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Conservation of wild bees and measuring pollination in cities – Functional design and evaluation of rehabilitated urban roadside vegetation

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And all the bees and trees, they weep for me
For they know the things that I can't see
I carry on my mind
The weight of self and time
Of all that can't become
Of all the dreams gone by

Rotem Bar Or
The Angelcy | Nodyssey

Male *Trachusa byssina* has a great view from a flower of *Lotus corniculatus* at an urban roadside in Freising, Germany.

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Summary

The intensification of land use has contributed significantly to changes in vital global systems. One of the defining modern types of land-use intensification is urbanization, inducing loss in insect biomass and diversity. However, insects contribute significantly to global ecosystem functioning, most prominently by pollinating wild and crop plants. Wild bees are among the most important pollinators and can exist in urban environments, provided that foraging and nesting resources are sufficiently available. To improve the environmental conditions for pollinators in cities, the design of biodiversity-friendly greenspace has lately come into focus, and especially thus far overlooked urban roadsides could offer great potential for ecological rehabilitation, serving as habitat and dispersal corridors for herbaceous plants and their pollinating insects in cities.

This doctoral thesis is based on three peer-reviewed publications addressing the successful rehabilitation of urban roadsides and their attractiveness for wild bees and other pollinators. By integrating taxonomic and functional aspects, it aims to improve urban rehabilitation, its functional evaluation, and wild bee conservation. Objectives were i) to implement a functional approach into the design of a habitat-specific wildflower mixture and evaluate plant establishment at urban roadsides by analyzing taxonomic and functional diversity, as well as community structuring; ii) to investigate the effects of local resource availability and urban land use on pollinator abundance and the pollination of phytometer plants to evaluate roadside rehabilitation; and iii) to measure the effects of the roadside vegetation and urbanization on wild bee taxonomic and functional diversity, and to derive trait-informed solutions for urban wild bee conservation. Thus, field experiments were conducted by creating 78 wildflower patches with a native seed mixture along five major roads in Munich (Germany), observing their establishment success and impact on pollinators and pollination along a gradient of urbanization.

In *Publication I*, the establishment of the wildflower patches along urban roadsides was examined, focusing on the site conditions and landscape factors that influence the process. Urbanization reduces plant species richness, but cities can still inhabit numerous native species depending on soil conditions, impervious surface cover, and habitat connectivity. In the study, taxonomic and functional diversity on 17 seeded wildflower patches and non-seeded control patches was sampled over two years (2020—2021) and analyzed with generalized linear mixed models, NMDS and PCoA. Key findings included higher taxonomic plant diversity in wildflower patches than controls, with species richness increasing at city boundaries and negatively correlated with soil organic matter. Functional richness of establishment and floral traits, as well as all traits combined, was higher in seeded patches than in control patches. Other functional indices showed varying sensitivity to soil and landscape variables. The seeding year was significant in the taxonomic and functional structuring of the wildflower communities, indicating seasonal variation that influences the outcome of urban roadside rehabilitation. Despite the artificial introduction, wildflower patches exhibited landscape-level effects on taxonomic and functional diversity within one year. The results demonstrate that seeding can significantly enhance urban biodiversity and habitat quality for pollinators, and post-treatment management is essential for long-term success. Integrating functional traits into native wildflower mixture design can further improve roadside habitats.

Publication II focuses on evaluating rehabilitated urban roadside vegetation using phytometer plants. Classic assessments of pollinators are time-consuming and costly, requiring extensive species knowledge. Phytometers can reduce these burdens by standardizing fruit production measurements, and analyzing plant-specific responses may enhance interpretability. Urban pollinator populations are shaped by local and landscape factors, including floral resources, impervious surfaces, and edge effects, complicating rehabilitation evaluations. We conducted a phytometer experiment on 34 urban wildflower and control patches (2020-2021). Control patches were low-cut roadside lawns. Fruit masses of *Fragaria* x *ananassa* and fruit numbers of *Ranunculus acris* and *Trifolium pratense* were used to measure pollination. Wild bee, honeybee, and hoverfly abundance were sampled monthly, and floral units were counted from June to August. We recorded distance to the city center, impervious surface area, and edge density within a radius of 500 m. Structural equation models (SEM) tested hypothesized relationships, revealing that rehabilitated local floral resources positively influenced pollinator abundance, and pollinator numbers increased with impervious surface cover and decreased at sites with high edge density. Pollination was almost exclusively indirectly influenced by the urban landscape, with phytometer-specific effects. Fruit masses of *F.* x *ananassa* were higher near the city center; impervious surfaces negatively affected *T. pratense* fruit numbers; edge density positively correlated with fruit numbers of *T. pratense* and negatively with those of *R. acris*. These findings highlight the complex interplay of local and landscape factors in shaping urban pollination dynamics. Overall, landscape characteristics predominantly shaped pollination, indicating the phytometers' efficiency in assessing urban landscape quality rather than local rehabilitation of roadside vegetation.

Publication III investigates the effects of wildflower patches on wild bee abundance, species richness, and functional diversity at urban roadsides. Urbanization significantly impacts wild bee communities, favoring some species while disadvantaging others based on their morphologies, phenologies, and habitat preferences. Generalist species usually adapt better to urban environments than specialists and excessive urban land use typically results in functionally homogenous communities. Urban roadside rehabilitation can support habitat connectivity and overall bee diversity, but studies in these habitats are rare. Therefore, vegetation at 78 wildflower and control patches was sampled, and wild bees were collected thrice yearly to assess abundance and species richness. Then, six bee traits were used to calculate functional dispersion. Landscape diversity, perimeter-area ratio of urban greenspace, and distance to the city center were measured within a radius of 500 m to analyze landscape-scale effects. Generalized linear mixed models (glmm) and generalized linear latent variable models (gllvm) were applied. Results showed that local vegetation diversity positively affected wild bee abundance and species richness, while functional dispersion also increased with landscape diversity and distance from the city center. Species with small body sizes, short lifespans, or low reproductive output were negatively associated with high vegetation diversity. Solitary bees were associated with high perimeter-area ratios of greenspace. The study highlights the importance of local forage and the need for targeted ecological interventions in urban landscapes. Identifying trait groups affected by urbanization can help optimize urban rehabilitation efforts for discriminated species.

The *General Discussion* summarizes the thesis' findings and reflects on the trait-informed approach used in the experiments for successful urban roadside rehabilitation. The impact of local floral resources and the urban landscape on the pollination of phytometer species is discussed. The question of how identifying wild bee groups discriminated by urbanization can improve their conservation in cities is examined. A scientific and practical synopsis suggests further research and a city-wide implementation of species-rich, flowering roadsides.

Zusammenfassung

Die Intensivierung der Landnutzung trägt erheblich zu den Veränderungen lebenswichtiger globaler Systeme bei. Eine der einflussreichsten Formen moderner Landnutzungsintensivierung ist Urbanisierung, die signifikant zum Verlust der Insektenbiomasse und -vielfalt beiträgt. Insekten tragen jedoch in erheblichem Maße zum Funktionieren der globalen Ökosysteme bei. Eine weit bekannte Funktion von Insekten ist die Bestäubung von Wild- und Nutzpflanzen. Wildbienen gehören zu den wichtigsten Bestäubern und können auch in städtischen Umgebungen existieren, sofern ausreichend Nahrungsressourcen und Nistmöglichkeiten vorhanden sind. Um die Umweltbedingungen für Bestäuber in Städten zu verbessern, ist in letzter Zeit die Grünflächengestaltung unter Biodiversitätsaspekten in den Mittelpunkt gerückt. Vor allem die bisher übersehenen städtischen Straßenränder könnten ein großes Potenzial für eine ökologische Aufwertung bieten, indem sie als Lebensraum und Ausbreitungskorridore für Pflanzen und Bestäuber in Städten dienen.

Diese Doktorarbeit basiert auf drei begutachteten Veröffentlichungen, die sich mit Fragen einer erfolgreichen Aufwertung von städtischen Straßenrändern und ihrer Attraktivität für Wildbienen und andere Bestäuber befassen. Durch die Integration von taxonomischen und funktionalen Aspekten sollten die Aufwertung von Straßenrändern, ihre funktionale Bewertung und der Schutz von Wildbienen verbessert werden. Ziele waren i) die Umsetzung eines funktionalen Ansatzes bei der Zusammenstellung einer lebensraumspezifischen Blühmischung heimischer Wildpflanzen, und die Bewertung der Pflanzenetablierung durch die Analyse ihrer taxonomischen und funktionalen Vielfalt sowie der Strukturierungsprozesse der Pflanzengemeinschaften; ii) die Auswirkungen der lokalen Ressourcenverfügbarkeit und der städtischen Flächennutzung auf die Abundanz von Bestäubern und Bestäubung von Phytometerpflanzen zu untersuchen, um die Aufwertung von Straßenrändern zu bewerten; und iii) die Auswirkungen der Straßenrandvegetation und der Urbanisierung auf die taxonomische und funktionale Vielfalt von Wildbienen zu erfassen, um Lösungen für den Schutz von Wildbienen in Städten abzuleiten. Dazu wurden in einem groß angelegten Feldexperiment 78 Blühflächen mit einer einheimischen Saatgutmischung entlang von fünf Hauptverkehrsstraßen in München angelegt. Anschließend wurden der Etablierungserfolg der Flächen und ihre Effekte auf Bestäuber und Bestäubung von Phytometern entlang eines Urbanisierungsgradienten beobachtet.

In *Publikation I* wurde die Etablierung von Blühflächen an städtischen Straßenrändern untersucht, wobei der Schwerpunkt auf den Standortbedingungen und Landschaftsfaktoren lag, die diesen Prozess beeinflussen. Im Allgemeinen verringert Urbanisierung die Pflanzenvielfalt, doch können in Städten je nach Bodenbeschaffenheit, sowie Versiegelungs- und Vernetzungsgrad immer noch zahlreiche heimische Arten vorkommen. In der Studie wurden 17 eingesäte und Kontrollflächen ohne Einsaat über zwei Jahre auf Ihre taxonomische und funktionale Vielfalt untersucht (2020-2021). Zu den wichtigsten Ergebnissen gehörte eine höhere Artenvielfalt in den Blühflächen im Vergleich zu Kontrollen, wobei diese an den Stadtgrenzen zunahm und negativ mit der organischen Bodensubstanz korrelierte. Die funktionale Vielfalt von Etablierungs- und Blütenmerkmalen („Traits“) sowie aller Merkmale zusammengenommen war in eingesäten Flächen höher als in Kontrollflächen. Andere funktionelle Indizes zeigten unterschiedliche Reaktionen gegenüber Boden- und Landschaftsvariablen. Das Aussaatjahr war für die taxonomische und funktionale Strukturierung der Pflanzengemeinschaften von Bedeutung, was auf jahreszeitliche Schwankungen hinweist, die das Ergebnis der Aufwertungsmaßnahmen beeinflussen. Trotz der künstlichen Einbringung zeigten die Blühflächen auf taxonomischer und funktioneller Ebene bereits innerhalb des ersten Jahres Reaktionen auf

Landschaftsebene. Die Ergebnisse demonstrieren, dass die Einsaat von Wildpflanzen die Artenvielfalt in Städten und die Qualität der Lebensräume für Bestäuber erheblich verbessern kann. Wobei ihre Pflege nach der Einsaat für den langfristigen Erfolg unerlässlich ist. Die Integration funktioneller Merkmale in die Gestaltung von heimischer Blühmischungen kann den Erfolg von Aufwertungsmaßnahmen erhöhen.

Publikation II fokussierte auf die Evaluation von Aufwertungsmaßnahmen an urbanen Straßenrändern mithilfe von Phytometerpflanzen. Klassische Methoden der Bestäubererfassung sind zeit- und kostspielig und bedürfen umfangreicher Artenkenntnisse. Phytometer können diese Hürden herabsetzen, indem an ihnen standardisierte Bestäubungsmessungen durchgeführt werden. Artspezifische Reaktionen der Phytometerpflanzen können dabei die Interpretierbarkeit verbessern. Urbane Bestäuberpopulationen werden durch lokale und landschaftliche Faktoren beeinflusst, unter anderem die Nahrungsverfügbarkeit, der Versiegelungsgrad und Randeffekte, die die Bewertung von Aufwertungsmaßnahmen erschweren. Daher führten wir ein Experiment mit Phytometern auf 34 städtischen Blüh- und Kontrollflächen durch (2020—2021). Kontrollflächen waren kurzgehaltener Scherrasen von Straßenrändern. Die Fruchtgewichte von *Fragaria* x *ananassa* und die Anzahl der produzierten Früchte von *Ranunculus acris* und *Trifolium pratense* wurden als Bestäubungsindikatoren herangezogen. Die Abundanz von Wildbienen, Honigbienen und Schwebfliegen, sowie die Anzahl von Blüteneinheiten wurden monatlich von Juni—August erfasst. Die Distanz zum Stadtzentrum, sowie der Anteil an versiegelter Fläche und die Randdichte wurden innerhalb eines Radius von 500 m kartiert. Strukturgleichungsmodelle (SEM) wurden angewendet, um zuvor aufgestellte hypothetische Zusammenhänge zu testen. Dabei zeigte sich, dass die Abundanz der Bestäuber positiv von den Aufwertungsmaßnahmen beeinflusst wurde, sowie an Untersuchungsflächen mit hohem Versiegelungsgrad anstieg und sich an Orten mit hoher Randdichte verringerte. Die Bestäubung der Phytometer war fast ausschließlich indirekt durch die städtische Landschaft gesteuert, dabei wurden artspezifische Unterschiede festgestellt. Die Fruchtgewichte von *F.* x *ananassa* waren nahe dem Stadtzentrum am höchsten; der Versiegelungsgrad beeinflusste die Fruchtanzahl von *T. pratense* negativ; die Randdichte korrelierte positiv mit der Fruchtanzahl von *T. pratense*, und negativ mit der von *R. acris*. Diese Ergebnisse betonen die Komplexität der Bestäubungsdynamik in Städten aufgrund der Interaktionen zwischen lokalen und landschaftlichen Faktoren. Zusammengefasst haben vorwiegend landschaftliche Charakteristika die Bestäubung beeinflusst, was die Eignung von Phytometern für die Bewertung der urbanen Landschaftsqualität aufzeigt, statt der lokalen Straßenrandaufwertung.

Publikation III untersuchte die Auswirkungen von Blühflächen auf die Abundanz, die Artenzahl und die funktionale Vielfalt von Wildbienen an städtischen Straßenrändern. Urbanisierung wirkt sich erheblich auf städtische Wildbienengemeinschaften aus und begünstigt einige Arten, während andere aufgrund ihrer Morphologie, Phänologie und Habitatpräferenzen benachteiligt werden. Generalistische Arten passen in der Regel besser in städtische Umgebungen als Spezialisten, und eine intensive städtische Landnutzung führt in der Regel zu funktional homogenen Bienengemeinschaften. Die Aufwertung von Straßenrändern kann die Vernetzung von Lebensräumen und die Vielfalt der Bienen fördern, jedoch gibt es bisher wenige Untersuchungen in diesen Lebensräumen. Daher wurde die Vegetation auf 78 Blüh- und Kontrollflächen beobachtet. Dreimal jährlich wurden Wildbienen erfasst, um die Abundanz und Artenzahlen zu ermitteln. Anschließend wurden sechs Merkmale der Bienen zur Berechnung der funktionalen Streuung (functional dispersion) herangezogen. Die Landschaftsvielfalt, das Verhältnis zwischen Umfang und Fläche der Grünflächen und die Entfernung zum Stadtzentrum wurden gemessen, um Effekte auf Landschaftsebene zu analysieren. Die Ergebnisse zeigen, dass sich die lokale Vielfalt der

Vegetation positiv auf die Abundanz und Artenzahlen von Wildbienen auswirkt, während die funktionale Streuung zusätzlich mit der Landschaftsvielfalt und der Entfernung zum Stadtzentrum zunimmt. Arten mit kleiner Körpergröße, kurzer Lebensdauer oder geringer Reproduktionsleistung wurden negativ mit einer hohen Vegetationsvielfalt in Verbindung gebracht. Solitärbienen profitierten von einem hohen Verhältnis zwischen Umfang und Fläche städtischer Grünflächen. Die Ergebnisse unterstreichen die Bedeutung lokaler Nahrungsressourcen und die Notwendigkeit gezielter ökologischer Eingriffe in städtischen Landschaften. Die Identifizierung von Merkmalsgruppen, die von der Verstädterung betroffen sind, kann dazu beitragen, städtische Aufwertungsmaßnahmen für bestimmte Arten zu optimieren.

Die *Allgemeine Diskussion* bietet eine Zusammenfassung der Ergebnisse der Arbeit und reflektiert den merkmalsbasierten Ansatz, der in den Experimenten für eine erfolgreiche Aufwertung städtischer Straßenränder angewendet wurde. Die Auswirkungen lokaler floraler Ressourcen und der städtischen Landschaft auf die Bestäubung von Phytometer-Arten werden diskutiert. Zudem wird die Frage beleuchtet, wie durch die Identifizierung von Wildbienengruppen, die durch die Urbanisierung benachteiligt werden, Artenschutz in Städten verbessern kann. Eine wissenschaftliche und praktische Zusammenfassung enthält Vorschläge für weitere Forschung und eine stadtweite Umsetzung von artenreichen, blühenden Straßenrändern.

1 Introduction

1.1 Anthropogenic impact on global natural systems and the biosphere

Humans have profoundly modified the global biomes and ecosystems over the past centuries. For example, about 30—50% of the terrestrial surface is used for resource exploitation, farming, settlements, or infrastructure (Crutzen, 2002). Human population size has increased tenfold during the past 300 years, and by increasing resource use and land transformation, natural systems have been inevitably changed, such as the global climate, with marked consequences for humans and the biosphere (Crutzen, 2002).

In the past decades, intensification of agricultural activity, resource exploitation, and urbanization have contributed significantly to the modification of natural landscapes, inducing significant shifts in the global biosphere. The accelerating loss of biodiversity can be traced back to the year 1500, and current species extinctions are calculated to be 100—1000 times higher than natural background rates (Barnosky et al., 2011). Thus, human activity is restructuring the biosphere globally, and, if not halted, will form a biostratigraphic horizon within a few centuries comparable to those of the five former mass extinctions in Earth´s history (Fonseca, 2009; Barnosky, 2014; Hochkirch et al., 2023). Human-induced species loss accelerated from the 19th century onwards, causing shifts in species distributions and driving invasions. This affects interactions among organisms and their environments, resulting in changes of vital ecological systems.

Insect trophic interactions contribute significantly to global ecosystem functioning due to their high species numbers, biomass, and omnipresence in all terrestrial ecosystems (Weisser and Siemann, 2008a). For example, herbivorous and detritivorous insects substantially influence biomass transformation, nutrient cycling, and carbon deposition (Hunter, 2001; Yang and Gratton, 2014). One of the most prominent ecosystem functions performed by insects is pollination, a mutualistic relationship between insects and herbaceous plants, in which insects seek nectar and pollen as food items while providing pollen transportation from one plant individual to another for plant reproduction and genetic exchange (Herrera and Pellmyr, 2008). Nearly 90% of all existing herbaceous plants rely on insects for reproduction, i.e., the availability of pollen from conspecifics (Ollerton et al., 2011) Ollerton et al., 2011). Wild bees are among the most important pollinators, and anthropogenic landscape change has significantly altered their populations in diversity, structure, and composition around the globe (Sánchez-Bayo and Wyckhuys, 2019). Worldwide, there are over 20.000 wild bee species, and the latest reports describe 2.138 species in Europe and 566 in Germany, of which 48% are rare or endangered (Michener, 2010; Westrich et al., 2011; Westrich, 2019; Ghisbain et al., 2023). Bees are, therefore, not only a crucial functional group in most populations of wild plants but also in agricultural systems, thus ensuring human food production (Ollerton et al., 2011; Noriega et al., 2018).

1.2 Urbanization impacts on biodiversity and ecosystems

Severe declines in insect biomass and diversity have been observed during the past decades due to anthropogenic landscape change (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Hochkirch et al., 2023). In the 21st century, one of the defining modern types of land-use change is urbanization, and global urban population growth is about 1% annually, with over 2.5 billion urban citizens to be added within the coming 30 years (UN, 2019). This implies a growing cover of urban land use with marked effects on pollinator diversity and pollination (Simkin et al., 2022). Urbanization occurs as a city densification process by building up on vacant lots and fallows or as urban expansion degrading (semi-)natural habitats. From an ecological point of view, impervious surface cover, chemical pollution, eutrophication, artificial night light, waterbody regulation, and the urban heat island effect are critical factors influencing urban populations across many taxa (Sánchez-Bayo and Wyckhuys, 2019). For example, Bennett et al. (2020) investigated the impact of global urbanization on pollen availability for plant populations and found disrupted plant-pollinator interactions in many cases. The rapid development of urbanization threatens the existence of pollinators and their functions. However, negative impacts on biodiversity and urban ecosystem functionality could be mitigated by including ecological principles in urban planning and respecting certain factors of habitat quality and functionality in greenspace design and management (Parris et al., 2018).

1.2.1 Impact of urbanization on plant communities

Increasing urban land cover reduces plant diversity, induced by losses of natural habitats, independent of geographic or climate region or elevation (Aronson et al., 2014). With increasing urbanization, plant communities usually show homogenization in phylogenetic and functional composition. However, depending on the intensity of urbanization, cities can sustain diverse plant communities, with rare species included, constituting so-called 'novel ecosystems‘, mainly formed by anthropogenic activity (Kowarik, 2011; Heger et al., 2019).

At a local scale, urban soils are most important for the respective vegetation. Many of them are technosols developed on anthropogenic waste materials, such as construction rubble of cement and bricks, causing high soil pH. They can also contain high amounts of nutrient elements (P, N, Ca), heavy metals (Cu, Zn, Pb, Hg), and organic pollutants from combustion processes, such as polycyclic aromatic hydrocarbons (PAH) (Yang and Zhang, 2015). Compared to naturally formed substrates, urban topsoil is characterized by higher compaction and changed microstructure, reduced microbial activity, decreased water infiltration and storing capacity, and lower gas exchange (Yang and Zhang, 2015). The properties of the resulting soils depend on historical and recent land use and result in variably distributed substrates with deviating physical, chemical, and biological conditions, strongly affecting the composition and diversity of the urban vegetation (Godefroid et al., 2007; Godefroid and Koedam, 2007). Besides soils, urban plant communities are shaped by local microclimatic conditions (Godefroid et al., 2007). Air temperature and humidity can vary considerably within the urban matrix, depending on the surrounding land use, such as impervious and greenspace cover. Plant-specific responses to this microclimatic variation influence the assembly of the urban communities, and increased urban temperatures alter their phenology by extending the growing season, starting earlier in spring and ending later in autumn (Godefroid et al., 2007; Melaas et al., 2016). Apart from abiotic factors, urbanization is commonly accompanied by the spread of non-native species. By suppressing less competitive natives, some of them have become dominant elements of the urban flora, invading urban vegetation and changing its composition and diversity (Kowarik, 2011; Gaertner et al., 2017).

At the landscape scale, several factors influence plant community assembly. For example, Godefroid and Koedam (2007) found urban vegetation patterns driven by different land-use types, and the density of built-up areas was most influential. Urbanization effects on plant diversity are reported to be negative overall, as plant communities are altered in their composition compared to habitats of more natural systems, resulting in homogenized species assemblages (McKinney, 2008). However, cities can harbor large numbers of species that tolerate anthropogenic disturbance and fit the urban environmental conditions (Kowarik, 2011). In fact, there is great yet untouched ecological potential for high plant diversity in urban grasslands, wastelands, parks, and gardens (Godefroid and Koedam, 2007; Klaus, 2013), and especially small, vegetated patches contribute significantly to urban plant diversity and habitat connectivity (Vega and Küffer, 2021).

A diverse urban flora can have significant effects on ecosystem functioning, depending on the actual type of urban green space. In cities, vegetated areas facilitate climate change adaptation and mitigation by cooling and increasing water uptake and storage (Georgi et al., 2012). Besides, urban green space can increase the diversity of urban pollinator insects, such as wild bees, compared to agricultural landscapes (Hall et al., 2017; Theodorou et al., 2020b). To achieve international biodiversity targets, as in the EU Biodiversity Strategy for 2030 (EU, 2020), the design and management of urban green space must, therefore, be adapted to benefit plant diversity, habitat quality, and accessibility.

1.2.2 Wild bee communities in cities

A steadily growing body of literature has studied the role of cities in wild bee diversity (Hall et al., 2017), and in fact, there is evidence that wild bees can thrive in urban environments, including more (rare) species compared to agricultural areas (Baldock et al., 2015; Theodorou et al., 2020b). However, the evidence on urbanization effects is conflicting (Fauviau et al., 2022) and depends on the type and intensity of urban land use. Low to medium urbanization is usually linked to positive effects, whereas high land-use intensity, as in areas with more than 60% impervious surface, has negative impacts on wild bee populations (Wenzel et al., 2020). To mitigate further losses of biodiversity and ecological functionality due to urban expansion, there is an urgent need to identify opportunities to support wild bees. In times of increasing economic pressure on agricultural land, vacant lots, and green space, a closer look at the relationships between the urban fabric and wild bee populations is necessary to provide practical solutions for city planners and conservationists (Baldock, 2020).

In cities, several factors influence the abundance, diversity, and community structure of wild bees at different spatial scales. Locally, floral resources are the crucial driver of wild bee population stability and diversity (Scheper et al., 2014). Flowering plants offer nectar and pollen for wild bees that serve as energy and protein sources for adults, as well as for raising their offspring. The main factors determining the quality of a foraging habitat for bees are the amount of floral display and respective food items provided per unit area, driving the number of individuals within a habitat (Roulston and Goodell, 2011). Secondly, the phylogenetic and functional diversity of the flowering plants positively affects the number of bee species that can feed on the plants (Choate et al., 2018). Due to different feeding strategies resulting from varying morphologies and host plant specializations, increasing plant species numbers is usually accompanied by an increase in wild bee diversity (Herrmann et al., 2023). Third, as wild bees vary greatly in their life-history traits, a high phenological consistency of food provision ensures the availability of wild bee resources over an entire vegetation period (Burkle et al., 2020).

Urban grasslands require adapted management if intended to support wild bee diversity. With extensive mowing and active management of invasive plant species, resource quality for wild bees can be preserved or improved, independent of the size of the resource habitat (Anderson et al., 2023). Bee-oriented management strategies should include the creation and maintenance of varying structures to comply with different nesting preferences, while the effects of urbanization on nesting behavior and reproduction of wild bees are so far understudied (Staab et al., 2018; Neumüller et al., 2022; Prendergast, 2023). Beyond habitat quality, competition with the domesticated honeybee can negatively affect urban populations of wild bees. This competition spans several levels, from direct aggressive interactions between honeybees and other pollinators over exploitative competition for floral resources to apparent competition by the transmission of parasites and pathogens (Geslin et al., 2017). In cities, high honeybee abundance or local hive densities can decrease the abundance of wild bees, hamper flower visitation rates of wild bees and resource availability, and subsequently reduce body sizes, resistance against parasitic and pathogen infestation, and overall fitness of wild bee individuals and colonies (Goulson and Sparrow, 2009; Ropars et al., 2019; Weissmann et al., 2021). While urban beekeeping grows in popularity, urban wild bee populations are affected negatively, and urban beekeeping is debated critically among ecologists (Egerer and Kowarik, 2020; Casanelles-Abella and Moretti, 2022).

Besides local conditions, urban land use affects the occurrence, diversity, and functionality of wild bee populations at several spatial scales (Buchholz and Egerer, 2020; Wenzel et al., 2020). The intensity of urbanization is thereby often defined as the proportion of impervious surface within differently sized buffer zones, which, at high levels, has detrimental effects on wild bees (Wenzel et al., 2020; Herrmann et al., 2023). To describe urbanization at the landscape scale, Shannon diversity of land-use types combines the presence and proportions of the different urban habitats. The effect of increasing urban landscape diversity on wild bees is mostly positive and affects their community assembly, pollination networks, and ecological functionality (Theodorou et al., 2017; Montagnana et al., 2021). Several types of green spaces usually occur in urban areas, varying in size, shape, and ecological quality. The proximity to each other and the distance to semi-natural habitats are essential factors for urban wild bee populations, as those areas function as species reservoirs in the urban matrix (Graffigna et al., 2023). Improved greenspace connectivity facilitates movement and genetic exchange by increasing habitat connectivity. Thus, species, functional, and intraspecific genetic diversity increase while inbreeding is reduced (Buchholz et al., 2020; Chau et al., 2023). Especially linear landscape elements, such as hedgerows, forest edges, or roadsides, serve as corridors between habitats, and edgy sites with high perimeter-area ratios significantly increase habitat accessibility (Griffin and Haddad, 2021; Fischer et al., 2022; Chau et al., 2023).

Abiotic factors, such as microclimatic conditions, including mean temperatures of air and soil, play a major role in wild bee ecology, while the responses of wild bees to annual climatic variability are species- and habitat-specific. In addition, climate-change impact is usually observed in analyzing long-term data, which, for insects, are difficult to procure. Both factors impede research on climate-change induced spatio-temporal trends in populations, and recent publications show that negative effects of weather variability on insect populations have been underestimated for the temperate zones, and especially warmer and drier winter conditions accelerated the widespread decline in insect biomass (Müller et al., 2023). Changes in phenology are strongest in spring-emerging species, as observed in pollinators and the respective food plants, while effects are often species- and trait-specific (Hegland et al., 2009; Cook et al., 2012). Extreme weather events, such as spring and summer droughts, can cause a phenological decoupling and spatio-temporal resource scarcity that affects species interactions and plant-insect networks (Forrest, 2015; Descamps et al., 2021). Although wild bees are a thermophilic group, climate change has a negative impact on their abundance (Kammerer et al., 2021). For cities specifically, the urban heat island effect (UHI), thermal heat waves, and drought events cause shifts in wild bee communities, affecting the species most sensitive to such extremes (Minckley et al., 2013). Thus, climate change negatively affects urban wild bee populations, while many aspects are not sufficiently understood (Hamblin et al., 2017; Hamblin et al., 2018).

1.2.3 Urban pollinator network and pollination

Interactions between species are the foundation of ecosystems, and all species are exposed to some form of antagonistic or mutualistic relationship (Theodorou, 2022). Urban ecosystems are mainly formed by anthropogenic influences that change community assemblages. This affects species interaction networks, and effects appear according to disturbance intensity (Geslin et al., 2013). Pollination can be investigated by analyzing interactions between plants and their pollinators and by measuring fruit or seed production of plants directly. However, the interplay of local and landscape-scale factors is difficult to disentangle for these highly complex networks (Theodorou et al., 2017).

Urbanization affects plant and bee species in their morphology, physiology, and behavior; thus, pollination networks are subsequently modulated at the level of species and their life-history traits (Theodorou et al., 2020a; Polidori et al., 2023). For example, pollination in plant species with radial floral morphologies increases with urbanization, attracting many generalist pollinators abundant in cities, including honeybees (Ferrari et al., 2024b). For less abundant or functionally specialized plants, pollen transfer is reduced in urban environments and could affect their seed or fruit production accordingly (Geslin et al., 2013; Irwin et al., 2018). Additionally, local factors influence pollination, such as the abundance of flowers. For example, the amount of floral display either increased or decreased the number of seeds per infructescence in *Lotus corniculatus*, depending on whether the sites were urban gardens or paved courtyards (Pellissier et al., 2012). Pollination success is, therefore, linked to the identity of a plant, and in pollination experiments, species-specific plant-environment interactions must be considered. Furthermore, local human disturbance alters plant-pollinator networks and pollination in plants. Hereby, not human population density itself affects pollinators negatively, but the intensity of human activity that increases in cities (Fauviau et al., 2022). Exposure to pesticides and heavy metals, as well as air pollution with nitrogen oxides (NO_x), ammonia (NH_3) or Ozone (O_3), can disrupt interaction networks by altering plant chemical cues or their detection and interpretation by pollinators, influencing the time and energy spent with foraging, thus the number of flower visits, pollen transfer rates and pollination success (Uhl and Brühl, 2019; Ryalls et al., 2022; Duque and Steffan-Dewenter, 2024). At the landscape scale, land-use effects strongly affect pollination networks, and while in urban areas, the number of interactions between pollinators and plants decreases, interaction evenness increases relative to semi-natural and agricultural areas (Geslin et al., 2013). Depending on the functional identity of plants and pollinators, interaction numbers can vary according to the landscape context. Nevertheless, flower visitation rates and plant reproductive success are significantly lower in urbanized areas (Geslin et al., 2013; Herrmann et al., 2023). Besides, urban landscape structures can induce phenological shifts and mismatches that change plant-pollinator networks and hamper pollination (Biella et al., 2022; Fisogni et al., 2022).

1.3 The urban filter: Trait-based structuring of urban plant and wild bee communities

1.3.1 Trait-based approaches in ecological research and restoration

Trait-based approaches in ecology have gained a lot of attention during the past 20 years, and publications in the field of functional ecology have increased significantly (Irschick et al., 2013). Functional traits are defined as morpho-physio-phenological properties of an organism that indirectly affect its fitness (Violle et al., 2007). Traits can be categorized into different types, which include reproduction, morphology, physiology, life history, behavior, ecology, and genetic characteristics of a species (Wong et al., 2019). They are, therefore, measurable only at the level of an individual in defined units that influence the ecological performance of organisms (McGill et al., 2006). Key ecological topics, e.g. species occurrences in specific habitats or regions, their role in communities and interaction networks, or species diversity and distribution patterns, are addressed in functional research. Yet, considering functional traits in experiments, organismal responses to environmental change or gradients are investigated mechanistically, and the processes and consequences of such responses for niche occupation, competition and interactions networks can be identified across space and time (McGill et al., 2006; 'response traits'; Violle et al., 2007; Irschick et al., 2013). Finally, aggregating information on the functional identities of species, weighted by their relative abundance, can be used to investigate ecosystem functioning, such as productivity, energy flow, or chemical cycling ('effect traits'; Violle et al., 2007; Weisser and Siemann, 2008b).

1.3.2 Urban filtering and functional diversity

Many wild species occur in cities, despite being built in disregard of any wildlife requirements. By investigating changes in functional diversity and trait-environment interactions, urbanization gradients are used to increase the understanding of the processes underlying species occurrence and community formation. With increasing intensity of urban land use, species that cannot endure specific environmental thresholds are removed, whereas species with higher plasticity to environmental change and anthropogenic disturbance still occur. The underlying filtering processes are based on species-specific traits in interaction with the environment (Buchholz and Egerer, 2020). Trait-based filtering causes urban communities to be functionally homogenous, with specialist species being deprived, whereas generalists similar in trait configurations cluster at highly urbanized locations (Wong et al., 2019).

Several indices are available to describe the functional diversity of communities (Table 1). These indices represent different facets of functional diversity and refer to the variety and distribution of traits among organisms in functional space. Therefore, functional trait space is defined as the multidimensional continuum formed by the various combinations of traits that occur within a community. Each trait represents an axis within this space, and the combination of traits identifies the ecological niche occupied by each species.

Table 1: Four functional indices representing different facets of functional diversity. The indices are statistically independent of each other. Hence, different research questions can be addressed, and interpretation of results must be done with respect to their definitions.

Index	Definition	Source
Functional richness	Volume of the functional space occupied by the community	Villéger et al. (2008)
Functional evenness	Regularity of the distribution of abundance in functional space	Villéger et al. (2008)
Functional divergence	Divergence in the distribution of abundance in functional space	Villéger et al. (2008)
Functional dispersion	Mean distance of individual species in functional space to the centroid of all species	Laliberté and Legendre (2010)

1.3.2 Functional community structuring in urban plants

Urban plant communities are significantly different in their taxonomic and functional composition compared to those of (semi-)natural habitats. Besides ecological factors that determine species' occurrence due to their evolutionary adaptations, human-driven criteria, such as human perception of aesthetics and historic land use, influence the composition of urban vegetation (Milanović et al., 2021). In cities, the functional diversity of plant communities is modulated by factors at different spatio-temporal scales. However, the scientific results on plant-environment interactions in cities are inconsistent. Aronson et al. (2016) proposed a framework that hierarchically modulates species distributions in cities, passing through a series of environmental, biotic, and anthropogenic filters, while response strength and directions vary across taxonomic groups. Given a pool of species within a biogeographical region, the resulting community is determined by (1) non-native plants, (2) facilitation, (3) the urban landscape and historical land use, (4) socioeconomic and cultural factors, and (5) trait-environment interactions. The traits in focus that primarily determine species occurrence and distribution are those modulating establishment, persistence, and reproduction (Shipley et al., 2006). Plants that have been associated with anthropogenic environments are bi- or perennial, C-strategists, wind-pollinated, mid-summer flowering, combine sexual and vegetative reproduction, wind dispersers, and depend on high light and nutrient availability (Lososová et al., 2006; Aronson et al., 2016). Others found non-native origin, drought resistance, high pH and nutrient tolerance, higher plant height, and annual phenology as advantageous traits in cities (Aronson et al., 2016).

1.3.3 Functional community structuring in urban wild bees

Despite the functional structuring of wild bee communities being an emerging topic, there is a lack of publications investigating indices of functional diversity. In their review, Buchholz and Egerer (2020) only found five studies that explicitly analyzed the effects of urbanization on the functional diversity of wild bees in different urban habitats. Buchholz et al. (2020) found that the functional dispersion of wild bees was affected by increasing habitat isolation and no influence of local plant richness in urban dry grasslands. Braaker et al. (2017) found functional dispersion to increase with increasing connectivity on greened urban rooftops, and on the ground, it additionally increased with flower abundance. Martins et al. (2017) found that functional dispersion is positively influenced by small-scale urbanization (250-m radius), whereas Hung et al. (2019) found a decrease in urban habitat fragments compared to natural reserves. Villalta et al. (2022) showed a decrease in an alternative functional diversity index ('FD', cf. Petchey and Gaston, 2002) with increasing urban land-use cover. Meanwhile, Banaszak-Cibicka and Dylewski (2021) compared rural, suburban, and urban bee habitats and found no differences in functional richness and evenness, but functional dispersion was higher in suburban and divergence in urban sites.

While limited studies are available on functional indices, many analyzed trait-environment interactions since identifying the traits affected by urban transformation can increase the understanding of the underlying processes (Wong et al., 2019). Nesting behavior, diet specialization, body size, and phenology are the main traits studied in urban contexts (Buchholz and Egerer, 2020). Depending on the species, wild bees use aboveground nesting structures, such as cavities of deadwood or living hollow trees, but reed galls and plant stems are also used. However, most of the species are ground nesting, creating self-dug cavities in varying substrates and exposures of different shapes and depths, or like many bumblebees (*Bombus* spec.), abandoned rodent or rabbit holes (Michener, 2010; Westrich, 2019). In many studies, species numbers of ground-nesting bees were found to decrease with increasing impervious surface cover, but the results are inconsistent across the literature (Fortel et al., 2014; Wilson and Jamieson, 2019; Buchholz et al., 2020; Banaszak-Cibicka and Dylewski, 2021; Zaninotto et al., 2021; Gathof et al., 2022).

Besides nesting behavior, wild bees show different levels of sociality, ranging from highly organized (eu-)social, over communal, to solitary lifestyles, or even parasitizing other bee species. Some studies found that social behavior is favored in cities, as division of labor and higher individual numbers can increase foraging efficiency and competitive abilities over solitary species. For example, colony-building bumblebees and socially organized sweat bees (*Lasioglossum* ssp.) are often observed in high abundances in urbanized environments (e.g. Hülsmann et al., 2015; Fischer et al., 2016; Geslin et al., 2016). Solitary bees are affected by urbanization as well, but effect directions differed among studies, and parasitic bees are often less abundant and diverse in intensively urbanized areas (Wilson and Jamieson, 2019; Banaszak-Cibicka and Dylewski, 2021; Zaninotto et al., 2021; Gathof et al., 2022). Though Buchholz et al. (2020) found parasitic bees favored by urbanization in urban dry grasslands. Parasitic bees are adapted to the phenology of their hosts and strictly bound to their spatial distribution. Habitats of high quality or an intermediate intensity of urbanization could, therefore, compensate for the negative effects of urbanization (Fortel et al., 2014). However, results are ambiguous across the few studies available, and further research must address existing knowledge gaps (Buchholz and Egerer, 2020).

Several wild bee species are oligolectic, i.e., diet specialists, and their foraging preferences range from plant families over genera to single species (Westrich, 2019). Occurrences of oligolectic wild bees are bound to the distribution of their host plants, and further habitat criteria must be met, such as the availability of nesting structures and materials in foraging distance and habitat reachability (Twerd et al., 2021). Those species are more sensitive to urban transformation, and polylectic species, i.e., generalist feeders, are often associated with urban environments (Buchholz et al., 2020; Banaszak-Cibicka and Dylewski, 2021).

Body sizes vary greatly among wild bee species and determine different aspects of their performance, e.g., dispersal and foraging ranges and transport capacities of pollen and nectar (Greenleaf et al., 2007). Several studies found larger bees in areas of increasing urbanization, possibly related to fragmented resource patches that can only be reached by covering higher distances (e.g. Zaninotto et al., 2021; Brasil et al., 2023). Nevertheless, others found the opposite (e.g. Gathof et al., 2022). Besides, there is evidence of a body-shrinking effect in reserve habitats in Spain due to a warming climate (Herrera et al., 2023), and similar effects may occur due to the urban heat island. Although body size is one of the most frequently analyzed wild bee traits, there are still many unknowns about general patterns in size-urbanization relationships. Inconclusive results may be caused by interactions between body size and physiological traits, such as thermal tolerance, morphological traits modulating flight performance, or environmental conditions, such as pollen quality influencing larval development and reproductive output (Hamblin et al., 2017; Gathof et al., 2022; Polidori et al., 2023; Ferrari et al., 2024b).

Phenological traits are affected by urbanization, thus influencing urban bee communities. Fewer spring-emerging species are found in urbanized areas, while species that occur in summer are more abundant (Twerd et al., 2021; Fisogni et al., 2022). Urban warming can affect early emerging bees twofold. On the one hand, a warmer urban climate causes shifts in the flowering phenology of plants, eventually leading to a temporal decoupling with pollinator emergence and reduced food availability for spring bees

(Harrison and Winfree, 2015). Although shift effects in phenology are evident, a phenological de-synchronization between early-flowering species and their pollinators has so far not been observed, and phenological shifts in plant-bee interactions need to be better understood (Buchholz and Egerer, 2020). On the other hand, spring emerging bees usually overwinter as imagines, which are negatively affected by warmer winter temperatures. Bee species that overwinter as adults have lower body weights, as energy consumption increases due to higher metabolic rates induced by changed hibernation conditions (Kemp et al., 2004; Fründ et al., 2013). Additionally, observations have been made in bumblebee queens and workers foraging in winter, and even second-generation winter colonies were produced in urban environments, using mass flowering shrubs as food resources (Stelzer et al., 2010). The extension of the vegetation period affects species that are active later in the year, and pre-winter conditions have species-specific effects on mortality rates, fat body, and performance of the following generation (Bosch et al., 2010; Sgolastra et al., 2011).

Consistent landscape effects in trait-based filtering were reported in the abovementioned studies. However, at varying scales, habitat types, sources of traits and landscape data, and different indices analyzed complicate the interpretation of the results. Up to now, it is impossible to predict general trends of urbanization-induced mechanisms that form urban wild bee communities. Local factors of habitat size and management are influential but not well covered by the literature, and especially how plant functional diversity and identities interact with wild bees needs further research (Blüthgen and Klein, 2011; Uyttenbroeck et al., 2017). Wild bee traits have been found to determine the occurrence of individual species with respect to urbanization at different scales. Therefore, understanding the relative significance of biotic and abiotic factors that shape ecological networks and their inherent interactions and functions is necessary to improve urban rehabilitation's effectiveness and efficiency (Aronson et al., 2016).

1.4 Rehabilitation of urban biodiversity and ecosystem functioning

Cities can include fragments of former species-rich (semi-)natural habitats and offer possibilities for wild plants and bees to form novel communities artificially shaped by anthropogenic land use. In modern cities, greenspace can support several species, although its creation and management is mainly based on non-ecological constraints (Kowarik, 2011). Thus, modern concepts that integrate biodiversity into urban development are needed to realize the potential of cities for biodiversity. There is a wide gap of knowledge on rehabilitation effectiveness and how it can be applied efficiently in the confined urban matrix (Gann et al., 2019). Additionally, in the face of global change, there is an urgent need to pay more attention to aspects of ecosystem functionality in urban rehabilitation (Kollmann et al., 2016). Finally, integrating scientific results into the daily decisions of planners and practitioners remains challenging (McDonnell and Hahs, 2013; Parris et al., 2018).

1.4.1 Green Infrastructure and its application in urban biodiversity rehabilitation

Rehabilitating urban greenspace is thought to maintain the functioning and resilience of ecosystems, support biodiversity, and improve public health in cities (Tzoulas et al., 2007). The concept of Green Infrastructure was first introduced in the 1990s and later developed by various scientists, practitioners, and organizations. Benedict and McMahon (2006) contributed to the foundation in defining and promoting the concept of a planned network of green areas to enhance city environmental quality. In 2013, the European Union adopted the ‘Green Infrastructure strategy’ to address environmental challenges in conservation and its role in sustainable development (European Commission, 2013). While this strategy's success varies and faces funding constraints, conflicting interests in land use, or regulatory barriers, it is ascribed a crucial role in mitigating the loss of species and ecosystem functioning (Chatzimentor et al., 2020).

There is no explicit formal definition of the term Green Infrastructure, which results in inconsistencies in its interpretation and usage by different actors, such as scientists and policymakers (Wright, 2011). However, regardless of the sources of definitions, they show great similarities across the literature, and their variation depends on the specific aspect in focus. These incorporate strategic, political, and regulatory aspects, methods in landscape and urban planning, conservation of biodiversity and ecosystems, and economic criteria framed by the concept of ecosystem services. These include climate change mitigation, water management, air quality, food provisioning, and human social cohesion and health (Chatzimentor et al., 2020). The following broad definition is based on the European Commission (2013), and Chatzimentor et al. (2020): Green Infrastructure refers to a strategically planned network of natural and semi-natural areas designed to improve ecosystem services and enhance human well-being. It encompasses urban and rural landscapes and emphasizes the interconnectedness of natural and built environments.

With growing populations and increasing building density, room for restorative interventions to support biodiversity is scarce in urban areas. To maintain and improve urban habitat quality, types and functions of Green Infrastructure with the highest impact potential must be identified. Prioritization in restoration and management can help to efficiently develop biodiverse and resilient ecosystems (Schaub et al., 2021; Sun et al., 2021). Several types of urban Green Infrastructure serve as habitats, such as wetlands and water bodies, parks, gardens, or remnants of a former natural landscape (Capotorti et al., 2023). Within the urban matrix, large green areas usually serve as species reservoirs, although often isolated by the surrounding impervious surface area. Other green structures, such as green rooftops, canals and riverbeds, river dikes, rail tracks, or roads, can serve as stepping stones and corridors to create an interconnected network of smaller and larger greenspace elements (Wright, 2011). Nevertheless, to fulfill the network function, the ecological quality of the connecting structures is the driver with the highest impact on its effectiveness. Therefore, the creation, rehabilitation, and management of Green Infrastructure need to be planned with respect to the species and functions to improve (Capotorti et al., 2023).

1.4.2 Urban Green Infrastructure for wild bees in cities

Wild bees are a highly synanthropic group, and urban wild bee habitats incorporate a wide range of different types. Bees are abundantly found in secondary habitats of anthropogenic origin, such as parks and gardens, the most frequently studied urban spaces (Westrich, 2019). Other types of urban bee habitats include sand and clay pits, spoil heaps, and other industrial wastelands and brownfields, where narrow niches often create refuges for specialized or rare species independent of anthropogenic disturbance intensity (Heneberg et al., 2016; Twerd et al., 2019; Twerd and Banaszak-Cibicka, 2019; Twerd et al., 2022).

Urban grasslands have lately come into focus as secondary habitats for plants and wild bees, offering great opportunities for plant and wild bee conservation (Klaus, 2013). Besides parks and gardens, meadows in residential areas and larger roadside verges can be considered grasslands, and harbor a wide range of plant species and provide foraging resources for wild bees (Muñoz et al., 2015; Buchholz et al., 2020; Felderhoff et al., 2022). Besides their different functions in the urban fabric, all grassland types have a regular mowing regime in common; depending on its intensity, different communities and species assemble (Steidle et al., 2022; Anderson et al., 2023). To increase their value for biodiversity, grasslands can be rehabilitated by introducing native seeds through mown material from local donor sites or sowing commercially available seed mixtures. Besides the species origins and applied techniques, other factors, such as pre-cultivation, tillage, exchange or removal of the soil, and local climatic conditions, need to be considered during grassland rehabilitation. These factors are crucial for the success of the intervention, and the composition of the applied seed material must be adapted to these factors (Klaus, 2013; Klaus and Kiehl, 2021).

Wild bee-promoting interventions need a holistic approach. Only increasing the foraging resources falls short if nesting structures in the near surroundings are missing, while wild bees are adapted to a wide range of different structures and substrates in different degrees of specialization. For example, offering bamboo or reed material (*Phragmites australis*), or drilled holes in wooden blocks or poles, is an effective way to support aboveground nesting wild bees in structurally poor environments (Prendergast, 2023). Moreover, this method has been successfully used to assess the diversity of wild bees and their interactions with other species and the environment in several experiments (Staab et al., 2018). Although most wild bees are soil nesters, the respective rehabilitation and research have so far not taken place in urban settings for this group. It is known that in agricultural areas with high proportions of bare soil, wild bee species richness increases (Tschanz et al., 2023). However, these results cannot easily be transferred to urban areas with high imperviousness, and methods to include nesting opportunities in urban Green Infrastructure design have yet not been tested.

Although there is a large body of research on urban wild bee communities and diversity, there are still many unknowns regarding urban rehabilitation. Research on technical solutions for wild bee conservation is lacking, and implementing biodiversity-friendly Green Infrastructure under current urban planning, administration, and regulation remains challenging (Chatzimentor et al., 2020).

1.4.3 Transforming barriers to corridors: Design and management of pollinator-friendly roadside vegetation

Roads are changing the landscapes in which they are built, causing habitat degradation or loss, increased mortality and disturbance of wildlife, division and isolation of populations, and invasion of common and exotic species (Andrews, 1990). Species most sensitive to roads are those poor in dispersal ability, bound to specific habitats, specialized behaviors, or endemic to a region (Andrews, 1990). Habitat fragmentation due to roads reduces gene flow and lowers genetic diversity (e.g. Keller and Largiadèr, 2003). Roads can occupy high proportions of land. For example, Phillips et al. (2021b) found 3694 km^2 hard road surfaces in Great Britain, covering 1.8% of land.

Besides the negative impact of roads, more recent research has pointed out the positive role roadside vegetation can play for pollinators and ecosystem service provision (Phillips et al., 2020b; Phillips et al., 2020a). Looking closer at urban areas, road verges cover considerable space and therefore offer opportunities to support biodiversity (Marshall et al., 2019). Sustaining habitat connectivity is one of the main quests in urban conservation. Roads permeate the urban fabric, and the ecological potential of roadside vegetation to function as corridors must be evaluated (Dániel-Ferreira et al., 2022). In doing so, the number and area size of high-quality secondary habitats can be increased to counteract growing habitat fragmentation (Fischer et al., 2022).

Rehabilitation of roadside vegetation can be oriented toward the restoration methods and techniques of natural or agricultural grasslands; however, there are specifics to be acknowledged. Roadsides experience high input of chemicals, heavy metals, salt, and microplastics (Phillips et al., 2021a). Littering, dog feces, and human trampling contribute to further degradation of the soils, exhibiting high levels of nutrients and compaction of shallow top layers (Frenne et al., 2022). Locally, the microclimatic urban conditions and water drainage lead to dry conditions and potential drought stress in summer. These environmental prerequisites must be considered implicitly when roadside vegetation is to be enhanced.

A cost-extensive way to enhance roadside vegetation lies in a change in its management. As they are usually mulched more than ten times yearly, decreasing the mowing intensity and removing the cut biomass can lead to satisfactory medium- or long-term results and benefit native plant species in the soil seed banks (O'Sullivan et al., 2017). However, many urban soils are depleted in seeds or invaded by neophytes dispersed via transportation routes (Ansong and Pickering, 2013). Sowing seed mixtures is, therefore, a practical solution to overcome urban problems of invasion, depleted soil seed banks, and limited dispersal of plants in combination with the isolation of many urban habitats (Bretzel et al., 2024). Newly built roadsides can easily be treated with a previously prepared standardized mixture.

When designing a seed mixture for roadsides, the local plant species pool is the basis for species selection, and the local soil and climatic conditions restrict the subset of species that fit the requirements. Wildflower mixtures are used to support wild bees and other pollinators. However, mixing herbaceous species with some less competitive grass species leads to quick soil closure and synergistic establishment effects in hot and dry conditions (Rojas-Botero et al., 2023). Further, species selection depends on the purpose of the greening type and is best informed by plant species traits. Flower colors and morphologies, plant phenologies, pollen and nectar load and components, and phylogenetic diversity determine which bee species will profit. Moreover, the redundancy of certain plant traits in a seed mixture covers the requirements of less competitive bee species (Burkle et al., 2020).

Trait-based approaches can improve the rehabilitation of urban habitats. However, although they are well advanced in plant ecological research, there are many unknowns regarding species of higher trophic levels, such as wild bees. To make further progress, evaluating practical solutions for wild bee conservation is necessary to identify:

i) wild bee habitats with rehabilitation potential;
ii) bee traits that are particularly affected by urban filtering; and
iii) functional groups of bees that are crucial to maintain the function of pollination.

1.5 Problem statement, objectives, and outline

Creating wildlife-friendly cities is critical in times of global change to counteract further species loss and maintain crucial ecosystem processes. Considering the predicted significant increases in land occupied by urban areas and immensely growing urban populations, nature conservation faces major challenges. Novel restoration approaches that integrate interactions between organisms and the environment must be considered and address the questions of how these interactions shape urban communities and how ecosystem functions can be maintained in human-dominated landscapes.

This doctoral thesis contributes further knowledge on the effective rehabilitation of roadsides as urban Green Infrastructure aimed to support wild bee communities and pollination. It is based on a city-wide field experiment in Munich, Germany. Over three years, urban roadsides were systematically rehabilitated by sowing a specifically designed wildflower mixture across an urbanization gradient. Their effects on wild bees and pollination were then investigated at different spatial scales to address the following objectives:

I. Testing a trait-based approach to design a habitat-specific wildflower mixture and evaluating plant establishment by analyzing the effects of the planting year, site conditions, and urbanization on taxonomic and functional diversity, as well as plant community structure.
II. Investigating the effects of roadside vegetation and urbanization on pollinator abundance, the causal interactions shaping pollination, and how results can be used to evaluate urban rehabilitation measures.
III. Analyzing the effects of the local vegetation and urbanization on wild bee taxonomic diversity, functional diversity, and urban filtering to derive trait-informed solutions for urban roadside rehabilitation.

These objectives correspond to three peer-reviewed articles published in international scientific journals, constituting the basis of this cumulative doctoral thesis (Figure 1). ***Publication I*** focuses on the application of a designed wildflower mixture sown at urban roadsides. It evaluates short-term effects of the planting year, the local soil conditions, as well as trait-based interactions with the urban environment, forming newly introduced roadside communities. In analyzing plant taxonomic and functional diversity, as well as urban filtering and community structuring, classic and trait-based aspects complement each other to form a comprehensive view of the rehabilitation success of urban roadsides. In ***Publication II***, three model plant species (‘phytometers') were used to measure the effects of local resource availability, i.e., plant diversity and floral density, on the abundance of wild bees, honeybees, and hoverflies. Additionally, cause-effect relationships between local vegetation, landscape factors, and pollinator abundance were analyzed to test the suitability of the phytometers for the functional evaluation of rehabilitation at the urban roadsides. Finally, ***Publication III*** assessed the effects of urban roadside rehabilitation and urbanization on wild bee abundance, taxonomic and functional diversity, as well as urban filtering. In this study, several wild bee traits were affected by increasing competition and urbanization. Based on this, trait-informed suggestions for urban conservation were made.

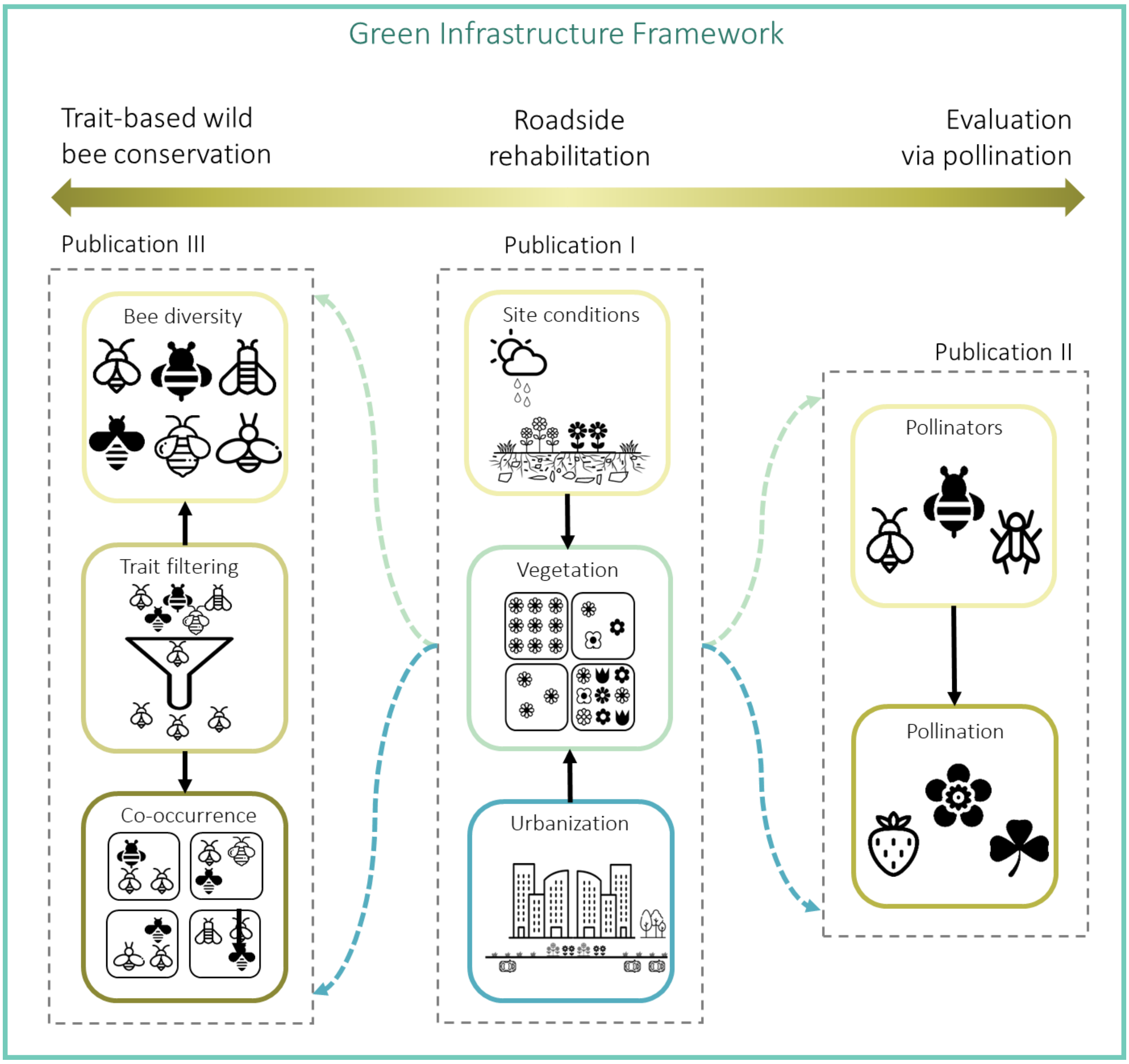


Figure 1: Graphical overview of the three publications included in the doctoral thesis, embedded in the Green Infrastructure Framework. **Publication I** (middle) focuses on the rehabilitation of urban roadside vegetation via sowing a native seed mixture. It evaluates the relative influence of the local site conditions, i.e., seasonal environmental variation and soil properties, and urban landscape characteristics on taxonomic and functional diversity and community assembly. In **Publication II** (right), plant diversity and flower availability of the rehabilitated roadside patches, as well as the urban landscape were investigated for their impact on pollinators, i.e. the abundances of wild bees, bumble bees and hoverflies, and the resulting effects on pollination success and quality based on three different phytometer species, namely *Fragaria* x *ananassa*, *Ranunculus acris*, and *Trifolium pratense*. The results were intended to be used for the evaluation of urban rehabilitation. **Publication III** (left) deals with the effects of roadside rehabilitation on urban wild bee diversity, functional urban filtering of urban bee communities, and how the functional analysis of species co-occurrence can be used to improve urban bee conservation. In summary, the thesis aims at covering significant topics in the conservation of urban biodiversity and ecosystem functioning, and in assessing the success of ecological interventions via phytometer plants.

2 Materials and Methods

2.1 Study region

The city of Munich served as study area for the implementation of the urban roadside experiment (city center: 48.13761, 11.57991; 515 m a.s.l.). The region has a temperate climate with a mean precipitation of 951 mm, and an average temperature of 10.7 °C (LfL, 2023). With over 1.5 million inhabitants and an area of 310 km2 (5100 km-2), Munich is rated Germany's third-largest city and among Europe's most densely populated areas (Eurostat, 2023; Munich city administration, 2023). Overall, seven major roads were selected for the project (Figure 2). Selection criteria were contiguous vegetated roadsides with a minimum width of 2 m and no planned construction sites that could have corrupted the experiment during the four-year project. The roads were required to cover a gradient of urban land-use intensity, such as dense and loose residential areas, industrial areas with high and dense development, infrastructural areas such as roads and railroad tracks, allotments, parks, fallows, other types of urban greenspace and areas of agricultural production.

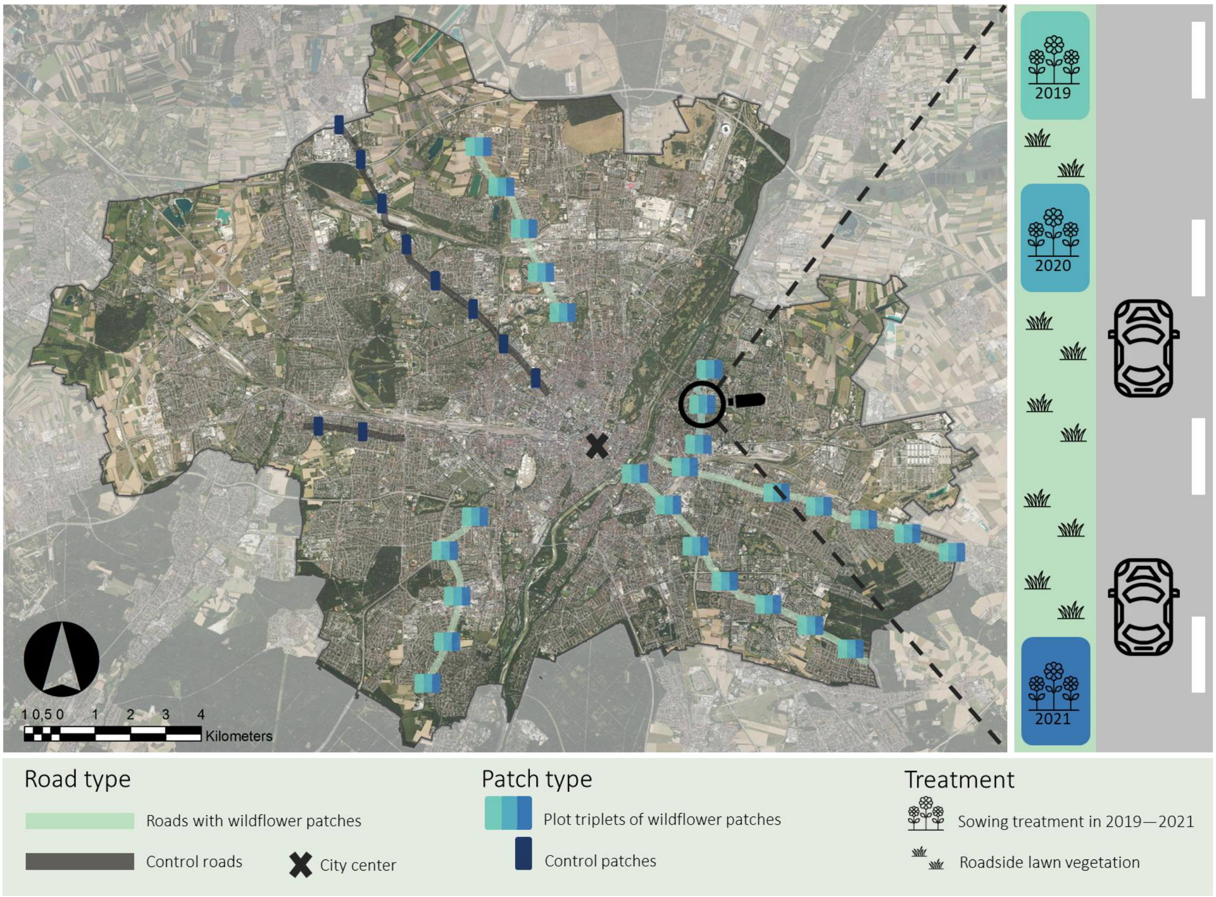


Figure 2: Map of the study area and schematic experimental design, providing an overview of Munich, the locations of the roads, and the layout of the experimental patches. Five roads were used for the sowing treatment (green roads), and wildflower patches were added yearly from 2019—2021, representing plot triplets, consisting of three gradually established wildflower patches in a 0—20—55 m distance array (light—dark blue); 26 plot triplets were established from the city center (black cross) to the borders, i.e., 1300 m away from each other. Two roads were used as control without sowing (grey roads), including ten control patches, consisting of short-trimmed roadside lawn vegetation (navy blue). Background map: DOP80 (Bayerische Vermessungsverwaltung, 2023; CC-BY 3.0).

2.2 Study design

Three contiguous wildflower patches were investigated at increasing distances, and the patches were seeded incrementally with a native wildflower mixture, hereafter referred to as 'site triplet'; 25 flowering patches were established along five roads in the year 2019. In 2020, additional patches were seeded at 20 m distance from the first flowering patches. In 2021, the distance of the third patch to the initially sown one was 75 m (Figure 2). The varying distances considered the maximum collecting distances of solitary wild bees as the most important target species group (Gathmann and Tscharntke, 2002). The minimum distance between the site triplet replicates was 1300 m to avoid spatial autocorrelation between the site triplets. Before seeding, plots were used as controls locally, i.e., non-seeded patches with low-cut grassy lawns, receiving the regular management of high-intensity mowing. Two separate roads served as additional controls where ten lawn patches without seeding were sampled. The high number of replicates was aimed at compensating for potential sampling failures, e.g., due to poor patch establishment or vandalism.

2.2.1 Wildflower mixture design

The native wild plant pool of the origin region 16 (Unterbayerische Hügel- und Plattenregion) served as a basis for species selection, with a focus on regional plant material (Durka et al., 2017; Bucharova et al., 2019). The target community was supposed to correspond to functional plant traits defined in consideration of the local conditions at urban roadsides, i.e., soils with high nutrient concentrations and contamination, such as salt, as well as extreme climatic conditions of drought and heat stress (Bretzel et al., 2024). In addition to ecological criteria, practical considerations for optimal performance at roadsides were considered, such as traffic safety and requirements for establishment and maintenance. Annual plant species originating from arable fields were incorporated, considering closure of bare soil and invasion resistance, fast provision of pollinator forage, and aesthetic aspects by rapid revegetation (Ligtermoet et al., 2022). Most importantly, several traits were included that are relevant for the local pollinator populations, such as phylogenetic diversity, varying phenologies, flower colors, and resource attraction (Table 2; Bucharova et al., 2021; Kuppler et al., 2023).

Several potential seed mixtures were assembled using functional criteria (Table 2). Plant trait information was obtained from the BiolFlor database (Klotz et al., 2002). From the pre-selected pool of 41 potential species, plants were hierarchically clustered based on Gower's distance (Botta-Dukát, 2005). In doing so, plants with similar characteristics were assigned to seven groups. Potential seed mixtures were composed by selecting species from every group, and the resulting mixtures were evaluated based on their phylogenetic diversity (Fornoff et al., 2017). Grasses were not included in the mixture, as they were assumed to be present in the local seed banks or to colonize from neighboring vegetation. Finally, 26 plant species out of eleven families were selected, mainly species of anthropo-zoogenic dry grasslands and herbaceous ruderal vegetation (Table 2). Compared to commercially available mixtures that usually include more than 30 species, the number of species in the roadside mixture was intentionally limited, considering costs and the relatively small dimensions of the experimental patches (Schaub et al., 2021). The autochthonous seed material was obtained from regional seed producer Johann Krimmer (Pulling, Germany).

Table 2: Plant species included in the seed mixture after trait-based clustering of the regional species pool. In total, 26 species from eleven families were selected that fitted the conditions at the urban roadsides and were attractive to the local pollinator population. Life cycle, flower color, type of main resource provision, pollen vectors, and flowering phenology (months of potential flowering) were considered to design the final seed mixture. The data was derived from the BiolFlor database (Klotz et al., 2002). Life cycle: an = annual, bi = bi-annual, per = perennial; main resource: pol = pollen, nec = nectar; phenology: month).

Family	Species	Life cycle	Flower color	Main resource	Pollen vector	Phenology
Apiaceae	*Daucus carota*	bi	white	pol/nec	short-tongued bees, flies, syrphids, wasps, beetles	06—09
	Pastinaca sativa	per	white	pol	short-tongued bees, flies, syrphids, wasps, beetles	07—09
Asteraceae	*Achillea millefolium*	per	white	pol	short-tongued bees, flies, syrphids, wasps, beetles	06—10
	Cyanus segetum	an	blue	pol/nec	bees, bumblebees, syrphids, wasps	06—10
	Centaurea jacea	per	purple	pol/nec	bees, bumblebees, syrphids, wasps	06—11
	Centaurea scabiosa	per	purple	pol/nec	bees, bumblebees, syrphids, wasps	07—08
	Cichorium intybus	per	blue	pol/nec	bees, bumblebees, syrphids, wasps	07—10
	Crepis biennis	bi	yellow	pol/nec	bees, syrphids, wasps, beetles	05—08
	Pentanema hirtum	per	yellow	pol/nec	bees, syrphids, wasps, beetles	06—07
	Pentanema salicinum	per	yellow	pol/nec	bees, syrphids, wasps, beetles	06—10
Boraginaceae	*Echium vulgare*	bi	purple/ pink	pol/nec	bumblebees, long-tongued bees	05—07
Brassicaceae	*Berteroa incana*	an	white	nec	bees, syrphids	06—10
Campanulaceae	*Campanula rapunculoides*	per	purple	pol	bees, syrphids	06—09
Caprifoliaceae	*Scabiosa columbaria*	per	blue	pol/nec	bees, bumblebees, syrphids, wasps	07—11
Caryophyllaceae	*Silene noctiflora*	an	white	nec	moths	06—09
Fabaceae	*Anthyllis vulneraria*	per	yellow	nec	bumblebees, long-tongued bees	05—08
	Lathyrus pratensis	per	yellow	nec	bumblebees, bees, syrphids	06—08
	Lotus corniculatus	per	yellow	nec	bumblebees, bees, syrphids	06—08
	Medicago falcata	per	yellow	nec	bumblebees, bees, syrphids	06—09
	Trifolium medium	per	red	nec	bumblebees, bees, syrphids	06—08
Lamiaceae	*Origanum vulgare*	per	purple	pol/nec	bumblebees, bees, syrphids	07—09
	Salvia pratensis	per	blue	pol/nec	bumblebees, long-tongued bees	05—08
	Thymus pulegioides	per	purple	nec	bumblebees, short-tongued bees, syrphids, flies, beetles	06—10
Malvaceae	*Malva moschata*	per	pink	pol/nec	bees, syrphids, flies, beetles	06—10
Ranunculaceae	*Delphinium consolida*	annual	blue	nec	bumblebees, long-tongued bees	05—08
	Papaver rhoeas	annual	red	nec/pol	bees, bumblebees, syrphids, flies, beetles	05—07

2.2.2 Patch establishment and management

The size of the experimental wildflower patches was 8 m^2 (2 m x 4 m). Before seeding, the aboveground turf and 5--10 cm of topsoil were removed, the subsoil was slightly loosened, and the patches were filled with a nutrient-poor sand-substrate mixture. The seed mixture was prepared in the lab using a precision scale, and every species had the same proportion of 1.23 g. For an even distribution, seeds were mixed with 31 g/m^2 of ground corn, hand-seeded at a seed density of 4 g/m^2, and then pressed onto the surface using a cylindrical roller or wooden boards. The experimental patches were not irrigated during the project period. All patches were marked with wooden posts to prevent accidental mowing and trampling by pedestrians (Figure 3). Additionally, information boards were put up to educate interested citizens and increase acceptability. Removal of foliage and mowing of the experimental plots took place in autumn, and the cut material was removed from the plots for nutrient regulation. After their establishment, the development of the sown patches was documented regularly during the project (Figure 4).

The pre-experimental vegetation was a shortly cut lawn dominated by few grasses and common herbaceous plants that tolerated the management, e.g., *Bellis perennis*, *Prunella vulgaris* or *Trifolium repens*. The prior management was a frequent mulching regime, with mowing 10–12 times during the year (Figure 5). This urban turf grass vegetation was used as local control as part of the site triplets, as well as ten control patches along the two control roads.

Figure 3: Plot establishment at urban roads in Munich. A) Wildflower patch a few months after seeding. B) Before seeding, the aboveground turf was manually removed, and the topsoil loosened. C) For better soil contact, the seed mixture was pressed to the surface with a cylindrical roller.

Pictures: Simon Dietzel

Figure 4: Example of wildflower patch development at Putzbrunner Straße (plot-ID RO018), Munich. Patch establishment from pre-existing low-cut roadside lawn, and sowing in **2019**, and during the following vegetation periods of **2020** and **2021**, each picture taken in mid—late June. Floral abundance and the number of plant species increased visibly, including plants attractive for pollinators, such as Achillea millefolium, Crepis biennis, Echium vulgare, Lotus corniculatus, or Salvia pratense.

Pictures: Sandra Rojas-Botero

Figure 5: Exemplary types of roadside lawns used in the experiments. In all cases, pre-existing roadsides received the regular management of high frequency mowing (> 10 times) per year. Lawns varied in widths of 3—5 m **(A—B)**, up to narrow strips of only 2—2.5 m **(C—E)**. Shading caused by tree foliage varied according to the density and age of the local population. The tested roads led from the city center to the outskirts, crossing varying land-use types. The prevailing vegetation consisted of species poor urban turf grass communities dominated by few grassy species adapted to the management and environmental conditions. Lawns were used as controls.

Pictures: Simon Dietzel

2.3 Data sampling and compilation

2.3.1 Vegetation sampling

The roadside vegetation was sampled on wildflower and control patches differently. To account for the floral resource diversity and abundance present at the time, flowering herbaceous plant species were identified, and the number of their floral units counted, including sown and spontaneous species (Baldock et al., 2015). Within the wildflower patches, frames of 50 cm x 50 cm were systematically placed five times to standardize sampling (Figure 6). The frames were not used for the controls; instead, species and floral units of the whole 8-m^2 patches were sampled, as flowering species were usually rare due to intense mowing. To standardize floral unit data of these two methods, we finally calculated mean floral density per m^2 per plot. Sampling was conducted from June—August 2019—2021. The data was used for *Publication II* and compiled accordingly.

To account for the total potential of floral resources for pollinators, all herbaceous species and their cover, including individuals in vegetative status, were recorded in one sampling round in June—July during all sampling years. Plant coverage was estimated following the Braun-Blanquet cover-abundance scale (Wikum and Shanholtzer, 1978). Again, frames were used for wildflower patches, entire control patches were sampled, and the data was finally harmonized by calculating plant cover per m^2. Using species and cover information, Shannon diversity per site and year was determined with the vegan R-package, version 2.6-4 (Oksanen et al., 2022). The data was used for *Publication III* and compiled accordingly.

In *Publication I*, controls were directly neighboring turf grass patches, similar in their management and vegetation to controls described in *Study design*. As local controls were successively transformed into wildflower patches, this was a practical solution to keep sampling standardized for the analysis of patch establishment, vegetation development, and plant functional community assembly. All species were identified with reference to the universal electronic reference list for the German flora (Jansen and Dengler, 2008). Data was compiled depending on the specific research questions of the three published experiments presented in this thesis.

Figure 6: Vegetation sampling was conducted monthly during 2019—2021, from June—August. **A)** Counting squares were placed five times within the patches of 8 m^2. **B—D)** Plant species and floral units were counted, and plant cover was estimated.

Pictures: Sandra Rojas-Botero & Simon Dietzel

2.3.3.1 Plant traits and diversity indices

In Publication I, the establishment, community assembly, and functional performance of the wildflower patches were evaluated. Therefore, we obtained trait information on all sampled plant species from two sources (Klotz et al., 2002; Carmona et al., 2021). We selected functional traits that characterized plant capacity to establish, endure, and disperse, as well as their attractiveness to pollinators. Although conditions of the urbanization gradient may influence the variability in trait values (Cochard et al., 2017; Johnson et al., 2018), we assumed that within-species functional differences would be less pronounced than the inter-species functional variation obtained from the databases (Siefert et al., 2015). In the analysis, plant height, specific leaf area, and seed mass were selected as continuous variables. All other traits were categorical (Johnson et al., 2018). That is, specific leaf area (SLA), which is associated with relative growth rate, palatability and response to nutrient and moisture gradients. Plant height is correlated to competitive abilities, especially regarding access to light. Furthermore, factors like life history and clonal growth play a role in determining the extent of local dispersal (Weiher et al., 1999), while seed mass affects dispersal distance, seedling germination, and growth rates. The selected floral traits provide insights into the phenology, type, and vector of pollination, as well as the physiology and morphology of the plant's sexual reproductive organs (Klotz et al., 2002), thus representing pollinator attractiveness (E-Vojtkó et al., 2022). The additionally used reproductive phenological traits offer information about potential plant-insect interactions and the availability of resources for associated pollinators over time (Benadi and Pauw, 2018; E-Vojtkó et al., 2022). Table 3 gives an overview of all selected plant traits, data types, and units used for the analysis.

Table 3: Plant traits included in Experiment I, categorized into establishment, persistence, and reproductive traits. Data was used in continuous and categorical forms from two different databases.

Category	Trait	Data type [unit]	Reference
Establishment/Persistence	Specific leaf area (SLA)	continuous [mm^2/mg]	Carmona et al. (2021)
	Plant height	continuous [m]	Carmona et al., 2021
	Seed mass	continuous [mg]	Carmona et al., 2021
	Life form	categorical	Klotz et al. (2002)
	Life span	categorical	Klotz et al., 2002
	Vegetative spread	binary	Klotz et al., 2002
	Strategy	categorical	Klotz et al., 2002
Reproduction/ Pollinator attractiveness	Flower color	categorical	Klotz et al., 2002
	Flower type	categorical	Klotz et al., 2002
	Reward	categorical	Klotz et al., 2002
	Pollination vector	categorical	Klotz et al., 2002
	Flowering start	ordinal	Klotz et al., 2002
	Flowering duration	ordinal	Klotz et al., 2002

In the seed mixture, the abundance of plant species was defined as the seed mass per species by assuming a 100% germination rate. Afterward, this hypothetical functional potential was compared with the plant composition of one-year-old plant communities of the wildflower and nearby control patches. To assess taxonomic diversity, we initially computed Shannon diversity per patch and year using the vegan R-package, version 2.6-4 (Oksanen et al., 2022). Besides, Pielou evenness was calculated by dividing Shannon diversity by the $\log_{10}$ of species abundance. The Community-weighted mean (CWM) for each trait was determined by averaging trait values and weighted by species abundance to reflect the trait value selected in each environment. The functcomp function of the FD R-package, version 1.0-12.1, was used, considering fuzzy coding for categorical traits (Laliberté and Legendre, 2010). To compare species based on their traits, we constructed a species-by-species Gower's distance matrix using the gawdis R-package, version 0.1.4 (deBello et al., 2021). Equal weight was assigned to each trait to allow fuzzy coded data. Quantitative traits underwent a $\log_{10}$ transformation before distance calculation.

Functional richness, functional evenness, and functional divergence were computed using the dbFD function of the FD package. Functional richness quantifies the niche space occupied by species within a community, independent of species abundance. Functional evenness is defined as the regularity of abundance distribution in a functional trait space, with higher values indicating a balanced niche occupancy and trait frequencies in communities. Functional divergence measures the degree to which abundance distribution in niche space maximizes divergence in functional characteristics within the community (Mason et al., 2005). A community with high functional divergence would have the most abundant species occurring at the extremes of the functional range. These multi-trait indices were computed for all recorded traits combined, traits related to the establishment and persistence of plant species, and floral traits.

2.3.3 Insect sampling

From 2019—2021, pollinator sampling took place three times a year, from June—August. Colored pans were used as traps 15 cm in diameter, filled with 400 ml of water and a drop of odorless detergent to remove water surface tension. The traps were sprayed with blue, white, and yellow luminescent paint (SparVar Leuchtfarbe, Spray-Color GmbH) to attract pollinators (Westphal et al., 2008). One pan trap of each color was attached to a single wooden pole and placed at vegetation height for 48 h (Figure 7). On control patches, the traps were placed 40 cm above the ground to prevent destruction by humans or pets. At least 25 days were in between the single sampling rounds.

Afterward, trapped honeybees, wild bees, and hoverflies were brought to the lab, sorted, and stored in 70% ethanol. Wild bees were then prepared and identified to species level using common identification keys for German taxa (Schmid-Egger and Scheuchl, 1997; Amiet et al., 1999; Scheuchl, 2000; Amiet et al., 2001, 2004; Scheuchl, 2006; Amiet et al., 2007; Amiet et al., 2010; Dathe et al., 2016; Amiet et al., 2017). Unknown or critical individuals were sent to wild bee expert Klaus Mandery for clarification.

Figure 7: Pollinators were sampled with pan traps monthly, from June—August (2019—2021). **A)** Pan traps were set up at vegetation height in the centers of the wildflower patches, attached to a wooden pole. **B)** Pan traps were colored with a luminescent paint in blue, white, and yellow, to attract different pollinator groups. **C)** Wild bees were prepared and identified to species level.

Pictures: Simon Dietzel

2.3.3.1 Wild bee traits and diversity indices

For analysis, we selected five key traits of wild bees, drawing upon insights from the review on trait-urbanization interactions by Buchholz and Egerer (2020). We sourced trait information from several identification keys of the Fauna Helvetica series and the existing literature on wild bee ecology (e.g., Westrich, 2019). To ensure data consistency, we derived trait values from similar and reliable sources (**Table 4**). Then, we calculated functional dispersion based on Gower's distances using the gawdis and FD packages (Laliberté and Legendre, 2010). We chose functional dispersion as an indicator for urban filtering processes that affect wild bees, as it remains independent of species richness and reflects the functional formation of wild bee communities, following the approach proposed by Laliberté and Legendre (2010). Functional dispersion represents the average distance in multidimensional trait space between individual species and the centroid of all species. In this calculation, the centroid's position in trait space is adjusted to the most abundant species, and distances to the centroid of individual species are weighted by their relative abundances (Laliberté and Legendre, 2010). At patches with strong urban filtering, species with similar traits tend to accumulate, resulting in low functional dispersion. Conversely, higher values of functional dispersion indicate increased trait diversity and niche partitioning within the community (Martins et al., 2017; Buchholz et al., 2020).

Table 4: Wild bee traits included in Publication III, incorporating morphological, behavioral, phenological, and foraging traits. Traits were used as continuous and categorical data from the Fauna Helvetica series for wild bee species identification and Westrich (2019).

Category	Trait	Measure [unit]	Source
Morphology	Body size of female bees	continuous [mm]	Fauna Helvetica Westrich (2019)
Behavior	Nesting location	categorical [above-/belowground]	Westrich (2019)
	Sociality	categorical [parasitic, solitary, facultative social, social]	Westrich (2019)
Phenology	Lifespan	continuous [weeks of female nesting activity]	Fauna Helvetica
	Voltinism	categorical [parasitic, univoltine, bivoltine, social]	Westrich (2019)
Foraging	Diet specialization	categorical [parasitic, oligolectic, polylectic]	Westrich (2019)

2.3.4 Pollination sampling

2.3.4.1 Phytometer selection and management

We utilized three phytometer species characterized by their complementary traits to assess pollination, following the recommendations by Strobl et al. (2018). These species included:

1. *Fragaria × ananassa* (Rosaceae), the garden strawberry, is a crop species known for its wide range of insect visitors. Although capable of self-pollination, it is a reliable indicator of pollination and is frequently employed to measure this ecosystem function (Klatt, 2013; Wietzke et al., 2018). We opted for the late-blooming Malwina cultivar to synchronize the strawberries' flowering phases and the wildflower patches. Frozen plantlets (organic frigo plants) were obtained from a commercial provider.
2. *Ranunculus acris* (Ranunculaceae), the meadow buttercup, is more likely to attract dipterans, such as hoverflies (Kipling and Warren, 2014).
3. *Trifolium pratense* (Fabaceae), the red clover, is commonly visited by long-tongued bees, such as bumblebees, but can also receive partial pollination from non-bee nocturnal insects (Kanduth et al., 2021; Alison et al., 2022). It has been successfully used in other urban pollination studies (Hegland, 2014; e.g., Theodorou et al., 2020a).

R. acris and T. pratense seedlings were cultivated from local seed material provided by Johann Krimmer, Pulling. In spring, all plants were pre-grown in individual pots within a greenhouse at TUM GHL Dürnast, Freising, under controlled conditions encompassing substrate, water, light, and temperature until flower buds became visible (Figure 8 A—B). After field exposition, i.e., pollinating the inflorescences at the wildflower and control patches, the plants were returned to the greenhouse for fruit development and ripening, again receiving standardized maintenance.

2.3.4.2 Pollination measurements

To ensure fruits were sampled exclusively from flowers exposed to the urban environment, we marked closed inflorescences with colored strings before field exposition. Additionally, any flower buds that emerged during the field exposition were similarly marked and included in the analysis. For each phytometer species, we placed three individuals per plot and adjusted watering based on prevailing weather conditions. To explore potential variations in plant responses to pollinator exclusion, we covered one flower on each plant with a meshed nylon bag (Figure 8 C). The exposure periods for the different phytometer species were as follows: *Fragaria* × *ananassa* was exposed from June to July (maximum 22 days), while *R. acris* (maximum 27 days) and *T. pratense* (maximum 27 days) were exposed from July to August. *Fragaria* × *ananassa* and *R. acris* were exposed in 2020 and 2021, whereas T. pratense was only in 2021. When the fruits were ripe, we harvested them for measurement, considering their color (*F.* x *ananassa, R. acris*) or degree of dryness (*R. acris*, *T. pratense*). We weighed the fruits of *F.* x *ananassa* with a precision scale and counted fruits of *R. acris* and *T. pratense* as indicators for ‘pollination quality‘ (Figure 8 I—J). We observed some flowers of *F.* x *ananassa* producing small, deformed, and lightweight fruits and even found flowers of all three species not producing any fruits (Figure 8 D—H). Therefore, we defined this as ‘pollination failure,’ accordingly, pollination success was analyzed relative to flowers that produced strawberries with a certain minimum weight or at least one fruit (*R. acris*, *T. pratense*).

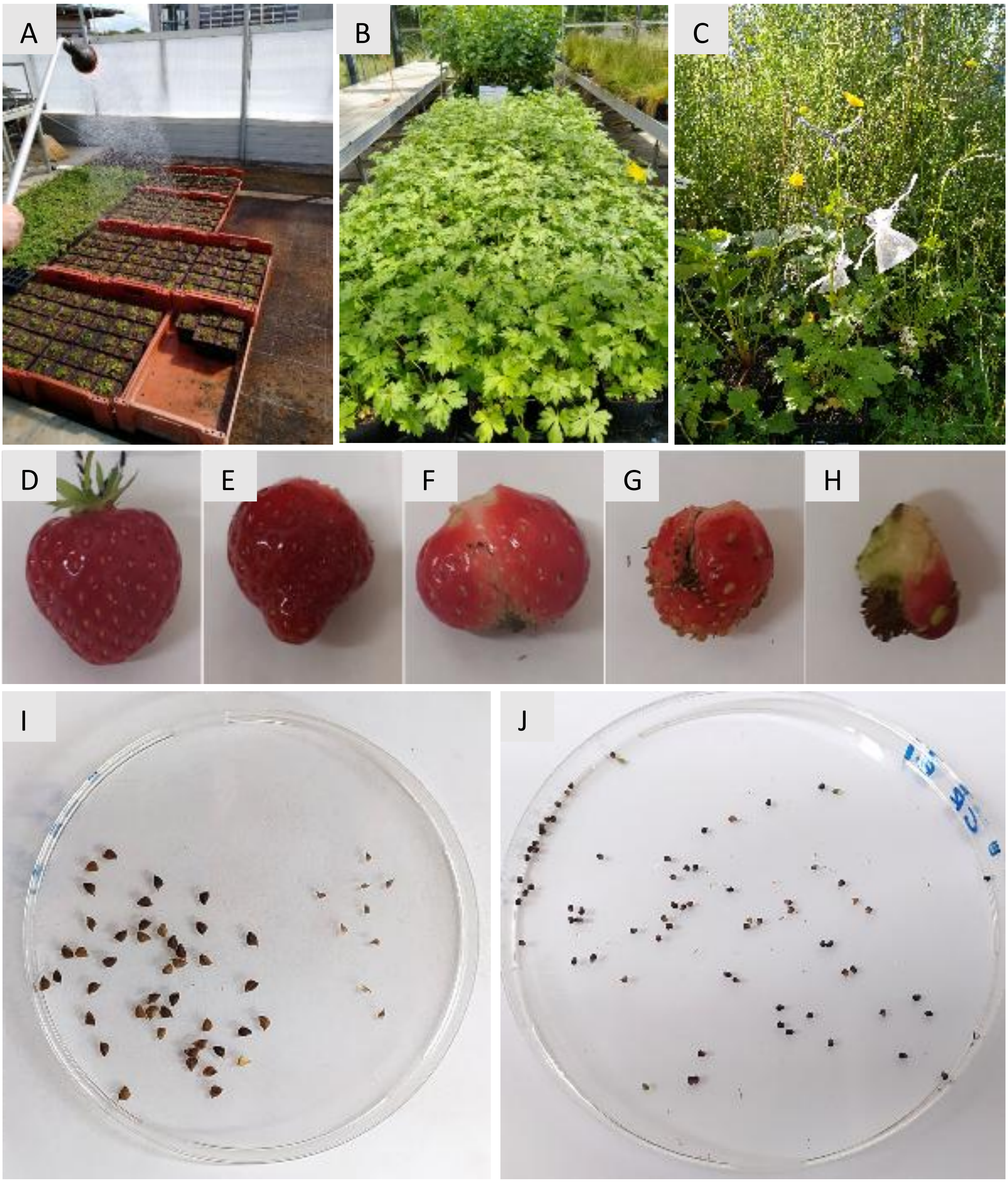


Figure 8: Phytometer plants were used to sample pollination success and quality along an urbanization gradient. **A—B)** Plants were kept under standardized conditions during rearing and after field exposure. **C)** Some flowers were covered with nylon bags to avoid pollination by insects. **D—H)** Strawberry fruit weights are sensible to the absence of insect pollinators, and fruit quality increases with pollinator abundance, in terms of color, and number of deformations. **I—J)** Fruit numbers of Ranunculus acris and Trifolium pratense were counted in the lab.

Pictures: Nadja Berger & Simon Dietzel

2.3.5 Local abiotic conditions

To gain insight into the role of local environmental conditions in vegetation establishment and the resulting functional communities, we collected soil samples by extracting the upper 10-15 cm of soil from ten randomly chosen locations within each wildflower patch using a soil corer with 3 cm in diameter. The soil bulk samples were air-dried and analyzed for soil texture, pH, organic matter, and salt, P, Mg, and K concentrations. The samples were analyzed at the Haeusler-Bodenanalysen Laboratory, Freising, Germany.

We set up a digital camera (Nikon D7500) with a circular fish-eye lens (EX-Sigma) covering a 180° field of view to assess shading over the wildflower patches. The camera was positioned at a height of 1 m, centered within each patch, to capture the local tree canopy cover, following the approach of Lagüela et al. (2011). To avoid overexposure to direct sunlight, the photographic documentation took place during early mornings, late afternoons, or cloudy days (Rich, 1990; Jonckheere et al., 2004). The images were processed using WinSCANOPY (Régent Instruments Inc.) to calculate the parameters of the Leaf Area Index (LAI) and the degree of sky openness (Rahman et al., 2018). LAI and openness were indicators for local shading levels within the study area. Control patches were not included in the sampling of local abiotic conditions, as they were only relevant for evaluating the seeding treatment according to the research questions of *Publication I*.

2.3.6 Urban land use

To include landscape effects in our analyses, we assessed the city landscape in a radius of 500 m around every experimental patch using ArcGIS 10 (Esri Inc., 2020). To gain publicly available land-use information in an appropriate resolution that is thus comprehensible for others, we used Open Street Map data (OSM; Open Street Map Contributors, 2020). We extracted information on different urban land-use types, such as industrial areas, transport infrastructures, green spaces, residential zones, agricultural production areas, and water bodies. To standardize OSM data, we followed the Corine Land Cover (CLC) classification (EEA, 2018). Land-use variables were then calculated, representing specific landscape factors used according to the research questions (Table 5).

Table 5: Analyzed landscape factors and the calculated variables used in the experiments within a radius of 500 m around every experimental patch.

Landscape factor	Variable [unit]	Research
Urbanization	Proportion of imperviousness [%] Landscape diversity [Shannon]	Impact of land-use intensity and habitat quality
Landscape quality	Edge density [m/m^2] Perimeter area ratio of greenspace [m/m^2]	Edge effects and relative importance of urban green space configuration
Patch location	Distance from the city center [km]	Corridor effects, functional filtering, and community shifting

2.4 Data analysis

The data was analyzed with R Software, version 4.1.2 (R Core Team, 2021). Before the statistical investigation, the raw data of every experiment was explored in depth, following the protocol by Zuur et al. (2010), i.e., checking for outliers, homogeneity, distribution, zero inflation, collinearity, interactions, and independence. Linear models were applied for all three publications. Normally distributed data was analyzed using the 'lme' function of the nlme R-package, version 3.1-157 (Pinheiro and Bates, 2022). Otherwise, non-normal and zero-inflated data was analyzed by deploying generalized linear mixed models (glmm) with Poisson, binomial, negative binomial, or Tweedie distributions, using the stats and glmmTMB R-packages, versions 4.1.2 and 1.1.4 (Brooks et al., 2017; Stoklosa et al., 2022). All models used the patch-triplet ID as a random factor to avoid auto-correlation. Full models included all relevant variables, and a stepwise model reduction approach was applied, considering decreasing AIC and p-values. For lme-models, the reduction was performed automatically, using the stepAIC function of the MASS R-package (Venables and Ripley, 2002). For glmms, model reduction was done manually or with the dredge function of the MuMIn R-package, version 1.46.0 (Barton, 2022). Model residuals were evaluated to examine model fits and quality using the performance and DHARMa R-packages, versions 0.10.4.1 and 0.4.4 (Hartig, 2021; Lüdecke et al., 2021). All results presented in *Publications I—III* represent the results of the final minimal models.

2.4.1 Specific analyses for Publication I

We used ordination analysis to investigate the taxonomic and functional community composition of the seed mixture, wildflower patches, and control patches. Based on Bray-Curtis dissimilarity calculations, the taxonomic compositions of the communities were compared using nonmetric multidimensional scaling (NMDS) by employing the metaMDS function of the vegan R-package. Principal Coordinates Analysis (PCoA) was conducted to investigate the CWM of functional plant traits with the pcoa function of vegan, based on Euclidean distances and negative Eigenvalues corrected with the 'Calliez' method. Permutational multivariate analysis of variance (PERMANOVA) was done with the adonis2 function of vegan to analyze the influence of the sowing treatment and two different years of wildflower patch establishment (2019, 2020). Differences within the treatment groups were tested with the betadisper function of vegan. In the linear regression analysis, Pielou evenness and all multi-trait functional diversity indices were fitted with a beta distribution using the betareg package (Cribari-Neto and Zeileis, 2010).

2.4.2 Specific analyses for Publication II

Experiment II used structural equation modeling (SEM) to analyze causal relationships between pollinator abundance, phytometer pollination, and local and landscape-scale factors. Based on scientific literature, we set up a theoretical framework comprising diverging effects of floral resources and the urban landscape, potentially affecting pollinator abundance positively with increasing local forage and habitat quality and negatively, e.g., by intensifying competitive pressures. We ran one SEM for each phytometer species using the piecewiseSEM R-package, version 2.1.2 (Lefcheck, 2016). A manual model reduction approach was applied by considering relevant information from the models, i.e., p-values, standard estimates, R^2, and Fisher's C. Model quality was checked by plotting SEM residuals with the residuals.psem function.

2.4.3 Specific analyses for Publication III

Generalized linear latent variable models (gllvm) were applied to study wild bee trait-environment interactions with the gllvm R-package, version 1.3.1 (Niku et al., 2019). We employed a fourth corner analysis by identifying species trait responses to local and landscape variables based on three matrices containing information on wild bee species abundance, environmental factors, and trait information. Additionally, we determined co-occurring indicator species by plotting two latent variables as an ordinal diagram. Model selection was done considering AIC and p-values, and the best model was selected by models with several specificities with likelihood ratio tests (anova R-function). The site triplets were set as random factor as in the regular linear regression analyses. Model fits were checked with the plot.gllvm function.

3 Manuscript Overview

This thesis is based on three original research articles published in international, peer-reviewed journals. Here, the contributions of the participating authors and graphical and written summaries of the publications are presented.

3.1 Publication I

Rojas-Botero, S., **Dietzel, S.**, Kollmann, J. & Teixeira, L. H. (2023). Towards a functional understanding of rehabilitated urban road verge grasslands: Effects of planting year, site conditions, and landscape factors. Flora, 152417. https://doi.org/10.1016/j.flora.2023.152417

Authorship contributions

Sandra Rojas-Botero: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review and editing, Visualization. **Simon Dietzel:** Methodology, Validation, Data curation, Writing – review and editing, Visualization. **Johannes Kollmann:** Conceptualization, Writing – review and editing, Supervision, Funding acquisition. **Leonardo H. Teixeira:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review and editing.

Graphical summary

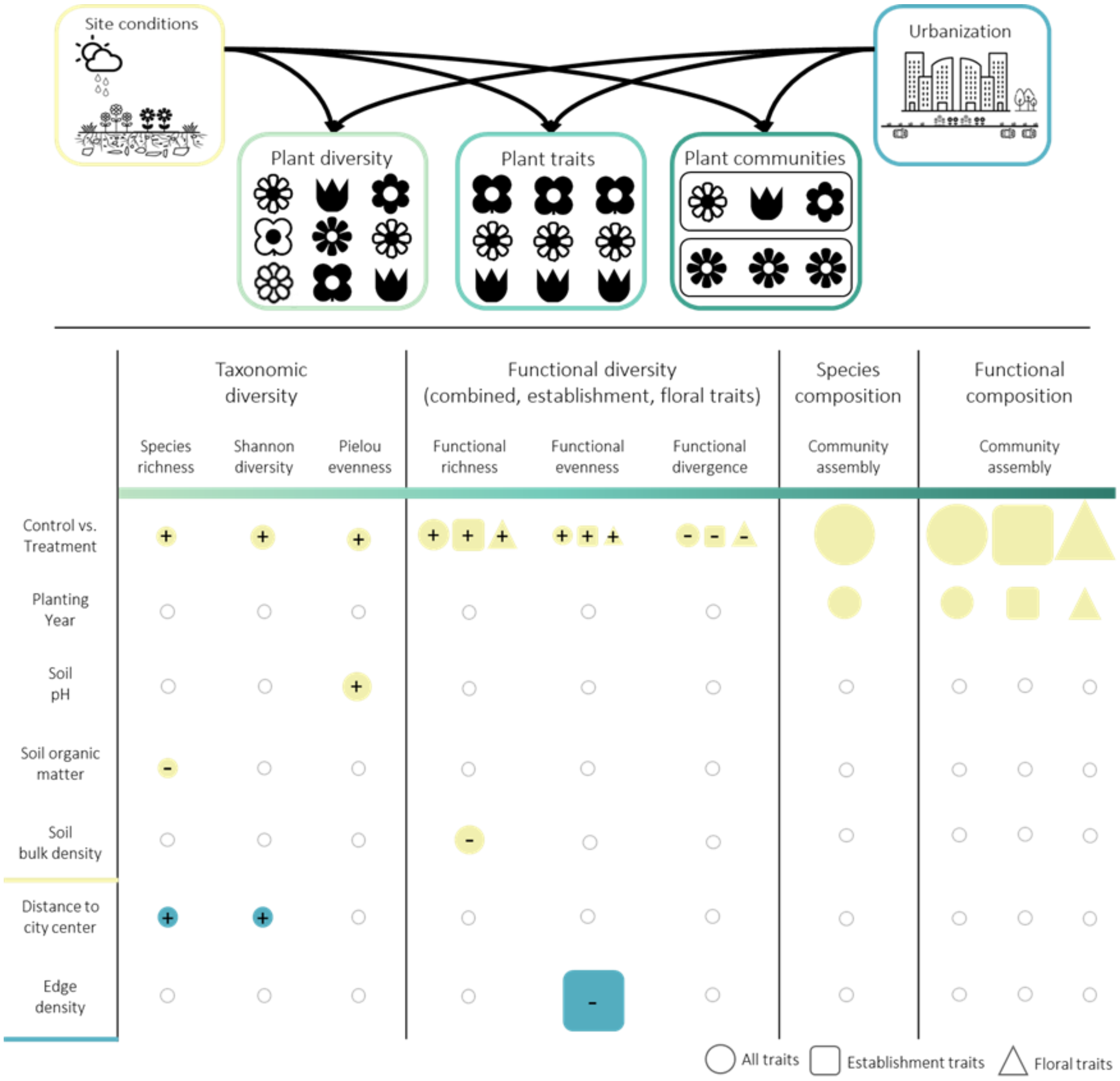


Figure 9: Graphical overview of the results of Publication I. The rehabilitation treatment significantly increased the taxonomic diversity, as well as the functional diversity of combined (circles), establishment (squares), and floral traits (triangles) of the urban roadside vegetation. The sizes of the symbols were adjusted to the result estimates of the respective models, and effect directions are depicted with +/-. Hollow grey circles indicate non-significant relationships (p>0.05). Planting-year effects and local soil conditions (yellow), as well as landscape scale urbanization characteristics (blue) along gradients of increasing edge density and distance from the city center positively affected taxonomic diversity (blue circles), and negatively functional evenness of establishment (blue square). Species and functional compositions of all trait categories were significantly different in the treatment sites compared to controls; additionally, the plant communities were modified by the seasonal variation among two different planting years.

Publication summary

In *Publication I*, environmental factors influencing wildflower patch establishment at urban roadsides were investigated (Figure 9). Plant species richness is, in general, negatively affected by urbanization, and urban functional filtering shapes the local plant communities. Despite the negative impact of urban land use, cities can harbor high numbers of native species, depending on several factors, such as the degree of imperviousness, habitat connectedness, and management. Transforming predominant species-poor lawns into diverse urban grasslands by seeding wildflower mixtures is a promising method to support urban plant and pollinator diversity. Plant establishment, persistence, and reproductive traits affect species dispersal, colonization, and plant-pollinator interactions in the urban landscape. By analyzing these functional traits, community development can be evaluated to minimize failure in rehabilitation.

We monitored vegetation on a subset of 17 one-year-old wildflower patches in 2020 and 2021 in June—July. Using the extended Braun-Blanquet cover-abundance scale, we used 50 cm x 50 cm frames to sample all vascular plants in abundance and richness. The nearby turf grass vegetation was similarly sampled within the same 2 m x 4 m patch dimension as controls. Soil conditions were recorded with a soil corer (3 cm diameter, 15 cm depth) at 10 randomly chosen positions. Soil texture, pH, organic matter content, and concentrations of NaCl, P, Mg, and K were identified by an external laboratory. To determine the effects of shading by trees and buildings on the patches, the leaf area index (LAI) was calculated using pictures taken with a 180° fish-eye camera lens and Win-SCANOPY software. At the landscape scale, we used the percentage of imperviousness, edge density, and the patch distance to the city center as explanatory variables. Using species abundance and functional trait data, Shannon diversity, Pielou evenness, community-weighted means (CWM), functional richness (Fric), evenness (Feve), and divergence (Fdiv) were calculated. We additionally calculated all response variables for the seed mixture by using species-specific seed masses, assuming a germination rate of 100%, to retrieve species abundance data to compare the field results with the theoretical optimum of the seeding treatment. The trait-based indices were determined for all traits combined, only for traits of establishment plus persistence, and only for floral traits. We used multivariate methods (NMDS, PCoA, PERMANOVA) and linear regression modeling to analyze taxonomic and functional community composition and the effects of the sowing years and treatments.

We observed 72 plant species, and 52% were included in the seed mixture. The wildflower patches contained significantly more species and showed higher Shannon diversity and Pielou evenness than controls. Besides, species richness was higher at the city boundaries and negatively correlated with soil organic matter, whereas Pielou evenness increased with soil pH. The species composition of the controls differed strongly from one-year-old wildflower patches and the seed mixture. The wildflower patches shared a high proportion of species, though there was a slight variation based on the seeding year. Other local or landscape factors had no influence. The functional composition of all traits combined and the functional trait groups differed between the treatments and the seed mixture. In contrast, the wildflower patches were more similar in terms of the year of seeding. Fric of combined traits was negatively correlated with soil bulk density. It was higher in wildflower patches of establishment traits, and their Feve was negatively affected by increasing edge density. Fric of floral traits was higher in wildflower patches than in controls. Finally, Fdiv of the three analyzed groups was consistently higher in controls than in wildflower patches.

With this experiment, we demonstrated that in urban areas, plant species richness is determined by local soil conditions and anthropogenic landscape characteristics and that trait-based filtering shapes roadside plant communities. Although artificially introduced by seeding, newly established communities showed local and landscape-level effects in species richness and functional diversity indices. However, even after the short time of one year after seeding, positive effects on species and functional diversity, and community assembly were detectable compared to the pre-existing typical roadside vegetation. The planting year modified the seeded communities, even though the exact composition of species was seeded every year. This variation makes the predictability of rehabilitation outcomes more difficult, although it is likely that post-treatment management plays a crucial role in further community development. We conclude that rehabilitation of roadside vegetation by seeding holds great ecological potential for urban biodiversity and can overcome species-specific dispersal barriers. Integrating functional aspects into wildflower mixture design can be a helpful tool to improve the habitat quality of roadsides for pollinators.

3.2 Publication II

Dietzel, S., Rojas-Botero, S., Kollmann, J., and Fischer, C. (2023). Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. Ecological Indicators *147*, 109980. https://doi.org/10.1016/j.ecolind.2023.109980

Authorship contributions

Simon Dietzel: Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review and editing, Visualization, Project administration. **Sandra Rojas-Botero:** Formal analysis, Investigation, Data curation, Writing – review and editing. **Johannes Kollmann:** Conceptualization, Methodology, Formal analysis, Resources, Writing – review and editing, Supervision, Project administration, Funding acquisition. **Christina Fischer:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – review and editing, Supervision, Project administration, Funding acquisition.

Graphical summary

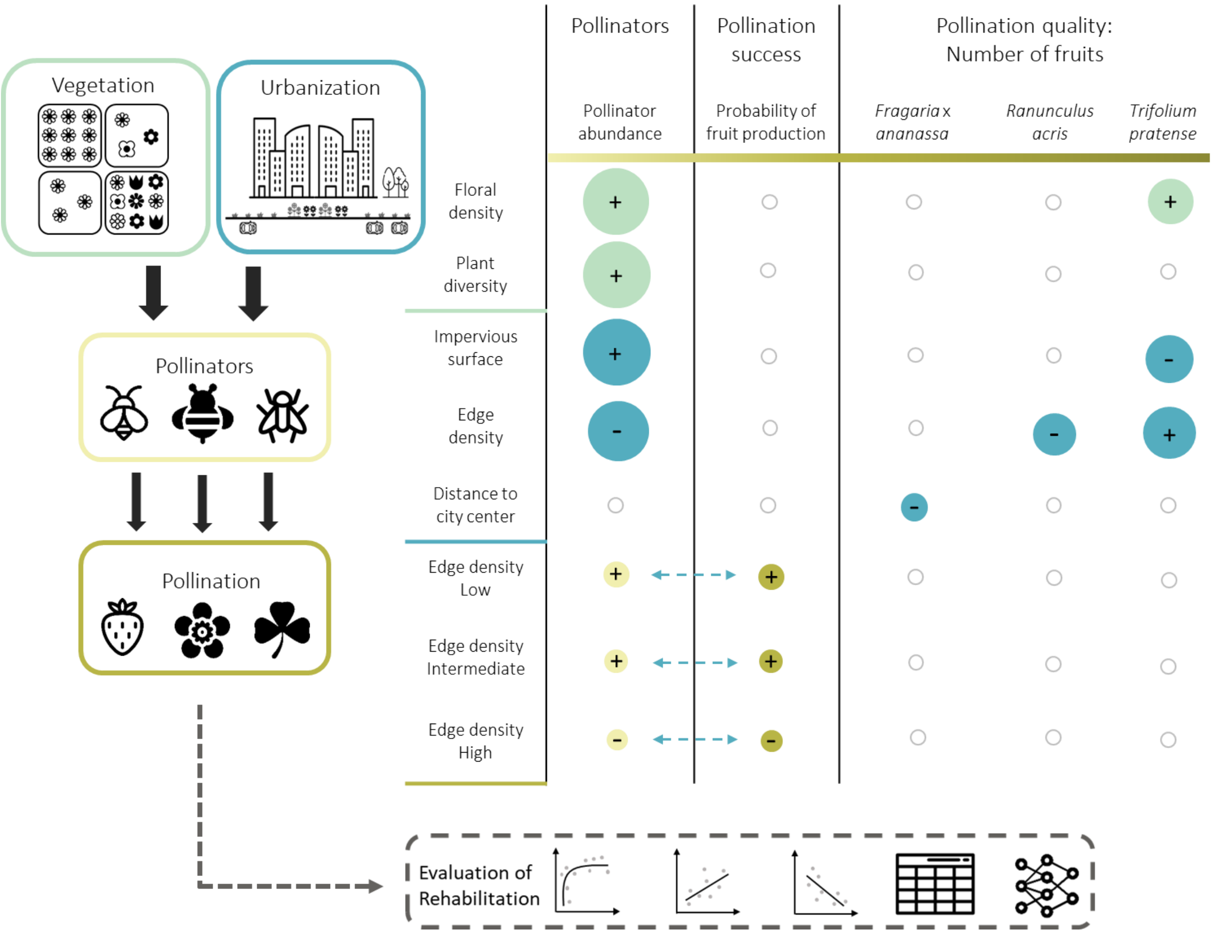


Figure 10: Overview of the main results of Publication II. *Fragaria* x *ananassa*, *Ranunculus acris* and *Trifolium pratense* were phytometer plants to evaluate the relative importance of roadside vegetation (green circles) and the urban landscape (blue circles) on pollinator abundance (light yellow) and pollination (dark yellow circles). The sizes of the circles were adjusted to the result estimates of the respective models, and effect directions are depicted with +/-. Hollow grey circles indicate non-significant relationships (p>0.05). Pollinator abundance was positively influenced by the increased floral density and plant diversity of the sowing treatment. Pollinator numbers also increased with impervious surface cover, but decreased with increasing edge density, indicating a concentration resp. dilution effect of pollinators at the landscape scale. The probability of fruit production of the phytometers increased with pollinator abundance. However, this was significantly modulated by an interaction with edge density (blue dashed arrows): In particularly edgy landscapes, pollinator abundance was no longer positively linked to pollination success. Finally, pollination quality, i.e. the number of fruits produced per flower, was not correlated with pollinator abundance. Instead, landscape-scale effects were detected, and species-specific correlations between fruit numbers and different landscape factors were indicated. The use of standardized model plants and measurements are discussed critically as a tool for evaluation of urban rehabilitation interventions.

Publication summary

Publication II focuses on evaluating enhanced urban roadside vegetation via phytometer plants (Figure 10). Evaluating pollinator rehabilitation measures usually requires species knowledge of several pollinator groups and is expensive in time and money. One method to reduce workload and costs could be the application of phytometer plants to observe pollination. A high level of methodological standardization is ensured by measuring fruit production under different environmental conditions. However, responses to surrounding conditions are plant-species-specific, depending on functional adaptations, such as flower morphology, color, or pollination type. Previous studies revealed local and landscape-scale factors shape urban pollinator populations manifold. In general, floral resources, impervious surface area, and edge effects control pollinator abundance, thus influencing pollination. These local-to-landscape interdependencies pose problems for the evaluation of urban rehabilitation quality. Hence, comparing phytometer species that differ in pollination traits may improve interpretability.

We, therefore, experimented on a subset of 34 urban wildflower and control patches in 2020—2021. Fruit masses of crop plant *Fragaria* x *ananassa* and fruit numbers of native wild plants *Ranunculus acris* and *Trifolium pratense* were used to measure pollination. Control patches were low-cut roadside lawns with regular management. The abundance of wild bees, honeybees, and hoverflies was sampled monthly with pan traps, floral units, and flowering plant species with counting frames from June—August. We recorded patch distance to the city center, percentage of impervious surface, and edge density of urban land-use types in a radius of 500 m. Based on the scientific literature, we set up a theoretical framework comprising causal relationships between pollinator abundance, phytometer pollination, and local and landscape-scale factors. This included diverging effects of floral resources and the urban landscape, potentially affecting pollinator abundance positively with increasing local forage and habitat quality and negatively, e.g., by intensifying competitive pressures. The probability of pollination success vs. failure was tested with a generalized linear mixed model.

The postulated relationships of the theoretical framework were tested with structural equation models (SEM). Pollination success was positively correlated with pollinator abundance but modulated by edge density, i.e., positive in areas of low to moderate edge density and negative in areas of high edge density. The SEMs showed positive effects of local resource availability and impervious surface on pollinator abundance, whereas edge density had a negative influence. Pollination was not directly controlled by pollinator abundance but indirectly affected by landscape-scale factors, and effect directions were phytometer-specific. Fruit masses of *F.* x *ananassa* were higher near the city center, impervious surface negatively affected *T. pratense* fruit numbers, and edge density was positively correlated with fruit numbers of *T. pratense* and negatively with those of *R. acris*. At the local scale, pollination was influenced by interacting factors that were challenging to unravel and hampering the evaluation of the quality of single patches, as increased resource availability and pollinator abundance did not result in improved pollination. Non-intuitively, pollinator abundance increased with imperviousness, whereas increasing edge density caused the opposite. This can be explained by a concentration vs. dilution effect, by which pollinators aggregate at flowering patches placed within intensively urbanized areas providing otherwise little forage (concentration), or pollinators spread in more heterogeneous landscapes, offering attractive resources in the surrounding area.

Overall, landscape characteristics almost exclusively shaped pollination. Hence, phytometers can be an efficient tool to assess urban landscape quality for pollinators and pollination. Our research demonstrated the efficacy of urban roadside rehabilitation to support pollinators and increase pollination of plants in intensively urbanized areas. Still, more research is required to understand the interplay of habitat quality and greenspace configuration to optimize ecological interventions in cities.

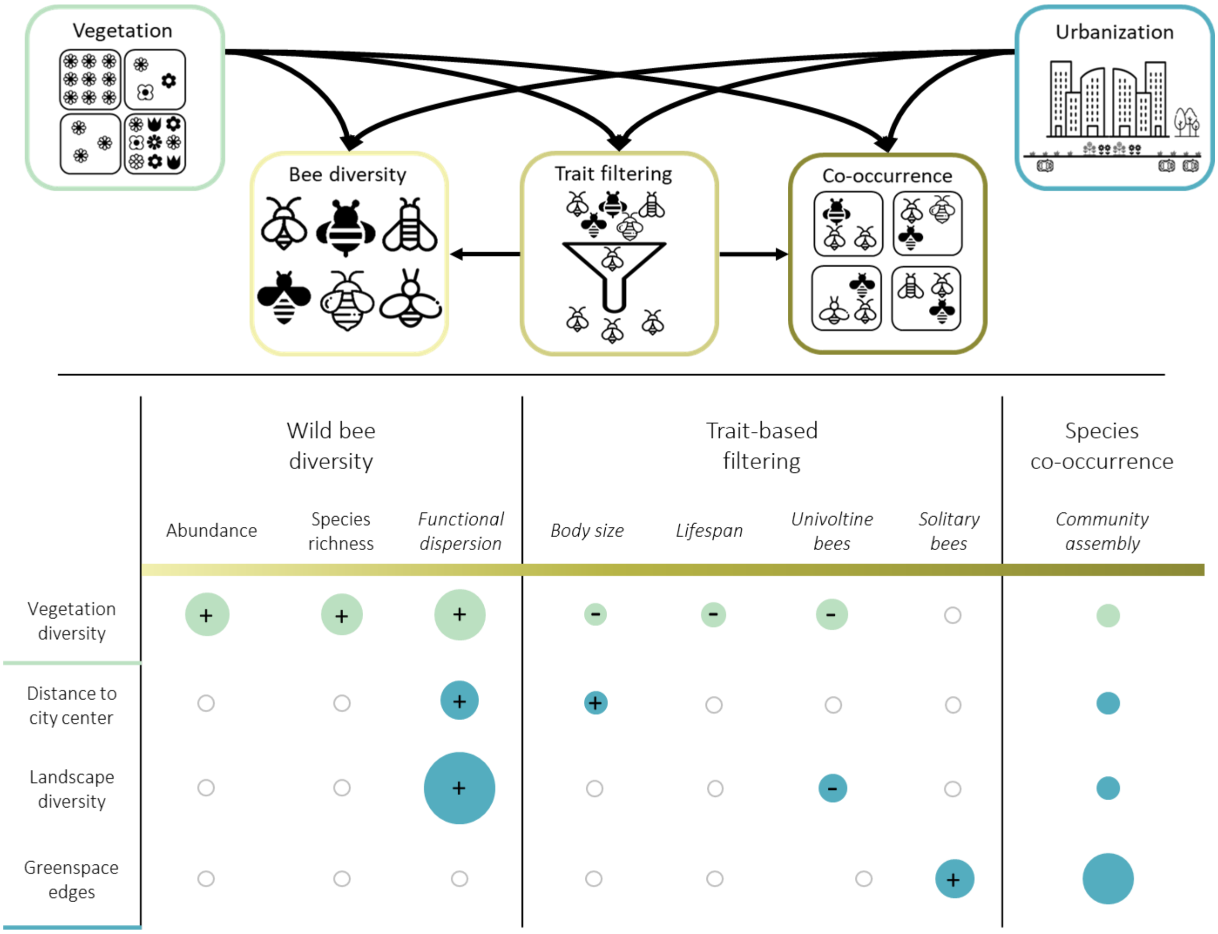
3.3 Publication III

Dietzel, S., Rojas-Botero, S., Dichtl, A., Kollmann, J. and Fischer, C. (2024). Winners and losers at enhanced urban roadsides: Trait-based structuring of wild bee communities at local and landscape scale. Biological Conservation 291, 110480. https://doi.org/10.1016/j.biocon.2024.110480

Authorship contributions

Simon Dietzel: Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review and editing. **Sandra Rojas-Botero:** Data curation, Investigation, Methodology, Validation, Writing – review and editing. **Anja Dichtl:** Data curation, Investigation, Visualization, Writing – review and editing. **Johannes Kollmann:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review and editing. **Christina Fischer:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review and editing.

Graphical summary



	Wild bee diversity			Trait-based filtering				Species co-occurrence
	Abundance	Species richness	*Functional dispersion*	*Body size*	*Lifespan*	*Univoltine bees*	*Solitary bees*	*Community assembly*
Vegetation diversity	+	+	+	-	-	-	○	●
Distance to city center	○	○	+	+	○	○	○	●
Landscape diversity	○	○	+	○	○	-	○	●
Greenspace edges	○	○	○	○	○	○	+	●

Figure 11: Graphical overview of the main result of Publication III, in which the effects of rehabilitated urban roadside vegetation (green circles) and the urban landscape (blue circles) on wild bee taxonomic and functional diversity indices were investigated. Additionally, urban filtering and community assembly of wild bees based on their functional traits were analyzed. The sizes of the circles were adjusted to the result estimates of the respective models, and effect directions are depicted with +/-. Hollow grey circles indicate non-significant relationships ($p>0.05$). Vegetation diversity positively affected wild bee diversity indices, and landscape scale functional filtering was detected near the city center and in low-diversity landscapes. Wild bees with low body sizes, short lifespans and limited reproductive output (univoltine species) were outcompeted at sites with high vegetation diversity. Additionally, univoltine bees were negatively affected by increasing landscape diversity, highlighting urban competitive pressures for specific trait groups. Solitary bees were favored by increasing availability of greenspace edges, which underlines the importance of small-scale urban green patches for wild bees. Finally, multi-factorial effects at the landscape scale filtered or favored functional groups. Analyzing patterns in species co-occurrence can improve the efficiency and successful outcomes of urban bee conservation.

Publication summary

Publication III investigated the effects of wildflower patches on wild bee abundance, species richness, and functional diversity at urban roadsides (Figure 11). As urban land use triggers functional filtering, it significantly affects the assembly of urban wild bee communities. Although wild bees can be favored by low to mid-urbanization intensity, functional groups are differently affected based on their varying morphologies, phenologies, and habitat preferences. For example, species that are specialized on specific host plants or nesting structures are more likely to be discriminated. In contrast, generalists with high plasticity to environmental change can cope with the anthropogenic environment. As urban intensity increases, wild bee communities are usually affected negatively, resulting in functionally monotonous communities. To overcome detrimental urbanization effects on wild bee populations, enhanced roadsides as part of a green infrastructural network can support habitat connectedness and overall species and functional diversity. However, studies on wild bees in urban roadside habitats are rare, and insights into trait-environment interactions at local and landscape scales are missing so far.

To understand the formation of wild bee diversity and functional composition at urban roadsides and how their communities are shaped by urban filtering, we set up a large-scale experiment in Munich (S Germany). Five major roads were selected, leading from the city center to the outskirts, and overall, 78 wildflower patches were created from 2019—2021. As controls, we used non-seeded, intensively mown patches with pre-existing vegetation. Vegetation diversity, landscape diversity, and the perimeter-area ratio of urban green space were sampled in three vegetation periods. Wild bees were sampled with pan traps thrice a year and identified to species level. Six traits were used to calculate the functional dispersion of the local communities and to identify functional groups favored or filtered by local and landscape scale conditions. To analyze wild bee abundance, species richness, and functional dispersion, generalized linear mixed effect models (glmm) were applied. A fourth corner analysis, based on a generalized linear latent variable model (gllvm), was employed to analyze trait-environment interactions and species co-occurrence, thus urban trait filtering.

Wild bee abundance and species richness were positively affected by local vegetation diversity, but they were independent of the landscape variables. Functional dispersion, however, increased with landscape diversity and distance from the city center, indicating functional filtering along the urban road corridors. We identified negative associations of species small in body sizes, short in lifespans, and low in reproduction rates (univoltine) with increased vegetation diversity. Besides, univoltine species were negatively affected by increasing landscape diversity; large body sizes were associated with high distances from the center, and high perimeter-area ratios of greenspace favored solitary bees. Five indicator species co-occurred at greenspace edges, and information on their habitat preferences provided trait-based suggestions for conservation.

The presented results underline the fundamental importance of local forage for wild bee populations in general and the necessity for ecologically and functionally improvement of hitherto overseen greenspace elements. Urban filtering could be detected using a trait-based analysis approach. By identifying trait groups affected by urbanization, conservationists can mechanistically understand the underlying processes that shape urban communities. This provides opportunities to optimize urban rehabilitation for specific habitats targeted at discriminated species groups. Sowing wildflower mixtures effectively improves local habitat conditions; however, we detected adverse effects of high vegetation diversity on some functional groups, indicating the need for sufficient food provision to reduce competitive pressure. Finally, landscape effects must be considered to support urban wild bees. Hence, expert knowledge in seed mixture design and wild bee species is needed to implement targeted ecological interventions in cities.

4 General Discussion

With urban rehabilitation, biodiversity-friendly roadsides for plants and pollinators can be created as urban Green Infrastructure. The ubiquitous lack of space in cities draws attention to areas that may appear ecologically unattractive at first glance. Under the Green Infrastructure framework, new paths are indicated to enhance small and marginal habitats and to improve the connectivity between isolated urban wild bee populations (Griffin and Haddad, 2021). By emphasizing positive edge effects and focusing on species traits, urban roadside rehabilitation can be raised to an integrative and sustainable approach that serves both the conservation of species and ecosystem functioning (Irschick et al., 2013). When created and managed appropriately, roadsides have been identified as attractive habitats for pollinators (Phillips et al., 2020b), but experiments on urban roads were lacking.

To support bees and other pollinators, increasing local floral abundance and plant diversity is one of the critical aspects. Therefore, 75 patches along five urban roads in Munich were experimentally sown with a native wildflower mixture from 2019—2021, specifically designed for the expected environmental conditions at urban roads. The resulting vegetation and its effects on the pollination of phytometers and the local bee fauna were investigated, and landscape-scale characteristics were considered. The results of *Publication I* indicate an interplay of yearly seasonal variation, local soil conditions, and landscape-scale urbanization effects that shape the newly established patches in their taxonomic and functional diversity and community composition (Figure 12). In *Publication II*, the effects of the local flora, i.e., plant diversity and floral density, on the pollination of three functionally different phytometer species were investigated. In doing so, we intended to employ the phytometer technique to evaluate the success of roadside rehabilitation in terms of pollinator abundance and plant pollination. We found strong positive relationships between increased local resource availability and the number of pollinators, and mainly landscape-scale effects modulated the pollination of the phytometers, depending on the species (Figure 12). The rehabilitated plant diversity positively influenced wild bee abundance, species richness, and functional diversity in *Publication III*. Analyzing bee functional diversity revealed a trait-based urban filtering effect along a gradient of landscape diversity and increasing proximity to the city center, and several bee traits (body size, reproductive output, sociality, lifespan) were found to interact with the urban environment (Figure 12).

This doctoral thesis aimed to learn about the successful rehabilitation of roadsides as Green Infrastructure aimed to support urban biodiversity. Integrating taxonomic and functional aspects into data analyses provided a comprehensive picture of the interactions between the local environmental factors, the urban landscape, and the studied plants and pollinators. The focus on functional traits was particularly insightful in understanding the interactions between functional traits and the environment, resulting in urban filtering in plants and wild bees. Subsequently, this information was used to develop proposals for optimizing urban roadside rehabilitation and wild bee conservation.

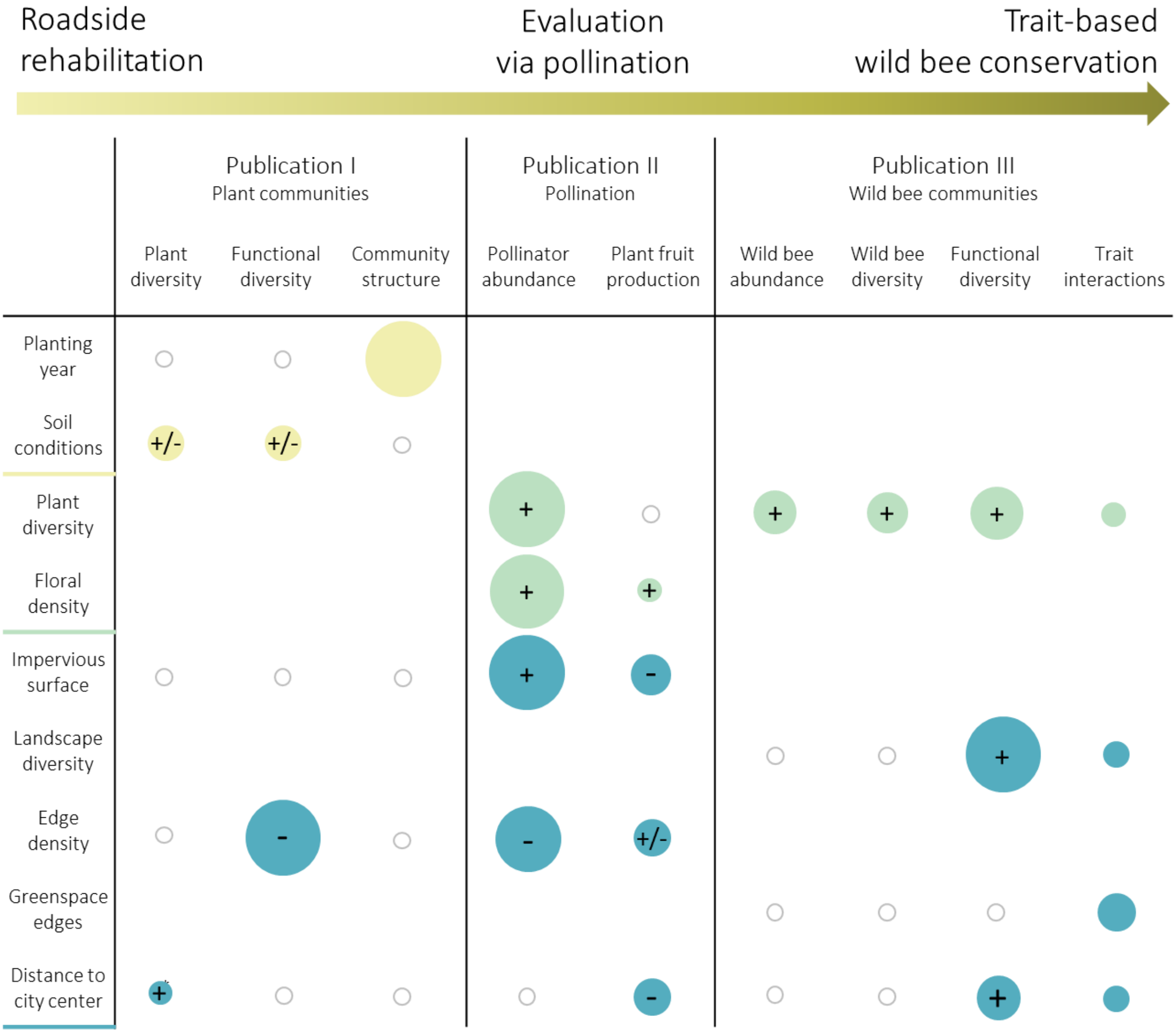


Figure 12: Aggregated results of the published articles presented in *Chapter 3*. By investigating plant establishment along urban roads, and how this rehabilitation affects pollination and wild bee communities, taxonomic and functional aspects of conservation were combined to display the integrative approach of this doctoral thesis. The sizes of the circles were adjusted to the result estimates (means) of the respective models, and effect directions are depicted with +/-. Hollow grey circles indicate non-significant relationships (p>0.05). Pairs of variables without symbol were not tested. **Publication I:** Urban roadsides were rehabilitated by sowing a native seed mixture, and varying effects of the planting year, soil conditions, and urbanization on plant taxonomic and functional diversity, as well as community structuring were found. **Publication II:** Increased local plant diversity and floral density positively affected the fruit production of phytometer plants. Landscape-scale effects of urbanization on pollination were phytometer-specific, indicated by different effect directions. **Publication III:** Plant diversity positively affected taxonomic and functional diversity of wild bees. Increasing landscape diversity and distance to the city center were positively correlated with bee functional diversity. Wild bee trait groups were differently affected by the local vegetation and landscape variables.

4.1 Trait-informed design of urban roadside vegetation and factors to be considered for successful rehabilitation

Successfully rehabilitating urban roadsides for biodiversity conservation requires knowledge about the used plant species and the targeted organisms. Trait-based aspects of the plants must be considered, as otherwise, the ecological intervention could fail, not showing any positive effects on pollinators compared to species-poor lawns or invaded roadside grasslands (Darst et al., 2024). The rehabilitation of many types of urban pollinator habitats can be oriented at traditional grassland restoration, as done in agricultural areas. This is particularly true for selecting the applied practical methods, including soil preparation, seeding, and management. However, several factors must be considered when planning and implementing urban roadsides. The rural character of these specific sites does not allow simply copying grassland mixtures or using hay transfer from species-rich grasslands. Their compositions resemble or originate from semi-natural habitats, and many of the included species may not establish at these sites due to their sensitivity to soil and climatic conditions, ultimately not worth the practical and financial effort.

Considering the lack of a natural equivalent habitat to restore, consulting plant traits has shown to be highly practical in seed mixture design and successful planting, as 24 of the 26 sown species were found in the patches. Plants of the existing regional species pool provide a sufficient foundation to design species and functionally rich mixtures for different purposes, such as supporting pollinators. For example, including annuals originated from agricultural fields to achieve a blooming aspect in the year of seeding, provides flowers for pollinators more quickly, and simultaneously increases social acceptance (Klaus, 2013). Creating trait-informed native seed mixtures has an advantage over hay transfer not only because of an exact design of the intended roadside plant community but also because it is less complex to implement considering the identification of suitable donor grasslands, the practical high effort during hay transfer, and the synchronization of harvest times and soil preparation.

Although a standardized seed mixture was used in all sites of this study, the planting year had a considerable influence on the resulting plant communities. Restoration measures can significantly differ in outcomes and deviate from the pre-defined targets, although methods and techniques were applied similarly (Strobl et al., 2019; Groves et al., 2020). Historical contingency plays a significant role in restoration. Depending on the yearly variation in precipitation and temperatures, resulting plant communities can significantly deviate, even almost two decades later (Groves et al., 2020). Weather extremes, such as drought or flood events after rehabilitation, can also change plant compositions or disrupt rehabilitation outcomes (Copeland et al., 2019). As seasonal forecasting is making great technological progress, it should generally be consulted to increase success in future restoration by adjusting planting activities to local weather, specifically in cities where extreme events are even more severe (Hagger et al., 2018). Establishing climate-resilient native vegetation along roads today needs consideration of tomorrow´s projected conditions (Seto et al., 2012; Hagger et al., 2018). In doing so, roadside wildflower plantings can significantly enhance urban cooling in densely built areas (Zhao et al., 2020). Nevertheless, there is a need for more experiments that examine the performance of species and mixtures on degraded soils in urban climates and how mixtures can be composed for maximizing interspecific synergistic effects under interacting urbanization factors at varying spatial scales (Rojas-Botero et al., 2023).

Soil conditions in the presented experiments were significant considering plant taxonomic and functional diversity. Indeed, soil conditions play a fundamental role in grassland restoration, and specifically, high organic matter and nutrient contents (P, N) are detrimental to successfully establishing diverse plant communities (Török et al., 2021). Roadside soil degradation parameters, such as physical compaction and accumulation of chemicals and nutrients, usually increase with road width and decrease with distance from the road (Mills et al., 2020; Zhou et al., 2020). When roadsides are newly constructed, soil properties, such as nutrient levels and water-retention abilities, can be determined initially. However, when this is not the case, considering the prevailing soil conditions at different locations besides the road is crucial, and explicitly considering soil-related plant traits can help adjust the species composition of the final seed mixture. To avoid failure in rehabilitation, soils should be pre-analyzed, or at least information on the used substrate during road construction and prior management must be available and integrated into seed mixture design. Nevertheless, urban roadsides experience permanent high nutrient inputs, which makes changes in their management inevitable (Mills et al., 2020). An extensification of management conditions before rehabilitation can provide insights into local soil productivity and seed bank conditions. Removing the cut material after mowing is a prerequisite to regulating nutrients, increasing soil quality, and increasing plant diversity in the medium and long term (Mills et al., 2020). Additionally, research has shown that employing insect-friendly mowing equipment and postponing mowing dates significantly reduces insect-killing rates at roadsides (Steidle et al., 2022).

4.2 Evaluation of rehabilitated urban roadsides via pollination and the impact of local and landscape-scale factors on species-specific interactions

Consistent with other research, increasing the habitat quality of roadsides resulted in higher pollinator abundance (e.g., Brown et al., 2024). Sowing native wildflowers is a well-proven method to restore pollinator habitats, and this experiment could be verified for urban roadsides despite the harsh conditions at these sites. In cities, rehabilitation can be geared towards multiple goals, such as increasing the functionality of the specific type of greenspace. Pollination is a crucial ecosystem function for wild plant populations and human food production (Free, 1993; Ollerton et al., 2011). Using pollination as an indicator for evaluating habitat quality and ecosystem functionality could be an innovative method to evaluate target-oriented rehabilitation (Dietrich et al., 2013). There is a strong need for standardized evaluation methods in restoration, and these methods need to be habitat-specific and adjusted to the previously defined targets (Kollmann et al., 2016). Optimally, the employed evaluation methods can be applied in the field by non-expert staff, are cost and time-efficient, and the obtained results must provide the possibility for clear interpretation (Strobl et al., 2018).

The phytometer plants used in *Publication II* ensured high standardization and easy-to-handle, low-cost procurement and maintenance. This experiment involved testing functionally different plants to explore species-specific sensitivity to local and landscape-scale variables influencing pollination and aimed to calibrate this promising method. Pollinator abundance is evidently shaped by local forage quality, quantity, and urbanization intensity (Roulston and Goodell, 2011). While roadside rehabilitation positively impacted pollinator abundance across the urban gradient, this increase was not captured in the pollination data of the phytometers. Instead, facilitation and inhibition of fruit production appeared differently in the plant species, although kept under similar conditions.

On the contrary, interactions were detected between plants and the landscape. Rather than local habitat quality, landscape characteristics determined the failure or success of fruit production and the number of fruits produced. Even more insightful, by using phytometers with different pollination ecologies, phytometer-specific sensitivity to urbanization revealed contrasting outcomes. Fruits of *Fragaria* x *ananassa* were heaviest when the plants were located near the city center. Increasing edge density resulted in higher fruit numbers of *Trifolium pratense* and caused decreasing fruit production in *Ranunculus acris*. *Trifolium pratense* fruit numbers were additionally impaired by the amount of impervious surface cover.

These mixed results raise further questions about the practicability of phytometers as evaluation tools. *Fragaria* x *ananassa* was only sensitive to the distance to the city center. Therefore, this species seems rather unsuitable for assessing the quality of urban landscapes. However, the indirect effects of a heat island effect on strawberry production could be demonstrated along a rural-to-urban gradient (Scherr and Jamieson, 2021), which provides a probable explanation for the result of our experiment. Employing different breeds could also have led to a deviating result in berry weights (Scherr, 2021). Measuring the influence of abiotic factors on pollination, such as land-use-modulated temperature, *F.* x *ananassa* could be a valid choice. However, we did not find direct land-use-pollination interactions, probably because the within-city urban gradient was not steep enough or simply because this species is not sensitive to land-use variables. In contrast, landscape effects on *R. acris* differed from those of *F.* x *ananassa,* although they share a common set of pollinators, such as hoverflies and other dipterans. Fewer fruits were produced in areas with high edge density, i.e., areas with potentially higher amounts of foraging plants. This result revealed an interesting pollination-landscape interaction and is in line with the result of pollinator abundance, which also decreased in these areas, however indirectly. As a pollen supplier, *R. acris* remains a very interesting species for further investigation of urban pollination, as it mainly attracts dipterans as an essential but understudied functional group (Orford et al., 2015). Flowers could be observed directly to identify the link between pollinators and fruit quantity. On the contrary, this would significantly increase the time spent in the field. *Trifolium pratense* reacted inversely, producing more fruits at high edge-density sites where *R. acris* generated less. At first sight, the results seem easy to interpret with increasing fruit numbers in less impervious areas and increased density of edges. Among the three species, *T. pratense* was the most sensitive phytometer to pollinator exclusion, never producing any fruit when flowers were covered with nylon bags. This makes it a very attractive species for further investigation. However, its narrow set of primary pollinators, in cities often abundant long-tongued bumblebees and honeybees, must be considered.

Overall, phytometers should be sensitive to the factors of interest, easy to maintain in the greenhouse, and quick to process in the lab. A trait-based selection of phytometer species can facilitate species selection. It should primarily consider the interrelated factors of plant flower morphology, gamy, and pollinator specificity to address the rehabilitation-specific targets or research questions as precisely as possible. Here, we presented the results of three functionally distinct species. Other species with comparable traits need to be tested to confirm the results. Assuming local resource availability and landscape quality linearly translate into increased pollinator abundance and pollination neglects the complex interactions between plants, among plants and pollinators, and among pollinators that take place under varying urban environmental conditions, especially at the local scale (Pellissier et al., 2013; McDougall et al., 2022). To improve knowledge, there is a need for research about phytometer-specific sensitivities to different landscape variables, how these translate into the evaluation of landscape-scale habitat quality and ecosystem functionality, and standardized frameworks and protocols for plant handling and data analysis. Since there is a high demand for quick and easy assessments of ecosystem functionality and rehabilitation success, phytometer plants are a promising tool at larger spatial scales; however, they are not yet applicable for large-scale assessments, and studies are missing so far.

4.3 Urban roads as green infrastructure for the preservation of wild bees and pollination

Depending on the quality of their accompanying vegetation, roads can be either barriers or corridors for wild organisms (Andersson et al., 2017; Dániel-Ferreira et al., 2022), and increasing the local abundance and diversity of foraging plants has considerable benefits for wild bees (Phillips et al., 2020b). However, the more significant ecological value of roadside rehabilitation lies in the network-like structure of the roads embedded in the urban landscape matrix. By creating urban green corridors along roads, city-scale landscape connectivity is the benchmark for effectively integrating wild bee conservation and preserving pollination (Bennett and Lovell, 2019). The results of this thesis indicate the ecological potential of urban roadsides. The Green Infrastructure concept can be used as a framework to unfold this potential, which can help mitigate the environmental consequences of transportation and urban development. Notably, looking at the mostly generalist species found during the experiments, roadsides can never replace larger (semi-)natural habitats that meet a wider range of different requirements for wild bees. Further experiments need to be done at roadsides, examining if the quality of the foraged nectar and pollen is affected by degraded urban soils and chemical pollution and how this could influence diversity, community compositions, health, lifespans, reproduction, and pollination of wild bees (Moroń et al., 2012; Ryalls et al., 2022; Duque and Steffan-Dewenter, 2024; Ferrari et al., 2024a). Additionally, research is needed that focuses on the social acceptance of a changed appearance of rehabilitated urban vegetation and how ecologically relevant, basic knowledge on urban biodiversity can be spread and strengthened among planners, architects, citizens, authorities, and policymakers (Klaus, 2013).

4.3.1 Trait-based filtering in wild bees: Raising urban conservation to the next level

Many wild bee species are synanthropic, i.e., species thrive in human-altered or human-created habitats, adapting well to urban environments due to their behavioral and physiological plasticity (Allasino et al., 2019; Brant et al., 2022). Wild bees are crucial in natural and anthropogenic environments by pollinating wild plants and crops. For decades, researchers have warned about their declines, and new ways of conservation need to be explored to mitigate species loss and maintain ecosystem functionality. The results of *Publication III* indicate the benefits of rehabilitated urban roadsides for bees, as their abundance and taxonomic diversity were positively affected. In this study, 78 species were found at the roadsides, accounting for 15% of all species in Bavaria (Voith et al., 2021), which is a high number considering the habitat type.

Until recently, wild bee research typically concluded at this juncture, emphasizing the beneficial impacts of plant-rich habitats on bee abundance and richness (Buchholz and Egerer, 2020). However, analyzing the environmental interactions of the roadside communities at the functional level revealed a landscape-scale decrease with rising urbanization intensity, and several functional groups were affected by different urban variables. Functional research provides the opportunity for a fundamental understanding of the interactions between organisms and environmental factors, representing a sophisticated view of wild bee conservation beyond traditional species-centric approaches. For holistic conservation of bees and their functions, rehabilitation requires a broader framework that includes not only enhancements of foraging habitats but also a landscape-scale integration of habitat requisites, such as different types of nesting opportunities above and belowground, optimally tailored to the local fauna (Drossart and Gérard, 2020; Neumüller et al., 2022).

For cities, identifying wild bee traits affected by urban filtering allows rehabilitation targets to be defined more precisely and prioritize interventions that benefit multiple bee species simultaneously, maximizing the impact of limited resources in terms of budgets and space. In the face of ever-growing urban cover, there is an urgent need for the rehabilitation and management adaptation of wild bee habitats to increase their resilience to increasing human and environmental disturbance (Müller et al., 2023; Polidori et al., 2023). The conservation effort must be expanded beyond recent activities if preserving urban biodiversity and securing its fundamental functions is the goal (IPBES, 2018). More research is needed that focuses explicitly on functional filtering in cities by using modern, sophisticated analysis tools, such as latent variable modeling or RLQ analysis at the city and global scale, and the effects of a landscape-wide integration of habitat elements that serve wild bee functional groups affected by urban filtering (Buchholz and Egerer, 2020). Trait-based analyses of local bee species pools can, therefore, provide valuable orientation for restoration and increase its efficiency, facilitate the reintroduction of locally extinct species, and improve the resilience of communities, ecosystems, and their functions (Winfree, 2010; Irschick et al., 2013).

4.4 Scaling up roadside rehabilitation at the city level and beyond

Removing barriers and creating corridors to improve dispersal and migration is paramount for plant and pollinator conservation (Winfree, 2010; Graffigna et al., 2023). Our findings can be used to improve the local habitat quality for pollinators, but more importantly, increase the habitat connectivity within the landscape and complement studies at non-urban roads (Phillips et al., 2020b). The trait-informed approach used for our experiments can be adapted for other cities, as the foundation for designing seed mixtures is the regional species pool, which is to be matched with the local habitat conditions, such as the microclimate and soils, and the functional targets, such as biodiversity or climate regulation. Identifying the vital local factors that favor the plant establishment is essential to determine whether plant species can be transferred to other urban locations. Creating the environmental conditions for plants to grow in strongly homogenized landscapes is critical for a city-wide implementation and will benefit habitat connectivity, bridging otherwise inhospitable environments (Griffin and Haddad, 2021; Graffigna et al., 2023). For wild bee conservation specifically, there is an urgent need to not only increase flower abundance and diversity but also to identify critical habitats and essential requisites (Bogusch et al., 2024). Target-oriented planning can improve the efficacy of bee-specific rehabilitation and decrease costs. By identifying functional groups affected by land-use intensification, measures, and management can be further adjusted. To implement pollinator-friendly rehabilitation and habitat management in cities, technical and socio-organizational aspects must be addressed. Besides technical aspects, to increase biodiversity and increase the functionality of roadsides in the long term, there is an urgent need for education among citizens and local authorities about the significance of urban green space for biodiversity, the functions of biodiversity-friendly roadsides, and the critical role of insects for ecosystem functioning and human food production (Klaus and Kiehl, 2021).

4.5 Practical synopsis for establishing biodiversity-friendly urban roadsides

From a technical point of view, reducing roadside management from an intense mowing regime to an extensive frequency of mowing events once or twice a year is a prerequisite. At locations with excessive vegetation growth, successively reducing the mowing frequency from three or four times to two times over several years is an option. Wherever possible, nutritious soils should be replaced with nutrient-low substrates, e.g., in the case of larger reconstruction projects. To reduce planning and implementation costs, pre-designed soil and native seed mixtures can be used for different newly established types of urban greenspaces, such as roadsides, watersides and dikes, flood plains, parks, or industrial areas, and other purposes, such as climate adaptation, water retention and storage, soil rehabilitation, or biodiversity. However, there are several technical and organizational obstacles, such as the existing mowing machinery, that cannot easily be replaced with insect-friendly equipment for financial reasons. A step-by-step approach could make management changes possible in the medium term, provided the administration is responsible for greenspace maintenance. Otherwise, public procurement procedures must consider technical requirements to increase insect survival during mowing. For biodiversity interventions to achieve long-term success, they must be complemented by educational initiatives. Raising awareness, acceptance, and spreading ecological knowledge among citizens, administrative officials, and policymakers are crucial factors in ensuring that conservation strategies are publicly supported (Parris et al., 2018). Additionally, integrating biodiversity aspects into official regulations and legislation is needed for city and landscape planning. For scaling up evidence-based knowledge and techniques of restoration and urban rehabilitation, a cultural change at the socio-organizational levels of education, legislation, funding, and subsidization is paramount.

Planting native wild plant mixtures at roadsides offers a promising urban rehabilitation opportunity. During the project, we faced technical questions, obstacles, and challenges that shall be briefly addressed below and were adopted from an article published in the practitioner journal ANLiegen Natur, written by the author of this thesis and colleagues (Dietzel et al., 2022).

4.5.1 Site criteria for urban flowering areas

Soil: Nutrient-poor substrates are beneficial for wildflowers at urban roadsides. Substrates mixed with sand or gravel can be used for newly established plantings. This prevents the invasion by neophytes, reduces biomass production and high vegetation growth (also in terms of traffic safety), and allows less competitive species to establish more successfully.

Site configuration: The broader and longer the roadside to be rehabilitated, the higher the success of the planting. Narrower edges of less than two meters could be enhanced by reducing mowing frequency. Vegetated strips in the middle of the road should not be used due to their trapping effect on insects. Our results suggest that even isolated small areas in highly urbanized areas can unfold ecological potential.

Shading: Avenues with old trees and dense canopies can cause intense shading and capture precipitation on their canopies. Additionally, tree transpiration removes water from the soil, causing dry conditions beneath the trees. Areas with young trees, low canopy cover, or completely open areas should be preferred.

Disturbance and contamination: Roadside edges are usually heavily disturbed and eutrophicated due to human trampling, dog feces, and chemical inputs. Planting should not be done at heavily frequented locations. Otherwise, even low barriers reduce the intensity of disturbance of passers-by. Information opportunities can promote acceptance and environmental awareness. Nevertheless, destruction and vandalism cannot be avoided entirely.

4.5.2 Site preparation and maintenance

Sowing: Within narrow strips, wild plants can easily be sown by hand or with a small seed drill. Almost all species were successfully established with a 4 g/m² seed density. Ground corn is recommended for better seed distribution (31 g/m²). The topsoil must be loosened, especially when using the existing soil substrate. The upper turf must be removed or milled twice. Care must be taken to avoid damaging tree roots. A final rolling ensures that the seeds are in contact with the substrate and not blown or washed away by wind or precipitation.

Plant selection mixture: The selection of plant species depends on the goals of the intervention, which can also be multifunctional, e.g., climate adaptation combined with biodiversity-friendly greenery. Frequent occurrence of drought stress and degraded soils limit the selection of suitable species. If rapid greening in the first year is wanted, flowering annual species can be integrated. A 25–50% grass component in the mixture can improve the establishment of target species and water infiltration and reduce the costs of expensive herbaceous seed material. Legumes should be used sparingly to avoid further nutrient input but should be included for adapted wild bees, such as bumblebees and many other specialized species.

Seed origin: Wild plant species of regional origin should be used. These are adapted to local conditions, and wild bees rely on the native wild flora. Using ornamental plants and species from agricultural flowering mixtures (Phacelia, sunflower, mustard, buckwheat, etc.) is not recommended for a long-term sustainable integration of native urban flora.

Plant diversity: It is worth considering their functional characteristics when selecting plants. The flowering mixture should represent a variety of growth forms, rooting, leaf area, biomass production, flowering duration, flowering time, and flower colors. Excessive tall growth forms should be avoided, as high roadside vegetation can restrict visibility for road users.

Maintenance: Depending on the site's productivity, mowing once or twice is required. To regulate nutrients at the site, the mowed material must be removed. The mowing date depends on the local conditions. Postponed summer mowing (June/July and late autumn) benefits insects and seed ripening and spread of the established wildflowers. On heavy soils, increased attention must be paid to possible invasions, and, if necessary, manual removal or adapted mowing must be applied. A narrow maintenance cut at the edges of flowering areas is visually appealing and prevents the overgrowth of traffic routes. In terms of contamination, the cut material is harmless and can be used or disposed of conventionally (Dittmer, 2024).

5 Concluding Remarks

Roads inflict damage on ecosystems. Locally, by degrading or destructing habitats of plants and wild bees, and at the landscape scale, by fragmenting habitats and wild populations. Thus, from an ecological perspective, the best road is the one that has not been built. Designing roadsides that increase the connectivity between habitats is, however, an effective tool to mitigate the impact of roads. The experiments of this study demonstrated how roadsides in cities could be successfully rehabilitated, which local and landscape-scale factors have an impact on plants and wild bee communities, and how pollination of phytometers can be used as an indicator for an efficient assessment of ecosystem functioning and urban landscape quality.

Native wild plants can be successfully established at urban roadsides. However, environmental and management factors must be manipulated or changed to secure and improve the outcome. Urban soils are the most crucial but easy-to-manipulate factor for plant community development. Therefore, soils should be exchanged with water-retaining, nutrient-poor substrates wherever possible. However, considering costs and funding budgets, this seems unrealistic for many interventions. Hence, applying management changes oriented at large-scale classic grassland restoration will improve the situation for urban pollinators in the medium term. Seeding is an appropriate and effective technique to overcome urban dispersal barriers for many wild plant species. However, local seed banks could still be vital and diverse in species, especially when more natural grassland areas are neighboring the sites. Thus, one should consider the local seed bank, exercise caution, and consult local experts before seeding. Seed mixture design is not limited to any natural vegetation type. Therefore, composing species mixtures can be optimized when it is guided by plant functional traits. When the rehabilitation is intended to improve the habitat quality for pollinators, flower traits can be emphasized in trait selection to meet the requirements of as many pollinators as possible.

Phytometers are a valuable tool for measuring environmental conditions and ecosystem functioning in urban areas. When phytometers are employed, several factors must be considered when choosing the appropriate plant species in light of the scientific questions or rehabilitation targets. Using phytometer plants allows for standardized data collection and comparison across different restoration projects and sites. Phytometer plants could also provide a cost-effective and straightforward method for long-term monitoring of restoration sites. By periodically assessing the condition of indicator plants over time, practitioners can track the trajectory of ecosystem recovery. In this thesis, I attempted a comparative approach to visualize the species-specific responses of phytometers at local and landscape scale factors in urban environments. This could be the first step in using standardized indicator species and establishing consistent monitoring protocols so that researchers and practitioners can more efficiently evaluate the success of restoration efforts.

Rehabilitation in cities targeted at wild bees can be successfully done by transforming urban roadsides into native wildflower corridors. Implementing green infrastructure along linear landscape elements, roofs, or building facades evidently increases bee diversity and the connectivity of urban habitats. Focusing on the local bee species pool to identify the species possibly profiting from the intervention is a first start. Zooming in on species abundances, distributions, and functional groups before starting an intervention is the golden standard, but it needs expert knowledge, and still, comprehensive trait databases do not exist. Trait information must be publicly available to make trait-based conservation approaches feasible for practitioners and conservationists. Secondly, identifying functional groups affected by urbanization needs standardized protocols and easy-to-handle analysis tools. Finally, research needs to address functional filtering in different landscape settings and identify fundamental trait-environment interactions to provide suggestions for basic countermeasures.

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Appendix

A1 Publication list

Peer reviewed publications

Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023. Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecological Indicators 147*, 109980.*

Rojas-Botero, S., **Dietzel, S.**, Kollmann, J., Teixeira, L.H., 2023. Towards a functional understanding of rehabilitated urban road verge grasslands: Effects of planting year, site conditions, and landscape factors. *Flora 309*, 152417.*[a]

Dietzel, S., Rojas-Botero, S., Dichtl, A., Kollmann, J., Fischer, C., 2024. Winners and losers at enhanced urban roadsides: Trait-based structuring of wild bee communities at local and landscape scale. *Biological Conservation 291*, 110480.*

Dietzel, S., Moosner, M., Seibold, S., Kollmann, J., 2025. When to mow and how? Short-term effects of river dike grassland management on arthropod abundance and species richness. *Journal of Insect Conservation*.[a] https://link.springer.com/journal/10841

*Included in the thesis

[a]Shared co-authorship

Further publications

Dietzel, S., Sauter, F., Moosner, M., Fischer, C., Kollmann, J., 2019. Blühstreifen und Blühflächen in der landwirtschaftlichen Praxis – eine naturschutzfachliche Evaluation. *ANLiegen Natur 41* (1), 73–86. https://www.anl.bayern.de/publikationen/anliegen/doc/an41129dietzel_et_al_2019_bluehstreifen_review.pdf

Dietzel, S., Fischer, C., 2020, Ausbreitungsbewegung von *Isodontia mexicana* (SAUSSURE, 1867), der Stahlblaue Grillenjäger in Bayern: Weitere Nachweise aus dem Stadtgebiet von München (Hymenoptera: Sphecidae). *Nachrichtenblatt der bayerischen Entomologen 69* (3/4). https://www.zobodat.at/pdf/NachBlBayEnt_069_0098-0099.pdf

Dietzel, S., Rojas-Botero, S., Fischer, C., Kollmann, J., 2022. Aufwertung urbaner Straßenränder als Anpassung an den Klimawandel und zur Förderung bestäubender Insekten. *ANLiegen Natur 44 (1*), 31–42. https://www.anl.bayern.de/publikationen/anliegen/doc/an44104dietzel_et_al_2022_aufwertung_strassenraender.pdf

Kollmann, J., **Dietzel, S.,** Moosner, M., Seibold, S., 2024. Auswirkungen der Deichmahd auf Vegetation und Arthropoden. *Wasserwirtschaft 114*, 26–31. https://doi.org/10.1007/s35147-024-2300-5

Poster presentations

Dietzel, S., Kollmann, J., Albrecht, H., Fischer C., 2019, Wildflower patches as urban green infrastructure and habitat for pollinators. GfOe conference, Muenster, 09.09.—13.09.

Rojas-Botero, S., **Dietzel, S**., Kollmann, J., 2021, Restored urban road vegetation offers floral resources for insect pollinators and contributes to climate regulation. SER World Conference on Ecological Restoration. 21.6.—24.6.

Dietzel, S., Rojas-Botero, S., Fischer, C., Kollmann, J., 2021, Bunte Bänder für unsere Städte in Zeiten des Klimawandels: Naturnahe städtische Blühflächen entlang von Verkehrsachsen zur Förderung der ökologischen Funktionalität. Symposium „Grüne Klimaarchitektur, Zentrum für Stadtnatur und Klimaanpassung, München, 22.09.

Moosner, M., **Dietzel, S**., Kollmann, J., Seinold, S., 2022, Short-term effects of mowing regime on arthropods in river dike grasslands – When and how to mow? GfOe conference, Metz, 21.11.—25.11.

Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023, Bunte Bänder: Effekte artenreicher Straßenränder auf die Reproduktion von Wildbienen und Wespen. Symposium „Animal Aided Design“, Zentrum für Stadtnatur und Klimaanpassung, München, 31.1.

Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023, Wild bee species richness, functional diversity, and trait filtering at urban roadsides. GfOe conference, Leipzig, 12.09.—16.09.