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Ecological restoration of urban grasslands in times of global change. Towards scientifically-informed practice based on mesocosm experiments

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SUMMARY

Urbanization is a major transforming force largely responsible for the degradation of ecosystems and biodiversity loss. Thus, urban ecosystems are usually deemed species-poor and homogenized, with little ecological value. Notwithstanding, in the past decades, the importance of urban ecosystems for improving human quality of life has gained visibility. Increasing initiatives strive to understand and rehabilitate the ecological integrity of urban ecosystems, particularly urban grasslands, which translates into ecosystem services, adaptation to climate change, and biodiversity protection. However, persistent knowledge gaps in understanding the capacity of urban grasslands to, e.g., resist biological invasions, improve their functioning, and adapt to climate change, call for diverse research approaches. By closing these gaps, it can be determined to what extent rehabilitation efforts are to produce the expected effects and what design criteria need prioritization.

This doctoral thesis aims to improve the understanding of the effects of global change on urban grasslands and to identify attributes that enhance their functioning under different environmental and biotic stressors. Specific objectives are: (i) to determine the magnitude of changes affecting the resistance of recently sown urban grasslands against invasive species, (ii) to understand the effect of climate change on the functioning of urban grasslands, and (iii) to evaluate the belowground responses of urban grasslands to climate change. Thus, I conducted experiments in a controlled environmental facility ('ecotron'), where abiotic and biotic conditions were manipulated. Mesocosm grasslands were designed to increase resistance to invasive alien species and enhance taxonomic and functional plant diversity.

The topic of **Publication 1** is the resistance of recently established grassland communities to an invasive alien species under the effect of environmental fluctuations. For this publication, a series of mesocosm experiments were conducted to test the effects of N fertilization, heat waves, and floodings on the invasion success of *Solidago gigantea* in bare soil sown with grassland seed mixtures. Two grassland communities were designed according to competitive trait hierarchies with different sowing patterns, reflecting variation in biotic resistance. Consistent effects of biotic resistance to the invasion of *S. gigantea* via competitive trait hierarchies were found across experiments. Communities dominated by species with high-competition traits were more resistant regardless of environmental fluctuation. The effects of abiotic fluctuations were less consistent and context-dependent. These results indicate that the biotic resistance of the communities is, in general, a primary concern for the restoration of grasslands under the pressure of invasive species. Species selection should include sets of traits conferring increased resistance to invasion.

Publication 2 addresses the multifunctionality of recently rehabilitated grasslands under climate change. In an ecotron experiment, two contrasting climate-change scenarios were simulated by manipulating temperature and [CO_2] concomitantly. Additionally, watering was controlled for 'average' vs. '50% reduced' volume of seasonal precipitation. Four grassland compositions with varying proportions of forbs:grasses were subjected to climate-change conditions, and indicator variables of ecosystem functions were measured and assessed through multifunctionality indices. Grassland communities responded to increased [CO_2] and temperature with more productivity, while lower precipitation negatively affected multifunctionality. Overall, communities with an even composition of forbs and grasses generally showed higher multifunctionality. It was observed that some functions were better performed in grasslands dominated by either grasses or forbs. This suggests that boosting certain functions in urban grasslands in times of climate change requires an objective-oriented approach to grassland design.

Publication 3 used the same environmental conditions described in Publication 2 to test the belowground responses of the four grassland communities to climate change. Given the importance of absorptive roots for controlling soil C allocation and resource acquisition, besides biomass allocation, root diameter, root tissue density, specific root length, and root length density were measured. The functional composition of grasslands determined biomass allocation, with grass-dominated communities producing more belowground biomass than forb-dominated ones and the opposite pattern registered aboveground. Contrastingly, fine root traits responded not only to functional composition but also to climate change. Reduced precipitation fostered conservative strategies belowground (i.e., high mean root diameter), while higher temperature and [CO_2] led to higher root tissue density and promoted exploration of lower soil layers. These results show that trait variation rather than biomass reflected belowground adjustments to climate change and reinforces the need to account for functional traits to design climate-resilient communities.

The **General Discussion** summarizes the publications' findings and contextualizes them in the current research gaps for the design and rehabilitation of urban grasslands. It puts together the aspects addressed in the thesis, i.e., biological invasions, multifunctionality, resilience, and adaptation to climate change, and how they may influence the successful establishment of urban grasslands. A reflection on the shortcomings and potentials of the utilized research approach is presented and contrasted with existing literature. Finally, practical recommendations for urban grassland rehabilitation were outlined in light of the research outcomes presented in this thesis.

ZUSAMMENFASSUNG

Urbanisierung ist ein besonders starker Eingriff in den Naturhaushalt und führt meist zur Degradierung natürlicher Ökosysteme und zu Verlusten an biologischer Vielfalt. Daher werden urbane Ökosysteme oft als homogen und artenarm wahrgenommen und ihr ökologischer Wert als gering eingeschätzt. Trotzdem gewinnt in den vergangenen Jahren die Bedeutung urbaner Ökosysteme für die Verbesserung der Lebensqualität von Menschen immer mehr Aufmerksamkeit. Viele Forschungs- und Umsetzungsprojekte beschäftigen sich mit der Untersuchung und Renaturierung der ökologischen Integrität urbaner Ökosysteme, insbesondere von Grünflächen, die spezielle Ökosystemdienstleistungen und damit ein hohes Potential für Biodiversitätsschutz, Vermeidung von Neobiota und Klimawandelanpassung bieten. Es gibt jedoch noch Wissenslücken im Verständnis wie urbanes Grünflächen ökologisch funktionieren, biologischen Invasionen widerstehen und sich an den Klimawandel anpassen können, was neue Forschungsansätze erfordert. Durch das Schließen solcher Wissenslücken kann besser geplant werden, inwieweit Renaturierungsmaßnahmen die erwarteten Effekte bringen oder welche Kriterien bei der Gestaltung urbaner Grünflächen priorisiert werden sollten.

Ziel der vorliegenden Dissertation ist ein verbessertes Verständnis von Effekten des globalen Wandels auf urbanes Grünland und ein Identifizieren von Eigenschaften, welche die Funktionalität dieser ‚Grünen Infrastruktur‘ unter bestimmten abiotischen und biotischen Stressfaktoren erhöhen. Konkrete Ziele sind: (i) abiotische und biotische Faktoren zu bestimmen, die die Invasionsresistenz kürzlich gesäten urbanen Grünlands bestimmen, (ii) die Auswirkungen von Klimawandel auf die ökologische Funktionalität dieser Vegetation zu verstehen, und (iii) die unterirdische Reaktion urbanen Grünlands an den Klimawandel zu untersuchen. Hierfür wurden aufwendige Experimente in Klimakammern (‚ecotron‘) durchgeführt mit Manipulation der abiotischen und biotischen Faktoren. In großen Wachstumsgefäßen (‚Mesokosmen‘) wurden Grünlandbestände angelegt, die eine spezifisch variierte taxonomische und funktionale Vielfalt und zu erwartende Invasionsresistenz hatten.

Das Thema von **Publikation 1** ist die Invasionsresistenz von kürzlich gesäten Grünland unter dem Einfluss von Umweltvariation. Für diese Publikation wurden drei Mesokosmenversuche durchgeführt, in denen die Auswirkungen von N-Düngung, Hitzewellen und Überflutungen auf den Etablierungserfolg des invasiven Neophyten *Solidago gigantea* untersucht wurden. Zwei unterschiedliche einheimische Grünlandmischungen wurden auf Basis funktioneller Eigenschaften mit unterschiedlicher Aussaatdichte angelegt. Die Konkurrenzstärke der einheimischen Pflanzengemeinschaften wies in allen Experimenten einen konsistenten Einfluss auf die Invasionsresistenz gegen *S. gigantea* auf. Die

Etablierung der invasiven Art nahm mit der Konkurrenzstärke der einheimischen Pflanzengemeinschaft ab. Die Auswirkung von Umweltvariation waren wenig konsistent und meistens kontextabhängig. Die Ergebnisse legen nahe, dass die Konkurrenzstärke der Pflanzengemeinschaften eine Priorität bei Anlage von urbanem Grünland sein sollte, v.a. bei potentieller Invasion durch Neophyten. Die Artenauswahl für solche Bestände müsste funktionelle Eigenschaften priorisieren, die die Konkurrenzstärke der Gemeinschaften erhöhen.

Publikation 2 untersucht die ökologische Multifunktionalität renaturierter Grünländer unter dem Einfluss von Klimawandel. In einem entsprechenden Klimakammer-Experiment wurden zwei Szenarien simuliert, und zwar mit unterschiedlicher Lufttemperatur und [CO_2], normalem und 50%-reduziertem Jahresniederschlag. Vier Pflanzengemeinschaften mit variierenden Mengenanteilen an krautige Pflanzen und Gräsern wurden diesen Klimawandelbedingungen unterzogen. Einzelne Ökosystemfunktionen wurden gemessen und durch Indikatoren der Multifunktionalität bewertet. Grünland unter erhöhter Lufttemperatur und [CO_2] wies eine höhere Produktivität auf. Im Gegensatz dazu hatte verringerter Niederschlag weitgehend negative Auswirkungen auf die Multifunktionalität der experimentellen Bestände. Gemeinschaften mit einem gleichmäßigen Mischverhältnis zwischen Gräsern und Kräutern zeigten eine Verbesserung der Multifunktionalität unter Klimawandelbedingungen. Einzelne Funktionen wurden entweder von gras- oder krautdominierten Gemeinschaften besser ausgeführt. Dies deutet darauf hin, dass um bestimmte ökologische Funktionen urbaner Grünländer in Zeiten des Klimawandels zu fördern, eine zielspezifische Gestaltung der Zusammensetzung der Saatmischungen erforderlich ist.

In **Publikation 3** wurden dieselben Umweltbedingungen wie in Publikation 2 verwendet, um die unterirdischen Reaktion von vier verschiedenen Grünlandmischungen an den Klimawandel zu evaluieren. Wegen der Bedeutung absorptiver Wurzeln für die Kohlenstoff-Allokation im Boden und die Ressourcengewinnung wurden Wurzeldurchmesser, Gewebedichte, Wurzellängendichte und Spezifische Wurzellänge neben der Biomasseverteilung in zwei Bodenhorizonten gemessen. Die funktionelle Zusammensetzung der Bestände bestimmte die Biomasseverteilung: Grasdominierte Gemeinschaften wiesen höhere unterirdische Biomasse auf als krautdominierte Gemeinschaften und das umgekehrte Muster wurde oberirdisch beobachtet. Im Gegensatz dazu reagierten die Feinwurzeln nicht nur auf die funktionelle Zusammensetzung, sondern auch auf den simulierten Klimawandel: Verringerter Niederschlag führte zu einer ‚konservativen' Strategie (d.h. höhere Durchmesser der Wurzeln), während erhöhte Lufttemperatur und [CO_2] zu größerer Wurzelgewebedichte führten und das Wurzelwachstum in der unteren Bodenschicht förderten. Diese Ergebnisse zeigen, dass Merkmalsvariation anstatt Biomasseverteilung unterirdische Anpassungen an Klimawandel reflektieren, und dies bestätigt die Notwendigkeit funktionelle Merkmale der Pflanzen zu betrachten, um klimaresiliente Gemeinschaften zu entwickeln.

Die **Allgemeine Diskussion** der Dissertation fasst die Erkenntnisse der drei Publikationen zusammen und stellt diese in den Kontext der aktuellen Wissenslücken zur Ökologie und Renaturierung urbaner Grünländer. Die wichtigsten Befunde der Dissertation betreffen invasive Neophyten, Multifunktionalität, Resilienz und Anpassung an den Klimawandel, und wie diese die erfolgreiche Etablierung urbanen Grünlands beeinflussen können. Es wird auch über methodische Grenzen des verwendeten Forschungsansatzes reflektiert und weitere Untersuchungen empfohlen. Abschließend werden praktische Empfehlungen zur Aufwertung urbanen Grünlands formuliert.

RESUMEN

La urbanización es una fuerza transformadora en gran medida responsable de la degradación de ecosystemas y la pérdida de biodiversidad. Por esta razón, los ecosistemas urbanos generalmente se consideran pobres en especies y altamente homogenizados, con un bajo valor ecológico. Sin embargo, en los últimos años, la importancia de los ecosistemas urbanos para el bienestar humano ha ganado visibilidad. Las iniciativas encaminadas a la comprensión y rehabilitación de la integridad ecológica de ecosistemas urbanos han incrementado, particularmente en praderas urbanas, lo que se traduce en el mejoramiento de los servicios ecosistémicos, la adaptación de las ciudades al cambio climático, y de paso la protección de la biodiversidad en estos espacios. No obstante, aún hay vacíos acerca de cómo estas praderas urbanas, especialmente en fases tempranas de establecimiento, resisten invasiones biológicas, mejoran su funcionamiento ecológico, y se adaptan a las condiciones de cambio climático. Cerrando estas brechas del conocimento se puede determinar en qué medida los esfuerzos de rehabilitación en estos ecosistemas pueden producir los efectos esperados y qué criterios en la planeación de la rehabilitación se deben priorizar.

Esta tesis tiene como objetivo mejorar la comprensión de los efectos de algunos factores de cambio global sobre praderas urbanas e identificar atributos que mejoran su funcionamiento aun bajo factores estresantes tanto abióticos como bióticos. Los objetivos específicos son: (i) determinar la magnitud de los cambios que afectan la resistencia de praderas urbanas recientemente sembradas ante especies invasoras, (ii) comprender el efecto del cambio climático en el funcionamiento ecológico de praderas urbanas, y (iii) evaluar las respuestas del componente subterráneo de estos ecosistemas al cambio climático. Para ello, realicé experimentos en una instalación de ambiente controlado (‘ecotrón’), en el que se manipularon condiciones abióticas y bióticas. Se diseñaron praderas experimentales en mesocosmos teniendo como criterios de selección de especies aumentar la resistencia a especies exóticas invasoras y de incrementar la diversidad funcional y taxonómica de las comunidades.

El tema de la **Publicación 1** es la resistencia de praderas urbanas recientemente sembradas a una especie exótica invasora bajo el efecto de variaciones ambientales. Tres experimentos con mesocosmos fueron realizadas para evaluar los efectos de la fertilización con nitrógeno, olas de calor e inundaciones, en el éxito de la invasion de *Solidago gigantea*. Dos comunidades de pradera fueron diseñadas considerando jerarquías de rasgos funcionales de las especies seleccionadas asociados a competencia; se establecieron con dos patrones de siembra, reflejando así variaciones en la resistencia biótica. Se encontraron efectos consistentes de la resistencia biótica a la invasión por *S. gigantea* a partir de las jerarquías de rasgos funcionales en todos los experimentos. Las comunidades dominadas

por especies cuyos rasgos funcionales se asociaron a alta competitividad fueron más resistentes a la invasión, independientemente de las fluctuaciones ambientales. Los efectos de las fluctaciones ambientales fueron en cambio menos consistentes y contexto-dependientes. Estos resultados indican que la resistencia biótica de las comunidades es la prioridad principal para la rehabilitación de praderas bajo la presión de especies invasoras. La selección de especies para la rehabilitación debe, por lo tanto, incluir rasgos funcionales que aporten al aumento en la resistencia a especies invasoras.

La **Publicación 2** estudia la multifuncionalidad de praderas urbanas recientemente rehabilitadas bajo condiciones de cambio climático. En un experimento de ecotrón, dos escenarios contrastantes de cambio climático fueron simulados, a través de la manipulación simultánea de temperatura y [CO_2]. Adicionalmente, el riego fue controlado para simular condiciones 'normales' vs. 'reducidas en 50%' con relación a la precipitation estacional. Cuatro comunidades de praderas con una variación en la composición de herbáceas no gramíneas vs. pastos se sometieron a condiciones de cambio climático. Se midieron variables indicadoras de funciones ecosistémicas y se evaluaron con índices de multifuncionalidad. Las praderas respondieron al incremento de temperatura y [CO_2] con mayor productividad, mientras que la reducción en precipitación afectó negativamente la multifuncionalidad. En general, comunidades con una composición uniforme de pastos y herbáceas no gramíneas mostraron mayor multifuncionalidad. Se observó además que algunas funciones fueron desempeñadas mejor en praderas dominadas por pastos o en aquellas dominadas por herbáceas no gramíneas. Los resultados sugieren que para estimular funciones particulares en praderas urbanas rehabilitadas bajo condiciones de cambio climático es importante considerar composiciones de especies orientadas a tales objetivos.

La **Publicación 3** utiliza las mismas condiciones ambientales descritas en la Publicación 2 para evaluar las respuestas del compartimento subterráneo de cuatro tipos de comunidades de praderas al cambio climático. Dada la importancia de las raíces absortivas en el control de la alocación de carbono en el suelo y la adquisición de recursos, se midió, aparte de la alocación de biomasa, el diámetro, la densidad de tejidos, la longitud específica y la densidad de longitud de las raíces. Se encontró que la composición funcional de las praderas determina la alocación de biomasa. Comunidades dominadas por pastos presentaron mayor biomasa subterránea que las dominadas por hierbas, mientras que el patrón opuesto se observó sobre la superficie. En contraste, los rasgos de las raíces absortivas respondieron no solo a la composición funcional sino también al cambio climático. La reducción de la precipitación promovió estrategias conservativas subterráneas, con un mayor diámetro promedio de raíces, mientras que el incremento de temperatura y [CO_2] condujo a una mayor densidad de tejido radicular y fomentó la exploración de capas más profundas del suelo. Estos resultados indican que la variación en rasgos funcionales, y no la biomasa, reflejan los cambios que demuestras los ajustes subterráneos de las comunidades al cambio climático, reforzando la necesidad de tener en cuenta los rasgos funcionales en el diseño de comunidades resilientes al cambio climático.

La **discusión general** sintetiza los resultados de las tres publicaciones y las contextualiza en los vacíos de investigación actuales con relación a la rehsbilitación de praderas urbanas. La discusión ensambla los aspectos abordados en la tesis, es decir, las invasiones biológicas, la multifuncionalidad, y la resiliencia y adaptación al cambio climático, y cómo estos pueden afectar el establecimiento exitoso de praderas urbanas. Se reflexionan las limitaciones y potencialidades del enfoque de investigación empleado y se contraste con la literatura disponible en la materia. Finalmente, se plantean recomendaciones prácticas para la rehabilitación de praderas urbanas con base en los resultados expuestos en esta tesis.

INTRODUCTION

Urbanization: degradation and rise of urban ecosystems

The transformation of land for urban development

Although global losses in biodiversity and ecosystem functions continue to be primarily driven by transformation for agricultural land use [1], the growth of urban areas[1] also implies profound impacts on the integrity of ecosystems. More than half of the global human population lives in cities (53% in 2018; [3]). With the projected urban population to grow by 2.5 billion over the next 30 years [1], urbanization poses unprecedented challenges for biodiversity and the functions and services derived from ecosystems in and around urban areas. Urbanization implies land-cover change and subsequent habitat loss and fragmentation, decreased carbon storage capacity in vegetation [4,5], and changes in biodiversity, e.g., species losses and introduction of neobiota, often producing homogenized species assemblages [6]. Moreover, habitat loss due to urbanization is caused by the intense transformation of the land into sealed areas. Semi-natural sites or agricultural lands converted into the urban fabric imply irreversible land-use changes because soils are severely compacted and sealed, and vegetation biomass is drastically reduced. Carbon sinks are significantly reduced with the loss of vegetation [7], while biogeochemical cycles are disrupted, contributing to altered local climate [7], and overall degraded ecosystem functioning.

Novelty in urban ecosystems

Apart from habitat loss due to urbanization, the remaining semi-natural or created urban ecosystems are characterized by altered species composition. First, urban areas are highly susceptible to invasion by non-native plant species because of their introduction, establishment, and spread [8,9]. Second, sensitive species may not survive urban site conditions and thus become locally or regionally extinct [10], while some natives benefit from urban conditions and increase in distribution and abundance. Therefore, plant communities in urban areas are usually transformed into hybrid or novel communities [10,11], which is typical for urban ecosystems [10,12–14]. While some non-native species become dominant and may alter ecosystem processes, novel community assemblages based on native and non-native species are common characteristics of urban ecosystems [11], eventually comparable in functioning to their more natural counterparts [15]. Indeed, the concept of ‘**novel ecosystems**’ is

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[1] Urban areas are defined according to the degree of urbanization and comprise cities plus town and semi-dense areas (also known as peri-urban or suburbs). This classification of ‘urban’ allows a clearer understanding of territories along the rural-urban continuum and an internationally comparable standard that facilitates building indicators in terms of the Sustainable Development Goals (SDG) of the UN. This is done using 1-km² grid cells, classified according to their population density, population size and contiguity (neighboring cells) [2].

useful in urban settings, where substantial transformations imply an irreversible change of ecosystems. Similarly, '**hybrid ecosystems**' refer to ecosystems where some historical attributes remain but are exposed to novel disturbance and management regimes compromising the return to historical conditions [11,16–18]. Furthermore, a characteristic of hybrid or novel urban ecosystems is that social values, purposes, and human interventions are needed for their existence, design, management, and restoration [10,11]. Although novelty in urban ecosystems has been deemed responsible for biotic homogenization across cities regionally and worldwide [6], evidence also has found novelty to foster diversity within cities (e.g., [19]) due to their heterogeneous habitats [10].

Functions and services of urban nature

The role of urban ecosystems in biodiversity protection

Although urbanization represents one of the main threats to biodiversity and may lead to biotic homogenization, cities can also be an opportunity to conserve native and even threatened biodiversity [5,20,21]. To what extent urban ecosystems support biodiversity and ecosystem functioning, with the subsequent delivery of ecosystem services, varies with anthropogenic and non-anthropogenic factors that operate at different scales. Land cover, composition, and configuration are critical in urban ecosystems [5]. While high levels of imperviousness in intensively built environments are detrimental to biodiversity, intermediately built areas of suburban districts tend to show higher species richness [22]. Furthermore, a heterogeneous urban configuration, including large patches of urban ecosystems or small ones forming corridors or stepping-stones (Figure 1), fosters biodiversity [21,23,24]. In addition, factors related to vegetation composition and structure of urban ecosystems are particularly relevant to increasing biodiversity in cities [23,25], especially if management is adapted for improved habitat quality and resource offer [25–27], or rehabilitation practices are implemented [11]. Notwithstanding, frequent small-scale anthropogenic disturbances, e.g., trampling, (re)construction, soil compaction, fertilization, pollution, and trash, can severely hinder the establishment of appropriate habitats and viable plant and animal species populations.

Figure 1. Exemplary green spaces depicting the heterogeneity in habitats that can be found in urban areas (S Germany) and potentially increase the opportunities for fostering biodiversity in cities, towns, and suburbs: a) forest, b) meadow, c) park, d) brownfield, e) road trees, f) vegetated road verges, g) private garden, h) allotment, and i) green roof. Landscape and local conditions, together with social values, may determine to what extent these are valuable elements for biodiversity. New designs, restoration, and adapted management strategies can influence the connectivity among these elements of urban green; this would improve their provision of ecosystem services and value for biodiversity. Photo credits (g and i): Johannes Kollmann.

Urban ecosystems benefit human well-being and contribute to climate change adaptation

Besides being arising options for biodiversity protection, urban ecosystems deliver ecosystem services (ESS) that translate into societal benefits [28,29], e.g., carbon sequestration, pollution removal, food production, water runoff mitigation, microclimate regulation, and space for recreation and contemplation [30]. This so-called multifunctionality of urban ecosystems implies that diverse and well-functioning urban ecosystems provide a range of benefits for citizens [28], maximizing synergies and diminishing trade-offs among the services delivered [31]. Even though the connection between biodiversity, ecosystem function, and ecosystem services is gaining evidence in natural and semi-natural ecosystems [32], the relationship between different aspects of biodiversity and the functioning of urban ecosystems has received relatively little attention [15].

Furthermore, urban ecosystems may be crucial for adapting to anthropogenic climate change [31]. Even though cities occupy only 2% of the total land, over 60% of global energy is consumed in cities, with 70% of greenhouse gas emissions and global waste deriving from them [33]. Thus, cities are significant drivers of climate change and are particularly vulnerable to its effects, including heat waves, droughts, hurricanes, and flooding [34]. Urban development and the significant removal of vegetation contribute to increased temperatures in cities, thus enhancing urban heat island effects [35] and the impact of heat waves [36]. Likewise, the sealing and compaction of soils reduce the ability to intercept, evapotranspire, store, and infiltrate rainwater, altering urban hydrology and amplifying flood risks. To counteract these adverse effects of climate change, urban green infrastructure (UGI) elements, such as road trees, green walls, and green roofs (see Box 1 for extended definition), diminish heat and energy consumption in urban settings [37]. Moreover, grasslands, trees, bioswales, and larger green areas reduce surface runoff by increasing water interception and evapotranspiration or retaining water in the soil and biomass [38].

Conservation and restoration of urban ecosystems

Nature and urbanization are not necessarily mutually exclusive

The United Nations Conference on Housing and Sustainable Urban Development presented the New Urban Agenda (NUA) [33], a desired global vision for a sustainable future in cities aligned with the Sustainable Development Goals [7] and the Paris Agreement adopted under the United Nations Framework Convention on Climate Change [33]. While acknowledging the challenges of growing urbanization and the need to warranty human well-being and reduce inequalities, the NUA recognizes the need to protect, conserve, and restore urban ecosystems to safeguard cities' biodiversity, reduce disaster risks, and mitigate and adapt to climate change [33]. By incorporating nature in the design and management of urban areas, ecosystem services such as carbon sequestration, local climate regulation, storm water mitigation, and water and air purification are expected to be locally delivered. Moreover, avoiding urban sprawl and land consumption can halt habitat loss, while cities can promote biodiversity through UGI [7] and thus achieve multiple benefits from urban ecosystems.

BOX 1: How to understand urban green infrastructure?

Urban green infrastructure (UGI) consists of strategically developed networks of natural, semi-natural, and novel ecosystems, e.g., ancient woodlands, meadows, public parks, private gardens, green streets, green roofs, and derelict land [39]. It is designed and managed to deliver a wide range of ecosystem services (ESS) [40] that provide multiple benefits to humans and integrate biodiversity in urban systems [29,31,39]. The broad concept of 'urban green infrastructure' refers primarily to terrestrial ecosystems but encompasses green and blue infrastructure (i.e., aquatic ecosystems such as channels, lakes, ponds, etc.).

The term urban green infrastructure goes beyond just renaming 'green space elements' of urban areas. It is also a planning tool that accounts for connectivity principles and multifunctionality. Thus, it is possible to determine what green spaces or urban ecosystems are properly part of the UGI network, and where it is necessary to improve the quality of existing elements or design new ones to strengthen connectivity and multifunctionality [41].

Types of urban ecosystems

While some urban ecosystems may retain relatively high levels of 'naturalness', others are highly 'artificial' but valuable elements of urban nature (Figure 2). Remnants of natural or semi-natural ecosystems (e.g., forests, grasslands, rivers, wetlands) can occasionally be found in expanding cities and present variable needs for restoration and management. In turn, intensively transformed ecosystems are prevalent in cities: Public parks, cemeteries, or roadside vegetation, which tend to be species-poor but still resemble some elements of native grasslands with sparse woody elements. Similarly, urban brownfields or wastelands facilitate the establishment of spontaneous native and non-native vegetation and the development of hybrid ecosystems on highly altered soils [42]. Finally, artificial ponds, wetlands, green roofs and facades, flowerbeds, and gardens are part of urban design in public or private spaces, with a commonly arbitrary design and species selection based on aesthetic and recreational goals.

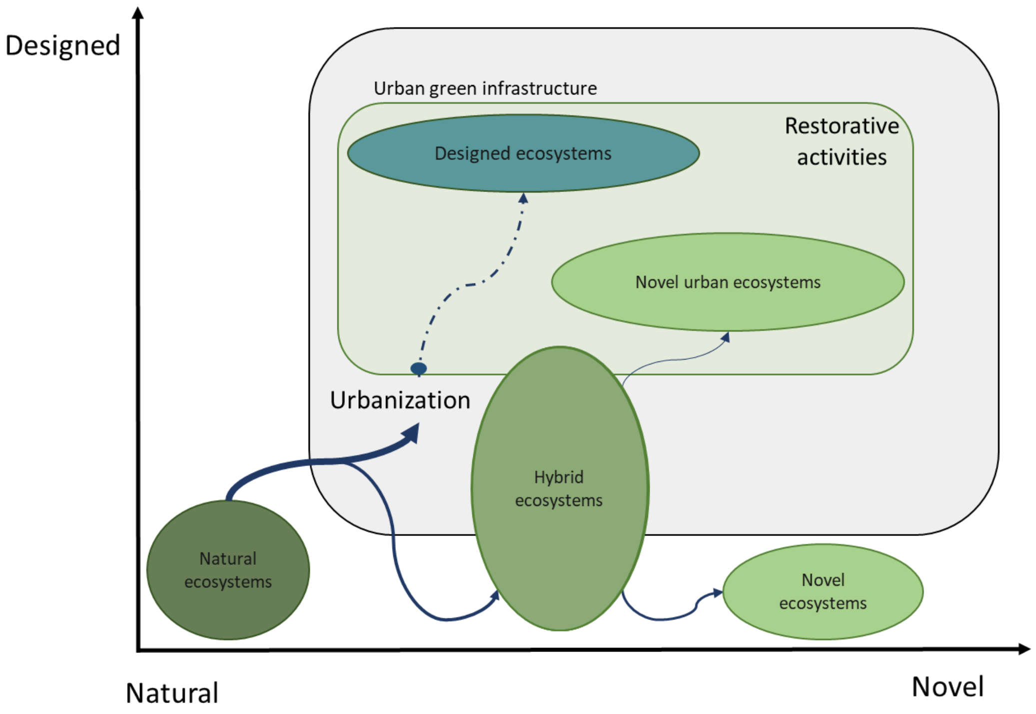

Figure 2. Types of urban ecosystems according to the degree of novelty and design. Urbanization implies the substantial transformation of natural and semi-natural areas ('natural ecosystems'), provoking shifts in ecosystems' biotic and abiotic properties in and around urban areas. Urban ecosystems can be considered 'hybrid' or 'novel' depending on the degree of transformation. Amidst urbanized areas, designed ecosystems may arise through direct human intervention to improve the ecological and aesthetic values of urban areas [16]. Urban green infrastructure (UGI) comprises a network of all urban ecosystems that deliver various services to urban dwellers. Adapted from [14].

Urban grassland as a pervasive element of urban green infrastructure

Grasslands are the predominant component of urban ecosystems [43–45]; they encompass, in a broad sense, lawns, meadows, private gardens, parks, brownfields, and roadsides [44,46,47]. Lawns dominated by turfgrasses are the most extended form of urban grasslands or grassland-like habitats, characterized by intensive management [45] and little ecological value [48]. Nevertheless, urban grasslands have a high potential for biodiversity conservation, ecosystem services, and climate change adaptation, especially in temperate urban areas [44,49–53], although their benefits have often been overlooked [47].

Recent approaches strive to convert lawns into species-rich meadows and improve their ecological value [27,28] and the array of functions and services derived from them [52,54,55], even in areas where they were not considered a meaningful element of UGI. For instance, urban roadsides, when composed of diverse herbaceous vegetation, represent a promising option to increase the cover of grassland-like vegetation in cities [56], which benefits species dispersal and enhances ecosystem services near the areas where people move [57,58]. Small patches of grassland vegetation may be the only representation of urban green in densely built areas [57,59]. Thus, they could substantially increase available green space in addition to parks and conservation areas [60]. Although small patches of herbaceous vegetation have limited conservation value in the long term, such interspersed vegetation patches constitute valuable space for urban biodiversity movement and ecosystem services [57,59,60].

Functioning of urban grasslands

Biodiversity is essential for ecosystem functioning, i.e., its capacity to sustain life over time [61]. Species richness, composition, and functional types are responsible for ecosystem resources and processes. During the past decades, various studies highlighted the role of biotic attributes of ecological communities, especially taxonomic and functional diversity, on single ecosystem functions and ecosystem multifunctionality [32,62,63], mainly in experimental and semi-natural grasslands [64]. When assessing an array of ecosystem functions, physical, geochemical, and biological processes can be described, as well as the supply of multiple ecosystem services under specific human demand [32]. Further research and management options can be defined based on multifunctionality assessments.

Furthermore, the aboveground biomass and its responses to biotic and environmental drivers is the most studied component of urban grassland functionality. Aboveground biomass production is often used as a proxy of ecosystem functionality [65] because the variability of functionality is largely explained by productivity and structural elements of the vegetation [66]. Nonetheless, the response of the belowground compartment is at least equally important [67] since roots largely control potential responses to environmental change [67,68], and the traits of plant roots have significant consequences for ecosystem functioning [67]. Moreover, grassland ecosystems have a large share of their biomass belowground [69]. In particular, absorptive roots inform about belowground C allocation [67,70] and mechanisms for water and nutrient acquisition [71], and thus can be crucial to grassland functioning under challenging conditions. Moreover, soil biota, i.e., bacteria, fungi, invertebrates, etc., are an essential component of the belowground functionality of grasslands [68] in urban contexts [15] and explain much of the variability in the function of soils under global change [68,70].

Urban ecosystem design and restoration

The United Nations Decade on Ecosystem Restoration declaration has made restoration ecology more visible. In a broad sense, ecosystem restoration “encompasses a wide continuum of practices, depending on local conditions and societal choice,” which for the urban case include practices to rehabilitate “degraded, modified ecosystems to more functional modified ecosystems” [72]. This initiative suggests the need to incorporate principles of restoration widely applicable to maximize net gain for native biodiversity, ecosystem health and integrity, and human health and well-being [73]. For instance, it highlights the need to align with the biodiversity, climate, and land-degradation neutrality goals of the Rio Conventions (CBD), United Nations Convention to Combat Desertification (UNCCD), and United Nations Framework Convention on Climate Change (UNFCCC) [73]. Moreover, restoration principles recognize a continuum of activities (the *restorative continuum* [74]) implemented in many ecosystems including urban ones [11], from remediation up to proper restoration, accounting for all types of knowledge [73], and the relevance of evidence-based science underpinning environmental practice [75]. The restoration (sensu lato) of urban ecosystems highlights the importance of raising the awareness of citizens and decision-makers to position urban ecosystems as a critical aspect of urban planning, with their potential for biodiversity conservation and ecosystem services. There are growing initiatives for increasing and improving UGI and urban ecosystem restoration, e.g., Green Cities Initiative[2] or Cities with Nature[3]. While remnants of ecosystems embedded in urban areas can be restored to stop degradation, the terms ‘restoration’ or ‘rehabilitation’ in the urban context also encompass establishing novel ecosystems [11].

A critical point in urban ecosystem restoration relates to ecological novelty and the fact that native and non-native species usually co-occur in UGI. Many non-native species in urban areas become invasive alien species (IAS). Usually, IAS escape from private gardens and public parks and rapidly spread and dominate hybrid and semi-natural ecosystems. Whereas decisions on species selection and management of private gardens remain a value-dominated issue, native species can provide similar benefits for citizens, and habitat and resources for specialized native fauna, even in combination with non-native species [11]. Nonetheless, restorative activities are needed to halt or control the further spread of IAS, which displace native species in different trophic levels, lead to enhanced biotic homogenization, and often produce ecosystem disservices [10].

Restorative activities in urban grasslands

Since grassland restoration is commonly based on seeds added to bare soil [56,76], restorative approaches in grasslands can support the short-term improvement of different aspects of ecological integrity. For instance, the preferential use of native species and evidence-based selection of traits, functional types, and compositions can meet invasion resistance targets, enhance multifunctionality and resilience to urbanization and climate change. Ultimately, despite urban grasslands not returning

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[2] https://www.fao.org/green-cities-initiative/en/
[3] https://citieswithnature.org/what-is-citieswithnature/

to historical conditions, potential ecological values may render them worth being rehabilitated or designed to reach urban reference systems in which aspects like species composition, functioning, and ecosystem services are considered. Reference conditions may thus be present in different regions where grassland-like systems have the desired characteristics regarding biodiversity and ecosystem services [11].

The enhancing and challenging role of climate change

Human-promoted increase of [CO_2] and other greenhouse gases (GHG) since 1750 has led to a higher temperature, changes in precipitation patterns, and more frequent and intense climate extremes, such as floods and heat waves [77], which negatively affect biodiversity and ecosystem functioning. In turn, ecosystem functioning is crucial for climate regulation because ecosystems substantially mediate biogeochemical cycles [28]. Different climate-change components can alter organisms' physiological responses, population dynamics, and community development, ultimately modifying the functioning of urban ecosystems and their attained services [78–80]. Thus, along with biodiversity effects, different components of global climate change can affect the responses of rehabilitated urban grasslands to alien plant invasions, their functioning, and derived ecosystem services.

Potential responses to invasions under climate change

Climate change can affect the performance of invasive and native species [81,82] and thus influence invasion outcomes [83]. Some IAS profit from altered environmental conditions, such as nutrient-rich soils [83], and can benefit from environmental fluctuations [84–86]. Under changed abiotic conditions such as those in urban areas, alien plants may modulate biomass production to become increasingly successful in hybrid and novel ecosystems, thus affecting ecosystem services [87]. Moreover, the magnitude and frequency of environmental fluctuations derived from climate change have critical roles in the ability of invasive species to capitalize on disturbances and shifts in resource availability and to become dominant [84].

Responses of ecosystem functioning to climate change

Changes in the availability of the primary resources of plants, i.e., CO_2, nitrogen, and water, and non-resource modifications (e.g., temperature) affect ecosystem functioning. Furthermore, biotic and abiotic processes can explain the differential effects of global change drivers on plant communities and their responses, which regulate ecosystem functioning [88]. While most evidence relates ecosystem multifunctionality, i.e., the ability of ecosystems to provide multiple functions, to species richness [64,89–91], possible impacts in ecosystem functioning due to climate change may relate best to more sophisticated aspects of biodiversity ([92] but see [93]), including functional composition [94,95].

Ecosystem's species and functional composition may thus modulate processes such as productivity, decomposition, and water and nutrient cycles, stocks of energy and matter [32], which are interrelated via networks of interactions and shared drivers [93,96].

Under climate change, modifications in, e.g., carbon cycling, have substantial implications for ecosystem functioning and the feedback to climate, given the CO_2-sink role of terrestrial ecosystems. Elevated temperature and higher [CO_2] increase C sequestration by plants [93,97], while water and nutrient availability determine whether terrestrial ecosystems benefit from a warmer and CO_2-enriched atmosphere [93,96,98]. Thus, in combination, climate-change components significantly affect ecosystem functionality outcomes that isolated drivers may not accurately explain [92,93,99]. Increases in atmospheric [CO_2], for instance, cascades through biological systems to affect many processes [100]. Ecosystem productivity usually increases under elevated [CO_2] because there is an increase in photosynthesis, a decrease in stomatal conductance, and an increased growth rate [98]. Nutrient demand increases to sustain plant growth under high [CO_2], whereas high water use efficiency maintains soil water availability due to lower plant transpiration rates [100]. Increased [CO_2] also enhances ecosystem respiration depending on soil water availability and soil type [93,101], thus producing differences in net C uptake. Moreover, larger biomass production means increased litter production and allocation of C to belowground processes [93,97].

Furthermore, the input of C controls the ‘sink’ role of terrestrial ecosystems, as most of this element is stored in the soil [102], while most CO_2 efflux stems from belowground [103]. Belowground processes are essential to understand the response of ecosystems to climate change [68,104]. In particular, the roots of plants contribute key ecosystem functions related to nutrient and water uptake, as well as belowground C allocation [105]. Hence, changes in ecosystem functioning, i.e., carbon, nitrogen, and water dynamics, due to rising [CO_2] cascade throughout all compartments of (urban) ecosystems.

The need for understanding urban grasslands in a changing world for evidence-based design and rehabilitation

Against this background, the function of urban grasslands to protect biodiversity and provide services is challenged by increasing global-change effects. While natural and semi-natural grasslands are the main focus of research on ecosystem functioning, restorative approaches in response to global change for identifying priorities in rehabilitating grasslands in urban areas, where modified abiotic and biotic conditions prevail. The restoration of urban grasslands expands from species selection aligned with biodiversity goals to the delivery of ecosystem services and the adaptation to urban conditions.

Fortunately, research on urban grassland restoration is increasing [46]. However, attributes and responses of urban grasslands submitted to restorative action are scarcely studied, and the potential to deliver essential ecosystem services, i.e., water infiltration, C storage, erosion control, etc., is poorly understood. These knowledge gaps about the design of urban grasslands under conditions of global change are addressed by this doctoral thesis.

1. The role of resident grassland communities, recently sown, in **reducing neophyte invasiveness** when interplaying with extreme weather events. Although increasing evidence on invasion patterns explains invasion success [106], to what degree biotic and abiotic constraints control the success of invasive species in grasslands is still poorly understood.
2. A fundamental role of urban grasslands is **multifunctionality** as a strategy to improve conservation values and support adaptation and resilience to climate change. With modest improvements in studies on urban ecosystem functionality [15,46,65], the question remains how designed grassland habitats with particular community compositions may function under climate change.
3. Although ecosystem responses to climate change significantly focus on the aboveground compartment, **belowground responses** remain obscure. Moreover, because of the particular conditions under which many urban grasslands establish, belowground responses can explain what community compositions and how these adjust to climate change conditions. Hence, species selection and community composition adaptation can be refined for more resilient urban grasslands.

The possibility of addressing the rehabilitation of urban grasslands and the properties that explain their response to common global change drivers is needed for planning and designing measures for better implementation of urban grasslands in UGI. Even though there are increased attempts to describe and understand the functioning of urban grasslands that contribute to biodiversity conservation and delivery of services in urban areas, a combination of challenges has rarely been studied. Integrating experimental and practical evidence must be based on an in-depth approach to, at times, unfeasible experiments offering insights into the practice of urban grassland rehabilitation.

Experiments in controlled environments to understand urban grasslands under climate change

A better understanding of the processes underpinning ecosystem functions and services and their possible alterations under climate change is necessary for developing management strategies aiming at innovation, mitigation, and adaptation of UGI [107]. Thus, studying ecosystems needs to combine multiple approaches to address questions of relevance for the future of ecosystems under increasing global-change inertia.

Controlled Environmental Facilities (sensu [108], with exemplary facilities therein) constitute an innovative tool that enables the simulation of environmental conditions with high precision and control, disentangling their influence on various ecosystems and revealing mechanisms of ecosystem response. The outcomes of experiments stemming from these facilities are a valuable input for parametrizing models of ecosystem- or global-based responses to environmental change [109,110] and for advancing experimental testing and theory development [107,108]. Multiple facilities with high-technology improvements, high fidelity, and control in simulating various environmental conditions susceptible to constant and automated monitoring have recently been established [108]. These facilities, broadly known as 'ecotrons', are replicated enclosures of variable dimensions that allow hosting samples of various ecosystems and in which one can simulate above- and belowground conditions (see TUM*mesa* in Materials and Methods). Moreover, the facilities enable the recording of energy and matter fluxes that support understanding various ecosystem functions.

Ecotron facilities help conduct experiments and deploy multiple advantages but are not free of trade-offs, whereby the missing complexity of natural systems may be the most important one [108,111]. Nonetheless, modern ecotrons circumvent some trade-offs via features that set them apart from traditional growth chambers, for example, by enabling the use of relatively large ecosystem samples (i.e., mesocosms) in rather large spaces. Moreover, the capacity to simulate a wide range of environmental conditions increases the abiotic complexity achieved in ecotrons with high accuracy and precision. Employing such control of crucial variables, climate-change experiments can reach projected ranges of environmental change [99,112], allowing for valuable predictions of ecosystem responses and the possibility of uncovering mechanisms of interest and understanding initial responses of ecosystems. Notably, the high level of control achieved in ecotrons allows for disentangling ecological effects from co-varying factors [108], and conducting multifactorial experiments that may produce different results from those of single-factor simulations [93]. At the same time, sampling the experimental units (soil, plants, animals, leachates, etc.) for analyzing particular functions and responses remains an activity of research teams guided by specific questions.

In ecotrons, research on specific ecosystem responses of (urban) grasslands is feasible because the stature of plants allows the manipulation of entire communities without compromising the realism of their vertical structure within the facilities [108]. Moreover, climate-change experiments in these facilities solve viability issues because field studies in actual urban settings are challenging. The lack of sufficient space, permits for using public space, vandalism, and safety concerns make it difficult to carefully assess environmental drivers or responses, for example, at the belowground level. Therefore, addressing the role of biodiversity in ecosystem functioning of urban grasslands *ex-situ* is often the only way to study some variables that are difficult to test in the field. If combined or complemented with results from other approaches based on field observations or common garden experiments, results can be even more enlightening and increase the external validity of the results [111].

OBJECTIVES AND OUTLINE

This thesis aims to investigate the drivers of global change on urban grasslands and identify the biotic properties that improve their performance under different biotic and abiotic stressors. In particular, the objectives are:

1. To determine the magnitude of changes affecting the **resistance of recently sown urban grasslands against invasive alien species**;
2. To understand the **effect of climate change on the functioning** of urban grasslands; and,
3. To evaluate the **belowground responses of urban grasslands** to climate change and to identify responsive compartments that adapt to change.

This dissertation is based on a strategic series of ecotron experiments in which experimental grassland communities were submitted to highly controlled environmental conditions to disentangle components of current global change. I centered the study of global change on designed urban grasslands for Central Europe to improve UGI. Ecological criteria include using native plants produced regionally and targeting ecological functions related to urban ecosystem services that gain relevance under the effects of climate change.

To achieve these objectives, I conducted three experiments under controlled conditions to test the selected ecological issues prioritized and reflected in this cumulative thesis (Publications 1–3). In the general introduction to the topic, I present the current state of knowledge on urban ecosystems and their risk and challenges under global change. Further, the materials and methods offer a general overview of the research describing the experimental setups and measurements. The summary of each publication highlights specific findings answering questions of biotic resistance, ecosystem functioning, and community responses under the pressure of global change factors, i.e., invasive alien species, eutrophication, and climate change. An overarching discussion brings the findings of the complete doctoral project into focus. I contrast the current literature on climate-change effects on grasslands, specifically in an urban context, with the results of the three publications. Moreover, I discuss what aspects need ecological theory to improve urban grassland design and rehabilitation as a strategy for biodiversity conservation and climate change adaptation and finishes with concluding remarks from both a scientific and a practical perspective (Figure 3).

Publication 1 [113] focuses on the impact of biotic (native biotic resistance and propagule pressure of alien species) and abiotic (N-fertilization, heat waves, and floodings) factors on the invasibility of recently sown native grasslands. Direct and indirect effects of the drivers of invasibility on the native grasslands were assessed. In **Publication 2** [114], the impact of the 'worst-case' climate change scenario (encompassing elevated [CO_2] and temperature) and decreased summer precipitation on the multifunctionality of engineered grasslands for urban roadsides was tested. Moreover, the influence of functional composition in modulating the responses was tested by controlling the proportion of grasses and forbs in the experimental grasslands. **Publication 3** [115] deals specifically with the belowground responses of urban grasslands to climate change scenarios and precipitation changes. By focusing the analyses on biomass allocation in the community and absorptive root traits, the objective was to understand early responses to climate change that help predict ecosystem feedback and highlight the results as input for more accurate modeling and practice of urban grassland rehabilitation.

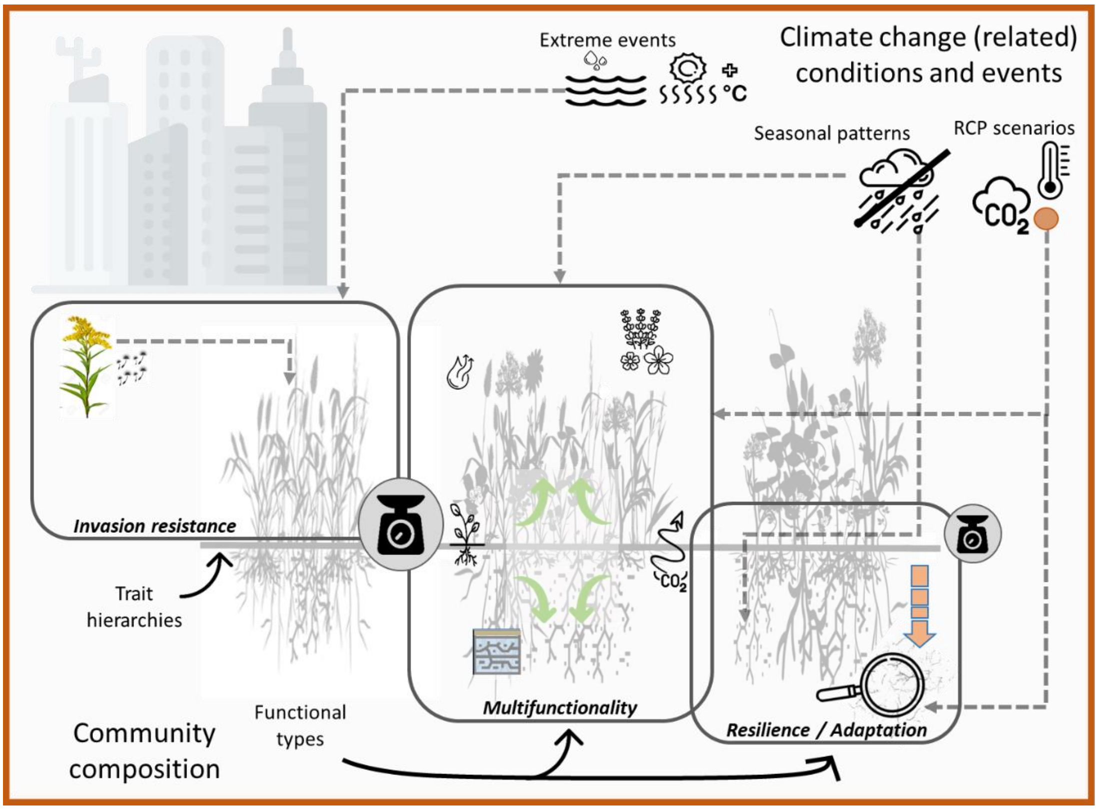

Figure 3. Graphic overview of the dissertation based on three publications drawing upon global change aspects studied in a controlled environment to understand their effects on different attributes of grasslands intended to deliver multiple benefits in urban contexts. This figure has been designed using images from Flaticon.com and Phylopic.org

MATERIALS AND METHODS

Greenhouse and ecotron experiments

The data for the publications presented in this thesis were collected from experiments conducted in the GHL Dürnast (Greenhouse Laboratory Center) and the ecotron facility of TUM*mesa* (Model EcoSystem Analyser) of the TUM PTC (Plant Technology Centre) located in Freising, Germany. Current vs. climate-change conditions adjusted for Central Europe were simulated in all experiments.

The greenhouse experiment included in **Publication 1**, testing for the effects of spatial sowing patterns, nutrient input, and community composition on the invasibility of engineered grasslands, took place in the GHL Dürnast (Figure 4). The facility allows reasonable control of light period and temperature. Trays (48 x 33 x 6 cm^3; 0.16 m^2) were located on floodable tables to establish the mesocosms.

Figure 4. TUM Greenhouse Laboratory Center Dürnast. One of the experiments supporting Publication 1 was conducted in this facility to study the response of grassland communities to the invasion of *Solidago gigantea*. Photo credits: (a) www.ghl.wzw.tum.de; (b) Andrea Frank & Johannes Prifling.

Furthermore, the second and third experiments described in **Publication 1** and the experimental setup supporting **Publications 2** and **3** were conducted in TUMmesa (Figure 5). This ecotron facility supports process-based ecological research in model ecosystems with high controllability. The chamber lighting consists of a LED-based system, allowing flicker-free illumination and PAR control. The achieved conditions within each ecotron unit produce minimal vibrations, noise, and air turbulence that could disturb any experiments. Moreover, a high-precision manipulation of individual environmental conditions such as [CO_2] and [O_3], as well as light intensity, temperature, and relative humidity, enable a reliable simulation of the conditions of interest for research. In TUM*mesa*, up to four walk-in chambers (2.4 x 3.2 x 2.2 m^3; area 7.7 m^2) and floodable plant tables were used with mesocosm of variable sizes according to each experimental design (see *Study Design*). The focus of the ecotron experiments was on the effects of extreme weather events (heat waves and floods) or climate-change scenarios on the invasibility (Publication 1), functionality (Publication 2), and belowground responses (Publication 3) of model grasslands.

4000K Warmweiß 100,0 %
6500K Kaltweiß 100,0 %
430nm Violett 100,0 %
475/490nm Blau 100,0 %
530nm Grün 100,0 %
630nm Orange 100,0 %
660nm Rot 100,0 %
730nm Infrarot 100,0 %
365/385/405nm UV A 100,0 %
325nm UV B 0,0 %
Gradient positiv 0,01 %/s
Gradient negativ 0,01 %/s
Lichtmessung:
PAR 616,32 µmol/m²s
UV 0,09 W/m²

Mischer LED
Mischer 25,51 %
Istwert +16,41 °C
Sollwert +16,61 °C
Pumpe LED

Platte 3 +23,29 °C
Platte 6 +22,39 °C
Platte 2 +24,00 °C
Platte 5 +23,34 °C
Platte 1 +22,36 °C
Platte 4 +24,54 °C
Fußbodentemperatur +24,42 °C

Figure 5. Ecotron facility TUM*mesa* used for experiments under controlled conditions. (a) Building of the ecotron, (b) main hall of the facility with eight walk-in climate chambers, (c) entrance window of one of the chambers containing mesocosms used in a previous experimental study conducted in 2018, and (d) a screenshot of the control panel located in front of each chamber. Photo credits: www.tummesa.wzw.tum.de/.

Study system

This thesis focuses on engineered grasslands of Central Europe. The model novel ecosystems were explicitly designed for urban settings [11], where anthropogenic influence hinders the establishment of strict near-natural grasslands. Therefore, I call the study system an 'engineered grassland.' Although it does not reflect natural or semi-natural grasslands, the overarching criteria for selecting the species of the studied engineered grasslands were that the species are native to Central Europe, and the seed material was of regional origin.

In total, 33 plant species were used for the experiments (Table 1). Further selection criteria followed specific requirements of the respective research aims outlined in each publication, e.g., documented competitiveness of the species (Publication 1), importance for urban pollinators of the region within and around Munich, Germany, flowering phenology, functional and phylogenetic diversity, and frequency in urban areas (Publications 2 and 3). I selected *Solidago gigantea* Aiton as a model species to test the invasibility of designed grasslands. It is a common invasive species in Central Europe, often used as ornamental in gardening and widely spread in urban and semi-natural areas in Europe [116]. All seed material used for composing the experimental grasslands was supplied by a regional seed producer based on local provenances (Johan Krimmer, Pulling, Germany) matching zone 16, corresponding to the area of the Munich Plane. The seeds of the invasive species used for the experiments in Publication 1 were collected in the surroundings of Freising, specifically in the riparian area of the river Isar (48°23’57’’ N, 11°45’16’’ E).

Experimental design

Publication 1

Greenhouse experiment 1: A greenhouse experiment was conducted to test the effect of competitive hierarchies in the native community, spatial sowing patterns, and soil nitrogen status on the recently sown grassland's invasibility by *S. gigantea* in a fully-factorial design. Mesocosm grasslands were established in trays (48 x 33 x 6 cm^3 [L x W x H]; 0.16 m^2). Two grassland types were sown, and the invasive species was concurrently added. The biomass of the native community and the invasive species harvested at the end of the experiment was taken as the response variable and assumed as a proxy of the community’s biotic resistance and invasion success, respectively.

Ecotron experiment 1: As mentioned above, grasslands with contrasting competitiveness based on trait hierarchies were exposed to extreme weather events related to climate change. The effect of interspersed heat waves and floods with a duration of 48 h each on the invasibility of grasslands with contrasting competitive ability was tested for 11 weeks. By the end of the experiment, the aboveground biomass of the native community and the alien invasive was harvested, oven-dried, and used for modeling invasibility as a response to biotic resistance through trait hierarchies, heat waves, and floods. A second ecotron experiment used the same two grassland compositions (low-competitive and high-competitive dominance) and submitted them to interspersed heat haves and floods in a 17-week timeframe. In addition, the propagule pressure of the invasive species was manipulated to test the effect of the number of introduction events and the density of added seeds. The final dry aboveground biomass of the native community and invasive alien species was collected for data analyses.

Table 1. Attributes of the study species selected for the experiments. Species used for the experiments constituting the three publications, and the key traits considered for species selection. Ecological Indicator Values [EIV] by [117] for moisture (1 very dry to 9 wet), reaction [pH] (1 strongly acidic to 9 alkaline and calcareous), nitrogen [N] (1 poorest to 9 very high nitrogen concentration), light (1 full shadow to 9 full sun exposition), temperature [Temp] (1 cold to 9 warm indicator), and salt (range from 0 not tolerant to 9 hypersaline soil tolerance). Plant height (m), SLA (specific leaf area; $mm^2 \cdot mg^{-1}$), SM (seed mass; mg) are mean values recorded for the species [118]. Flowering months of the year, flower color, and pollen vectors [119]. In EIV, X represents indifferent behavior, ~ represents variable behavior with immediately surrounding levels. Nomenclature from WFO (World Flora Online), http://www.worldfloraonline.org. Accessed on: 16 Feb 2023

Publication	Species	Family	EIV						Height	SLA	SM	Flowering month	Flower color	Pollen vector
			Moist	pH	N	Light	Temp	Salt						
2, 3	*Daucus carota* L.	Apiaceae	4	x	4	8	6	0	0.70	17.00	0.98	Jun–Sep	white	beetles, flies, syrphids, wasps, medium-tongued bees
2, 3	*Pastinaca sativa* L.	Apiaceae	4	8	5	8	6	0	0.81	18.58	3.71	Jul–Sep	yellow	
2, 3	*Achillea millefolium* L.	Asteraceae	4	x	5	8	x	1	0.36	13.53	0.19	Jun–Oct	white	bees, bumble bees, wasps, bombylides, syrphids
2, 3	*Centaurea jacea* L.	Asteraceae	x	x	x	7	x	0	0.50	19.06	1.61	Jun–Nov	purple	
2, 3	*Centaurea scabiosa* L.	Asteraceae	3	8	4	7	x	0	0.60	14.67	8.15	Jul–Aug	purple	
2, 3	*Cichorium intybus* L.	Asteraceae	4	8	5	9	6	0	0.75	25.12	2.57	Jul–Oct	blue	
2, 3	*Crepis biennis* L.	Asteraceae	6	6	5	7	5	0	0.75	27.39	1.16	May–Aug	yellow	
2, 3	*Centaurea cyanus L.*	Asteraceae	x	x	x	7	6	0	0.55	31.40	4.13	Jun–Oct	blue	
2, 3	*Pentanema salicinum* (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort.	Asteraceae	6~	9	3	8	6	1	0.46	26.67	0.33	Jun–Oct	yellow	
2, 3	*Pentanema hirtum* (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort.	Asteracee	3	8	3	7	6	0	0.34	19.48	0.78	Jun–Jul	yellow	
2, 3	*Echium vulgare* L.	Boraginaceae	4	8	4	9	6	0	0.51	14.45	2.80	May–Jul	pink	hymenopterans
2, 3	*Berteroa incana* (L.) DC.	Brassicaceae	3	6	4	9	6	0	0.37	19.46	0.54	Jun–Oct	white	syrphids, bees
2, 3	*Campanula rapunculoides* L.	Campanulaceae	4	7	4	6	6	0	0.70	38.17	0.15	Jun–Sep	violet	bees
2, 3	*Scabiosa columbaria* L.	Caprifoliaceae	3	8	3	8	5	0	0.40	19.33	1.87	Jul–Nov	blue	bees, bumble bees, wasps, bombylides, syrphids

Publication	Species	Family	EIV						Height	SLA	SM	Flowering month	Flower color	Pollen vector
			Moist	pH	N	Light	Temp	Salt						
2, 3	*Silene noctiflora* L.	Caryophyllaceae							0.35	21.90	1.04	Jun–Sep	pink	moths
2, 3	*Anthyllis vulneraria L.*	Fabaceae	3	7	2	8	6	0	0.27	15.28	2.45	May–Aug	yellow	hymenopterans
2, 3	*Lathyrus pratensis* L.	Fabaceae	6	7	6	7	5	0	0.58	25.80	12.13	Jun–Aug	yellow	hymenopterans
2, 3	*Lotus corniculatus* L.	Fabaceae	4	7	3	7	x	0	0.31	18.20	1.24	Jun–Aug	yellow	bees
2, 3	*Medicago falcata* L.	Fabaceae	3	9	3	8	6	0	0.63	20.50	2.03	Jun–Sep	yellow	hymenopterans
2, 3	*Trifolium medium* L.	Fabaceae	4	6	3	7	6	0	0.43	20.16	2.04	Jun–Aug	red	hymenopterans
2, 3	*Origanum vulgare* L.	Lamiaceae	3	8	3	7	x	0	0.48	26.70	0.10	Jul–Sep	purple	bees, bumble bees, wasps, bombylides, syrphids
2, 3	*Salvia pratensis* L.	Lamiaceae	3	8	4	8	6	0	0.62	22.55	2.13	May–Aug	blue	bumble bees
2, 3	*Thymus pulegioides* L.	Lamiaceae	4	x	1	8	x	0	0.20	22.56	0.12	Jun–Oct	purple	bees, bumble bees, wasps, bombylides, syrphids
2, 3	*Malva moschata* L.	Malvaceae	4	7	4	8	6	0	0.52	20.03	2.30	Jun–Oct	pink	
2, 3	*Papaver rhoeas* L.	Papaveraceae	5	6	7	6	6	0	0.45	25.09	0.13	May–Jul	red	short-tongued bees, syrphids, flies, beetles
2, 3	*Delphinium consolida* L.	Ranunculaceae	4	8	5	6	7	0	0.21	24.86	1.27	May–Aug	blue	bumble bees
2, 3	*Lolium perenne* L.	Poaceae	5	7	7	8	6	0	0.44	26.97	1.89	May–Oct	-	Wind
2, 3	*Poa pratensis* L.	Poaceae	5	x	6	6	x	0	0.39	19.03	0.23	May–Jun	-	
1, 2, 3	*Dactylis glomerata* L.	Poaceae	5	x	6	7	x	0	0.57	23.68	0.89	May–Jul	-	
1, 2, 3	*Festuca rubra* L.	Poaceae	6	6	x	x	x	0	0.44	13.97	0.99	Jun–Jul	-	
1	*Festuca ovina* L.	Poaceae	x	3	1	7	x	0	0.24	22.55	0.57	May–Aug	-	
1	*Arrhenatherum elatius* (L.) P.Beauv. ex J.Presl & C.Presl	Poaceae	x	7	7	8	5	0	0.99	29.51	2.49	Jun–Oct	-	

Publication 2

Ecotron experiment 2: Grassland-like communities designed for urban road verges were established and tested in mesocosms (Figure 6). Four community compositions based on the manipulation of forbs vs. grasses were sown in 70 x 40 x 22.5 cm^3 (L x W x H) trays. Climate-change scenarios RCP2.6 and RCP8.5, resembling current (1980–2019) vs. worst-case conditions (2100), were applied over six weeks. Moreover, precipitation was controlled to represent average current values of seasonal rainfall vs. reduced early-summer precipitation (-50%). Eight indicator variables of grassland functioning were measured, i.e., above- and belowground biomass, vegetation cover and height, flower density, water retention and loss via evapotranspiration, and soil respiration. Single functions were assessed, and two multifunctionality approaches were calculated.

Publication 3

Ecotron experiment 2: Based on the abovementioned experiment, belowground responses to climate change were studied by analyzing biomass allocation and the response of absorptive root traits. Besides measuring biomass allocation and the ratio between above- and belowground biomass, four morphological root traits were measured following standardized procedures: root diameter, root tissue density, specific root length, and root length density. The effect of climate change components and the functional composition of the experimental grassland were tested as predictors of belowground responses.

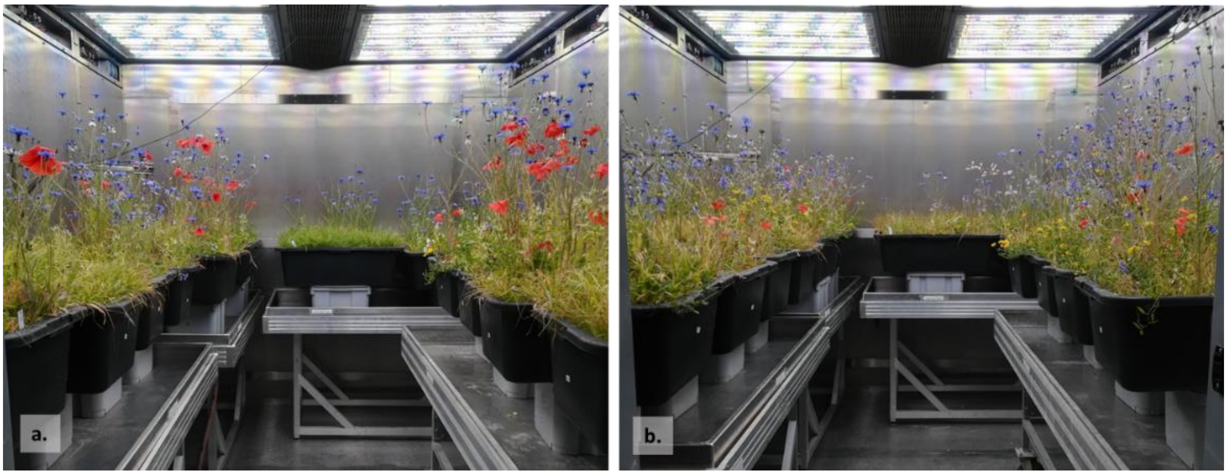

Figure 6. Walk-in chambers of TUM*mesa* ecotron with mesocosm grasslands used for Publications 2 and 3. Communities with four functional compositions were subjected to two climate scenarios (a, RCP2.6; b, RCP8.5). Temperature and [CO_2] were manipulated in each chamber, while simulated precipitation (normal vs. reduced) was randomized for each table containing four experimental communities.

Data sampling

Performance of native communities in resistance to invasion and invasion success

Invasion resistance of native communities was measured as biomass production (Publication 1). Biomass was determined by harvesting all aboveground plant parts at the end of the experiment by clipping above 1 cm of the soil level. Harvested material was oven-dried at 65 °C for 48–72 h before weighing. Likewise, the harvested aboveground biomass of the invasive species was oven-dried, weighted, and assumed as a proxy for invasion success.

Ecosystem functioning of experimental urban grasslands

After 10 weeks of establishment, measurements were taken in the mesocosms to evaluate indicators of single functions of engineered urban grassland and then calculate multifunctionality following two approaches (see [62]). Biomass production was determined at the end of the experiment by harvesting aboveground biomass, as described in the previous section. Belowground biomass was collected by sampling two cores per mesocosm (total depth 15 cm) with a soil corer of 8 cm diameter. Each soil core was split into two depths and processed separately. The sub-cores were washed using a set of sieves to separate the roots from the soil. The resulting root material was oven-dried at 60 °C for 72 h. Floral production was estimated on the 43rd day of grassland development. All mature floral buds and open floral units (sensu [120]) were counted in each mesocosm. Vegetation cover was visually estimated for the mesocosm's total area (0.21 m^2) and expressed in percentage. Vegetation height was calculated based on the average of six random height measurements with a pocket rule within each mesocosm.

Soil respiration rate was measured in four sampling rounds during the 10th week of the experiment in a vegetation-free portion of each mesocosm with an environmental gas Analyzer for CO_2 (EGM-4. PP Systems) and a cylindrical PVC chamber (height = 150 mm, diameter = 100 mm). The resulting soil respiration measurements per mesocosm were averaged to include a unique mean value in the analyses. Water retention and loss were measured following a water-and-weight protocol [121]. In the 9th week, each mesocosm was weighted (T1), and then 15 L of water was added to simulate a heavy rain event. One hour after watering, the mesocosms were weighed again (T2), and the difference between them was considered as the amount of water captured (Capture = T2 − T1). The mesocosms were weighed again after 24 h (T3), resulting in the amount of water lost (Loss = T2 − T3). Water lost by T3 after T2 was assumed to be evapotranspiration.

Absorptive root traits of experimental urban grasslands

The belowground cores obtained from the mesocosm experiment mentioned in the previous section were split into two soil depths (0–6 and 6–15 cm) and processed independently. Cleaned roots were used to measure morphological traits. Before oven-drying the root samples, a representative subsample per core and depth was dyed with toluene blue, rinsed, and spread over an acrylic tray partially filled with water to obtain high-resolution images in an EPSON V700 Photo scanner. Afterward, the images were processed with the software WinRHIZO (Pro STD4800, Regent Instruments) to get the following traits: root diameter (mm), root tissue density ($g \cdot cm^{-3}$), specific root length ($m \cdot g^{-1}$), and root length density ($cm \cdot cm^{-3}$).

Analytical tools

All data processing and analyses were conducted in R Versions 3.5.3 and 4.1.2 [122]. For statistical analyses, linear or linear mixed models were built, depending on the nature of the experimental design and the suitability of the analyses for the data structure. Furthermore, structural equation models were employed to conduct path analyses to disentangle the direct and indirect effects of the explanatory variables on the community responses (Publication 1). Data transformation (e.g., log-transformation and scaling of response and explanatory variables, respectively) was done whenever needed for improved calculations and adjustment to model assumptions. Model appropriateness was tested in all cases. Post-hoc analyses and model simplification were done when appropriate (Publications 2 and 3).

SUMMARY OF PUBLICATIONS

This thesis is based on three original research contributions to international, peer-reviewed journals. Hereunder, I present the publication status, the contribution of the participating authors, a graphical abstract, and a concise summary of each publication.

PUBLICATION 1: Competitive trait hierarchies of native communities and invasive propagule pressure as determinants of invasion success during grassland establishment

Rojas-Botero, S., Kollmann, J., Teixeira, L.H. (2022). Competitive trait hierarchies of native communities and invasive propagule pressure consistently predict invasion success during grassland establishment. *Biological Invasions* 24: 107-122. https://doi.org/10.1007/s10530-021-02630-4.

Author contributions: LHT and JK conceived and designed the experiments; **SR-B** and LHT conducted the experiments; **SR-B** and LHT collected, analyzed, and interpreted the data; **SR-B** and LHT led the writing and editing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Graphical abstract

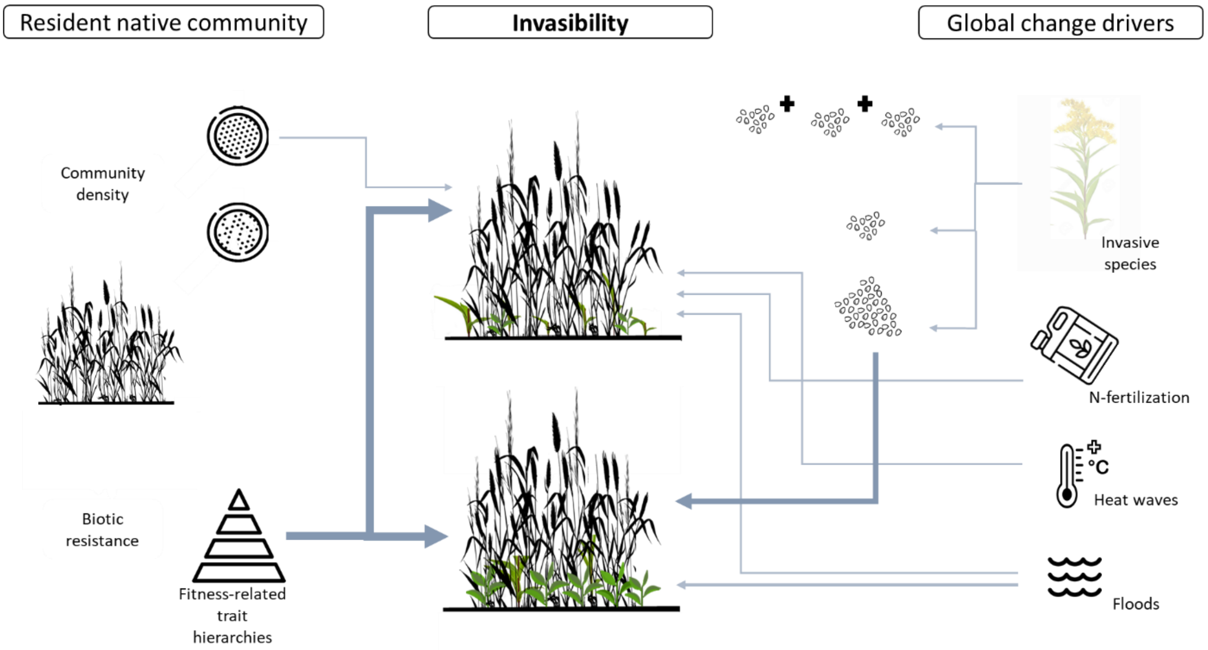

Figure 7. Graphical abstract of Publication 1 showing environmental and biotic aspects affecting the invasibility of recently sown grasslands, studied using greenhouse and ecotron experiments. Thick lines portray the most relevant drivers. This figure has been designed using images from Flaticon.com and Phylopic.org

Summary of Publication 1

Publication 1 underlines the challenging role of invasive plant species in the rehabilitation of grasslands, primarily when such rehabilitation is based on mixture-sowing onto prepared soil. In the paper, the ability of a resident native community to reduce invasibility is addressed from the hypothesis of hierarchies of fitness-related traits of the species and community density as drivers of biotic resistance. Conversely, invasiveness was studied as a function of the propagule pressure of the invader species. Furthermore, environmental fluctuations such as eutrophication, floods, and extreme temperatures were identified as drivers of invasibility.

One greenhouse and two ecotron experiments were conducted to test what biotic and abiotic factors determine the successful establishment of invasive species in a recently sown grassland system. Two grassland communities with five native grass species, but designed with contrasting abundances, were sown and submitted to environmental fluctuations (N-fertilization, heat waves, and floods). Additionally, seeds of the invasive species *Solidago gigantea* were introduced with varying densities and frequency. The biomass of the invasive species and the native community were assumed as proxies for invasion and restoration success, respectively. Direct and indirect effects of the biotic and abiotic drivers were tested to understand their contribution to invasibility.

Biotic resistance resulting from competitive trait hierarchies was a consistent driver of biotic resistance across experiments, and grasslands dominated by highly competitive species were more resistant to *S. gigantea*. Similarly, clumped seeding patterns in grasslands increased biotic resistance and thus decreased the invader's biomass. A high density of *S. gigantea* seeds reaching the grasslands early in the assembly process increased invasion success and revealed the importance of priority effects. Environmental fluctuations had positive, neutral, or adverse effects on invasibility and underlined a context-dependence impact on invasion success.

Based on these results, the crucial role of biotic resistance derived from the trait composition in a community highlights the importance of trait selection when designing grassland mixtures and the control of invasive species in rehabilitation projects, particularly in the early stages of grassland establishment.

PUBLICATION 2: Low precipitation consistently reduces multifunctionality of urban grasslands

Rojas-Botero, S., Teixeira, L.H., Kollmann, J. (2023). Low precipitation due to climate change consistently reduces multifunctionality of urban grasslands in mesocosms. *PLOS ONE* 18(2): e0275044. https://doi.org/10.1371/journal.pone.0275044

Author contributions: **SR-B**, LHT, and JK conceived the ideas and designed the methodology; **SR-B** and LHT collected the data; **SR-B** and LHT analyzed the data; **SR-B** led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Graphical abstract

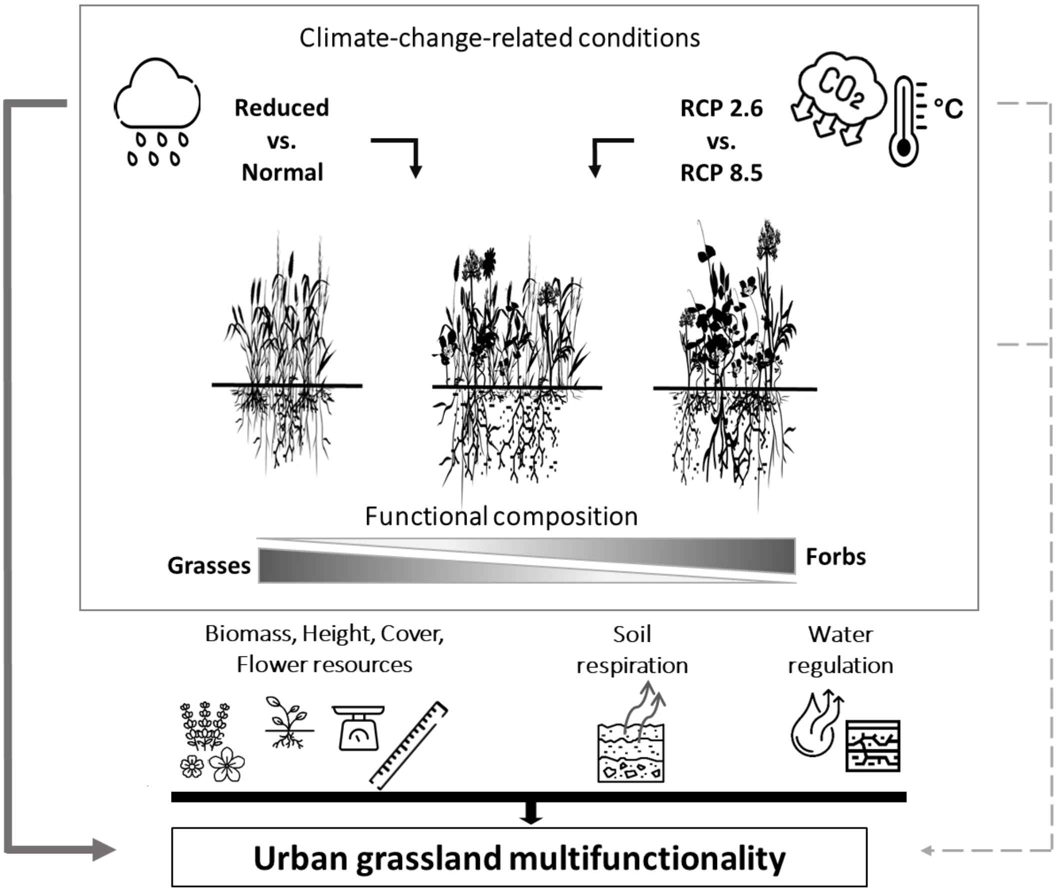

Figure 8. Graphical abstract of Publication 2 showing the aspects of grassland functioning investigated in an ecotron experiment with simulated climate change scenarios. Thick lines portray the most consistent drivers of ecosystem functions. This figure has been designed using images from Flaticon.com and Phylopic.org

Summary of Publication 2

This publication focuses on assessing young grassland multifunctionality, considering the sowing of native-species-based mixtures of grasslands designed for delivering multiple services on urban roadsides and their responses to climate-change-related environmental conditions.

Two climate change IPCC scenarios representing the ‘Paris Agreement’ vs. ‘worst case’ (RCP2.6 vs. RCP8.5) were simulated by jointly manipulating [CO_2] and temperature scenarios for climate change. Additionally, the experiment manipulated precipitation to simulate average vs. -50% seasonal rainfall. Also, the functional composition of the grassland mixtures was controlled for varying proportions of grasses vs. forbs to test its mediation of climate change effects on individual functions and multifunctionality. Eight indicator variables of above- and belowground ecosystem functions mainly related to productivity and water regulation were measured, and two multifunctionality indices were calculated.

Elevated [CO_2] and temperature increased carbon cycling via higher plant production (biomass, cover, height, flowers) and soil respiration. In turn, reduced precipitation negatively affected all grassland productivity indicators, while the communities' functional composition explained plant production indicators. Climate change and precipitation interactively affected water regulation since higher [CO_2] enhances plant water efficiency and reduces water loss. Thus, grasslands showed similar evapotranspiration (water circulation) under RCP8.5 regardless of the precipitation treatment, and higher water retention in soil was observed with reduced precipitation under RCP2.6. The two calculated multifunctional indices underscore the negative effect of decreased precipitation on grassland functioning, especially under RCP2.6. The analysis of single functions showed trade-offs in single functions being best performed by either grass-dominated (e.g., plant cover, belowground biomass) or forb-dominated grasslands (e.g., flower production, aboveground biomass).

The study highlights the importance of assessing the combined effects of climate-change-related variables on grassland functioning and the relevance of considering their functional composition when designing urban grasslands to promote biodiversity and climate change resilience in urban greening.

PUBLICATION 3: Root traits of grasslands rapidly respond to climate change, while community biomass mainly depends on functional composition

Rojas-Botero, S., Teixeira, L.H., Prucker, P., Kloska, V., Kollmann, J., Le Stradic, S. (2023). Root traits of grasslands rapidly respond to climate change, while community biomass mainly depends on functional composition. *Functional Ecology* 37(7): 1841-1855. https://doi.org/10.1111/1365-2435.14345

Author contributions: **SR-B**, LHT, JK, and SLS conceived the ideas and designed the methodology; **SR-B**, LHT, and SLS conducted the experiment; **SR-B**, PP, VK, LHT, and SLS collected the data; **SR-B** and PP analyzed the data; **SR-B** led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Graphical abstract

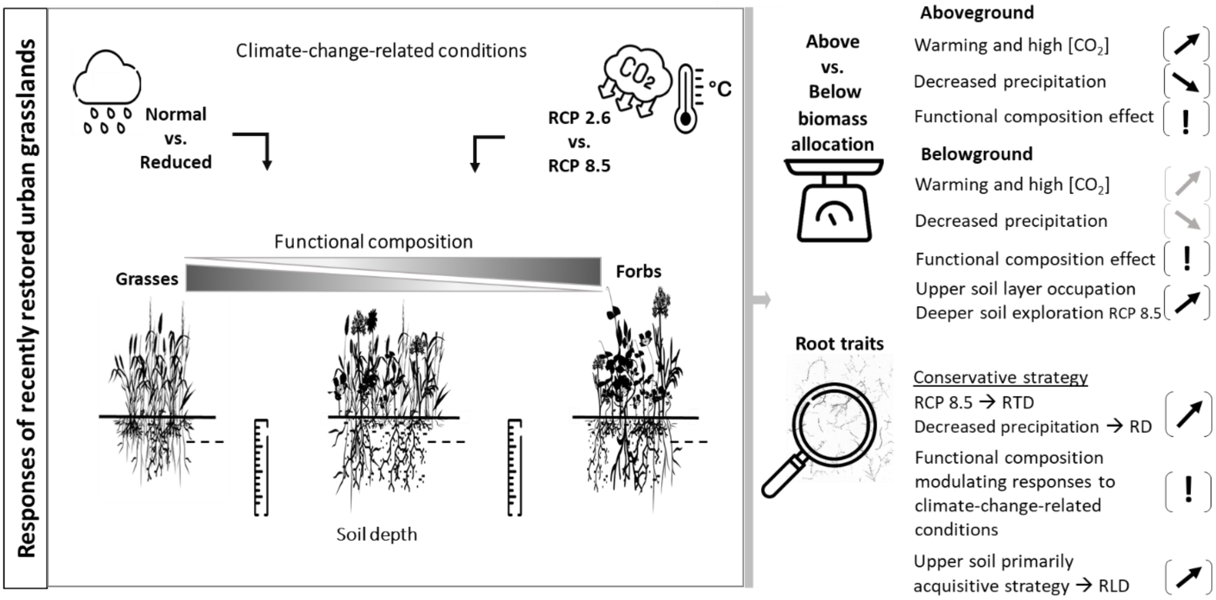

Figure 9. Graphical abstract of Publication 3 portraying the effects of simulated climate change scenarios, precipitation, and functional composition on grasslands' biomass allocation and root traits. Symbols in brackets summarize the results. This figure has been designed using images from Flaticon.com and Phylopic.org

Summary of Publication 3

In this study, I investigated the effect of climate-change-related conditions and functional composition on biomass allocation and the trait responses of fine roots of mesocosm grasslands established for testing their potential performance in urban road verges. The focus on roots lies in their importance for soil carbon allocation, resource acquisition, and the need to understand their responses to climate change.

In an ecotron experiment, I simulated two contrasting IPCC climate change scenarios (RCP 2.6 and 8.5) based on [CO_2] and temperature, and applied average vs. reduced seasonal precipitation of early summer. The effects of functional composition were assessed by varying the proportion of grasses and forbs in the mesocosm. I measured above- and belowground biomass, root diameter, root tissue density, specific root length, and root length density.

Aboveground biomass and root traits responded significantly from the early phase of establishing grasslands. Belowground grassland biomass tended to increase under simulated RCP8.5 scenario (i.e., higher temperature and [CO_2]) and to decrease under reduced precipitation. Notably, the functional composition of the grasslands was crucial for biomass allocation, with grass communities producing more belowground biomass than forb-dominated ones and the opposite pattern observed aboveground. It also modulated the responses of some root traits to climate change. A higher root diameter indicated a more conservative strategy under reduced precipitation, while elevated temperature and [CO_2] led to higher root tissue density. Moreover, root biomass mainly occupied the upper soil layer, while a warm and CO_2-enriched environment promoted root exploration in the lower soil layer. Nevertheless, grass-dominated communities quickly colonized all available soil volume, while forb-dominated communities remained clumped in the upper layer.

The results highlight that trait variation, instead of biomass allocation, reflected adjustments of young grasslands to climate change conditions. In turn, the grassland's functional composition is crucial for biomass allocation, reinforcing the importance of designing urban grasslands based on functional information to increase their resilience to climate change.

GENERAL DISCUSSION

Factors to be considered for the design of multifunctional urban grasslands

Rehabilitating or designing urban grasslands has increasingly followed ecological criteria beyond traditional approaches guided by aesthetics and cost-effective selection of species and techniques [11]. Recent calls for practices supported in the EU recognize the value of urban nature for protecting biodiversity and its connection to human well-being. Thus, the understanding of urban green infrastructure as a nature-based solution with high potential for achieving an array of objectives for sustainable urbanization, especially in times of enhanced effects of global change, reinforces the critical role of evidence-based design and management of urban grasslands and grassland-like habitats as pervasive elements of urban green infrastructure (UGI).

It is difficult to address multiple challenges in restoring or rehabilitating ecosystems in urban areas, where many intertwined factors are in play. Thus, there is a need to design appropriate studies to help understand ecological processes and derive relevant and applicable knowledge for urban greening planning and implementation. The studies presented in this thesis tackle significant challenges to which urban grasslands are subjected. For instance, the greenhouse and ecotron experiments presented in Publication 1 [113] provided insightful evidence of influencing factors underpinning the resistance of recently sown grasslands against broadly expanded IAS in urban areas. Moreover, Publication 2 [114] explored the drivers of multifunctionality in experimental urban grasslands under climate change conditions simulated in ecotrons. Finally, Publication 3 [115] presented the responses of belowground traits and community biomass allocation of model urban grasslands to climate change, and pointed out relevant aspects to consider for an informed selection of grassland composition (Figure 10).

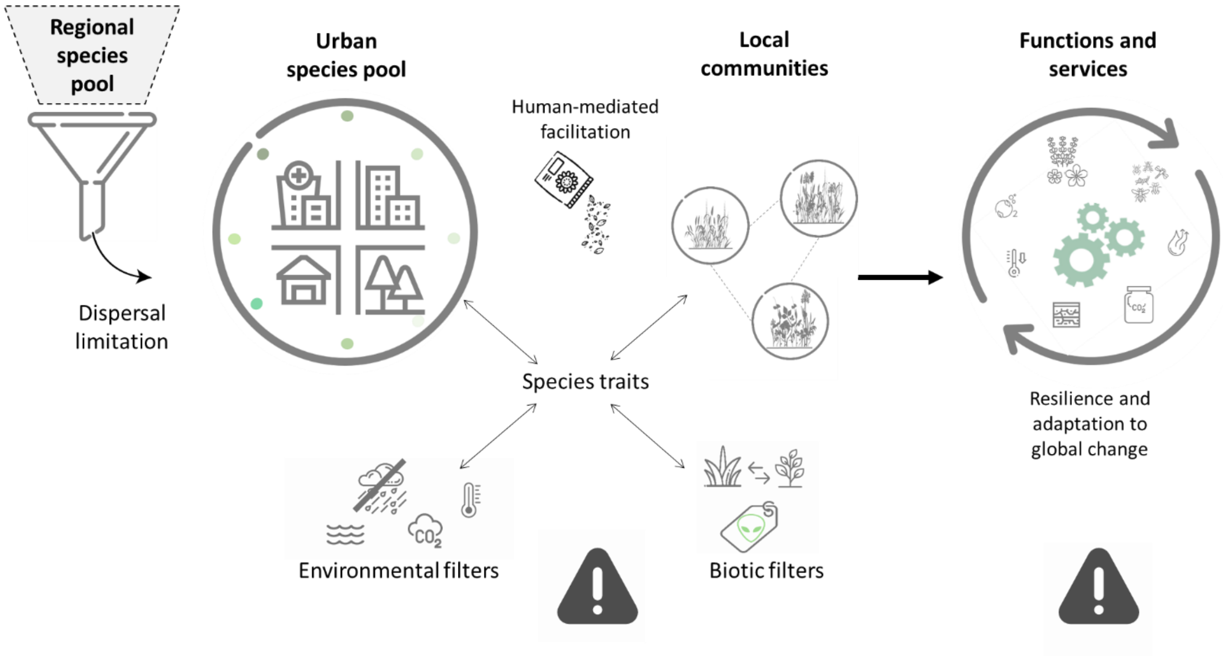

Figure 10. The rehabilitation of urban grasslands addresses key limitations for community assembly. This thesis presents insights into challenges for the rehabilitation of urban grasslands. Sowing seed mixtures of native species is the first step to overcoming dispersal limitation in urban grasslands. However, sown species are additionally subjected to environmental and biotic filters (e.g., climate change, N-fertilization, and competition with invasive species). These filters and the attributes of the plant communities, particularly functional composition, may determine whether the communities will resist invasion and environmental stress while performing ecological functions. The knowledge gained with the contributions presented here seeks to inform the practice of urban grassland design and enhance the multifunctionality and resilience of these ecosystems. This figure has been designed using images from Flaticon.com and Phylopic.org

Relevant aspects when rehabilitating urban grasslands with high invasion resistance

Because biological invasions disturb ecosystem processes and threaten native species diversity, reducing the impact of invasive species is crucial for accomplishing the desired goals of urban ecosystems. Therefore, a function of urban grasslands is biotic resistance to invasion, especially in the early phases of establishment, even under challenging environmental conditions [123]. Nonetheless, urban areas bear attributes that make them highly vulnerable to biological invasions and act as hubs for invasive species spreading in the surrounding regions.

It has been argued that environmental fluctuations may favor the dispersal and establishment of invasive alien species (IAS), which can cope with disturbances and use the excess resources faster than native plant communities (nutrients, water, light, etc.; [82,84,85,124]). Under a changing climate, urban areas experience enhanced environmental and resource fluctuations (heavy rain, nitrogen inputs), likely fostering invasion success in disturbed areas. Notwithstanding, the experiments with simulated floods and heat waves in Publication 1 [113] showed that these fluctuations do not have consistently favorable effects on the invasiveness of a model alien species common in urban areas (i.e., *Solidago gigantea*). Previous studies have shown that invasive species can benefit from environmental fluctuations [82]. Still, the effect on resident communities strongly depends on different aspects of the fluctuation (e.g., duration, magnitude, and frequency), invader identity [125,126], its adaptation to fluctuations [124], and interactions with the traits of the resident species [127].

While environmental fluctuations were context-dependent on their effects on invasion success, biotic resistance was a consistent determinant, and species attributes of natives and invasive species played a key role. On the one hand, across the conducted experiments, the resident communities had a consistent effect explaining the ability to resist the spread of invasive species during community assembly. Communities with a high abundance of species with greater competitive performance always performed best at decreasing invasive species establishment.

The experiments presented in Publication 1 [113] showed that a model community deploying traits allowing for enhanced fitness (e.g., canopy cover, height, biomass) increased the capacity to limit the establishment of invaders and thus positively correlated with invasion resistance [123]. On the other hand, the evidence provided also demonstrates the critical role of the propagule pressure of invasive species to determine their establishment success in recently sown grasslands. High propagule pressure, in this case, high densities of incoming seeds of IAS, enhances its ability to preempt or modify niches [128] and become over-dominant in assembling communities.

The biotic control highlights that resistance against IAS depends on functional traits and the identity of the native community, conferring advantageous characteristics [125,129], and enabling inhibitory mechanisms such as asymmetric competition and soil legacies [130]. The biotic resistance effect throughout the experiments of Publication 1 [113] also underscores the role of 'priority effects,' i.e., the capacity of a species to 'arrive first' and take advantage of favorable conditions during community assembly [131,132]. Sowing native mixtures and limiting the dispersion of propagules of invasive species in rehabilitating areas has proven to be a cost-effective strategy to hamper the dominance of invasive species [132–134]. The early arrival of native species or mixtures, even with a few days of difference (reviewed in [135]), combined with scarce or low-density arrivals of IAS, might be crucial to determining assembly outcomes and invasion success [113].

Although the exclusion of IAS in urban ecosystems may be unrealistic, rehabilitating urban grasslands should focus on species richness and identity and fitness-related traits [123], especially in areas with high pressure of IAS. As climate change becomes more conspicuous and hence extreme weather events increase in frequency, rehabilitating urban grasslands based on attributes of the native species in sowed mixtures provides extra insurance against invasions, regardless of potential environmental fluctuations. However, highly competitive species that could cope with IAS and limit their establishment, especially those with a high affinity for nutrients or eutrophic areas, can also limit the colonization of less competitive native species. Thus, management practices are necessary to allow or facilitate the enrichment of grassland communities, for instance, via adaptive management and 'phased introductions' of target species during grassland restoration [135–137], which may occur even several years after initial seeding [137]. An adaptive approach to grassland rehabilitation in invaded areas could aim at (i) promoting more resistant communities assembled in a critical point of grassland rehabilitation, thus decreasing the establishment of invasive neophytes taking advantage of recently disturbed areas (bare soil prepared during grassland rehabilitation); (ii) fostering the introduction of additional target species in additional interventions; and (iii) hampering the further establishment of IAS arriving in later points to an established grassland.

Rehabilitated urban grasslands to increase multifunctionality and settle functional trade-offs

Urban grasslands are subjected to human influence. While grassland communities may function as invasion barriers, a complex of other desired functions in urban areas, i.e., multifunctionality, might benefit from competitive species and taxonomic and functional diversity. Numerous multifunctionality studies have been conducted in semi-natural and agricultural grasslands, focusing on taxonomic diversity and, less often, on functional attributes of plant communities. The multifunctionality assessment presented in Publication 2 [114] considered the relative abundance of two coarse plant functional groups (grasses and forbs). It investigated to what degree the functional composition contributes to ecosystem functions of particular interest for UGI, considering the influence of climate change conditions. Publication 2 [114] used an ecotron experiment simulating the rehabilitation of urban grasslands for road verges under two contrasting climate change scenarios projected by IPCC (RCP2.6 and RCP8.5) [138]. In this case, soil conditions (substrate quality and depth) and plant species (according to specific goals) are closer to those occurring in current roadside grassland rehabilitation in central Europe [139]. Thus, insightful knowledge resulted from studying simulated climate change conditions on the multifunctionality of urban grasslands.

While a warmer and CO_2-enriched atmosphere has multiple effects on ecosystems and biogeochemical cycles, functions performed in recently rehabilitated urban grasslands could positively affect early growth. Productivity-related functions were enhanced in the early phases of rehabilitation due to CO_2

fertilization when there was no resource limitation (soil nutrients or water). In contrast, as experienced in atypical years with early summer precipitation scarcity [140], water stress reduced productivity-related functions (i.e., biomass, cover, height, and flower production). Similarly, the study suggests the ability of urban grasslands to circulate water to perform transpirational cooling functions might be compromised under precipitation scarcity. The reduced stomatal conductivity due to the higher availability of CO_2 also hampered water loss through transpiration [98,100], while the water is instead used for the further building of plant tissues or maintained in the soil. With less stomatal conductance under a climate change scenario like RCP8.5, water losses were not substantially different between reduced or average precipitation, and the communities released less water for transpiration cooling.

There is consensus that biodiversity effects on ecosystem multifunctionality are mediated by different parameters of the community's functional structure [8,141,142]. Furthermore, Publication 2 [114] underscores that the functional composition of the communities also mediated climate change effects on grassland multifunctionality. The study addressed a gap given the scarcity of studies on ecosystem multifunctionality under simulated climate change and that account for the role of functional composition. Previous scientific contributions studied single functions in ecotron or field experiments simulating climate change and controlling functional composition or focused mainly on soil multifunctionality. For instance, it has been found that soil multifunctionality in temperate grasslands under experimental climate change was driven by the functional diversity of the plant community [141], especially in the early stages of grassland rehabilitation [143]. Accurate assessments of climate change impacts on soil functionality must account for plant functional composition as it may counteract environmental effects [144] by exerting cascade effects on soil organisms and multifunctionality [145]. Publication 2 [114], adding to the currently available knowledge, focuses on a set of functions of relevance for urban grasslands.

Among the functional compositions presented in Publication 2 [114], trade-offs arose due to single functions performed best by one or another functional composition, while overall multifunctionality was highest in grasslands evenly composed of grasses and forbs (i.e., F50). This aspect suggests complementarity effects in grassland functioning in community F50. Even for functions best performed by only-grass (F0) or only-forb (F100) communities, F50 represented an effective way to outweigh the benefits of such compositions. For example, grasslands with an even composition of grasses and forbs depicted the highest ratio height:cover under climate change and performed best under precipitation scarcity. In equal proportions, the two functional groups are more beneficial in urban grasslands than forb-dominated seed mixtures, which may benefit pollinator promotion in urban areas, or grass-dominated mixtures, which are preferred for rapid coverage and soil stabilization. Considering previous findings on the drivers of grassland multifunctionality [146,147], one could argue it is not only species richness but functional composition pointing to niche partitioning and complementarity between functional groups (e.g., [148]) as a determinant factor in achieving higher ecosystem multifunctionality, even under the challenging conditions of climate change.

Even though invasion resistance was not explicitly investigated along with other functions in Publication 2 [114], there is abundant evidence, though not fully supported across studies, on the effect of diversity on invasion. Considering the findings of Publication 1 [114] underscoring the importance of fitness-related traits for invasion resistance, I suggest species-rich communities with balanced proportions of functional types may benefit bundles of functions as assessed in Publication 2 [114] and the resistance against IAS. Moreover, areas under high IAS pressure might be rehabilitated via approaches prioritizing competitive species, followed by secondary interventions and phased species introductions aiming at increasing diversity [137]. An insightful aspect arising from Publications 1 and 2 [113,114] is the possibility of rehabilitating urban grasslands, weighing certain ecosystem functions over others as required in urban contexts, e.g., high biodiversity over biomass productivity. Designing urban grasslands able to reach different outcomes of multifunctionality (sensu [32]) benefit from ecological knowledge by pondering restorative activities based on, e.g., species taxonomic or functional composition and traits, the role of priority effects and the possibility of fostering, at larger scales in the urban landscape, diverse ecosystem services bundles.

The role of urban grassland rehabilitation for adaptation to climate change

A critical point outlined in this dissertation is the consideration of the establishment and adaptation of grasslands to roadside conditions in urbanized areas. With the expectation that climate change will bear enhanced influence in cities, i.e., with even higher temperatures, increased inputs of CO_2, and a higher vulnerability to exceptionally dry growing seasons, there is a need to understand how young grassland communities adapt to such conditions. Plant productivity, measured as above- and belowground biomass production, has been a frequent object of study in grassland experiments, also in urban areas [15,65], and a variable responding to environmental change. While productivity-related functions can be controlled by manipulating the functional composition of urban grassland and grassland-like habitats, the question remains: what attributes may contribute to improving the adaptation to changing climate under climate change and the performance of ecosystem functions?

Since much of grassland biomass occurs belowground, and urban soils may have a crucial role in C storage [68], at least some morphological attributes of grassland roots may explain strategies for adaptation of communities to climate change and, ultimately, their functionality. Plant diversity influences belowground biological properties and processes [149–152] and resilience to conditions such as drought [143]. Moreover, taxonomic and functional type diversity fosters diversity of root traits, e.g., forbs have lower specific root length and root length density than grasses [153]. The presence of diverse trait values may lead to higher resistance and resilience to environmental stress [153–155], especially in the early stages of community establishment [140] by varying resource acquisition strategies and resource partitioning [156]. Additionally, root traits greatly influence soil physical properties of fundamental importance to soil function, including soil aggregate stability, saturated hydraulic conductivity, and water movement through soil layers [149,157,158]. Thus, it is critical to understand how belowground functional aspects of the communities perform and may explain the resilience of urban grasslands to climate change and harsh abiotic conditions in cities.

Publication 3 [115] investigated how different young grassland communities responded to simulated climate change in terms of biomass allocation and fine root traits. It was found that the functional composition of the communities was the main driver of biomass allocation. In contrast, climate change conditions, i.e., climate change scenario for temperature and [CO_2] and seasonal precipitation, played a secondary role, especially belowground. Under climate change, community root traits were better indicators of early adaptation to changes and pointed out possible consequences of such trait modification on the delivery of correlated ecosystem functions. For instance, water scarcity fostered higher values in the mean root diameter in grasslands to protect the hydraulic integrity of roots and, thereby, indirectly could likely affect, e.g., soil stability, which benefits from thin and abundant roots [149]. Similarly, elevated temperature and [CO_2] provoked increased mean values of root tissue density due to the increased availability of C to construct tissue and further develop roots in deeper soil layers. In contrast, reduced precipitation stimulated root production in the upper soil layers (high root length density), where water input from precipitation is rapidly captured. Since the functional composition also modulates the responses of functional traits to changing environmental conditions associated with climate change, Publication 3 [115] also underscores how grassland composition can offer opportunities to provide a range of complementary root traits to deliver different functions. The presence of grasses in designed mixtures seems to modify the direction of responses of root traits to climate change, suggesting that grasses largely determine the community response of root traits to climate change. In mixtures containing grasses and forbs, root production of particular grass species may be favored by becoming more abundant belowground [159]. Thus, grass roots partially drive the community traits under climate change. Functional composition controls biomass allocation, determines root traits, and modulates trait responses to climate change. Thus, functional aspects also become essential to designing urban grasslands and better predicting potential responses to climate change.

Moreover, an aspect worth mentioning in this experiment that assessed biomass production in the young communities, is the effect of soil nutrient status and age of the communities. The obtained enhanced biomass production responded to sufficient nutrient availability to support plant growth above- and belowground, given the young age of the communities and the starting characteristics of the prepared urban substrate for sowing communities. Given the shallow soil depth and the age of the plants, root length density was higher in upper soil layers, allowing for intense exploration of resources where perhaps the involvement of soil microbiota, e.g., arbuscular mycorrhiza, can become crucial to improve the provision of nutrients to plants (P uptake and transfer to the host plant). At the same time, N-fixing species in communities containing forbs can also increase nutrient availability in further phases of community development [160], overcoming nutrient limitations to community productivity. This implies that an additional avenue of research should include the study of mycorrhiza associations in urban soils, with their challenging characteristics, which could improve soil attributes and growth conditions of urban grassland communities [161]. In addition, the preparation of substrates with heterogeneous characteristics may increase the resilience of the belowground compartment of grasslands to the effects of climate change conditions.

Scalability of findings in a real-life context

It is often argued in the literature that experiments mimicking climate change should be very close to reality to contribute valuable information about the potential future fate of plant communities and ecosystems and that such studies still lack [107]. On the other hand, others posit that current summarized climate-change experiments are within projected changes in some variable ranges, e.g., temperature [99]. It has been highlighted that long-term and short-term variability, or extreme events, should be considered because the latter may be more important for community structure and ecosystem functioning [162]. This dissertation tackles both approaches, i.e., mimicking climate change, by simulating two projected scenarios, and extreme events. Moreover, the experiments considered interacting variables of climate change. There is evidence that extreme events are context-dependent, and various factors related to the extreme event may be necessary for the effects to be noticeable. The climate change simulation showed interactive effects of the environmental variables on multifunctionality. It demonstrated how the responses could be eventually modulated by the functional composition of the communities [163], thus improving the mechanistic understanding of climate change's influence on grassland communities. Notably, the responses obtained suggest potential complementary effects between the functional groups studied, affecting the capacity of urban grasslands to continue delivering bundles of benefits. Despite explicitly noting that some responses may change over time and acclimatization may cause the magnitude and direction of effects to change, these presented contributions offer a valuable overview of rehabilitated urban grasslands responses in the short term.

Furthermore, testing a comprehensive set of projected future conditions in combination with realistic field conditions is generally not feasible. I prioritized experiments that manipulated factors of ecological relevance most likely to change and be enhanced in urban areas and addressed full-factorial combinations of the tested variables. Additional human-mediated changes and disturbances were, therefore, out of the scope of the experiments but are arguably sources of variation in the responses. Nonetheless, the effect of rehabilitation measures on the functionality of urban grasslands and grassland-like vegetation via the sowing of species-rich seed mixtures remains valuable. This focus is also supported by studies on real urban grasslands, pointing out that enhanced plant diversity can increase the multifunctionality of urban soils and their role in mitigating the effects of climate change [15].

The feasibility of urban grassland rehabilitation may require secondary interventions, which, in turn, may increase rehabilitation costs [135]. A trade-off that arises from the publications presented is that assembling a resistant resident community against IAS may also challenge the establishment of target species, which do not necessarily deploy high-competitive traits. In areas with high pressure of IAS, a first restorative intervention could imply the sowing of robust competitor species, while secondary interventions at later points may promote the enrichment with less competitive species that play specific roles desired in urban grasslands (e.g., resources for urban pollinators).

Practical recommendations for urban grasslands under climate change

An overarching theme of this dissertation is the importance of a theory- and evidence-based design of resistant and resilient grasslands for rehabilitation in urban areas where goals and services associated with urban green infrastructure are desired. When designing seed mixtures to rehabilitate grassland communities in urban areas, the most suitable criteria for selecting species will depend on several factors and potential arising trade-offs in applying these criteria. For instance, the specific goal for rehabilitating urban grasslands may guide the prioritization of particular traits and species, e.g., carbon sequestration, plant diversity, resources for pollinators, containment for IAS, etc. Moreover, beyond the ecological principles outlined in this dissertation, feasibility aspects for the implementation are worth considering, e.g., budget limitation on the amount of seed material or species that can be acquired, the availability of the species, the knowledge and will to implement adjustments for the implementation and maintenance of urban grasslands (Figure 11).

Seed limitation is often crucial in establishing plant communities in urban greenspaces [164]. Thus, sowing seed mixtures seems an essential strategy for rehabilitating grasslands in urban areas. Additionally, other biotic and abiotic limitations compromise the establishment of communities in different stages of the life story of plants in urban areas (see, e.g., [165,166]). Human activity and soil characteristics are some of the many urban drivers that may limit and shape plant communities at local scales [164]. At the same time, pervasive conditions related to climate change (e.g., temperature, [CO_2] and precipitation) pose challenges to the persistence and functioning of urban grasslands. Here, I contribute to further enriching research on restorative approaches to urban ecosystems by identifying ecological processes influencing the establishment and functioning of native urban grasslands and establishing attributes of species mixtures that promote their functioning and derived services in resilient urban areas. Finally, species selection is suggested based on specific goals, which translate into the inclusion of taxonomic and functionally diverse plant species addressing suits of services expected from urban grasslands.

Figure 11. Exemplary urban grasslands undergoing rehabilitation (above, road verges in Munich, below, parking lot in Freising, S Germany). Species-poor and frequently mown lawns were rehabilitated by designing mixtures of native species subsequently sown in prepared bare soil. Species selection primarily followed suitability criteria for native pollinators recorded in urban areas and accounted for a diverse composition in functional traits and plant families. Management was adapted for a single mowing event by the end of the growing season.

CONCLUDING REMARKS

Sowing seed mixtures is the most reasonable strategy for rehabilitating diverse urban grasslands and grassland-like habitats and overcoming the most common limitations to plant establishment in urban areas. Because of the importance of recreating and managing urban grasslands for enhanced ecosystem services, research on attributes of sown grassland communities and their responses to environmental conditions is crucial to ensure that defined rehabilitation goals and desired levels of services are delivered. Drivers associated with global change, i.e., urbanization itself and the influence of climate change, pose a significant role in understanding multiple interplaying aspects affecting grassland performance, multifunctionality, and resilience.

An essential outcome of this thesis is that to achieve high levels of functionality, which are closely associated with the different goals of grassland on the larger scale of an urban landscape, special attention needs to be paid to the functional composition of designed grasslands. Although multiple purposes cannot be equally achieved or inevitable trade-offs arise, the conclusions drawn from Publications 1–3 underscore the role of trait hierarchies for increasing resistance against IAS and functional types and their relative abundances to increase ecosystem functioning. Thus, high levels of taxonomic and functional diversity, along with even composition between forbs and grasses, may increase the resilience and functioning of urban grasslands under climate change, especially in the early phases of grassland rehabilitation and during the growing season.

Multiple anthropogenic factors in real urban settings may pose new difficulties to improved attributes securing high levels of multifunctionality. A thorough assessment of site conditions, prevailing environmental challenges, and prioritized goals should be conducted and complemented by carefully selecting species and their share in potential mixtures. Plant species richness has positively influenced the functioning of grasslands. This thesis complements earlier findings by emphasizing the role of grasses and forbs (and their diverse traits) and their abundance in grasslands to influence their functioning. Thus, a designed urban grassland community can display a wide range of complementary effects in different ecosystem compartments, translating into bundles of benefits to help adapt cities to increasing climate change effects.

Under global change, urban green infrastructure, specifically urban grasslands and grassland-like habitats, will be vital in dealing with climate-change mitigation and adaptation, though challenged in their integrity and functionality. Nonetheless, the adverse effects of climate change can be counteracted by the compositional attributes of the target community. Therefore, there is a great potential for designing and implementing urban grasslands whereby selecting species in light of specific targets is desirable and feasible.

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APPENDIX

A1 Publication List

A1 Publication List[4]

Peer-reviewed journal publications

2023

Dietzel, Simon; **Rojas-Botero, Sandra**; Kollmann, Johannes; Fischer, Christina (2023): Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. In *Ecological Indicators* 147, p. 109980.

Englmeier, Jana; Mitesser, Oliver; Benbow, M. Eric; Hothorn, Torsten; Hoermann, Christian von; Benjamin, Caryl; … **Rojas-Botero, Sandra**; et al. (2023): Diverse effects of climate, land use, and insects on dung and carrion decomposition. In *Ecosystems* 26 (2), pp. 397–411.

Englmeier, Jana; Rieker, Daniel; Mitesser, Oliver; Benjamin, Caryl; Fricke, Ute; Ganuza, Cristina; … **Rojas-Botero, Sandra**; et al. (2023): Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria. In *Ecography*, e06807.

Fricke, Ute; Redlich, Sarah; Zhang, Jie; Benjamin, Caryl S.; Englmeier, Jana; Ganuza, Cristina; … **Rojas-Botero, Sandra**; et al. (2023): Earlier flowering of winter oilseed rape compensates for higher pest pressure in warmer climates. In *Journal of Applied Ecology* 60 (2), pp. 365–375.

Rojas-Botero, Sandra; Teixeira, Leonardo H.; Kollmann, Johannes (2023): Low precipitation due to climate change consistently reduces multifunctionality of urban grasslands in mesocosms. In *PloS one* 18 (2), e0275044.

Rojas-Botero, Sandra; Teixeira, Leonardo H.; Prucker, Paula; Kloska, Veronika; Kollmann, Johannes; Le Stradic, Soizig (2023): Root traits of grasslands rapidly respond to climate change, while community biomass mainly depends on functional composition. In *Functional Ecology* 37(7), pp. 1841-1855

Tobisch, Cynthia; **Rojas-Botero, Sandra**; Uhler, Johannes; Kollmann, Johannes; Müller, Jörg; Moning, Christoph et al. (2023): Conservation-relevant plant species indicate arthropod richness across trophic levels: Habitat quality is more important than habitat amount. In *Ecological Indicators* 148, p. 110039.

Tobisch, Cynthia; **Rojas-Botero, Sandra**; Uhler, Johannes; Müller, Jörg; Kollmann, Johannes; Moning, Christoph et al. (2023): Plant species composition and local habitat conditions as primary determinants of terrestrial arthropod assemblages. In *Oecologia* 201 (3), pp. 813–825.

Uphus, Lars; Uhler, Johannes; Tobisch, Cynthia; **Rojas-Botero, Sandra**; Lüpke, Marvin; Benjamin, Caryl et al. (2023): Earlier and more uniform spring green-up linked to lower insect richness and biomass in temperate forests. In *Communications Biology* 6 (1), p. 1052.

2022

Benjamin, Caryl S.; Uphus, Lars; Lüpke, Marvin; **Rojas-Botero, Sandra**; Dhillon, Maninder Singh; Englmeier, Jana et al. (2022): Modelling the Relative Abundance of Roe Deer (Capreolus capreolus L.) along a Climate and Land-Use Gradient. In *Animals* 12 (3), p. 222.

Englmeier, Jana; Hoermann, Christian von; Rieker, Daniel; Benbow, Marc Eric; Benjamin, Caryl; Fricke, Ute; … **Rojas-Botero, Sandra**; et al. (2022): Dung-visiting beetle diversity is mainly affected by land use, while community specialization is driven by climate. In *Ecology and evolution* 12 (10), e9386.

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[4] https://scholar.google.de/citations?hl=de&user=4co4UpoAAAAJ

Fricke, Ute; Redlich, Sarah; Zhang, Jie; Tobisch, Cynthia; **Rojas-Botero, Sandra**; Benjamin, Caryl S. et al. (2022): Plant richness, land use and temperature differently shape invertebrate leaf-chewing herbivory on plant functional groups. In *Oecologia* 199 (2), pp. 407–417.

Fricke, Ute; Steffan-Dewenter, Ingolf; Zhang, Jie; Tobisch, Cynthia; **Rojas-Botero, Sandra**; Benjamin, Caryl S. et al. (2022): Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types. In *PloS one* 17 (4), e0264881.

Ganuza, Cristina; Redlich, Sarah; Uhler, Johannes; Tobisch, Cynthia; **Rojas-Botero, Sandra**; Peters, Marcell K. et al. (2022): Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. In *Science advances* 8 (18), eabm9359.

Redlich, Sarah; Zhang, Jie; Benjamin, Caryl; Dhillon, Maninder Singh; Englmeier, Jana; Ewald, Jörg; … **Rojas-Botero, Sandra**; et al. (2022): Disentangling effects of climate and land use on biodiversity and ecosystem services—A multi-scale experimental design. In *Methods in Ecology and Evolution* 13 (2), pp. 514–527.

Rojas-Botero, Sandra; Kollmann, Johannes; Teixeira, Leonardo H. (2022): Competitive trait hierarchies of native communities and invasive propagule pressure consistently predict invasion success during grassland establishment. In *Biological Invasions* 24 (1), pp. 107–122.

Welti, Ellen A. R.; Zajicek, Petr; Frenzel, Mark; Ayasse, Manfred; Bornholdt, Tim; Buse, Jörn; … **Rojas-Botero, Sandra**; et al. (2022): Temperature drives variation in flying insect biomass across a German malaise trap network. In *Insect conservation and diversity* 15 (2), pp. 168–180.

2021

Uhler, Johannes; Redlich, Sarah; Zhang, Jie; Hothorn, Torsten; Tobisch, Cynthia; Ewald, Jörg; … **Rojas-Botero, Sandra**; et al. (2021): Relationship of insect biomass and richness with land use along a climate gradient. In *Nature Communications* 12 (1), p. 5946.

2020

Rojas-Botero, Sandra; Solorza-Bejarano, Jairo; Kollmann, Johannes; Teixeira, Leonardo H. (2020): Nucleation increases understory species and functional diversity in early tropical forest restoration. In *Ecological Engineering* 158, p. 106031.

2017

Rojas-B., Sandra Liliana (2017): Estructura y composición florística de la vegetación en proceso de restauración en los Cerros Orientales de Bogotá (Colombia). In *Caldasia* 39 (1), pp. 124–139.

Other publications

Dietzel, Simon; **Rojas-Botero, Sandra**; Fischer, Cristina; Kollmann, Johannes (2022): Aufwertung urbaner Straßenränder als Anpassung an den Klimawandel und zur Förderung bestäubender Insekten. In ANLiegen Natur 44.

Vargas, Orlando; León, Olga Adriana; **Rojas, Sandra Liliana** (2021): Protocolo para el monitoreo de la restauración ecológica en los páramos. In Mauricio Aguilar Garavito, Wilson Ramírez (Eds.): Evaluación y seguimiento de la restauración ecológica en el páramo Andino. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Bogotá, D.C., pp. 74–95.

Rojas Botero, Sandra Liliana (2017): El banco de semillas del humedal Tibanica y su potencial para la restauración de su vegetación acuática. In G. Guillot Monroy, G. A. Pinilla A. (Eds.): Estudios ecológicos en humedales de Bogotá. Aplicaciones para su evaluación, seguimiento y manejo. Universidad Nacional de Colombia, Sede Bogotá, Facultad de Ciencias; Bogotá, Colombia, pp. 169-192.

Conference participations

Nov 2022	**URBIO International Conference** Leipzig, Germany Restored urban roadside vegetation offers opportunities for climate regulation and enhancement of resources for urban flower-visitors [oral presentation]
Nov 2022	**Joint SFE^2-GfÖ-EEF Conference on Ecological Sciences** Metz, France Grassland root traits respond rapidly to climate change, while functional type composition explains differences in biomass allocation [oral presentation]
Jun 2022	**IAVS Annual Symposium** Madrid, Spain Multifunctionality of restored urban grasslands is consistently affected by decreases in precipitation under climate change [poster presentation]
Jun 2020	**SER World Conference** Quebec, Canada [online surrogate] Restored urban road vegetation offers floral resources for insect pollinators and contributes to climate regulation [poster presentation]
Sep 2019	**Annual Meeting GfÖ** Münster, Germany Effects of extreme weather events, competitive hierarchy, and propagule pressure on the invasion success of *Solidago gigantea* in experimental grasslands [oral presentation]
Aug 2015	**8th Colombian Conference of Botany** Manizales, Colombia Vegetation communities and regeneration patterns in areas under ecological restoration in the Eastern Hills of Bogotá, Colombia [poster presentation] Restoration of vegetation dynamics using soil seed bank translocation in Andean forests [poster presentation]
Apr 2015	**4th Ibero-American and Caribbean Conference on Ecological Restoration** Buenos Aires, Argentina Nucleation as a strategy to overcome barriers to natural regeneration in the Eastern Hills of Bogotá, Colombia [oral presentation] Participatory ecological restoration in rural areas of High Mountain in Bogotá, Colombia: Achievements and challenges [poster presentation]