–576

Nentwig W, Bacher S, Kumschick S et al (2018) More than "100 worst" alien species in Europe. Biol Invasions 20:1611–1621. https://doi.org/10.1007/s10530-017-1651-6

Nentwig W, Blick T, Bosmans R, Gloor D, Hänggi A, Kropf C (2019) Spinnen Europas. Version 10.2019. Online https://www.araneae.nmbe.ch

Novgorodova TA, Gavrilyuk AV (2012) The degree of protection different ants (Hymenoptera: Formicidae) provide aphids (Hemiptera: Aphididae) against aphidophages. Eur J Entomol 109:187–196. https://doi.org/10.14411/eje.2012.025

Oksanen AJ, Blanchet FG, Friendly M, et al (2017) Package 'vegan'. https://cran.r-project.org/web/packages/vegan/vegan.pdf

Packer JG, Delean S, Kueffer C et al (2016) Native faunal communities depend on habitat from non-native plants in novel but not in natural ecosystems. Biodivers Conserv 25:503–523. https://doi.org/10.1007/s10531-016-1059-0

Payne EH, Gebregziabher M, Hardin JW et al (2018) An empirical approach to determine a threshold for assessing overdispersion in poisson and negative binomial models for count data. Commun Stat Simul Comput 47:1722–1738. https://doi.org/10.1080/03610918.2017.1323223

Pearson DE (2009) Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. Oecologia 159:549–558. https://doi.org/10.1007/s00442-008-1241-5

Pekár S (2004) Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae). J Arachnol 32:31–41. https://doi.org/10.1636/s02-15

Pekár S, Toft S, Hrušková M, Mayntz D (2008) Dietary and prey-capture adaptations by which *Zodarion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the Formicinae. Naturwissenschaften 95:233–239. https://doi.org/10.1007/s00114-007-0322-3

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Procheş Ş, Wilson JRU, Richardson DM, Chown SL (2008) Herbivores, but not other insects, are scarce on alien plants. Austral Ecol 33:691–700. https://doi.org/10.1111/j.1442-9993.2008.01836.x

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol Invasions 8:927–939. https://doi.org/10.1007/s10530-005-5103-3

Roháčová M, Drozd P (2009) How many heteropteran species can live on alien goldenrods *Solidago canadensis* and *S. gigantea* in Europe? Biologia (Bratisl) 64:981–993. https://doi.org/10.2478/s11756-009-0151-2

Romero GQ, Vasconcellos-Neto J (2004a) Foraging by the flower-dwelling spider, *Misumenops argenteus* (Thomisidae), at high prey density sites. J Nat Hist 38:1287–1296

Romero GQ, Vasconcellos-Neto J (2004b) Beneficial effects of flower-dwelling predators on their host plant. Ecology 85:446–457. https://doi.org/10.1890/02-0327

Russo L, Nichol C, Shea K (2016) Pollinator floral provisioning by a plant invader: quantifying beneficial effects of detrimental species. Divers Distrib 22:189–198. https://doi.org/10.1111/ddi.12397

Sala OE, Chapin FS, Armesto JJ et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sanders D, Platner C (2007) Intraguild interactions between spiders and ants and top-down control in a grassland food web. Oecologia 150:611–624. https://doi.org/10.1007/s00442-006-0538-5

Schirmel J, Bundschuh M, Entling MH et al (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. Glob Chang Biol 22:594–603. https://doi.org/10.1111/gcb.13093

Seeney A, Eastwood S, Pattison Z, Willby NJ, Bull CD (2019) All change at the water's edge: invasion by non-native riparian plants negatively impacts terrestrial invertebrates. Biol Invasions 21(6):1933–1946. https://doi.org/10.1007/s10530-019-01947-5

Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013

Tanasevitch AV (2020) Linyphid spiders of the World. http://old.cepl.rssi.ru/bio/tan/linyphiidae. Accessed 10 June 2020

Tanner RA, Varia S, Eschen R, Wood S et al (2013) Impacts of an invasive non-native annual weed, *Impatiens glandulifera*, on above-and below-ground invertebrate communities in the United Kingdom. PLoS ONE 8(6):e67271. https://doi.org/10.1371/journal.pone.0067271

Weber E (2000) Biological flora of Central Europe: *Solidago altissima* L. Flora 195:123–134. https://doi.org/10.1016/S0367-2530(17)30960-X

Westrich P (2019) Die Wildbienen Deutschlands, 2nd edn. Eugen Ulmer Verlag, Stuttgart

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. Divers Distrib 12:443–455. https://doi.org/10.1111/j.1366-9516.2006.00265.x

Wise DH (1979) Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving pider species (Araneae: Araneidae). Oecologia 41:289–300

World Spider Catalog (2019) World Spider Catalog. Version 20.5. Natural History Museum Bern. http://wsc.nmbe.ch, accessed on 10 October 2019

Supplementary material

Supplementary material Table 1: Dominating herbaceous vegetation in native comparison plots

Site	Dominant native herbaceous plants
4_solidago_native	*Urtica dioica*
5_solidago_native	*Urtica dioica*
6_solidago_native	*Lythrum salicaria*
7_solidago_native	*Berteroa incana; Achillea millefolium; Brassica sp.*
8_solidago_native	*Lythrum salicaria; Urtica dioica;*
9_solidago_native	*Urtica dioica; Cirsium sp.*
10_solidago_native	*Cirsium* sp; *Rumex acetosa*
11_solidago_native	*Urtica dioica; Foeniculum vulgare*
12_solidago_native	*Urtica dioica; Cirsium sp.*
13_solidago_native	*Cirsium sp; Artemisia vulgaris*
14_solidago_native	*Artemisia vulgaris; Urtica dioica*
15_solidago_native	*Urtica dioica; Foeniculum vulgare; Lapsana communis*
16_solidago_native	*Medicago x varia; Artemisia vulgaris; Achillea millefolium; Silene sp.; Berteroa incana*
17_solidago_native	*Urtica dioica*
18_solidago_native	*Artemisia vulgaris; Cirsium sp.*
19_solidago_native	*Saponaria* sp.; *Mentha* sp.; *Rubus caesius*
20_solidago_native	*Lapsana communis*
21_solidago_native	*Urtica dioica; Rubus caesius; Lythrum salicaria*
2a_impatiens_native	*Urtica dioica; Convolvulus arvensis*
3a_impatiens_native	*Urtica dioica*
4a_impatiens_native	*Cirsium sp.*
5a_impatiens_native	*Urtica dioica*
6a_impatiens_native	*Urtica dioica; Lythrum salicaria*
7a_impatiens_native	*Urtica dioica; Lythrum salicaria*
8a_impatiens_native	*Lythrum salicaria; Phragmites sp; Lamium sp.*
9a_impatiens_native	*Urtica dioica; Convolvulus arvensis; Sambucus nigra*
10a_impatiens_native	*Urtica dioica; Rubus caesius; Lapsana communis*
11a_impatiens_native	*Urtica dioica; Convolvulus arvensis*
12a_impatiens_native	*Urtica dioica*
13a_impatiens_native	*Urtica dioica*
14a_impatiens_native	*Urtica dioica; Chenopodium album*
15a_impatiens_native	*Urtica dioica; Lythrum salicaria*
16a_impatiens_native	*Urtica dioica; Lythrum salicaria; Artemisia vulgaris*
17a_impatiens_native	*Urtica dioica; Lapsana communis*
18a_impatiens_native	*Urtica dioica*
19a_impatiens_native	*Urtica dioica; Rubus sp.*
1a_impatiens_native	*Urtica dioica; Cirsium sp.*
20a_impatiens_native	*Urtica dioica*

Supplementary material Table 2: Cumulated numbers of collected spider specimens per family and guild classification after Cardoso et al. (2011). Individual numbers are shown for plots invaded by American goldenrods (*Solidago canadensis and/or S. gigantea*), invaded by Himalayan balsam (*Impatiens glandulifera*) and for their native reference plots, respectively.

Spider family	**no web**	**American goldenrods**		**Himalayan balsam**	
		Invaded	**Native**	**Invaded**	**Native**
Araneidae	no	8	15	7	4
Dictynidae	no	1	6	2	7
Linyphiidae (Micronetinae)	no	0	1	1	3
Linyphiidae (Linyphiinae)	no	0	0	2	0
Pisauridae	no	4	20	13	13
Tetragnathidae	no	7	24	18	20
Theridiidae	no	14	22	12	22
Anyphaenidae	yes	2	2	4	4
Cheiracanthiidae	yes	0	1	0	1
Clubionidae	yes	3	2	4	0
Philodromidae	yes	32	31	22	41
Salticidae	yes	1	5	1	2
Thomisidae	yes	122	86	32	40

Chapter VI

Synthesis and outlook

Tobias Bauer

Synthesis of Chapter II –IV

Urban grasslands are once again shown to host species-rich and flourishing arthropod assemblages. They neither host conspicuously low numbers of species nor individuals. 10,704 spiders and 2660 ground beetles were sampled (Chapter II), which is well within the range reported from rural grasslands with similar sampling efforts/periods (ARAMOB 2025, but also see Schirmel 2021). 86 species of spiders (Araneae) and 55 species of ground beetles (Araneae) were sampled with pitfall traps and sweep netting from 27 urban grasslands during a limited sampling period over the vegetation period. However, 18 species of spiders and 17 species of ground beetles of conservation according to red lists of the federal state (Nährig *et al.* 2003, Trautner *et al.* 2005) were found in this study, which is rather surprising and demonstrates the high potential of urban grasslands for arthropod conservation in general. Nonetheless, the results of chapter IV show that living in urban areas may come at a cost, with higher environmental stress potentially leading to developmental instabilities and higher activity rates and boldness.

Species of conservation concern (cc) were mainly comprised of xerothermic specialists that prefer dry conditions and low vegetation heights. In general, species of cc remained virtually absent in the most humid and high-grown urban grasslands, which assemblages mostly consisted of common, eurytopic species. The reasons for this remain unclear. A higher sensitivity of endangered wetland species to cutting in summer, which induces more rapid changes in local conditions, may play an important role as well as the rather uniform and structurally poor vegetation encountered. An experimental approach in urban humid grasslands that compares different management systems, including partial mowing and further decreased mowing intensities, could shed light on this problem. For example, Buchholz *et al.* (2018) have shown that infrequently managed urban grassland has a much higher potential for harbouring stenotopic species of humid habitats, especially Linyphiidae (dwarf spiders). Although intensive management did not cause a loss of species of cc in our setting, it negatively affected the number of caught specimens. Landscape factors only played a minor role in our analyses, corroborating the hypothesis that local factors and management play a crucial role in shaping arthropod communities of urban grasslands (e.g. Philpott *et al.* 2014, Buchholz *et al.* 2018). On the other hand, Chapter III shows that urban grassland patches could not compensate the loss of a large grassland reserve located in the same landscape (Hemm *et al.* 2012). Several rare xerothermic spider species found in the reserve were missing from urban grasslands, potentially linked to area or disturbance sensitivity in some species and rather uniform vegetation structures due to management in urban grasslands. Nonetheless, some species were only found outside the reserve in grasslands with different soil or humidity conditions. This again demonstrates the crucial importance of local factors (Philpott *et al.* 2014) and large, well-preserved and little disturbed habitat patches within urban areas (Beninde *et al.* 2015). For a maximum impact of conservation efforts, urban grassland should be extensively managed and consist of well-preserved large and several small habitat patches with varying local conditions, ranging from dry to humid patches. When large patches of dry urban grassland become available, e.g. through conversion of inner city or industrial areas, they should be mainly preserved and not used for construction or further urban consolidation. The Landschaftspark Tegeler Stadtheide, a former airport and large patch of dry grassland, is a modern example on how to develop such areas

and harmonize demand for housing and biodiversity conservation, allowing future generations to experience nature and biodiversity close to the city (Grünberlin 2024).

Outlook and management implications

The results of this study strongly advocate for semi-natural dry grassland presence, restoration or creation in cities and coincides with an increased appreciation of even small dry grassland patches in other landscapes (e.g. Eurasian Dry Grassland Group 2025, Rösch *et al.* 2015). Dry, sparsely vegetated and extensively managed grassland is one of the most promising and powerful tools local stakeholders and administration have for (arthropod) species conservation in temperate regions, as it often naturally present in cities due to anthropogenic activities and soil alteration, such as the nature reserve "Alter Flugplatz" (Hemm *et al.* 2012, Zimmermann 2011). Furthermore, it may be developed/restored from turf grass or eutrophied grassland in parks when managed correctly and the geological and climatic conditions are fitting (Klaus 2013). Native seed material, which is widely available in Germany and other countries (Jedicke *et al.* 2022), can be used for establishing (dry) urban grassland on seed-depleted urban soils. Following an internal technical report of our results and other investigations, this was also recognized by the administration in Karlsruhe, which have now successively increased the amount of urban grassland managed extensively to 25% (Gartenbauamt Karlsruhe 2025). Further efforts also include partial mowing of grasslands to maintain cover and hideouts as well as overwintering retreats (Knapp *et al.* 2022). However, to maintain or restore dry and sparsely vegetated grassland conditions in cities, the continuous removal of biomass is necessary. In addition, an increased mowing frequency or earlier cutting dates to further remove superfluous soil nitrogen and restore nutrient-poor conditions might even be essential at some localities (Bakker *et al.* 2012). Some grasslands with mesic conditions in the study showed clear signs of eutrophication, probably due to dog excrement and nitrogen input by traffic (Cape *et al.* 2004). Subjected to increased mowing frequencies, they likely develop a sparser and more open vegetation than encountered during the study, which will facilitate a greater number of locally endangered arthropods. Mowing is often underestimated in its importance in species-rich grassland conservation and restoration, and topics revolving around mowing and biodiversity are often very superficially communicated by non-governmental conservation agencies in Germany (e.g. NABU 2024). A (further) well-meant decrease in mowing frequencies of dry urban grassland might have a negative effect on species of cc as an increase in soil nitrogen due to anthropogenic and natural deposition (e.g. through nitrogen fixation by species of Fabaceae) might alter vegetation density and height leading to changes in microclimatic conditions and the loss of xerothermic arthropod species (e.g. Markl *et al.* 2022). In addition, the effects of city and park trees and their foliage, especially of species with high N content, may also been an underestimated factor for (dry) urban grassland management and restoration. Decomposing foliage of trees can counteract restoration efforts towards a nutrient-poor state in urban grassland soils through nutrient release from decomposition (Thompson & Kao-Kniffin 2019) and foster conditions not suitable for xerothermic species via shading of grassland. On the other hand, a further decrease in cutting frequencies, e.g. mowing only partially every other year, may facilitate stenotopic species in mesic and humid grassland, especially from the species-rich group of dwarf spiders (Linyphiidae) (Buchholz *et al.* 2018) and also reduce stress and disturbance rates for larger insects such as

grasshoppers. Cutting times and management intensity therefore represent a three-edged sword: On the one hand, mulching and increased mowing frequencies likely reduces the population density of grassland arthropods and creates higher disturbance rates, but, on the other hand, increased mowing frequencies for a certain period **with** removal of biomass can create nutrient-poor and more open conditions that foster xerothermic species of cc. In contrast, in mesic and humid urban grassland, very extensive or irregular management may again foster some stenotopic species of humid conditions by creating relatively stable habitats with little disturbance. This demonstrates that there is no universally valid manual for biodiversity-friendly management in cities. Management must be in line with local environmental conditions of the grassland, with results from arthropod monitoring guiding all decisions on the future of the applied measures.

For improving our understanding of urban grassland management and restoration, following research questions may be of interest:

How does further benign neglect and irregular management of already extensively managed urban grassland influence nutrient cycling in the soil, vegetation and arthropod biodiversity over the long term?

How strong is the influence of the urban matrix on species diversity and abundance in direct comparison of similar-sized urban and rural dry grasslands?

Can species-rich urban grasslands and their arthropod communities be restored from decades-long turf grass cultivation only by a change in management?

How strong is the influence of urban trees on nutrient accumulation and arthropod species compositions in extensively managed urban grassland?

Does increasing connectivity and permeability, for example by extensive and biodiversity-friendly management of roadsides, actively benefit isolated, but extensively managed urban grasslands?

The future of urban grassland

Although often stated to be comparatively cheap (e.g. Klaus 2013), extensive management of grassland requires special machinery for biomass removal and should be accompanied by biodiversity-friendly mowing techniques (Steidle *et al.* 2022) and input of native seed material on depleted soils. In addition, human resources are needed to organize and implement mowing regimes, monitor species occurrences and design signs and webpages informing the public. In summary, this leads to higher costs of extensive management (1-2 cuts per year, biomass removal) in comparison with 3-5 times mulching and self-composting (Gartenbauamt Karlsruhe, pers. comm.). One repeatedly encountered criticism of urban grassland management and restoration is therefore whether such resources should not rather be spent on rural meadows or nature reserves, as cities are men-made and urban grasslands can, given their localization in urban areas and inherent high artificiality and even higher isolation, not maintain biodiversity at a similar level. While it is true that the urban matrix acts as a filter for some species and functional groups as established above, this holds true for rural landscapes as well, especially those dominated by

intensive agriculture (e.g. Duflot *et al.* 2014). Although semi-natural urban grasslands in Europe are under pressure due to climate change, consolidation and other urban-specific threats, they usually do not face destruction or deterioration by agricultural intensification nor abandonment, which are currently the greatest threats to semi-natural grasslands in rural areas ranking even before climate change (Shipley *et al.* 2024). Based on this severe crisis alone, it could be argued that urban grassland is under less pressure than its rural counterpart. Further, urban grasslands in cities are usually part of urban green spaces and managed by a single local administration and are therefore not under agricultural pressure. Measures such as a reduction in cutting frequencies are much easier to implement at a landscape level compared to rural areas with an array of farmers with different ideas on best practices. Lastly, the maybe most important argument for creation, restoration or maintenance of species-rich urban grassland is the conservation of biodiversity within city limits as a potential experience for citizens. Routine experience of biodiversity is crucial to understanding needs and aims of species conservation (Dean *et al.* 2019, Prévot *et al.* 2018). As currently over 50% of the global population lives in cities, a large fraction of people will only experience biodiversity frequently when it is present in their direct surroundings. In addition, not only green space *per se,* but also urban biodiversity is increasingly recognized as a positive influence on human physical, mental and social health as well as overall well-being (Marselle *et al.* 2021). A systematic conservation of biodiversity and species-rich grassland in cities does therefore not only benefit species and satisfy ecologists. It could allow billions of people to experience nature on a daily basis and would benefit humanity on a magnitude of different levels.

Synthesis of Chapter V

Urban areas are rich in alien plants (Kowarik 2008). Although alien plants have, in general, negative effects on native species (Schirmel *et al.* 2016), they can also facilitate native taxa. Himalayan Balsam and American goldenrod species are often described as one of the most invasive plant invaders of terrestrial habitats (e.g. Moroń *et al.* 2009, Tanner & Gange 2020) in Europe, while simultaneously acting as a habitat analogue or food source for several native species, especially generalists such as bumble bees or some true bugs (e.g. Davis *et al.* 2018, Roháčová & Drozd 2009). Our results demonstrate contrasting effects of both invaders on native spiders. With no negative effects found on overall spider abundance, Himalayan balsam had negative effects on Philodromidae and free hunters, while American goldenrod negatively influenced web-builders, but was inhabited by more crab spiders (Thomisidae). The massive bloom of both alien plants in late summer falls into a time that is very poor in flower supply, especially in urban habitats. It is surprising that only goldenrod attracted more crab spiders, which are visually attracted by flowers (Heiling *et al.* 2006). The reasons for this remain unclear, but may be related to the structure of the flower in Himalayan balsam or a restricted set of pollinators that visit the plant. The negative effects in Himalayan balsam may be related to its die off in winter and a high number of ants visiting plant lice (Trophobiosis). Although a relatively large number of spider specimens were recorded in the study (409), the one-time sampling during flowering season may mask a negative effect of both plant invaders on crab spiders during earlier grow stages. Both plants build dense stands that outcompete native species locally. Only the late bloom can be used by crab spiders for lurking on

pollinators. However, thomisids usually mate in spring and early summer (Arachnologische Gesellschaft 2025). This means that the adults only encounter the flowerless stages of plant development and may be negatively affected by a dominance of both plant invaders, as they outcompete native flowers with an earlier bloom. In addition, the dense stands of these plants are structurally poor in comparison with mixed stands of native plant species consisting of grasses and forbs, which may also explain the negative effects of Himalayan Balsam. Web building spider abundance is, for example often positively related to increased vegetation structure (Gómez *et al.* 2016). Both plants outcompete native, structurally rich plant communities, often consisting of a mixture of grasses and forbs. On the other hand, the rich bloom of goldenrod offers plenty of habitat for the juveniles that are active in late summer, which is, as described above, very poor in flower supply.

Figure X: Mowing limits the dominance of invasive American goldenrod (*Solidago* sp.) in urban greenspaces of Karlsruhe to areas difficult to access by machines and workers. Karlsruhe, September 2018.

Management implications

Both plant invaders clearly altered native plant-dwelling spider communities and presence of functional groups. However, they were both inhabited by a large number of native spider individuals, mainly juveniles. This raises questions concerning the removal of these alien plant

invaders in urban habitats, especially during bloom season. Mechanical mulching of flowering plants, as it often happens along roadsides, may be detrimental to local spider populations, especially crab spiders as they were found in very high numbers especially on goldenrod. On the other hand, a dominance of these plant invaders may have negative effects on several groups of arthropods due to outcompeting native species and dense stands that only flower once and very late in summer (Moroń *et al.* 2009, Tanner & Gange 2020). When necessary, removal of both invaders should therefore happen before the flowering season. As the management of green spaces in Karlsruhe creates a mosaic of different vegetation types, ranging from small forest stands to extensively managed grassland over neglected edge areas, targeted removal of Himalayan Balsam and goldenrod is usually not necessary as these plants do not become dominant. Usually, dense stands are only observed locally and remain restricted to small-scale areas (Fig. X) that are not frequently mown in summer.

Alien plants as part of urban green spaces?

Alien plants have become a major part of urban vegetation, especially in novel habitats, over the last decades (Kowarik 2008, 2018). Nonetheless, there is an ongoing debate on how to handle alien plants in general, especially those coined as invasive (e.g. Davis *et al.* 2011, Simberloff & Vilà 2011). The perception of invasive alien plants by local citizens is mostly negative, but also slightly conflictive. For example, In South Africa a majority of citizens perceived plant invaders as negative, but their importance in providing ecosystem services were recognized by a surprisingly large part of the study group (Potgieter *et al.* 2019). In Switzerland, invasive plants are perceived predominantly as negative (Junge *et al.* 2019). In Germany, invasive plants are perceived negatively, especially by a movement that advocates for biodiversity-friendly gardens by mainly using native plants (e.g. Witt 2017). However, several invasive plant species are still readily available in the ornamental plant trade. From an applied conservation and economic perspective, it is clear that the costs of wide-ranging control and eradication of the majority of invasive alien plants clearly outweighs the benefits, at least in Central Europe. As proposed by Kowarik (2018), control and eradication, especially in early stages of invasion, may be important in nature reserves and similar habitats to preserve historic conditions, but in novel habitats control of alien plants may conflict with local interests and wilderness supply in urban areas. Invasive alien plants form a stable part of novel ecosystems such as many urban green spaces and their role as a habitat analogue and food source for native species, especially arthropods, is far from well understood, often conflictive and strongly depending on the taxonomic or functional group studied (e.g. Dudek *et al.* 2016, Hanley *et al.* 2014, Potgieter *et al.* 2019, Schirmel *et al.* 2016, Smith *et al.* 2016, Tallamy *et al.* 2010). Future research should aim at harmonizing perception by citizens, their positive and negative impacts on native biodiversity as well as further ecosystem services and disservices provided by invasive alien plants. This would allow generating more nuanced and individual pictures of invasive alien plant species, helping in the understanding of countermeasures against plant invasions in nature reserves in the public opinion as well as creating a broader acceptance of invasive alien plants as an important part of novel ecosystems in cities.

For improving our understanding of the role of alien plants in urban ecosystems, following research questions may be of interest:

Does lurking for prey on invasive pollinators alter the diet composition of crab spiders in comparison to native plants?

Does the same species of pollinators use certain invasive plants in an urban as well as in a rural setting?

Do large, uniform and unmanaged stands of invasive Solidago or Impatiens-plants alter overwintering success of epigeic spiders and other arthropods?

Does mechanical management of invasive plants, for example along roadsides or during flowering season, lead to local population declines in generalistic plant-dwelling predators such as crab spiders due to habitat loss and higher mortality rates?

How many different pollinator species use invasive goldenrod species or other plant invaders along an urbanization gradient?

Chapter VII

References (Chapter I and VI)

Aerts, R., Honnay, O., & Van Nieuwenhuyse, A. (2018) Biodiversity and human health: mechanisms and evidence of the positive health effects of diversity in nature and green spaces. British medical bulletin 127: 5-22.

Allen, R. C. (2009) The British industrial revolution in global perspective. Cambridge University Press.

Alrahma, A.M., Al Suwaidi, H., AlGurg, R. *et al.* (2023) Results from the United Arab Emirates 2022 report card on physical activity for children and adolescents. Journal of Exercise Science & Fitness 21: 218-225

Arachnologische Gesellschaft (2025) Atlas der Spinnentiere Europas. Retrieved from: https://atlas.arages.de (03.01.2025)

Aram, F., García, E.H., Solgi, E., & Mansournia, S. (2019) Urban green space cooling effect in cities. Heliyon 5: e01339

ARAMOB (2025) Ökologische Daten für die Forschung. Retrieved from: https://aramob.de/de/home. (10.01.2025)

Arnberger, A., & Eder, R. (2012) The influence of green space on community attachment of urban and suburban residents. Urban Forestry & Urban Greening 11: 41-49

Aronson, M. F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., *et al.* (2017) Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment, 15: 189-196

Bach, A., Jedamski, J., Daniels, B., & Roß-Nickoll, M. (2025) From lawns to meadows: spiders (Arachnida: Araneae) as indicators to measure urban grassland restoration success. Urban Ecosystems 28: 1-14

Bach, A., Raub, F., Höfer, H., Ottermanns, R., & Roß-Nickoll, M. (2024) ARAapp: filling gaps in the ecological knowledge of spiders using an automated and dynamic approach to analyze systematically collected community data. Database 2024: baae004.

Bach, A., Roß-Nickoll, M., Holstein, J., Ottermanns, R., Raub, F., Triebel, D. *et al.* (2023) Improved access to arachnological data for ecological research through the ARAMOB data repository, supported by Diversity Workbench and NFDI data pipelines. Arachnologische Mitteilungen: Arachnology Letters 66: 79-85.

Bakker, J.P., Van Diggelen, R., Bekker, R.M., & Marrs, R.H. (2012) Restoration of dry grasslands and heathlands. Restoration ecology: the new frontier: 173-188

Batáry, P., Kurucz, K., Suarez-Rubio, M., & Chamberlain, D. E. (2018) Non-linearities in bird responses across urbanization gradients: A meta-analysis. Global Change Biology 24: 1046-1054

Batten L A. (1972) Breeding bird species diversity in relation to increasing urbanisation. Bird study 19: 157-166.

Baumgarten, B., & Rucht, D. (2013) Die Protestierenden gegen „Stuttgart 21 "einzigartig oder typisch?. Stuttgart 21: Ein Großprojekt zwischen Protest und Akzeptanz: 97-125

Baxter-Gilbert, J., Riley, J. L., & Whiting, M. J. (2019) Bold new world: urbanization promotes an innate behavioral trait in a lizard. Behavioral Ecology and Sociobiology 73: 1-10

Behnisch, M., Poglitsch, H., & Krüger, T. (2016) Soil sealing and the complex bundle of influential factors: Germany as a case study. ISPRS International Journal of Geo-Information 5: 132.

Beninde, J., Veith, M., & Hochkirch, A. (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecology letters 18: 581-592

Blick, T., Finch, O.-D., Harms, K.H., Kiechle, J., Kielhorn, K.-H., Kreuels, M., Malten, A. *et al.* (2016) Rote Liste und Gesamtartenliste der Spinnen (Arachnida: Araneae) Deutschlands. 3. Fassung, Stand April 2008, einzelne Änderungen und Nachträge bis August 2015. Naturschutz und Biologische Vielfalt 70: 383-510.

Blum P. (2004) Erlebnis Hardtwald. Der Traum in Grün. Der Kleine Buch Verlag

Boal, C.W., & Dykstra, C.R. (2018) Urban raptors: ecology and conservation of birds of prey in cities. Island Press

Botkin, D.B., & Beveridge, C.E. (1997) Cities as environments. Urban ecosystems 1: 3-19

Bowler, D.E., Buyung-Ali, L., Knight, T. M., & Pullin, A.S. (2010) Urban greening to cool towns and cities: A systematic review of the empirical evidence. Landscape and urban planning 97: 147-155

Branco, M., Nunes, P., Roques, A., Fernandes, M.R., Orazio, C., & Jactel, H. (2019) Urban trees facilitate the establishment of non-native forest insects. NeoBiota 52: 25-46

Bruns, A. (2014) The environmental impacts of megacities on the coast. In: Megacities and the Coast: 22-69

Buchholz, S., Gathof, A.K., Grossmann, A.J., Kowarik, I., & Fischer, L.K. (2020) Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. Landscape and Urban Planning 196: 103731

Buchholz, S., Hannig, K., Möller, M., & Schirmel, J. (2018) Reducing management intensity and isolation as promising tools to enhance ground-dwelling arthropod diversity in urban grasslands. Urban Ecosystems 21: 1139-1149.

Cai, Z., La Sorte, F. A., Chen, Y., & Wu, J. (2023) The surface urban heat island effect decreases bird diversity in Chinese cities. Science of the Total Environment 902: 166200.

Cape, J.N., Tang, Y.S., Van Dijk, N., Love, L., Sutton, M.A., & Palmer, S.C.F. (2004) Concentrations of ammonia and nitrogen dioxide at roadside verges, and their contribution to nitrogen deposition. Environmental Pollution 132: 469-478

CBD (2007) Cities and Biodiversity: Engaging Local Authorities in the Implementation of the Convention on Biological Diversity. UNEP/CBD/COP/9/INF/10

Choi, J., & Kim, G. (2022) History of Seoul's parks and green space policies: focusing on policy changes in urban development. Land 11: 474

Cohen, B. (2015) Urbanization, City Growth, and the New United Nations Development Agenda. The Official Journal of the World Coal Industry 3:4-7

Colding, J., Gren, Å., & Barthel, S. (2020) The incremental demise of urban green spaces. Land 9: 162

Coppel, G., & Wüstemann, H. (2017). The impact of urban green space on health in Berlin, Germany: Empirical findings and implications for urban planning. Landscape and Urban Planning 167: 410-418

Crespo, L.C., Silva, I., Borges, P.A., & Cardoso, P. (2014) Assessing the conservation status of the strict endemic Desertas wolf spider, Hogna ingens (Araneae, Lycosidae). Journal for Nature Conservation 22: 516-524

Davis, E.S., Kelly, R., Maggs, C.A., & Stout, J.C. (2018) Contrasting impacts of highly invasive plant species on flower-visiting insect communities. Biodiversity and Conservation 27: 2069-2085

Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J. *et al.* (2011) Don't judge species on their origins. Nature 474: 153-154.

Dawson, R. (2018) How are cities planning to respond to climate change? Assessment of local climate plans from 885 cities in the EU-28. Journal of cleaner production, 191, 207-219

De Coster, G., Van Dongen, S., Malaki, P., Muchane, M., Alcántara-Exposito, A., Matheve, H., & Lens, L. (2013) Fluctuating asymmetry and environmental stress: understanding the role of trait history. PLoS One: 8: e57966

Dean, A.J., Barnett, A.G., Wilson, K.A., & Turrell, G. (2019) Beyond the 'extinction of experience'–Novel pathways between nature experience and support for nature conservation. Global Environmental Change 55: 48-57.

Deilami, K., Kamruzzaman, M., & Liu, Y. (2018) Urban heat island effect: A systematic review of spatio-temporal factors, data, methods, and mitigation measures. International journal of applied earth observation and geoinformation 67: 30-42.

Des Roches, S., Brans, K.I., Lambert, M.R., Rivkin, L.R., Savage, A.M., Schell, C. J., *et al.* (2021) Socio-eco-evolutionary dynamics in cities. Evolutionary Applications 14: 248-267

Diener, A., & Mudu, P. (2021) How can vegetation protect us from air pollution? A critical review on green spaces' mitigation abilities for air-borne particles from a public health perspective-with implications for urban planning. Science of the Total Environment 796: 148605

Dostál, P., Müllerová, J., Pyšek, P., Pergl, J., & Klinerová, T. (2013) The impact of an invasive plant changes over time. Ecology letters 16: 1277-1284.

Du, H., Cai, W., Xu, Y., Wang, Z., Wang, Y., & Cai, Y. (2017) Quantifying the cool island effects of urban green spaces using remote sensing Data. Urban Forestry & Urban Greening 27: 24-31

Dudek, K., Michlewicz, M., Dudek, M., & Tryjanowski, P. (2016) Invasive Canadian goldenrod (*Solidago canadensis* L.) as a preferred foraging habitat for spiders. Arthropod-Plant Interactions 10: 377-381

Duflot, R., Georges, R., Ernoult, A., Aviron, S., & Burel, F. (2014) Landscape heterogeneity as an ecological filter of species traits. Acta Oecologica 56: 19-26

Dzhambov, A.M., & Dimitrova, D.D. (2014) Urban green spaces′ effectiveness as a psychological buffer for the negative health impact of noise pollution: A systematic review. Noise and health 16: 157-165.

Ebeling, S.K., Hensen, I., & Auge, H. (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. Diversity and Distributions 14: 225-233

Eckert, S., Möller, M., & Buchholz, S. (2017) Grasshopper diversity of urban wastelands is primarily boosted by habitat factors. Insect Conservation and Diversity 10: 248-257

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R., & Nentwig, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Global ecology and biogeography 16: 440-448

Environmental Atlas Berlin (2021): Impervious soil coverage in Berlin. Retrieved from: https://www.berlin.de/umweltatlas/en/soil/impervious-soil-coverage/2021/map-description (14. Jan. 2025)

Eurasian Dry Grassland Group (2025) Eurasian Dry Grassland Group. Retrieved from https://edgg.org. (21.02.2025)

Eurostats (2025) Performance of the agricultural sector. Retrieved from https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Performance_of_the_agricultural_sector (02.02.2025)

Farrell, C.R. (2016) Immigrant suburbanisation and the shifting geographic structure of metropolitan segregation in the United States. Urban Studies 53: 57-76.

Fekete, R., Valkó, O., Fischer, L.K., Deák, B., & Klaus, V.H. (2024) Ecological restoration and biodiversity-friendly management of urban grasslands–A global review on the current state of knowledge. Journal of Environmental Management 368: 122220.

Fenoglio, M.S., Rossetti, M. R., & Videla, M. (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. Global Ecology and Biogeography 29: 1412-1429.

Firebaugh, G. (1979) Structural determinants of urbanization in Asia and Latin America, 1950-1970. American Sociological Review 44: 199-215.

Garreau, J., (1992) Edge City: Life on the New Frontier. Knopf Doubleday

Gartenbauamt Karlsruhe (2025) Artenreiche Grünpflege. Retrieved from: https://www.karlsruhe.de/umwelt-klima/stadtgruen-wald/baeume-und-stadtvegetation/naturnahe-gruenpflege (01.01.2025)

Gartenbauamt Karlsruhe (2025) https://www.karlsruhe.de/umwelt-klima/stadtgruen-wald/baeume-und-stadtvegetation/naturnahe-gruenpflege

GDV (2023) Versiegelungsstudie: Ludwigshafen ist die am stärksten versiegelte Stadt in Deutschland. Retrieved from https://www.gdv.de/gdv/medien/medieninformationen/versiegelungsstudie-ludwigshafen-ist-die-am-staerksten-versiegelte-stadt-in-deutschland--133126 (02.03.2025)

Genovesi, P. (2005) Eradications of invasive alien species in Europe: a review. Biological invasions 7: 127-133

Gezer, Ö. & Popp, M. (2013) Das große Aufräumen. Der Spiegel 30/2013

Gilbert, B., & Levine, J.M. (2013) Plant invasions and extinction debts. Proceedings of the National Academy of Sciences, 110: 1744-1749

Giménez-Nadal, J.I., Molina, J.A., & Velilla, J. (2022) Trends in commuting time of European workers: A cross-country analysis. Transport Policy 116: 327-342

Gleeson, B., & Low, N. (2000) Cities as consumers of the world's environment. Consuming cities: The urban environment in the global economy after the Rio Declaration: 1-29

Godefroid, S., & Ricotta, C. (2018) Alien plant species do have a clear preference for different land uses within urban environments. Urban Ecosystems 21: 1189-1198

Gómez, J.E., Lohmiller, J., & Joern, A. (2016) Importance of vegetation structure to the assembly of an aerial web-building spider community in North American open grassland. The Journal of Arachnology 44: 28-35

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L. *et al.* (2008) Global change and the ecology of cities. science 319: 756-760

Grossmann, A.J., Herrmann, J., Buchholz, S., & Gathof, A.K. (2022) Dry grassland within the urban matrix acts as favourable habitat for different pollinators including endangered species. Insect Conservation & Diversity 16: 97-109

Grünberlin (2024) Landschaftspark Tegeler Heide. Retrieved from https://gruen-berlin.de/projekte/urbane-freiraeume/landschaftsraum-tegel-tegeler-stadtheide/ueber-das-projekt. 10.02.2025

Grutters, B.M., Pollux, B.J., Verberk, W.C., & Bakker, E.S. (2015) Native and non-native plants provide similar refuge to invertebrate prey, but less than artificial plants. PLoS One 10: e0124455

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS one 12: e0185809.

Hanley, M.E., Awbi, A.J., & Franco, M. (2014) Going native? Flower use by bumblebees in English urban gardens. Annals of Botany 113: 799-806.

Harvey, J.A., Heinen, R., Armbrecht, I., Basset, Y., Baxter-Gilbert, J. H., Bezemer, T. M., *et al.* (2020) International scientists formulate a roadmap for insect conservation and recovery. Nature Ecology & Evolution 4: 174-176

Heiling, A.M., Cheng, K., & Herberstein, M.E. (2006) Picking the right spot: crab spiders position themselves on flowers to maximize prey attraction. Behaviour 143: 957-968.

Hemm, V., Meyer, F., & Höfer, H. (2012) Die epigäische Spinnenfauna (Arachnida, Araneae) in Sandrasen, Borstgrasrasen und Ruderalfluren im Naturschutzgebiet „Alter Flugplatz Karlsruhe “. Arachnologische Mitteilungen 44: 20-40.

Hesse, M., & Siedentop, S. (2018) Suburbanisation and suburbanisms–Making sense of continental European developments. Raumforschung und Raumordnung| Spatial Research and Planning 76: 97-108

Holgersen, S., & Malm, A. (2015) “green fix” as crisis management. or, in which world is Malmö the world's greenest city? Geografiska Annaler: Series B, Human Geography 97: 275-290.

Horák, J. (2018) The role of urban environments for saproxylic insects. Saproxylic Insects: Diversity, Ecology and Conservation: 835-846

Hulme, P.E. (2021) Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. One Earth 4: 666-679

Hutchings, P., Willcock, S., Lynch, K. *et al.* (2022) Understanding rural–urban transitions in the Global South through peri-urban turbulence. Nature Sustainability 5: 924–930

IUCN (2023) Cities and nature. Retrieved from: https://iucn.org/resources/issues-brief/cities-and-nature. 21.02.2025

Jacobs II, P.W., & Conlin, D.A. (2014) Campus Martius. Cambridge University Press.

Jaret, C., Ghadge, R., Reid, L.W., & Adelman, R.M. (2009) The measurement of suburban sprawl: an evaluation. City & Community 8: 65-84.

Jedicke, E., Aufderheide, U., Bergmeier, E., Betz, O., Brunzel, S., Eckerter, P., *et al.* (2022) Gebietseigenes Saatgut–Chance oder Risiko für den Biodiversitätsschutz? Ein Thesenpapier zur Umsetzung des § 40 BNatSchG. Naturschutz und Landschaftsplanung 54: 12-21

Junge, X., Hunziker, M., Bauer, N., Arnberger, A., & Olschewski, R. (2019) Invasive alien species in Switzerland: Awareness and preferences of experts and the public. Environmental management 63: 80-93.

Klaus V.H. (2013) Urban grassland restoration: a neglected opportunity for biodiversity conservation. Restoration Ecology 21: 665-669.

Knapp, M., Štrobl, M., Venturo, A., Seidl, M., Jakubíková, L., Tajovský, K., *et al.* (2022) Importance of grassy and forest non-crop habitat islands for overwintering of ground-dwelling arthropods in agricultural landscapes: A multi-taxa approach. Biological Conservation 275: 109757.

Knoll, M., Lubken, U., & Schott, D. (Eds.). (2017) Rivers lost, rivers regained: Rethinking city-river relations. University of Pittsburgh Press.

Kondo, M.C., Fluehr, J.M., McKeon, T., & Branas, C.C. (2018) Urban green space and its impact on human health. International journal of environmental research and public health 15: 445

Kowarik, I. (2008) On the role of alien species in urban flora and vegetation. Urban ecology: An international perspective on the interaction between humans and nature: 321-338

Kowarik, I. (2011) Novel urban ecosystems, biodiversity, and conservation. Environmental pollution 159: 1974-1983

Kowarik, I. (2018) Urban wilderness: Supply, demand, and access. Urban Forestry & Urban Greening: 29: 336-347

Kühn, I., Brandl, R., & Klotz, S. (2004) The flora of German cities is naturally species rich. Evolutionary ecology research 6: 749-764

Langgut, D. (2022) Prestigious Early Roman gardens across the Empire: The significance of gardens and horticultural trends evidenced by pollen. Palynology 46: 1-17

Lawler, D. (2018) The global cities with the most and least green space. Axios. Retrieved from: https://www.axios.com/2018/05/03/the-cities-with-the-most-green-space-around-the-world. (12.01.2025)

Lazić, M.M., Kaliontzopoulou, A., Carretero, M.A., & Crnobrnja-Isailović, J. (2013) Lizards from urban areas are more asymmetric: using fluctuating asymmetry to evaluate environmental disturbance. PloS one: 8: e84190

Lee, K.S. (2007) Infant mortality decline in the late 19th and early 20th centuries: the role of market milk. Perspectives in Biology and Medicine 50: 585-602

Leonard, L. (2023) How to Be More Sustainable in Suburbia. EcoWatch. Retrieved from https://www.ecowatch.com/suburban-sustainability-tips-ecowatch.html (17.2.2025)

Lepczyk, C.A., Aronson, M.F., & La Sorte, F.A. (2023) Cities as sanctuaries. Frontiers in Ecology and the Environment, 21: 251-259

Leveau, L. M., Bocelli, M. L., Quesada-Acuña, S.G., González-Lagos, C., Tapia, P.G., *et al.* (2022) Bird diversity-environment relationships in urban parks and cemeteries of the Neotropics during breeding and non-breeding seasons. PeerJ 10: e14496.

Lin, K. L. (2010) Determining key ecological indicators for urban land consolidation. International Journal of Strategic Property Management 14: 89-103

Litman, T. (2020) Parking management best practices. Routledge.

Lokatis, S., & Jeschke, J. M. (2022) Urban biotic homogenization: Approaches and knowledge gaps. Ecological Applications 32: e2703.

Lokatis, S., Jeschke, J. M., Bernard-Verdier, M., Buchholz, S., Grossart, H. P., Havemann, F., *et al.* (2023) Hypotheses in urban ecology: building a common knowledge base. Biological Reviews 98: 1530-1547

Loughran, K. (2020) Urban parks and urban problems: An historical perspective on green space development as a cultural fix. Urban Studies 57: 2321-2338.

Lu, M., Zhou, C., Wang, C., Jackson, R. B., & Kempes, C. P. (2024) Worldwide scaling of waste generation in urban systems. Nature Cities 1: 126-135.

Markl, G., Hinneberg, H., & Tarmann, G. (2022) Drastic decline of extensive grassland species in Central Europe since 1950: Forester moths of the genus *Jordanita* (Lepidoptera, Zygaenidae) as a type example. Ecology and Evolution 12: e9291

Marselle, M.R., Hartig, T., Cox, D.T., De Bell, S., Knapp, S., Lindley, S. *et al.* (2021) Pathways linking biodiversity to human health: A conceptual framework. Environment international 150: 106420

Mattijssen, T., Buijs, A., Elands, B., & Arts, B. (2018) The 'green'and 'self'in green self-governance–a study of 264 green space initiatives by citizens. Journal of Environmental Policy & Planning, 20: 96-113

Mazza, G., Tricarico, E., Genovesi, P., & Gherardi, F. (2014) Biological invaders are threats to human health: an overview. Ethology Ecology & Evolution, 26:112-129

McKinney, M.L. (2008). Effects of urbanization on species richness: a review of plants and animals. Urban ecosystems, 11, 161-176.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., *et al.* (2018) Body-size shifts in aquatic and terrestrial urban communities. Nature 558: 113-116

Mi, Z., Guan, D., Liu, Z., Liu, J., Viguié, V., Fromer, N., & Wang, Y. (2019) Cities: The core of climate change mitigation. Journal of Cleaner Production 207: 582-589

Modelski, G. (2003) World cities: -3000 to 2000. Faros 2000

Möller, M., Blick, T., & Buchholz, S. (2019) Spinnen der Trockenrasen in und um Berlin–Vielfalt, Verbreitung und Gefährdung. Arachnologische Mitteilungen: Arachnologische Mitteilungen 58: 52-61

Moroń, D., Lenda, M., Skórka, P., Szentgyörgyi, H., Settele, J., & Woyciechowski, M. (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. Biological Conservation 142: 1322-1332.

NABU (2024) Mähfreier Mai. Retrieved from: https://nabu-bretten.jimdoweb.com/tiere-pflanzen/naturmomente-1/m%C3%A4hfreier-mai-1 (10.01.2025)

Nährig, D., Harms, K. H., Rausch, H., Schwaller, W., Spelda, J., Bellmann, B. H., *et al.* (2003) Rote Listen und Checklisten der Spinnen in Baden-Württemberg. LUBW. Mannheim. 203 pp.

Nentwig, W., Bacher, S., Kumschick, S., Pyšek, P., & Vilà, M. (2018) More than "100 worst" alien species in Europe. Biological invasions 20: 1611-1621.

Nguyen, M.H., & Jones, T.E. (2022) Predictors of support for biodiversity loss countermeasure and bushmeat consumption among Vietnamese urban residents. Conservation Science and Practice 4: e12822.

Niemets, K., Kravchenko, K., Kandyba, Y., Kobylin, P., & Morar, C. (2021) World cities in terms of the sustainable development concept. Geography and Sustainability, 2 304-311

Niemiera, A.X., & Holle, B.V. (2009) Invasive plant species and the ornamental horticulture industry. Management of invasive weeds: 167-187

Nowak, D.J., & Greenfield, E.J. (2012) Tree and impervious cover change in US cities. Urban Forestry & Urban Greening 11: 21-30

Paap, T., Burgess, T. I., & Wingfield, M. J. (2017) Urban trees: bridge-heads for forest pest invasions and sentinels for early detection. Biological invasions 19: 3515-3526

Packer, J.G., Delean, S., Kueffer, C. *et al.* (2016) Native faunal communities depend on habitat from non-native plants in novel but not in natural ecosystems. Biodiversity Conservation 25:503–523

Padovani, R.J., Salisbury, A., Bostock, H., Roy, D. B., & Thomas, C.D. (2020) Introduced plants as novel Anthropocene habitats for insects. Global change biology 26: 971-988.

Partecke, J., Schwabl, I., & Gwinner, E. (2006) Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecology 87: 1945-195

Paudel, S., & States, S. L. (2023) Urban green spaces and sustainability: Exploring the ecosystem services and disservices of grassy lawns versus floral meadows. Urban forestry & urban greening 84: 127932.

Paul, J. (2022) Work from home behaviors among US urban and rural residents. Journal of Rural Studies 96: 101-111.

Philpott, S. M., Cotton, J., Bichier, P., Friedrich, R. L., Moorhead, L. C., Uno, S., & Valdez, M. (2014) Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. Urban Ecosystems 17: 513-532.

Pincetl, S. (2013) Urban ecology and nature's services infrastructure: Policy implications of the million trees initiative of the city of Los Angeles. In: urbanization and sustainability: Linking urban ecology, environmental justice and global environmental change: 61-74

Piquet, A., Piano, E., Tolve, M., & Isaia, M. (2024) City as a filter: urban density affects taxonomic and functional diversity of foliage dwelling spiders. Landscape Ecology 40: 3

Potgieter, L. J., Gaertner, M., O'Farrell, P. J., & Richardson, D. M. (2019) Perceptions of impact: invasive alien plants in the urban environment. Journal of environmental management, 229: 76-87

PRB (2007) World population. Retrieved from https://www.prb.org/resources/world-population-highlights-2007-urbanization. (18.12.2024)

Prévot, A. C., Cheval, H., Raymond, R., & Cosquer, A. (2018) Routine experiences of nature in cities can increase personal commitment toward biodiversity conservation. Biological conservation 226: 1-8

Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. Journal of Biogeography 25: 155-163

Reckien, D., Lwasa, S., Satterthwaite, D., McEvoy, D., Creutzig, F., Montgomery, M. *et al.* (2018) Equity, environmental justice, and urban climate change. In Climate change and cities: Second assessment report of the urban climate change research network (pp. 173-224). Cambridge University Press.

Rega-Brodsky, C. C., Aronson, M. F., Piana, M. R., Carpenter, E. S., Hahs, A. K., Herrera-Montes, A. *et al.* (2022) Urban biodiversity: State of the science and future directions. Urban Ecosystems 25: 1083-1096

Richardson, D. M., & Rejmánek, M. (2011) Trees and shrubs as invasive alien species–a global review. Diversity and distributions 17: 788-809.

Riffat, S., Powell, R., & Aydin, D. (2016) Future cities and environmental sustainability. Future cities and Environment 2: 1-23.

Rodriguez, L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological invasions 8: 927-939.

Rogers, A. M., Yong, R. Q., & Holden, M. H. (2023) The house of a thousand species: The untapped potential of comprehensive biodiversity censuses of urban properties. Ecology 105: e4225

Roháčová, M., & Drozd, P. (2009) How many heteropteran species can live on alien goldenrods *Solidago canadensis* and *S. gigantea* in Europe? Biologia 64: 981-993

Rösch, V., Tscharntke, T., Scherber, C., & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia 179: 209-222

Rosenzweig, M.L. (1995) Species Diversity in Space and Time. Cambridge University Press, New York

Roser, M. (2023) Employment in Agriculture. Retrieved from https://ourworldindata.org/employment-in-agriculture. (12.2.2025)

Salter, C. M., Ahn, R., Yasin, F., Hines, R., Kornfield, L., Salter, E. C., & Burke, T. F. (2015) Community noise, urbanization, and global health: Problems and solutions. Innovating for Healthy Urbanization: 165-192

Salvati, L. (2014) The spatial pattern of soil sealing along the urban-rural gradient in a Mediterranean region. Journal of Environmental Planning and Management 57: 848-861

Sánchez, F. G., Solecki, W.D., & Batalla, C.R. (2018) Climate change adaptation in Europe and the United States: A comparative approach to urban green spaces in Bilbao and New York City. Land use policy 79: 164-173

Schäfer, J., Weiser, H., Winiwarter, L., Höfle, B., Schmidtlein, S., & Fassnacht, F.E. (2023) Generating synthetic laser scanning data of forests by combining forest inventory information, a tree point cloud database and an open-source laser scanning simulator. Forestry: An International Journal of Forest Research 96: 653-671

Schirmel, J. (2021) COVID-19 pandemic turns life-science students into "citizen scientists": Data indicate multiple negative effects of urbanization on biota. Sustainability 13: 2992

Schirmel, J., Bundschuh, M., Entling, M.H., Kowarik, I., & Buchholz, S. (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. Global change biology: 22: 594-603

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen *et al.* (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574: 671-67

Shipley, J.R., Frei, E. R., Bergamini, A., Boch, S., Schulz, T., Ginzler, C., *et al.* (2024) Agricultural practices and biodiversity: Conservation policies for semi-natural grasslands in Europe. Current Biology 34: R753-R761

Simberloff, D., & Vilà, M. (2011) Non-natives: 141 scientists object. Nature 475: 36

Small, E.C., Sadler, J.P., & Telfer, M.G. (2002) Carabid beetle assemblages on urban derelict sites in Birmingham, UK. Journal of Insect Conservation 6: 233-246

Smil, V. (1999) Detonator of the population explosion. Nature 400: 415-415

Smith, J.N., Emlen, D.J., & Pearson, D.E. (2016) Linking native and invader traits explains native spider population responses to plant invasion. PLoS One 11: e0153661.

Smith, L.S., Broyles, M.E., Larzleer, H.K., & Fellowes, M.D. (2015) Adding ecological value to the urban lawnscape. Insect abundance and diversity in grass-free lawns. Biodiversity and conservation 24: 47-62

Soanes, K., & Lentini, P.E. (2019) When cities are the last chance for saving species. Frontiers in Ecology and the Environment 17: 225-231

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot *et al.* (2020) The worldwide impact of urbanisation on avian functional diversity. Ecology Letters 23: 962-972

Stadtwiki Karlsruhe (2025) Heldbock. Retrieved from: https://ka.stadtwiki.net/Heldbock (21.02.2025)

Stankowski, S. J. (1972) Population density as an indirect indicator of urban and suburban land-surface modifications. US Geological Survey Professional Paper 800: 219-224.

Stark, B.L. (2014) Urban gardens and parks in pre-modern states and empires. Cambridge Archaeological Journal, 24: 87-115

Statistisches Landesamt (2025) Bevölkerungsentwicklung Stadtgebiet Karlsruhe. Retrieved from https://www.statistik-bw.de/BevoelkGebiet/GebietFlaeche/01515020.tab?R=BT271 (21.02.2025)

Steidle, J.L., Kimmich, T., Csader, M., & Betz, O. (2022) Negative impact of roadside mowing on arthropod fauna and its reduction with 'arthropod-friendly'mowing technique. Journal of Applied Entomology 146: 465-472

Straka, T. M., Radchuk, V., Kowarik, I., von der Lippe, M., & Buchholz, S. (2025) Urbanization Impacts Top Predators and Alters Biotic Interactions in Predator–Prey–Mutualistic Communities of Urban Dry Grasslands. Ecology and Evolution 15: e70791.

Straka, T.M., von der Lippe, M., Voigt, C. C., Gandy, M., Kowarik, I., & Buchholz, S. (2021) Light pollution impairs urban nocturnal pollinators but less so in areas with high tree cover. Science of the Total Environment 778: 146244.

Sukkopp, H., & Wittig, R. S. (1998) Ein Fachbuch für Studium und Praxis. Spektrum Akademischer Verlag

Tallamy, D.W., Ballard, M., & D'Amico, V. (2010) Can alien plants support generalist insect herbivores?. Biological invasions 12: 2285-2292.

Tanner, R.A., & Gange, A.C. (2020) Himalayan balsam, *Impatiens glandulifera*: its ecology, invasion and management. Weed Research 60: 4-7

Thompson, G.L., & Kao-Kniffin, J. (2019) Urban grassland management implications for soil C and N dynamics: a microbial perspective. Frontiers in Ecology and Evolution 7: 315

Trautner, J., Bräunicke, M., Kiechle, J., Kramer, M., Rietze, J., Schanowski, A., *et al.* (2005) Rote Liste und Artenverzeichnis der Laufkäfer Baden-Württembergs (Coleoptera: Carabidae). LUBW, Mannheim

Tubby, K.V., & Webber, J.F. (2010) Pests and diseases threatening urban trees under a changing climate. Forestry 83: 451-459

Twerd, L., & Banaszak-Cibicka, W. (2019) Wastelands: their attractiveness and importance for preserving the diversity of wild bees in urban areas. Journal of insect conservation 23: 573-588

United Nations (2020) Generating power. Retrieved from: https://www.un.org/en/climatechange/climate-solutions/cities-pollution. 21.02.2025

Unterweger, P.A., Rieger, C., & Betz, O. (2017) The influence of urban lawn mowing regimes on diversity of Heteroptera (Hemiptera). Heteropteron 48: 7-21

Van Wilgen, B.W., Witt, A.B., Beale, T., & Kiambi, S. (2017) A preliminary assessment of the extent and potential impacts of alien plant invasions in the Serengeti-Mara ecosystem, East Africa. Koedoe: African Protected Area Conservation and Science, 59: 1-16

Venn, S. J., Kotze, D. J., Lassila, T., & Niemelä, J.K. (2013) Urban dry meadows provide valuable habitat for granivorous and xerophylic carabid beetles. Journal of insect conservation 17: 747-764

Venn, S., & Kotze, D.J. (2014) Benign neglect enhances urban habitat heterogeneity: Responses of vegetation and carabid beetles (Coleoptera: Carabidae) to the cessation of mowing of park lawns. European Journal of Entomology 111: 703-714

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., & Stopak, D. (2021) Insect decline in the Anthropocene: Death by a thousand cuts. Proceedings of the National Academy of Sciences 118: e2023989118

Walker, W.H., Bumgarner, J.R., Walton, J.C., Liu, J.A., Meléndez-Fernández, O.H., Nelson, R.J., & DeVries, A.C. (2020) Light pollution and cancer. International Journal of Molecular Sciences 21: 9360

Wang, J., Liu, X.D., & Lu, J. (2012) Urban river pollution control and remediation. Procedia Environmental Sciences 13: 1856-1862

Wauters, L.A., Lurz, P.W., Santicchia, F., Romeo, C., Ferrari, N., Martinoli, A., & Gurnell, J. (2023) Interactions between native and invasive species: A systematic review of the red squirrel-gray squirrel paradigm. Frontiers in Ecology and Evolution 11: 1083008

Weeks, J.R. (2010) Defining urban areas. In: Remote sensing of urban and suburban areas: 33-45

Weijs-Perrée, M., Dane, G., & van den Berg, P. (2020) Analyzing the relationships between citizens' emotions and their momentary satisfaction in urban public spaces. Sustainability 12: 7921

Wessolek, G. (2008) Sealing of soils. Urban Ecology: An international perspective on the interaction between humans and nature: 161-179

Whitlock, M.C., McPeek, M.A., Rausher, M.D., Rieseberg, L., & Moore, A.J. (2010) Data archiving. The American Naturalist 175: 145-146

WHO (2017) Urban green spaces: a brief for action. 22 pp. Retrieved from: https://iris.who.int/bitstream/handle/10665/344116/9789289052498-eng.pdf (21.02.2025)

Witt, R. (2017) Das Wildpflanzen Topfbuch. Ausdauernde Arten für Balkon, Terrasse und Garten. Lebendig, pflegeleicht, nachhaltig Selbstverlag Reinhard Witt

Wong, K., Zhang, Y., Tsou, J. Y., & Li, Y. (2017) Assessing impervious surface changes in sustainable coastal land use: A case study in Hong Kong. Sustainability 9: 1029

Yang, L., Qian, F., Song, D. X., & Zheng, K. J. (2016) Research on urban heat-island effect. Procedia engineering 169: 11-18.

Yao, L., Chen, L., Wei, W., & Sun, R. (2015) Potential reduction in urban runoff by green spaces in Beijing: A scenario analysis. Urban Forestry & Urban Greening 14: 300-308

Yeh, A.G. (2011) High density living in Hong Kong. In: Proceedings of the Cities, Health and Well-being conference, London School of Economics and Alfred Herrhausen Society in partnership with the University of Hong Kong, Hong Kong: 31-32

Yu, Q., Ji, W., Pu, R., Landry, S., Acheampong, M., O'Neil-Dunne, J. *et al.* (2020) A preliminary exploration of the cooling effect of tree shade in urban landscapes. International Journal of Applied Earth Observation and Geoinformation 92: 102161.

Zang, J., Zhang, T., Chen, L., Li, L., Liu, W., Yuan, L., *et al.* (2021) Optimization of modelling population density estimation based on impervious surfaces. Land 10: 791

Zeller, V., Towa, E., Degrez, M., & Achten, W. M. (2019) Urban waste flows and their potential for a circular economy model at city-region level. Waste management 83 83-94

Zenkteler, M., Foth, M., & Hearn, G. (2022) Lifestyle cities, remote work and implications for urban planning. Australian Planner 58: 25-35

Zhang, B., Xie, G., Zhang, C., & Zhang, J. (2012) The economic benefits of rainwater-runoff reduction by urban green spaces: A case study in Beijing, China. Journal of environmental management 100: 65-71

Zhang, H. (2024) Urban green space management in ancient Chinese capitals: Case studies of Chang'an, Lin'an and Beijing. International Planning History Society Proceedings 20: 863-878

Zhang, L., You, S., Zhang, M., Zhang, S., Yi, S., & Zhou, B. (2022) The effects of urbanization on air pollution based on a spatial perspective: Evidence from China. Frontiers in Environmental Science 10 1058009.

Zhang, X.Q. (2016) The trends, promises and challenges of urbanisation in the world. Habitat international 54: 241-252

Zimmermann, P. (2011) Der „Alte Flugplatz Karlsruhe ": ein neues Naturschutzgebiet. Carolinea 69: 139-163

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Status and author contributions included in the thesis

The idea of a project that investigates the arthropod fauna of urban grassland in Karlsruhe originated in field observations by the author during his employment as a scientific trainee at the State Museum of Natural History Karlsruhe (Jul. 2016-Jun. 2018). Extensive pre-fieldwork surveys of urban grasslands in Karlsruhe were conducted by the author and Daniela Warzecha in 2017.

Chapter II (a)

Bauer, T., Höfer, H., & Schirmel, J. (2024) Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes. Insect Conservation and Diversity 17: 811-825. https://doi.org/10.1111/icad.12746

All fieldwork and spider determination was done by Tobias Bauer by bicycle, without assistance. Verification of single spider specimens was done by various experts (see Chapter II). Extensive verification of carabid material was necessary and done by Tobias Bauer from December 2021- June 2023. All arthropod material was sorted by Tobias Bauer and partly by Teagan Wernicke (intern at SMNK from 20.05.2019 - 28.06.2019). For other contributions of each author, please see Chapter II.

Chapter II (b)

Bauer, T., Höfer, H., & Schirmel, J. (2024) Spider assemblages (Arachnida: Araneae) in urban grassland patches in Karlsruhe (Baden-Württemberg, Germany). Arachnologische Mitteilungen: Arachnology letters 68: 1. https://doi.org/10.30963/aramit6801

Original draft and Appendix were written by Tobias Bauer and metadata enrichment of the dataset were done by Tobias Bauer and Hubert Höfer. All authors commented extensively on the manuscript. For contributions on methodology please see chapter II(a).

Chapter III

Bauer, T., Höfer, H., & Schirmel, J. A Large urban reserve and many small urban grassland fragments together effectively preserve local grassland spider diversity in a city, finished draft

Original idea for the analyses by Tobias Bauer. Tobias Bauer wrote the original draft, prepared the datasets and analysed data. All authors commented on the methodology and text.

Chapter IV

Rech, F., Narimanov, N., **Bauer, T.**, & Schirmel, J. (2022) Urbanization increases fluctuating asymmetry and affects behavioral traits of a common grasshopper. Ecology and Evolution 12: e9658 (1-10). https://doi.org/10.1002/ece3.9658

For author contributions, please see Chapter IV

Chapter V

Bauer, T., Bäte, D. A., Kempfer, F., & Schirmel, J. (2021) Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season. Biological Invasions 23: 1473-1485. https://doi.org/10.1007/s10530-020-02452-w

For contributions of each author, please see Chapter V

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Academic studies

10/2013 – 06/2016	**Agrarbiologie (M. Sc.)** Universität Hohenheim, 70599 Stuttgart, Germany Focus**:** Landscape Ecology Content of studies: Ecology, biodiversity conservation, sustainable land use
10/2011 - 12/2013	**Agrarbiologie (B. Sc.)** Universität Hohenheim, 70599 Stuttgart, Germany
10/2008 – 09/2011	**Biologie (B. Sc.)** Universität Hohenheim, 70599 Stuttgart, Germany

Professional experience

Since 04/2023	Project staff, FLIP („Förderung der Lebensqualität von Insekten & Menschen durch perfekte Wiesenwelten“, RWTH Aachen, State Museum of Natural History Karlsruhe)
10/2022-3/2023	Freelancing work in conservation

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10/2018-09/2021	PhD-Scholarship holder, Friedrich-Ebert-Stiftung e.V.
Since 10/2018	External PhD student, RPTU (Environmental Science, Landau)
07/2018 -09/2018	Project staff, State Museum of Natural History Karlsruhe
07/2016 – 06/2018	Scientific assistant, State Museum of Natural History Karlsruhe, Department of Zoology (Hubert Höfer)
2011-2015	Supervisor, Practical course „Spiders of Hohenheim“ (Prof. Dr. Johannes Steidle) Biology (B. Sc.) 4th semester
05/2014-05/2017	Determination of spider samples in Projekt „Fauna von Schutzäckern“ and co-author of project report
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Memberships

Arachnologische Gesellschaft e.V. (AraGes)

Zoologische Gesellschaft für Arten- und Populationsschutz e.V. (ZGAP)

Naturgarten e.V. (Verein zur Förderung naturnaher Gärten)

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Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT)

Editorial work

Editor-in-Chief of Arachnologische Mitteilungen/Arachnology letters

Subject editor, Check List (Pensoft) (Araneae of Eurasia & Neotropics)

Publications

Bach, A., Lauterbach, S., Astrin, J. J., Thorns, H. J., & **Bauer, T.** (2024) A master in disguise? The rediscovery of *Misumena bicolor* Simon, 1875 (Araneae: Thomisidae). Zootaxa 5529: 175-185

Bauer, T., Höfer, H., & Schirmel, J. (2024) Dry grasslands in urban areas can harbour arthropod species of local conservation concern and should be prioritised for biodiversity-friendly mowing regimes. Insect Conservation and Diversity 17: 811-825

Tchilinguirian, J., Lamare, L., Laval, C., & **Bauer, T.** (2023) Redécouverte de *Philodromus parietalis* Simon, 1875 (Araneae, Philodromidae) en France après 91 ans et synthèse des données existantes. Revue Arachnologique 10: 23-29

Raub, F., Bach, A., **Bauer, T.**, & Höfer, H. (2023) Data paper publication in Arachnologische Mitteilungen–Goals, review criteria, editorial procedures, format, data management and mobilization. Arachnologische Mitteilungen 66: iii-iv.

Bauer, T., Falato, R., & Pantini, P. (2023) *Xysticus grallator* Simon, 1932 new to mainland Italy (Araneae, Thomisidae). Check List 19: 713-718

Narimanov, N., **Bauer, T.**, Bonte, D., Fahse, L., & Entling, M. H. (2022). Accelerated invasion through the evolution of dispersal behaviour. Global Ecology and Biogeography 31: 2423-2436

Bauer, T. (2022) Remarks on the type material of *Poecilochroa loricata* Kritscher, 1996 (Araneae: Gnaphosidae). Zootaxa 5169: 97-100.

Bauer, T., Thorns, H. J., & Guttenberger, J. (2022) Rediscovery of the extremely rare running crab spider *Philodromus (Artanes) poecilus* (Thorell, 1872) in Bavaria, Germany, after 141 years (Araneae, Philodromidae). Check List 18: 583-591.

Bauer, T., & Wendt, I. (2022) La araña toro, *Macrothele calpeiana*, repeatedly imported to Germany (Araneae: Macrothelidae). Fragmenta entomologica 54: 69-72

Breitling, R., & **Bauer, T.** (2022) What, if anything, is *Lycosa accentuata* Latreille, 1817?– Review of a nomenclatural conundrum (Araneae: Lycosidae). Zoosystema 44: 197-207

Bauer, T. (2021) Ant-eating twigs and stalks: the natural prey of *Tmarus* and *Monaeses* (Araneae: Thomisidae) in the Western Palaearctic, analysed by using online-accessible wildlife photography. Arachnologische Mitteilungen 62: 61-66

Bauer, T., Bäte, D. A., Kempfer, F., & Schirmel, J. (2021) Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season. Biological Invasions, 23: 1473-1485

Bauer, T. (2021) The camouflaged silken retreat of *Viridasius* sp. (Araneae: Viridasiidae). The Journal of Arachnology 48: 339-342

Bauer, T., Bushell, M. & Ziegler T. (2020) Ein Portrait der stark gefährdeten Desertas-Tarantel *Hogna ingens* (Blackwall, 1857), der wahrscheinlich größten Wolfspinne der Welt. ZGAP Mitteilungen 1/2020: 31-34

Bauer, T. (2020) First record of the crab spider *Epicadus camelinus* (O. Pickard-Cambridge, 1869) in Peru (Araneae, Thomisidae, Stephanopinae). Check List 16: 1551-1555.

Lauterbach, S., Hörren, T., & **Bauer, T.** (2020) *Stenochrus portoricensis* neu für Nordrhein-Westfalen, mit Anmerkungen zur Verbreitung und Habitaten weiterer eingeschleppter Zwerggeißelskorpionarten in Europa (Arachnida: Schizomida). Arachnologische Mitteilungen 60: 50-54.

Bauer, T., Lemke, M., & Pantini, P. (2020) *Xysticus brevidentatus* new to Bosnia and Herzegovina (Araneae: Thomisidae), with remarks on the habitat and distribution. Arachnologische Mitteilungen 60: 34-37

Bauer, T., Bayer, S., Derschmidt, E., & Höfer, H. (2019) Description of the egg sac of *Paratrachelas maculatus*, with notes on its establishment in urban regions of Germany and Austria (Araneae: Trachelidae). Arachnologische Mitteilungen 57: 26-30

Bauer, T., Feldmeier, S., Krehenwinkel, H., Wieczorrek, C., Reiser, N., & Breitling, R. (2019) Steatoda nobilis, a false widow on the rise: a synthesis of past and current distribution trends. NeoBiota 42: 19–43

Guttenberger J., Guttenberger L., **Bauer T.** (2018) *Prinerigone vagans* new to Poland (Araneae: Linyphiidae), with comments on taxonomy and distribution. Arachnologische Mitteilungen/Arachnology Letters 55: 75-78

Bauer, T., Raub, F., Höfer H. (2018): Notes on the behavior and the pendulous egg-sacs of *Viridasius* sp. (Araneae, Viridasiidae). Journal of Arachnology 46: 155-158

Bauer, T. & Höfer, H. (2017) Erstnachweis von *Oxyopes lineatus* in Deutschland und faunistisch-taxonomischen Anmerkungen zu weiteren besonderen Arten aus Baden-Württemberg (Araneae: Lycosidae, Oxyopidae, Salticidae, Thomisidae, Trachelidae). Arachnologische Mitteilungen 53: 29-37

Breitling, R., **Bauer, T**., Schäfer, M., Morano, E., Barrientos, J. A. & Blick, T. (2016) Phantom spiders 2: More notes on dubious spider species from Europe. Arachnologische Mitteilungen 52: 50-77

Breitling, R., **Bauer, T.**, Grabolle, A., Oger, P., Pantini, P., Van Keer, J., Pfliegler, W. P., Jantscher, E. & Dolanský, J. (2016) East meets West: on the true identity of *Cheiracanthium*

rupestre and *Xysticus albomaculatus* (Arachnida: Araneae: Eutichuridae, Thomisidae). Arachnologische Mitteilungen 52: 38-49.

Bauer, T., Wendt, I., Holstein, J. & Gabriel, G. (2016) *Crossopriza lyoni* new to Germany (Araneae: Pholcidae). Arachnologische Mitteilungen 52: 4-6

Breitling, R. & **Bauer, T.** (2015) Remarks on synonyms of European *Larinioides* species (Arachnida: Araneae: Araneidae). Arachnology 16: 305-310

Breitling, R., Lemke, M**., Bauer, T.**, Hohner, M., Grabolle, A. & Blick, T. (2015) Phantom spiders: notes on dubious spider species from Europe. Arachnologische Mitteilungen 50: 65-80

Bauer, T., Freudenschuss, M. & Grabolle, A. (2015) *Plexippoides flavescens* (O. Pickard-Cambridge, 1872) and *Menemerus marginatus* (Kroneberg, 1875), new records for Pakistan (Aranei: Salticidae). Arthropoda Selecta 24: 87-90

Freudenschuss, M., **Bauer, T.** & Sciberras, A. (2013) *Menemerus fagei* new to Malta and Europe (Araneae: Salticidae). Arachnologische Mitteilungen 46: 6-8

Bauer, T. & Grabolle, A. (2012) Erstnachweise von *Paratrachelas maculatus* in Österreich und Deutschland (Araneae, Corinnidae). Arachnologische Mitteilungen 44: 77-80

Statement on the usage of Artificial intelligence (AI) in this dissertation

No AI models nor AI detectors were used whatsoever.

Karlsruhe, 15 October 2025 Tobias Bauer

Sustainability statement

To reduce carbon emissions and air pollution related to the project, the fieldwork of Chapter II and Chapter V was done by bicycle. Whenever possible vials were re-used. All material of Chapter II and V is deposited at the State Museum of Natural History Karlsruhe.

Karlsruhe, 15 October 2025 Tobias Bauer