

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

**CIDADES COMO LABORATÓRIOS DE EVOLUÇÃO: UMA BROMÉLIA COMO
MODELO DE ESTUDO DA ADAPTAÇÃO DE PLANTAS AO AMBIENTE
URBANO**



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Resumo

A urbanização traz uma mistura complexa de mudanças no ambiente, aumentando a pressão sobre a diversidade das espécies locais. No entanto, pouco se sabe ainda como os impactos ecológicos decorrentes da urbanização afetam a evolução das populações de plantas que vivem nas cidades. A proposta desta tese foi abordar diferentes aspectos da urbanização como causadores de mudanças em espécies e comunidades de plantas, assim como contribuir com estudos genéticos e evolutivos de uma espécie nativa de bromélia (*Tillandsia aeranthos* (Loisel.) L.B.Sm.) que ocorre em ambientes urbanos no sul do Brasil. O Capítulo III apresenta uma revisão sistemática global que integra várias áreas da Ecologia Urbana para sumarizar como as espécies e comunidades de plantas estão respondendo a urbanização e quais os principais agentes dessas respostas (*Urban Drivers*). Após avaliar 171 estudos publicados nos últimos onze anos, foi revelado que a maioria deles relatou consequências negativas da urbanização. Os *Urban Drivers* mais citados como responsáveis pelas mudanças nas espécies e comunidades vegetais foram “mudança da cobertura do solo” e “invasão biótica”. Dentre as consequências negativas mais relatadas, temos redução de riqueza de espécies vegetais, menor disponibilidade de polinizadores, homogeneização do ambiente, invasão de espécies não nativas, alterações nos tempos dos eventos fenológicos e dificuldades para o crescimento das plantas. No entanto, foi avaliado que algumas espécies apresentam evidências de adaptação a essas adversidades por meio de sua plasticidade fenotípica e também pela evolução de características que tornam os indivíduos resilientes ao ambiente urbano. O Capítulo IV, trata dos efeitos da urbanização na diversidade genética, estrutura genética e adaptação local em *T. aeranthos*. Seu metabolismo CAM é vantajoso para colonizar com sucesso as áreas urbanas, geralmente mais secas, tornando esta espécie um excelente modelo para o estudo de como as plantas podem se adaptar a estes ambientes. Para testar se haveria diferenças nos padrões genéticos entre populações que ocorrem em ambientes urbanos e não-urbanos, utilizamos uma amostragem na forma de transectos, distribuídos ao longo de um gradiente de urbanização. A fecundação cruzada obrigatória permitiu que esta espécie mantivesse altos níveis de diversidade genética, sem diminuição na diversidade genética com o aumento da urbanização. Em concordância com este resultado, a fragmentação causada pela urbanização não foi suficiente para separar as populações urbanas e não-urbanas através das análises de estrutura genética. A falta de

correlação entre os *outlier loci* detectados através do escaneamento genômico e o índice de urbanização encontrado em nosso estudo corrobora com os demais índices de diversidade genética, não sendo afetados pela urbanização. Portanto, pode-se supor que a dispersão pode ocorrer por pólen ou sementes entre populações urbanas e não-urbanas, sendo estes os principais determinantes da manutenção da diversidade genética nas populações de *T. aeranthis*. Por outro lado, o Capítulo V apresenta um estudo sobre a produção e a viabilidade de sementes de *T. aeranthis*, como forma de comparar um dos aspectos de seu sucesso reprodutivo em ambientes urbanos e não-urbanos. A produção de sementes não apresentou diferença estatisticamente significativa em relação ao gradiente de urbanização, porém a taxa de germinação diminuiu com o aumento da urbanização. Como o desenvolvimento da semente depende estritamente da fertilização cruzada bem-sucedida, é provável que tenha ocorrido uma falha no desenvolvimento da semente posterior à fertilização. Os resultados obtidos na presente tese contribuirão com os estudos avaliando os efeitos da urbanização em espécies vegetais, especialmente em ambientes tropicais, que ainda são menos representados em escala global.

Abstract

Urbanization brings complex changes to the environment, increasing pressures on local species diversity. However, little is known about how the ecological impacts resulted from urbanization affect the evolution of plant populations living in cities. The purpose of this thesis was to address different aspects of urbanization causing changes in plant species and communities, as well as to contribute to genetic and evolutionary studies of a native species of bromeliad (*Tillandsia aeranthos* (Loisel.) L.B.Sm.) that occurs in urban environments in southern Brazil. The Chapter III presents a global systematic review that integrates several areas of Urban Ecology, summarizing how plant species and communities are responding to urbanization and which are the main agents of these responses (*Urban Drivers*). After evaluating 171 studies published in the last eleven years, we found that most of them reported negative consequences of urbanization. The *Urban Drivers* most cited as responsible for changes in plant species and communities were “land cover change” and “biotic invasion”. Among the most reported negative consequences, we have reduced plant species richness, lower availability of pollinators, environment homogenization, invasion of non-native species, changes in the timing of phenological events and difficulties for plant growth. However, it was evaluated that some species show evidence of adaptation to these adversities through their phenotypic plasticity and also through the evolution of characteristics that make individuals resilient to the urban environment. In Chapter IV we described the effects of urbanization on genetic diversity, genetic structure and local adaptation in *T. aeranthos*. Its CAM metabolism is advantageous for successfully colonizing the generally drier urban areas, making this species an excellent model for studying how plants can adapt to these environments. To test whether there would be differences in genetic patterns between populations that occur in urban and non-urban environments, we used sampling in the form of transects, distributed along an urbanization gradient. Obligatory cross-fertilization has allowed this species to maintain high levels of genetic diversity, with no decrease in genetic diversity with increasing urbanization. In agreement with this result, the fragmentation caused by urbanization was not enough to separate urban and non-urban populations through genetic structure analyses. The lack of correlation between the *outlier loci* detected through genomic scan and the urbanization index in our study corroborates the other genetic diversity indices not being affected by urbanization. Therefore, it can be

assumed that dispersion can occur by pollen or seeds between urban and non-urban populations, which are the main determinants of the maintenance of genetic diversity in *T. aeranthos* populations. On the other hand, Chapter V presents a study on the production and viability of *T. aeranthos* seeds, as a way of comparing one of the aspects of its reproductive success in urban and non-urban environments. Seed production showed no statistically significant difference in relation to the urbanization gradient, but the germination rate decreased with increasing urbanization. As seed development is strictly dependent on successful cross-fertilization, it is likely that was a failure in the post-fertilization development of the seed. The results obtained in this thesis will contribute to studies evaluating the effects of urbanization on plant species, especially in tropical environments, which are still less represented on a global scale.

Capítulo I
Introdução geral

Introdução geral

A urbanização e as ameaças à biodiversidade

A atividade humana está alterando permanentemente o planeta Terra. As mudanças geoquímicas, climáticas e biológicas em escala global causadas pelos humanos levou os cientistas a propor uma nova época, o Antropoceno, convenientemente colocado com seu início em meados do século XX (Waters *et al.*, 2016).

Uma das maiores particularidades do Antropoceno é o rápido aumento da urbanização em todo planeta e as consequências dessa urbanização para o meio ambiente. A proporção da superfície global que é classificada como urbana é atualmente estimada em aproximadamente 3% e esta proporção continuará aumentando. Em 2018, 55% da população mundial residia em áreas urbanas, em comparação com apenas 30% em 1950, refletindo uma mudança na distribuição espacial das populações das áreas rurais para as áreas urbanas. Espera-se que o crescimento da população urbana continue, de modo que a população urbana mundial atingirá cinco bilhões em 2028 e seis bilhões em 2041 (Parris, 2016; United Nations, 2018).

Embora as áreas urbanas ocupem apenas 3% da superfície global, o crescimento urbano impõe grandes desafios à conservação da biodiversidade. Em comparação com outras atividades humanas que causam a perda de habitats, a expansão da urbanização é a mais duradoura, pois já induziu a uma grande transformação de paisagens, produzindo algumas das maiores taxas de extinção local e frequentemente eliminando a grande maioria das espécies nativas locais (McKinney, 2002). Portanto, em uma era de expansão urbana global, entender como a urbanização afeta a biodiversidade e como as espécies se adaptam aos ambientes urbanos são fundamentais para a conservação da biodiversidade (McKinney, 2002; Aronson *et al.*, 2014).

Os processos biofísicos associados à construção das cidades são frequentemente semelhantes, fazendo com que o habitat urbano imponha condições e desafios semelhantes para a persistência de espécies não humanas. Parris (2016) classificou esses processos biofísicos como primários (p. ex. remoção da vegetação existente; construção de prédios, estradas e outras infraestruturas urbanas; substituição de superfícies permeáveis por impermeáveis; poluição) e secundários (p. ex. perda de habitat, fragmentação e isolamento;

mudanças climáticas; poluição do ar, água e solo), sendo os processos secundários consequências ecológicas dos primários. Esses processos biofísicos da urbanização podem ter efeitos sobre espécies, populações e comunidades inteiras, alterando a quantidade, qualidade, arranjo temporal e espacial de recursos dos quais microrganismos, fungos, plantas e animais dependem para sobreviver, como abrigo, ninhos, alimentos, água, luz solar e nutrientes (Parris, 2016).

A disciplina de Ecologia Urbana surgiu a partir da necessidade de compreender toda a complexidade das relações entre a comunidade biológica e o ambiente urbano. A Ecologia Urbana pode ser definida como a ecologia de todos os organismos – incluindo humanos – em ambientes urbanos, bem como ambientes que são impactados pela construção, expansão e a operação das cidades (Douglas *et al.*, 2011; Parris, 2016). O amadurecimento dessa disciplina nos últimos anos está permitindo avaliar como as mudanças ambientais em decorrência da urbanização afetam a ecologia populacional das espécies, a estrutura da comunidade e os processos ecossistêmicos (Donihue & Lambert, 2015).

Apesar do aumento considerável no número de estudos nesta área, o impacto da urbanização em plantas ainda é pouco compreendido. A maioria dos estudos recentes em Ecologia Urbana concentra-se em animais, particularmente mamíferos, artrópodes e pássaros, com menos estudos avaliando os efeitos da urbanização em plantas (Aronson *et al.*, 2014; Johnson, Thompson, & Saini, 2015; Rivkin *et al.*, 2019).

Sem dúvida, os centros urbanos, são uma das principais fontes de emissões de gases de efeito estufa e, portanto, também são responsáveis pelas mudanças climáticas globais. O exemplo melhor documentado de modificação climática antropogênica é o efeito da ilha de calor urbana (*Urban Heat Island* - UHI): as cidades tendem a ter temperaturas mais altas do ar e da superfície do que seus arredores rurais. Diversas características dos ambientes urbanos podem causar a formação da UHI. Estas incluem, por exemplo, o aumento de superfícies impermeáveis (gerando redução do albedo – poder de reflexão de uma superfície) e a redução de áreas cobertas por vegetação e água (causando redução da perda de calor devido ao resfriamento evaporativo) (Grimm *et al.*, 2008).

Estudos apontam algumas das mais severas consequências para as espécies e comunidades de plantas devido às mudanças climáticas, como redução na riqueza de espécies devido à filtragem de espécies que não são adaptadas a habitats mais quentes (Albrecht & Haider, 2013; Chen *et al.*, 2014; Concepción *et al.*, 2017; Yu *et al.*, 2021) e

aumento do estresse hídrico devido ao aumento dos níveis de dióxido de carbono e ozônio nas áreas urbanas (Calfapietra, Peñuelas, & Niinemets, 2015; Lahr *et al.*, 2015; Lahr, Dunn, & Frank, 2018; Zipper *et al.*, 2017; Barradas & Esperon-Rodriguez, 2021). Porém, um dos efeitos mais pronunciados e documentados são as mudanças na fenologia das plantas, o que pode ser utilizado como um bioindicador para a detecção de mudanças climáticas (Jochner & Menzel, 2015). Muitos estudos envolvendo análises fenológicas utilizando tanto abordagens espaciais (comparação entre ambiente urbano e rural) como temporais (comparações ao longo de décadas/séculos de urbanização) detectaram mudanças nos padrões fenológicos em plantas, como avanços nos períodos de desdobramento, coloração e queda das folhas, floração e amadurecimento dos frutos (Neil, Landrum, & Wu, 2010; Jeong *et al.*, 2011; van Vliet *et al.*, 2014; Massetti, Petralli, & Orlandini, 2015; Comber & Brunson, 2015; He *et al.*, 2016; Davis, Major, & Taylor, 2016; Yakub & Tiffin, 2017; Li *et al.*, 2017; Qiu, Song, & Li, 2017; Lee, 2017; Lindh, McGahan, & Bluhm, 2018; Oliveira *et al.*, 2019; Su *et al.*, 2019; Cochard *et al.*, 2019; Kondratyeva *et al.*, 2020; Fisogni *et al.*, 2020; Fitchett & Raik, 2021). Uma dessincronização entre a épocas de floração e os polinizadores pode levar as espécies a um isolamento reprodutivo, especialmente em plantas que têm uma curta duração da floração (Jochner & Menzel, 2015). Consequentemente, os vários efeitos das mudanças climáticas sobre as espécies provavelmente modificarão a rede de interações ao nível de comunidade. A resposta de algumas espécies às mudanças climáticas pode constituir um impacto indireto nas espécies que delas dependem (Bellard *et al.*, 2012).

A poluição do ar, da água e dos solos causada pela urbanização também afeta negativamente as plantas, podendo trazer impactos no seu crescimento e desenvolvimento (Huang *et al.*, 2013; Vujić *et al.*, 2015; Bouraoui *et al.*, 2019; King & Hovick, 2020; Turmukhametova & Shadrina, 2020; Su *et al.*, 2021); reduções na concentração de clorofila e de taxas fotossintéticas (Molnár *et al.*, 2018; Xiao *et al.*, 2021) e interrupção das trocas gasosas estomáticas pela deposição de material particulado nas folhas (Singh *et al.*, 2020; Singh, 2021).

A contínua expansão das cidades altera as paisagens de vegetação nativa e agrícola transformando-as em áreas cobertas por superfícies impermeáveis. Em muitos casos, o habitat que resta é fragmentado em pequenas áreas ou manchas, que tendem a ser isoladas umas das outras por uma paisagem inóspita formada pela infraestrutura urbana (Parris,

2016). Quando os habitats são fragmentados em pequenas áreas, eles são suscetíveis a mudanças ao longo do tempo. Pequenas manchas de habitat são vulneráveis a efeitos de borda – mudanças nas condições físicas e biológicas que ocorrem na fronteira de dois ecossistemas ou tipos de habitat. Em habitats terrestres, estes podem incluir mudanças microclimáticas (por exemplo, aumento da radiação, temperatura e vento, diminuição da umidade), invasão de espécies exóticas, aumento da pressão de herbívoros e predadores, influxo de poluentes, mudanças na ciclagem de nutrientes, mudanças na dinâmica populacional das espécies e aumento da perturbação por humanos (Grimm *et al.*, 2008; Williams *et al.*, 2009; Hahs & McDonnell, 2013). Essas mudanças podem levar à redução da frequência e abundância de espécies de plantas nativas e aumento da prevalência da flora exótica introduzida, levando à extinção local de muitas espécies de plantas nativas das cidades e a criação de novas comunidades de plantas urbanas (Hahs *et al.*, 2009; Williams, Hahs, & Vesk, 2015). Do mesmo modo, espécies que sobrevivem à perda de habitat podem ser altamente suscetíveis à extinção local, já que a fragmentação do habitat deve selecionar um conjunto previsível de espécies que carregam características relacionadas à persistência de metapopulações ou persistência apesar do baixo tamanho populacional. Por exemplo, espécies com capacidade de dispersão limitada e baixa produção de sementes são mais vulneráveis à extinção por falhas na recolonização de habitats. Da mesma forma, espécies que são fortemente dependentes de outros organismos numa relação mutualista (por exemplo, polinizadores especializados para reprodução), correm maior risco de extinção pela fragmentação (Williams *et al.*, 2009).

Em suma, as cidades são ecossistemas, nos quais muitos organismos interagem e prosperam. Como em qualquer ecossistema, os sistemas urbanos são caracterizados por seus conjuntos de espécies, bem como por seus ambientes químicos e físicos, cujos componentes interagem para governar os processos ecológicos, como ciclagem de nutrientes e fluxo de energia (Grimm *et al.*, 2008; Donihue & Lambert, 2015). No entanto, os ecossistemas urbanos são caracterizados pelos fortes impactos antropogênicos. A contínua expansão da urbanização é inevitável em todo o planeta, e manter a diversidade e a função das comunidades biológicas assim como seus serviços ecossistêmicos associados, dentro e perto das cidades é uma tarefa muito difícil (Grimm *et al.*, 2008). Compreender como os fatores abióticos, bióticos e antropogênicos moldam as comunidades locais podem levar a práticas que garantem o futuro de cidades sustentáveis (Aronson *et al.*, 2016).

Dinâmicas evolutivas em ambientes urbanos

A urbanização vem com uma mistura complexa de mudanças no ambiente que se repetem consistentemente nas cidades, aumentando a pressão sobre a diversidade das espécies locais remanescentes (Johnson & Munshi-South, 2017). Os estudos em Ecologia Urbana fornecem cada vez mais evidências de como essas mudanças ambientais afetam a ecologia das espécies, a estrutura da comunidade e os processos ecossistêmicos. No entanto, sabemos muito menos sobre como os impactos ecológicos da urbanização afetam a evolução das populações de organismos que vivem nas cidades (Donihue & Lambert, 2015; Johnson & Munshi-South, 2017), e como essa evolução pode influenciar os processos e padrões ecológicos por meio de dinâmicas ecoevolutivas (Alberti, 2015). Uma das questões cruciais no debate sobre os efeitos ecológicos em decorrência da urbanização é se as espécies serão ou não capazes de se adaptar rápido o suficiente para acompanhar o ritmo acelerado dessas mudanças. Mesmo quando as espécies são capazes de persistir no ambiente a curto prazo, a redução prolongada no tamanho da população ameaça a sua persistência a longo prazo por meio de uma série de efeitos demográficos e genéticos previsíveis para as populações (Lande, 1988).

Por exemplo, a fragmentação e degradação dos habitats naturais em decorrência da urbanização frequentemente reduz o tamanho e aumenta o isolamento das populações nativas (Haddad *et al.*, 2015). Isto ocorre porque a fragmentação reduz o tamanho das manchas de habitat e aumenta o isolamento espacial dessas manchas, com uma matriz circundante inóspita. À medida que a extensão da matriz cresce, o tamanho dos fragmentos reduz, assim como a dispersão entre eles (Cheptou *et al.*, 2017). Espera-se que esses processos ecológicos aumentem a estocasticidade nas frequências alélicas por meio da deriva genética e dos efeitos fundadores e diminuam a dispersão e o movimento de alelos (ou seja, fluxo gênico) em paisagens urbanas (Johnson & Munshi-South, 2017). Mudanças nos fatores bióticos e abióticos geradas pela urbanização também podem alterar a seleção natural e impulsionar a evolução adaptativa (Donihue & Lambert, 2015). As primeiras evidências de evolução em resposta à urbanização incluem algumas das primeiras demonstrações de adaptação contemporânea na natureza. Por exemplo, o aumento da frequência da forma escura da mariposa *Biston betularia* Linnaeus (*peppered moth*) em resposta à poluição industrial elevada em torno das cidades do início do século XIX a meados do século XX

(Kettlewell, 1955). Apesar desse exemplo clássico, os estudos focados na evolução em ambientes urbanos só ganharam força recentemente (Rivkin *et al.*, 2019).

As consequências evolutivas das alterações ambientais nos sistemas urbanos têm sido amplamente estudadas do ponto de vista da genética de populações, com ênfase particular em como a fragmentação do habitat resulta em mudanças estocásticas mais pronunciadas nas frequências alélicas. A deriva pode diminuir a diversidade genética, reduzindo o potencial evolutivo das populações ao lidar com novos ambientes (Frankham, Ballou, & Briscoe, 2010). É esperado que este processo aumente em muitas espécies à medida que a extensão da urbanização aumenta. Por exemplo, habitats fragmentados levaram à redução da diversidade genética dentro das populações e maior diferenciação genética entre as populações urbanas de *Linaria vulgaris* Mill. (Bartlewicz *et al.*, 2015), em comparação com populações em habitats não urbanizados. Por outro lado, a urbanização não levou a uma perda da diversidade genética, e algumas medidas de urbanização até foram correlacionadas ao aumento da diversidade genética em populações de *Trifolium repens* L. (Johnson *et al.*, 2018). Embora o resultado do aumento dos efeitos da deriva (e a possível consequência na redução da diversidade dentro das populações) tenha sido identificado em várias cidades em outros organismos (Rivkin *et al.*, 2019), poucos estudos examinaram em detalhes quais características do ambiente urbano (por exemplo estradas, edifícios) afetam a demografia populacional em plantas. Padrões esperados de diversidade e estrutura genética baseados nos estudos realizados em habitats fragmentados (não-urbanos) oferecem previsões de como as plantas responderiam à urbanização. Porém, a forma rápida como ocorre a alteração da paisagem pela atividade humana fornecerá novos conhecimentos em relação à evolução das espécies nas cidades. Até recentemente, a adaptação à fragmentação antropogênica era considerada improvável, pois os processos evolutivos eram considerados ineficientes em escalas de tempo de algumas décadas. No entanto, estudos recentes demonstraram que a adaptação de traços de história de vida pode ocorrer em escalas de tempo curtos, com mudanças evolutivas observáveis em até apenas duas gerações (Kinnison & Hendry, 2001; Bodbyl Roels & Kelly, 2011).

Um efeito importante da fragmentação é o aumento da variabilidade nas condições abióticas e na estocasticidade demográfica que as pequenas populações estão sujeitas, gerando vários níveis de seleção nas populações. Os efeitos demográficos e genéticos populacionais alteram a forma como as espécies respondem à seleção (Cheptou *et al.*, 2017).

Ao reduzir o fluxo gênico entre manchas, a fragmentação pode melhorar a adaptação local de uma espécie na paisagem presente nas cidades. Por exemplo, pode ocorrer seleção diversificadora (seleção disruptiva) entre manchas causada por fatores abióticos (por exemplo, deterioração do habitat, efeitos de borda) ou fatores bióticos (por exemplo, perda de interação com organismos mutualistas). Consequentemente, a adaptação local e a deriva podem gerar populações localmente diferenciadas, mesmo em escalas de tempo curtas (Cheptou *et al.*, 2017). Por outro lado, a fragmentação pode selecionar espécies que possuem uma maior amplitude de nicho ecológico (ou seja, uma estratégia mais generalista), que permitam às espécies lidar com a heterogeneidade do habitat. Organismos que podem permanecer com sucesso nos habitats de borda e até mesmo na matriz terão mais habitats disponíveis para colonização e serão menos isolados (Cheptou *et al.*, 2017). Espécies que são especialistas podem sofrer mais com as flutuações de habitat do que espécies generalistas. Consequentemente, serão selecionadas estratégias de história de vida que aumentem a aptidão média em toda a paisagem (Comins, Hamilton, & May, 1980). De fato, uma maior frequência de plantas com traços generalistas (como dispersão pelo vento, baixa estatura e presença de sementes pequenas) nos ambientes urbanos foi encontrada em estudos de riqueza filogenética das comunidades de plantas urbanas (Knapp, Winter, & Klotz, 2017; Lopez, Urban, & White, 2018; Silva-Junior *et al.*, 2018; Cui *et al.*, 2019; El-Barougy *et al.*, 2021). Já espécies especialistas e aquelas com baixa dispersão são mais afetadas negativamente pela urbanização, confirmando que a fragmentação pode exercer tal seleção (Huang *et al.*, 2013; Mccune & Vellend, 2013; Everingham, Hemmings, & Moles, 2019; Oliveira *et al.*, 2020; Yang *et al.*, 2021).

O efeito final da fragmentação na dinâmica populacional de uma determinada espécie depende do grau em que a dispersão entre fragmentos é impedida. Uma alta dispersão pode manter uma população panmítica mesmo em paisagens severamente fragmentadas. Já uma dispersão menos efetiva resultará em dinâmicas metapopulacionais, onde as populações funcionam de forma independente, e as manchas experimentam extinção regular e subsequente recolonização. Uma fragmentação mais severa deixará manchas isoladas, como ilhas, onde as extinções locais não serão mais contrabalançadas pela colonização (Cheptou *et al.*, 2017). A probabilidade da dispersão ocorrer, por sua vez, depende da extensão espacial da fragmentação (distância entre manchas), da facilidade com que os indivíduos podem se dispersar pela matriz (permeabilidade da matriz) e da capacidade de dispersão da espécie.

Assim, espécies diferentes responderão à mesma paisagem de forma diferente (Hanski, 1991; Ricketts, 2001; Cheptou *et al.*, 2017).

Quando os tamanhos efetivos da população dos fragmentos são pequenos, pode haver seleção para melhores estratégias de dispersão entre os fragmentos. Em pequenas populações muitas vezes os cruzamentos se darão inevitavelmente entre aparentados, resultando em uma diminuição da aptidão devido à depressão endogâmica (Ricketts, 2001). Uma das consequências pode ser o aumento da seleção a favor de maior dispersão entre manchas como forma de evitar a depressão endogâmica. Desta forma, bons dispersores terão acesso a mais manchas e, portanto, a recursos mais abundantes (Cheptou *et al.*, 2017). Por outro lado, espera-se que a fragmentação também selecione contra a dispersão, pois a matriz hostil entre os fragmentos aumenta o risco de o organismo não encontrar um habitat adequado para seu estabelecimento (Bonte *et al.*, 2012). Por exemplo, uma das primeiras demonstrações dos efeitos de ambientes urbanos fragmentados na seleção de plantas foi realizada em *Crepis sancta* (L.) Babc. (Cheptou *et al.*, 2008). Esta planta apresenta variação hereditária para a proporção de sementes dispersantes e não-dispersantes, e experimentos mostraram que a fragmentação do habitat urbano impõe a seleção para a produção de mais sementes não-dispersivas, já que estas são mais propensas a pousar em substratos adequados próximos à planta-mãe, para germinação em habitats urbanos. Logo, a fragmentação nos ambientes urbanos pode impor seleção às populações de plantas, o que pode resultar em adaptação se as populações tiverem a variação genética adaptativa necessária para responder (Rivkin *et al.*, 2019). Entretanto, exemplos tão claros dos efeitos de ambientes urbanos na evolução por seleção natural existem em poucos sistemas, representando uma lacuna para a compreensão da evolução em ambientes urbanos.

Como as alterações físicas e demográficas da fragmentação afetam as espécies de maneiras diferentes, eles também podem interromper as interações entre as espécies, causando uma cascata de efeitos no nível da comunidade local. Estudos inspirados na biogeografia de ilhas mostram que espécies são perdidas em pequenos fragmentos, especialmente espécies que preferem habitats específicos (Laurance *et al.*, 2002). Essas extinções locais afetam as interações mutualísticas e antagônicas das espécies. Por exemplo, declínios de polinizadores, dispersores de sementes e predadores insetívoros em fragmentos da Floresta Amazônica podem diminuir o sucesso reprodutivo das plantas enquanto aumentam a herbivoria (Laurance *et al.*, 2002). De fato, a diminuição das populações e/ou

atividade de polinizadores é um dos efeitos melhor estudados quando se trata de fragmentação, e descobriu-se que isso impede a reprodução de plantas que vivem nas cidades e que são dependentes de polinizadores (Aguilar *et al.*, 2006; Lhotte, Affre, & Saatkamp, 2014; Leong, Kremen, & Roderick, 2014; Irwin, Warren, & Adler, 2018; Oliveira *et al.*, 2019; Hou *et al.*, 2019). As plantas também podem possuir adaptações que ajudem a compensar os efeitos demográficos da fragmentação. Pequenas populações de plantas podem enfrentar uma escassez de parceiros, o que pode favorecer sistemas de cruzamento menos exigentes. De fato, a autocompatibilidade e a autofertilização em plantas são frequentemente associadas a populações pequenas (Baker, 1955), permitindo que essas espécies tenham sucesso reprodutivo em ambientes urbanos com menor frequência ou até mesmo na ausência de polinizadores (Ushimaru, Kobayashi, & Dohzono, 2014).

As características fenotípicas determinam a capacidade de uma espécie colonizar e estabelecer uma população em ambientes urbanos (Rivkin *et al.*, 2019). Entretanto, atualmente, não se sabe se os traços relacionados ao estabelecimento e proliferação de populações em áreas urbanas são resultado de características ancestrais, adaptação recente, plasticidade fenotípica (incluindo mudanças epigenéticas) ou uma combinação desses atributos. Múltiplos processos bióticos e abióticos determinam o subconjunto de espécies presentes nas cidades (Williams *et al.*, 2009; Aronson *et al.*, 2016). Além disso, embora a adaptação rápida nas cidades tenha sido encontrada em algumas espécies de plantas e animais (Johnson & Munshi-South, 2017), não está claro se isso é um fenômeno comum. Desvendar a importância relativa da adaptação versus plasticidade para o sucesso de uma espécie em uma determinada cidade contribuirá para entender como e por que algumas espécies, mas não outras, são capazes de colonizar e persistir em ambientes urbanos (Rivkin *et al.*, 2019). Para descobrir se as diferenças nas características entre populações urbanas e não-urbanas representam adaptações genéticas em vez de plasticidade não hereditária, métodos genômicos podem ser usados para examinar assinaturas de rápida adaptação à urbanização (por exemplo, escaneamentos genômicos: Harris & Munshi-South, 2017; Theodorou *et al.*, 2018). Análises de expressão gênica também podem ser usadas para identificar divergências adaptativas e os fundamentos genéticos das respostas à urbanização (Harris, O'Neill, & Munshi-South, 2015). Juntas, essas abordagens esclarecerão a importância relativa e as interações entre características ancestrais, adaptação rápida e

plasticidade fenotípica na determinação do sucesso ecológico das populações urbanas (Rivkin *et al.*, 2019).

As cidades alteram drasticamente o ambiente abiótico e biótico, o que pode influenciar a seleção natural nas populações urbanas. Apesar dessa simples previsão, os agentes que afetam a aptidão podem ser difíceis de discernir, em parte porque as mudanças ambientais nas cidades variam de simples a complexas. A urbanização inclui mudanças ambientais ao longo de múltiplas dimensões interativas, como a quantidade de superfície impermeável, temperatura, poluição (solo, ar, água, luz e som), disponibilidade de recursos, bem como a abundância e diversidade de concorrentes, predadores e mutualistas. Essa multidimensionalidade pode aumentar drasticamente a complexidade dos ambientes aos quais as populações devem se adaptar e pode tornar desafiadora a descoberta de agentes específicos de seleção. Identificar generalidades sobre a força, a forma e os agentes de seleção em ambientes urbanos permitiriam uma compreensão mecanicista dos processos adaptativos associados à urbanização (Rivkin *et al.*, 2019). Compreender as aplicações ecológicas e ecossistêmicas mais amplas da evolução urbana para espécies nativas representa uma importante prioridade para pesquisas futuras em ecologia evolutiva urbana. A integração dessas pesquisas pode ajudar a projetar estratégias que facilitem a adaptação das espécies à urbanização, melhorar a previsão de declínios populacionais e desenvolver planos de conservação e manejo apropriados (Alberti, 2015). A identificação dos impulsionadores da evolução nas cidades e a história evolutiva das espécies que as habitam pode ser usada para construir novas comunidades resilientes às pressões urbanas e melhorar a conservação da biodiversidade global.

A família Bromeliaceae

Bromeliaceae (3782 espécies, Gouda *et al.*, atualização contínua) é uma das maiores famílias de plantas com flores encontradas quase exclusivamente nos Neotrópicos (Stevens, 2013). Esta família é reconhecida como um dos melhores exemplos de radiação adaptativa – existe uma enorme diversidade de formas de vida, desde formas terrestres com raízes funcionais até epífitas completamente independentes do seu substrato para a nutrição (Benzing, 2000). Uma série de inovações que exigem a integração de um conjunto de características bioquímicas, anatômicas, fisiológicas e do organismo, permitiu a colonização

e especiação bem-sucedida das bromélias em ambientes novos e sob estresse (Benzing, 2000; Crayn *et al.*, 2004, 2015; Givnish *et al.*, 2007, 2011, 2014; Males, 2016; Palma-Silva *et al.*, 2016).

As bromélias são plantas típicas do Novo Mundo, com distribuição geográfica que vai desde os estados da Virgínia, Texas e Califórnia, nos Estados Unidos (limite norte), ao norte da Patagônia, na Argentina (limite sul). A única exceção é *Pitcairnia feliciana* (A. Chev.) Harms & Mildbr distribuída no oeste da África, na região da Guiné, o que parece ter sido um evento de recente dispersão a longa distância (Givnish *et al.*, 2004). O Brasil apresenta uma grande diversidade de bromélias com 56 gêneros (24 endêmicos) e 1.386 espécies (1.186 endêmicas) (Flora e Funga do Brasil, 2022). Especificamente, a Mata Atlântica apresenta uma grande riqueza de espécies (Martinelli *et al.*, 2008), sendo as epífitas dentre as Angiospermas com o maior número de registros neste bioma (37,6%) (Ramos *et al.*, 2019).

Tradicionalmente, Bromeliaceae estava dividida em três subfamílias: Pitcairnioideae, Tillandsioideae e Bromelioideae (Smith & Downs, 1974; 1977; 1979). No entanto, análises filogenéticas realizadas com marcadores plastidiais indicaram o reconhecimento de oito subfamílias (Givnish *et al.*, 2007, 2011): Brocchinioideae, Lindmanioideae, Tillandsioideae, Hechtioideae, Navioideae, Pitcairnioideae, Puyoideae e Bromelioideae. Estima-se que as bromélias surgiram no Escudo das Guianas há cerca de 100 milhões de anos atrás (Ma), durante o Período Cretáceo, com as subfamílias existentes começando a divergir há apenas 19 Ma (Givnish *et al.*, 2011). Os mesmos autores sugerem que as bromélias começaram a ocupar os Andes, a Amazônia, a América Central, o Caribe e o Escudo brasileiro entre 15 e 10 Ma.

Esta família é constituída por plantas terrestres, rupícolas e epífitas, herbáceas, variando de plantas delicadas e de pequeno porte, como *Tillandsia recurvata* (L.) L., com alguns centímetros de comprimento, até plantas de grande porte, como *Puya raimondii* Harms, encontrada nos Andes, que chega a atingir mais de 10 metros de altura (Smith & Downs, 1977). As bromélias apresentam grande variabilidade de formas, sendo em geral plantas bem características e ornamentais. Segundo Rizzini (1997) e Benzing (2000) os diferentes habitats e, especialmente, a natureza do substrato influenciam no aspecto da planta, que pode variar amplamente em tamanho e coloração das folhas, assim como na morfologia das flores. A evolução de uma ampla diversidade de cores e formas de estruturas

florais atraíram os mais variados polinizadores, como insetos, morcegos e beija-flores (Benzing, 2000). Os beija-flores podem ser considerados os principais agentes polinizadores da família (Benzing, 2000; Dias *et al.*, 2014). Em um estudo de polinização com beija-flores, realizado em regiões da Mata Atlântica, as bromélias representaram 36% da flora ornitófila e 33% das flores mais ricas em néctar (Buzato, Sazima, & Sazima, 2000). Embora a maioria das bromélias seja polinizada por vertebrados, principalmente beija-flores e morcegos, as abelhas estão entre os visitantes mais frequentes de algumas espécies de corola curta com características ornitófilas. No entanto, poucos estudos identificaram insetos como polinizadores eficazes de bromélias (Kamke *et al.*, 2011). Essas plantas podem possuir frutos carnosos que são consumidos e dispersados por aves, e o tanque formado pelas suas folhas, em grande parte das espécies, permite o armazenamento de água e nutrientes, servindo para sua própria nutrição e fornecendo um microambiente favorável que proporciona alimento, abrigo e local de reprodução para diversos animais associados (Benzing, 2000; Fleming & Muchhala, 2008; Dias *et al.*, 2014).

Apesar de serem plantas quase exclusivamente herbáceas, é notável sua diversidade ecológica, visto que as espécies são encontradas em diferentes tipos de substratos, bem como nos mais variados habitats (Fischer & Araujo, 1995; Benzing, 2000), constituindo um sistema de estudo favorável às abordagens ecológicas e evolutivas.

Tillandsioideae, o gênero Tillandsia e o epifitismo

A Subfamília Tillandsioideae Harms é a maior das oito subfamílias atualmente estabelecidas para a família Bromeliaceae, apresentando a maior distribuição geográfica dentre elas (Givnish *et al.*, 2007, 2011). As duas principais origens do epifitismo em bromélias se deram nesta subfamília, com o soerguimento do norte dos Andes ca. 15 Ma e em Bromelioideae (epífitas com tanque), com o soerguimento das Serras do Mar e da Mantiqueira na região da Mata Atlântica durante o Plioceno-Pleistoceno (Givnish *et al.*, 2014).

Espécies atmosféricas do gênero *Tillandsia* são epífitas que não formam tanque e que dependem quase exclusivamente de tricomas foliares absorventes para absorção de água e nutrientes (Benzing, 2000). As raízes dessas epífitas são frequentemente reduzidas, servindo apenas para fixação no substrato (Pittendrigh, 1948; Benzing, 1990). Os tricomas abundantes

tornam suas folhas secas altamente refletivas, possivelmente reduzindo a perda de água e a fotoinibição (Pierce *et al.*, 2001). Conjuntos densos de tricomas desse gênero são altamente eficientes na captura de umidade quando combinados com suas folhas pequenas e estreitas que capturam eficientemente gotículas finas da atmosfera (Martorell & Ezcurra, 2007). As bromélias atmosféricas toleram melhor a dessecação do que as espécies de tanque, mas têm taxas mais baixas de fotossíntese por unidade de massa foliar (Benzing & Burt, 1970; Benzing & Renfrow, 1974; Reyes-García, Griffiths, & Rincón, 2008), e quase todas têm fotossíntese CAM (Crayn *et al.*, 2004).

As epífitas em geral são um grupo composto por mais de 31.000 espécies pertencentes a 84 famílias de plantas, representando uma importante proporção da flora mundial (Zotz *et al.*, 2021). São plantas que utilizam outras plantas como substrato para o crescimento, sem extrair delas nenhum recurso hídrico ou nutriente (Benzing, 1990). As epífitas vasculares germinam e crescem sobre forófitos (árvores-suporte) adquirindo uma distribuição espacial horizontal (entre as espécies de forófitos) e vertical (dentro dos forófitos, desde a base do fuste até a copa). A maioria das epífitas é angiosperma, sendo Orchidaceae e Bromeliaceae as famílias com maior número de representantes desse grupo de plantas (Zotz, 2013). A maior diversidade de epífitas é geralmente encontrada em habitats tropicais úmidos, como florestas nubladas e florestas tropicais (Gentry & Dodson, 1987; Benzing, 1990; Nieder, Prosperí, & Michaloud, 2001).

A maioria dos estudos sobre epífitas estão concentrados na morfologia, ecofisiologia e taxonomia dessas plantas (Benzing, 1978, 1990; Zotz, 2004; Wanek & Zotz, 2011). No entanto, mesmo com o grande número de angiospermas epífitas, pouco se sabe sobre a ecologia populacional deste grupo (Mondragón-Chaparro *et al.*, 2006; Matallana *et al.*, 2010; Zotz *et al.*, 2010). Como as epífitas estão sujeitas a pressões seletivas semelhantes, dado o habitat específico que ocupam, é esperado que elas compartilhem semelhanças em suas características demográficas, respostas das populações, padrões de mortalidade, sobrevivência e reprodução (Mondragon, Valverde, & Hernandez-Apolinar, 2015). Recentemente, biólogos da conservação começaram a se concentrar na ecologia populacional de epífitas, já que este grupo de plantas possui uma grande sensibilidade às mudanças climáticas globais, e tem grande potencial como ferramenta de avaliação para o estabelecimento do estado de conservação de florestas tropicais (Hsu *et al.*, 2012).

A estratégia de dispersão mais difundida entre as epífitas é a anemocoria, com a produção de grandes quantidades de sementes pequenas e leves, aumentando assim a probabilidade de que pelo menos algumas delas cheguem a locais seguros (Madison, 1977; Hughes *et al.*, 1994). Em populações de plantas epífitas, a dispersão de sementes pode acontecer de duas formas: as sementes permanecem próximas à sua fonte (ou seja, no mesmo forófito) ou deixam seu forófito original. Neste último caso, as espécies confrontam o processo altamente arriscado de cruzar a matriz de habitat onde os forófitos estão imersos e, eventualmente, encontrar um local seguro para germinação e crescimento (Mondragon *et al.*, 2015). Apesar do alto risco envolvido neste processo, o fato de tantas epífitas apresentarem adaptações de dispersão de sementes a longa distância torna evidente que suas vantagens evolutivas superam seus custos (Horvitz & Schemske, 1986). Provavelmente a maior vantagem para as epífitas dispersarem suas sementes a longas distâncias seja a maior possibilidade de colonização de novas manchas de habitat que podem ser efêmeras e/ou livres de competição (Mondragon *et al.*, 2015). Entretanto, observações de campo sugerem que a maioria das sementes tendem a cair perto da planta mãe, enquanto a dispersão de sementes a longa distância é relativamente rara (Mondragón-Chaparro *et al.*, 2006; Paggi *et al.*, 2010; Chaves *et al.*, 2021). Eventos de dispersão de sementes a longa distância são importantes para o aumento do fluxo gênico e para a expansão das áreas de distribuição das espécies através da fundação de novas populações.

As epífitas são atualmente consideradas um dos grupos de plantas mais ameaçadas. Isso se deve em parte à sua dependência da presença/disponibilidade de árvores hospedeiras e ao fato de que a maioria das epífitas satisfaz suas necessidades de nutrientes e água diretamente da atmosfera (Benzing, 1998; Zotz *et al.*, 2010; Obregon *et al.*, 2011), o que as torna vulneráveis a potenciais mudanças atmosféricas. Mudanças climáticas globais como aumento da temperatura e diminuição da precipitação já são percebidas atualmente, além do aumento da concentração atmosférica de CO₂ (Murphy *et al.*, 2004; Stainforth *et al.*, 2005). Estima-se que essas mudanças, principalmente a redução da umidade atmosférica, afetarão drasticamente o desempenho de epífitas e, portanto, sua dinâmica populacional (Benzing, 1990; Zotz *et al.*, 2010; Müller, Albach, & Zotz, 2018). Embora muitas epífitas apresentem metabolismo CAM, temperaturas alguns graus acima do ótimo noturno resultam em dessecação do tecido ou aumentam os déficits de saturação nas massas de ar circundantes, o que reduz a condutância estomática e, portanto, a disponibilidade de CO₂ para a fotossíntese

(Benzing, 1998). Em adição a isso, as mudanças no uso da terra e perda de habitats através do desmatamento podem diminuir a abundância e a diversidade de epífitas devido ao impacto das atividades humanas nas florestas em que habitam (Hietz, 1997; Wolf, 2005; Köster *et al.*, 2009; Köster, Nieder, & Barthlott, 2011; Adhikari, Fischer, & Fischer, 2012; Chaves *et al.*, 2021). A mudança na diversidade e composição de espécies epífitas após um distúrbio antropogênico tem sido associada a dois processos: restrições na dispersão e alteração das condições microclimáticas no habitat remanescente (Mondragon *et al.*, 2015).

A maioria das epífitas apresenta sistemas de reprodução mistos, que em muitos casos incluem mecanismos que favorecem a fecundação cruzada. Essa variação nos sistemas de reprodução reflete na diversidade genética, no entanto, relativamente pouco foi revelado sobre a estrutura genética desse grupo de plantas em habitats fragmentados, e menos ainda em ecossistemas urbanos (Izuddin & Webb, 2015; Quail *et al.*, 2022). Além disso, os padrões de dispersão de sementes das epífitas permitem que este grupo colonize novos habitats, sendo capazes de atingir altos níveis de abundância em paisagens urbanas (Fenster & Martén-Rodríguez, 2007; Chaves *et al.*, 2021). Como resultado, as epífitas são um grupo ideal para o estudo da conectividade das plantas em paisagens urbanas e para ajudar na compreensão dos mecanismos evolutivos envolvidos nas respostas das plantas frente à urbanização.

Capítulo II
Objetivos

Objetivos

Objetivo geral

Abordar diferentes aspectos da urbanização como causadores de mudanças em espécies e comunidades de plantas, assim como contribuir com estudos genéticos e evolutivos de uma espécie nativa de bromélia (*Tillandsia aeranthos*) que ocorre em ambientes urbanos no sul do Brasil.

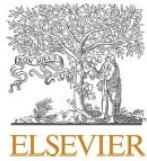
Objetivos específicos

- a. Revisar na literatura os aspectos da urbanização que geram respostas em espécies e comunidades de plantas em escala global;
- b. Caracterizar a diversidade e a estrutura genética de *T. aeranthos* usando marcadores moleculares do tipo AFLP, ao longo de dois gradientes de urbanização, utilizando uma amostragem na forma de transecto;
- c. Testar se há diferenciação alélica em populações amostradas ao longo dos transectos e se esta está correlacionada com o gradiente de urbanização;
- d. Detectar *outlier loci* ao longo dos transectos que possam estar potencialmente ligados à divergência adaptativa relacionada com as mudanças causadas pela urbanização;
- e. Buscar indícios dos efeitos da urbanização no sucesso reprodutivo, através da avaliação da produção e na viabilidade de sementes de populações de *T. aeranthos* ao longo de um gradiente de urbanização.

Capítulo III

*Urbanization driving changes in plant species and communities— A
global view*

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Urbanization driving changes in plant species and communities – A global view

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ABSTRACT

The urban landscape is becoming the environment most familiar to most of humanity, which has consequences for society, the environment, and biodiversity. Here, we present a systematic review of current research integrating several areas of urban ecology to evaluate how plants are responding to urbanization. We found that most studies were conducted in Europe and North America. The most represented biome was that of Temperate Broadleaf and Mixed Forests. The majority of studies reported negative consequences of urbanization. The Urban Drivers most commonly cited as responsible for changes in plant species and communities were Land Cover Change and Biotic Invasion. In general, urbanization reduces the richness of plant species and pollinators' availability. It also homogenizes the environment, promotes the invasion of non-native species, causes changes in phenological events, and presents difficulties for plant growth. However, some species show evidence of adaptation to these adversities through their phenotypic plasticity and the evolution of traits that make individuals resilient to the urban environment. Although it has been established that urbanization imposes novel selective pressures resulting in unique adaptations to city life, patterns of changes in biodiversity in response to urbanization can vary by region, biomes, city history, and the taxa studied. The Urban Drivers responsible for floristic responses work simultaneously by modifying the environment. Therefore, it is challenging to predict response patterns of plants under urban growth. It is necessary to outline strategies for continuous monitoring to document the progress of species in perpetuating themselves in the face of urbanization.

1. Introduction

Urbanization is a complex socio-economic process with numerous consequences for different levels of society, the environment, and biodiversity (United Nations, 2018). The urban landscape is becoming the most familiar environment for most of humanity, despite covering a small proportion of the Earth's surface (Niemelä, 2011). More than half of the world's people currently live in urban areas, with 55 % of the world's population residing in urban areas in 2018, compared with 30 % in 1950, reflecting a shift in the spatial distribution of populations from rural to urban areas (Parris, 2016; United Nations, 2018). Urban population growth is expected to continue, such that the world's urban population will reach five billion in 2028 and six billion in 2041 (United Nations, 2018).

Urbanization leads to primary (e.g., removal of existing vegetation and construction of urban infrastructure) and secondary (e.g.,

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habitat loss, fragmentation and isolation, climatic changes, pollution of air, water, and soil) processes that represent many challenges to the persistence of non-human species (Parris, 2016). Cities have distinctive characteristics due to the changes that happen to the land in urban areas. All ecosystems are affected by the same broad suite of state factors (Chapin et al., 2002), such as climate, substrate, resident organisms, relief, and the system's history. The urban ecosystem is no different. However, urban biotic communities are also highly influenced by anthropogenic impacts. Natural areas, agriculture, and forests are primarily replaced by predominantly built-up surfaces, changing cities' environment, which significantly impacts the physical environment, ecosystem processes, and ecology of organisms that live in cities (Grimm et al., 2008; McDonnell and MacGregor-Fors, 2016).

Biological introductions and human disturbance, combined with primary and secondary urbanization processes, impact species' births, deaths, immigration, and emigration rates. These combined factors lead to population growth or decline, which in turn may further alter intra- and interspecific interactions in different groups of organisms (Parris, 2016). Understanding the relative roles of abiotic, biotic, and anthropogenic filters that shape local communities provides a deeper understanding of community assembly, leading to practices that ensure the future of sustainable and biodiverse cities (Aronson et al., 2016).

The impacts of urbanization on biodiversity and ecosystems, especially on a global scale, are insufficiently understood. Previous work has established that urban areas impose novel selective pressures resulting in unique adaptations to city life (Niemelä, 2011). Although generalizations about the effect of urban areas on biodiversity are often made, actual patterns can vary by region, biomes, and city history (Müller et al., 2013; Niemelä, 2011). Furthermore, understanding which species are likely to benefit and which are likely to be detrimentally impacted will be important for biodiversity conservation and ecosystem services in an increasingly urbanized world (Williams et al., 2015). To improve our understanding of ecology in urban ecosystems, there is a need for comparative research worldwide (McPhearson et al., 2016).

The discipline of urban ecology has provided increasing evidence of how environmental changes affect species' population ecology, community structure, and ecosystem processes (Donihue and Lambert, 2015). Specific trends of living organisms' responses to urban stressors have been predicted based on prior knowledge of ecology and evolution (Johnson et al., 2015). Most of the recent studies in urban evolutionary ecology have focused on animals, particularly mammals, arthropods, and birds, and fewer studies have examined the effects of urbanization on plant evolution (Aronson et al., 2014; Johnson et al., 2015; Rivkin et al., 2019). Previous reviews on the topic of urban ecology have specified issues regarding the possible responses of plants to the biotic and abiotic changes that occur in urban areas (e.g., Alberti et al., 2017; Aronson et al., 2016; Cadotte et al., 2017; Eckert et al., 2010; Harrison and Winfree, 2015; Jochner and Menzel, 2015; Johnson et al., 2015; Rai, 2016; Williams et al., 2015, 2009). However, how the impacts of urbanization drive the evolution of living organisms in cities remains poorly understood (Donihue and Lambert, 2015; Johnson and Munshi-South, 2017; Rivkin et al., 2019).

Most studies examine only a few populations in one city (Johnson and Munshi-South, 2017). However, cities worldwide have different development histories and urbanization varies in intensity. Moreover, cities are inserted in different biomes and climates that can lead to a variety of responses in local biodiversity. The different contexts in which cities have developed their histories provide an excellent opportunity to understand the repeatability and pace of evolution in response to human activity. Considering this, we still need to understand more deeply the effects that this inevitable increase in urbanization will bring to the environment to facilitate the establishment of resilient and sustainable urban ecosystems (Johnson and Munshi-South, 2017; Niemelä, 2011).

In this article, we do a comprehensive systematic review of what has been found in the last eleven years of publications in urban ecology, focusing on plant species and communities worldwide. Our goals were to (1) summarize how urbanization drives plant changes in species and communities worldwide, (2) to understand whether plants respond to urban environments via phenotypical plasticity or through adaptation, (3) and to analyze whether Urban Drivers generate different responses based on the biome and urban density in plant species and communities. We also aimed to integrate several areas that fall under urban ecology to evaluate species plant and communities' structure changes in response to Urban Drivers.

2. Methods

We undertook a broad systematic review of peer-reviewed articles reporting data about the effects of urbanization in two ecological levels (species and communities) in vascular plants worldwide. We focused on studies and observations made completely in the field, comparing the results obtained between urban and non-urban areas (e.g., natural, agricultural, and green areas). We also included studies reporting comparisons between different time points in the history of increasing urbanization in various cities. We did not include studies exclusively performed with urban environment simulations in laboratory/greenhouse or those that evaluated flora that did not occur spontaneously in the study area.

From June 2020 to January 2022, we searched the literature in the Web of Science (WoS) database. The related search keywords were "urban plants" AND "species richness" OR "ecology" OR "genetic" OR "evolution" OR "adaptation" OR "pollinators" OR "reproduction" OR "dispersion" OR "physiology." We considered the matches to our search terms within the topic, title, keywords, and abstract. Studies meeting the inclusion criteria were: i) published in a peer-reviewed journal, ii) written in English, iii) reporting observational or experimental field data about effects of urbanization in plants, iv) published between 2010 and 2021. We recorded the studies in a spreadsheet, and relevant information was extracted and allocated into categories to summarize the methodologies used in the articles and the obtained results.

We classified the studies' methods according to the designed approach: urban–non-urban gradient, urban vs. non-urban (spatial comparison between urban and non-urban habitats), or temporal (changes over years of urbanization). We also recorded locations globally, considering the 14 terrestrial biomes of the world according to Dinerstein et al. (2017) (updated version of the Terrestrial Ecoregions of the World from Olson et al., 2001). When the city of the study was provided, we classified them as "megacity" if they have

more than 1 million inhabitants, in keeping with the United Nations' World Economic Situation and Prospects (United Nations, Department of Economic and Social Affairs, 2018), or as "small cities" if they have fewer than 1 million inhabitants. We also recorded the variables analyzed in each study. We categorized them into major areas to overview the main variables studied over the past eleven years. The variables allowed us to identify the following principal major areas reviewed: "community traits" (e.g., species richness and abundance, vegetation cover, demography, non-native species richness, herbivory, species conservation status), "physical environment" (e.g., land use, temperature, precipitation, evapotranspiration, soil properties, air and soil pollution, habitat type, percentage of impervious surfaces, carbon dioxide [CO₂] concentrations), "morphological traits" (e.g., diameter at breast height, leaf area, shape, number of leaves, size), "physio-chemical traits" (e.g., leaf content [carbon and nitrogen], biomass, photosynthesis, stomatal conductance, thermal and shade tolerance, gas exchange measurements), and "reproductive biology" (e.g., phenology [flowering], flower morphology, pollination, reproductive success, seed dispersion, germination, and fruiting).

The responses of plant species and communities to urbanization were categorized according to the following Urban Drivers: biotic invasion, climate, human activities, land cover change, and pollution (Alberti et al., 2017; Aronson et al., 2016; Piana et al., 2019; Pickett et al., 2011). Biotic invasion represents the introduction of non-native species in the habitat. Climate refers to climate changes in urban areas, especially warming. Human activities are how humans directly act on urban biodiversity (e.g., through gardening practices). Land cover change refers to fragmentation and land conversion, and pollution is attributed to environmental contamination through soil and air pollutants. These responses were classified as negative (urban habitats negatively affect fitness), neutral (when species' and communities' responses do not differ between urban/rural habitats), or positive (species and communities are successful in the urban environment, maintaining the ecological balance). If a study found several responses, we considered each one individually according to the abovementioned criteria.

3. Results

The number of studies evaluating plant responses to urbanization has increased over the past ten years (Fig. 1). We found 171 studies that fit our selection criteria. Most of the studies were carried out in temperate biomes (113), with Temperate Broadleaf and Mixed Forests most represented with 102 studies (Fig. 2). Most studies took place in Europe and North America (60 and 43, respectively). Forty studies were conducted in Asia, 14 in South America, eight in Africa, and only seven in Oceania (Fig. 2).

Most of the studies (89) used the urban–non-urban gradient to describe how urbanization drives changes in species and communities. Forty-two studies used a simple comparison between urban and non-urban habitats, and eighteen used the temporal approach to explain how urbanization is changing species and communities over the years. In addition, 22 studies used combinations of these approaches. Most of the studies (103) were conducted with comparisons in different plant communities, and 68 studies analyzed specific species. Thus, analyses involving general community traits are among the most studied. Further details on the methodologies used in the studies to determine plants' responses to urbanization are found in Supplementary Table 1.

The most commonly cited Urban Drivers responsible for changes in plants in the reviewed literature (Fig. 3) were land cover change (129) and biotic invasion (56). Pollution was the least cited (Fig. 3). Overall, the studies identified varied responses in plants, often showing the same species or community demonstrating beneficial, neutral, or harmful responses, depending on which major areas were analyzed (Supplementary Table 2). However, most studies (133) reported negative responses (Supplementary Table 2). Table 1 summarizes how plants are responding to urbanization.

4. Discussion

4.1. Urbanization and urban drivers

The responses of plants to urbanization can be complex and varied (Table 1; Supplementary Table 2). More than one Urban Driver may be responsible for some community and plant traits changes, or several different changes may result from one driver. The

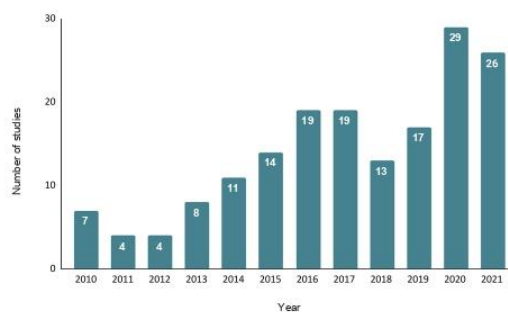


Fig. 1. Number of studies relating changes in plant species and communities in response to urbanization between 2010 and 2021.

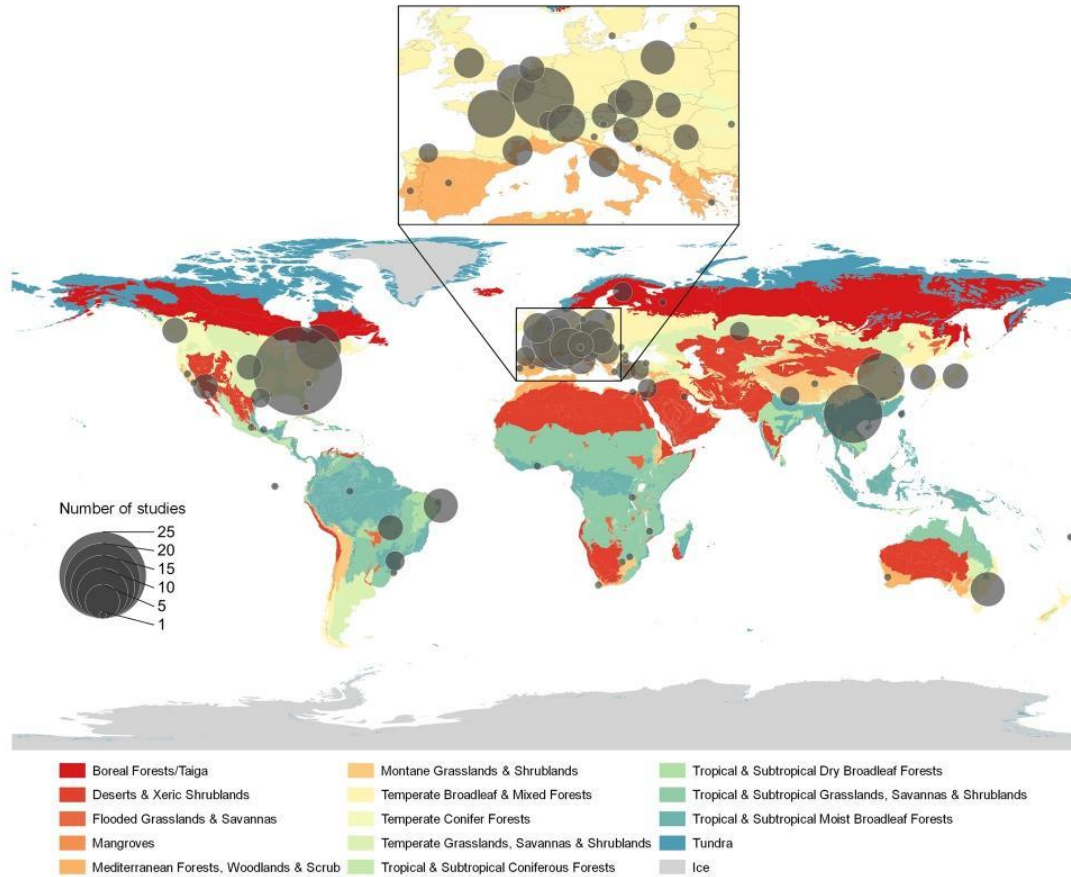


Fig. 2. Number of studies relating changes in plant species and communities in response to urbanization within their locations on biomes according to Dinerstein et al. (2017) (updated version of the Terrestrial Ecoregions of the World from Olson et al., 2001).

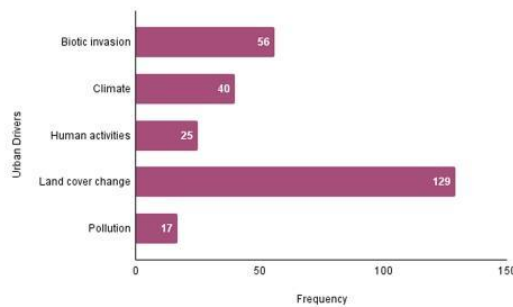


Fig. 3. The frequency at which Urban Drivers are held responsible for changes in plant species and communities based on the literature review from the last eleven years.

consequences are a network of responses connected to various drivers, making systematic cause-and-effect classification through frameworks in urban environments difficult (Aronson et al., 2016; Williams et al., 2015). We found that urbanization mainly negatively affects plants compared with neutral and positive responses, both in megacities and small cities. They result from a single driver or by combination among different Urban Drivers.

Table 1

Negative, neutral, and positive examples of responses of plants to six Urban Drivers. The data was compiled based on a literature review from the last eleven years of publications of the effects of urbanization on plant species and communities.

Urban Drivers	Negative	Neutral	Positive
<i>Land cover change</i>	Lower plant cover; prevalence of abiotic pollination and dispersion; lower ability to reproduce sexually; reduction of dispersal ability between fragments; lower reproductive success; higher proportions of non-native, generalist, and disturbance-tolerant species	Species richness remains stable; reproduction modes did not change in response to urbanization	Urbanization of grasslands areas keep high nature conservation value through the favoring of insect-pollinated species; adaptations to attract more pollinators; reproduction modes changes in response to urbanization; biotic differentiation
<i>Climate</i>	Higher abundance of non-native species adapted to warmer conditions; phenological events start earlier; asynchrony between the phenology of plants and pollinators; decrease in species richness; changes in photosynthetic rates; lower water use efficiency	No changes in the timing of phenological events	Thriving of native thermophilous species; urban areas as a refuge for endangered species with affinities for hot and dry surfaces
<i>Pollution</i>	Decrease in species richness; delays in phenology; higher leaf nitrogen concentration; lower content of chlorophyll-a; associated arthropod biota affected through the reduction in palatability; higher weed coverage	Inconsistent changes in leaf morphology	More species with higher affinities to nutrient soil content
<i>Human activities</i>	Facilitation of the spread of non-native plant species by roads and railways; increase in ornamental non-native species in urban gardens, with lower functional richness; beneficial of human dispersed plants; higher abundance of species with lower conservation value; decrease in species richness	–	Human preferences for showy flowers may are good for pollinators in urban areas, favoring animal-pollinated plants
<i>Biotic Invasion</i>	Loss of species richness by the colonization of non-native species phylogenetically similar to the resident species; reduction in the diversity of native species; evolution of non-native species to compete with natives; pollinators preference for non-native species; species turnover;	Native species keeping fitness front invasion of non-native species	Increase of total plant species richness

4.2. Urban Drivers and their effects on plant species and communities

4.2.1. Land cover change

When it comes to urbanization, fragmentation due to land cover change is the central axis of biodiversity loss. A considerable amount of the reviewed literature described decreased species richness in plant communities related to land cover change (Abd El-Wahab, 2016; Albrecht and Haider, 2013; Anderson et al., 2020; de Araújo et al., 2021; Aronson et al., 2015; Bigirimana et al., 2011; Cochard et al., 2017; Deák et al., 2016; Dolan et al., 2011; Fekete et al., 2020; Glisic et al., 2021; Güler, 2020; Heneidy et al., 2021; Kalusová et al., 2019; Kolbe et al., 2016; Kumli et al., 2021; Lopez et al., 2018; Lowry et al., 2020; Melliger et al., 2018; Nero, 2019; Peng et al., 2019; Planchuelo et al., 2020a; Salgado et al., 2021; Silva-Junior et al., 2018; Tian et al., 2015; du Toit et al., 2020; Vakhlamova et al., 2014; Vallet et al., 2010a; Wang et al., 2020a; Wang et al., 2020b; Wu et al., 2013; Yan et al., 2019; Zhang et al., 2016) - Supplementary Table 2). The disturbance created by land cover changes, fragmenting landscapes from native vegetation to areas covered by impervious surfaces, homogenizes the physical environment. In consequence, the urbanization process creates similar environments that select identical traits and life histories in both native and non-native species, causing a reduction in species richness and shifts in the community's composition (species turnover) (Aronson et al., 2016; Brice et al., 2017, 2016; Dolan et al., 2017; Freitas et al., 2020; McKinney, 2006; Paquin et al., 2020).

Studies with functional-trait approaches have demonstrated specific features of plants selected by the urban environment leading to habitat homogenization since low functional-trait diversity in communities was detected in several cases (Anderson et al., 2020; Concepción et al., 2017; Melliger et al., 2018; Milanović et al., 2021; Nock et al., 2013; Ribeiro et al., 2019; Trentanovi et al., 2013). Some of the responses to habitat homogenization were a higher presence of generalist and disturbance-tolerant species (Everingham et al., 2019; Huang et al., 2013; Mccune and Vellend, 2013; Oliveira et al., 2020; Yang et al., 2021), ruderal species (Bigirimana et al., 2011; Wang et al., 2020a, 2020b; Zhang et al., 2020), and pioneers (Concepción et al., 2015; Nero, 2019; Pennington et al., 2010) as well as a decline in phylogenetic richness (Cui et al., 2019; El-Barougy et al., 2021; Knapp et al., 2017; Lopez et al., 2018; Silva-Junior et al., 2018). In these studies, we found a convergence of selected traits in urban habitats related to loss of animal-related characteristics (e.g., shifts to self- and wind-pollination and dispersal), fast growth rates (e.g., short stature and small seeds), long flowering periods, and demanding resource-use strategy (e.g., softer wood, larger leaves, lower leaf mass per area). Reductions in the number of functional groups of organisms decrease the efficiency by which whole communities capture biologically essential resources, which is

acknowledged as critical for community stability and functioning (Cardinale et al., 2012). These findings raise that analyzing functional traits in plants is more potent in capturing species' response to environmental filtering driven by urbanization (Anderson et al., 2020; Dolan et al., 2017) beyond just tabulating changes in species richness.

At the same time, some studies revealed that native plant communities could be resilient to fragmentation, keeping their diversity (Fekete et al., 2020; Hahs and McDonnell, 2013; Landis and Leopold, 2014; Lechuga-Lago et al., 2017; Santos et al., 2016; Schwoertzig et al., 2016). The persistence of native species in urban areas shows us that we have alternatives to face the consequences of urbanization. The city's structures can provide favorable and heterogeneous environments for stress-adapted native species and even endangered species (Dallimer et al., 2012; Fekete et al., 2020; Heneidy et al., 2021; Paquin et al., 2020; Planchuelo et al., 2020b; Qian et al., 2020; Schmidt et al., 2014; Schmiedel et al., 2015; Sonti et al., 2021; Trammell et al., 2020). Investigating the functional traits and ecological strategies of native species adapted to fragmented environments can help establish conservation priorities, using local native adapted species for urban greening purposes. Also, forests and protected areas close to urban environments have been essential in maintaining and sending propagules of native species to fragmented areas (Blood et al., 2016; Davis et al., 2015; Gulezian and Nyberg, 2010).

Because of low habitat fragment connectivity in urban environments, insect-pollinated species can experience a lower quality of pollinator services in terms of decreased visitation rate and the lowered ability of pollinators to carry pollen between fragmented populations (Bartlewicz et al., 2015; Geslin et al., 2013), bringing different consequences for populations and communities. In most cases, both self-compatible and self-incompatible plants showed a decrease in reproductive success due to the reduction of the variety of pollinators, their low effectiveness, and low visit frequency, often reducing the seed set (Hou et al., 2019; Irwin et al., 2018; Leong et al., 2014; Lhotte et al., 2014; Oliveira et al., 2019). *Teucrium pseudochamaepitys*, an endangered species in Southern France, experienced low reproductive success, despite effective pollination in urban habitats (Lhotte et al., 2014). Lhotte et al. (2014) showed a lower diversity of pollinators, with *Apis mellifera* ensuring 97 % of pollination. They demonstrate that changes in land use threaten the short-term persistence of populations due to competition.

However, other studies suggested that pollinators may also be mobile between urban fragments (Filiz et al., 2015; Kobayashi et al., 2018; Van Rossum, 2010; Verboven et al., 2014). Verboven et al. (2014) analyzed the pollinator frequency in *Trifolium repens*, a species pollinated mainly by generalist bumblebees. Generalist species with large foraging ranges were previously found not to be strongly affected by urban land use (Bates et al., 2011). This finding reinforces that plant species that are not supported by these generalist pollinators are not the most suitable species for conservation efforts in cities.

Species that do not depend on pollinators for reproduction can maintain their reproductive success when performing selfing under conditions of lower pollinator availability (Ushimaru et al., 2014). The ability to tolerate fragmentation with traits that allow reproduction by selfing has also been identified by analyzing genetic diversity in *Viola gypoceras* in Kyoto, Japan (Toma et al., 2015). This study found no significant difference in allelic richness between the urban fragmented and suburban forests.

Genetic studies can be valuable for describing how plant populations have responded to habitat fragmentation due to land cover change. Molecular markers described limited gene flow between urban and rural populations (Bartlewicz et al., 2015; Emel et al., 2021; Wodkiewicz and Gruszczyńska, 2014) detected through high genetic structure between populations. On the other hand, there can be a failure to detect a genetic response to habitat fragmentation due to insufficient time having elapsed since fragmentation, as seen by Delnevo et al. (2021). Despite the current intense fragmentation, they found similar levels of genetic diversity across populations and a weak spatial genetic structure in *Conospermum undulatum* in Western Australia, highlighting the importance of considering the historical habitat dynamics when investigating fragmentation consequences in long-lived plants (Delnevo et al., 2021). These authors related that the currently fragmented populations of *C. undulatum* were part of a continuous population 70 years ago, resulting in the present weak genetic structure.

Knowing the reproductive system of a species and how populations respond to fragmentation through genetic studies is an effective way of evaluating the success of a species in the face of urbanization. Studying plant species with alternatives to biotic pollination and species pollinated by animals that can move between fragments is essential to establish which species are suitable for creating green areas. Above that, maintaining protected forest areas close to cities would be a more effective way to maintain more specific plant-pollinator relationships, maximizing species richness and ecosystem stability.

4.2.2. Climate

Fragmentation only is often insufficient to explain plant species' distributions in urban landscapes (Williams et al., 2009). Fragmentation in urban habitats includes the introduction of materials that are not biologically active covering the soils in urban habitats, allowing additional drivers to be responsible, on a smaller or larger scale, for decreasing the number of species (Grimm et al., 2008; McKinney, 2002). These drivers include climate (which increases the phenomenon of the Urban Heat Island [UHI]) and soil and air pollution (Pickett et al., 2011). These particularities associated with urban areas significantly impact species in anthropogenic habitats (Williams et al., 2009). Indeed, increased temperatures in cities were related to reduced species richness by filtering out species not adapted to warmer habitats (Albrecht and Haider, 2013; Chen et al., 2014; Concepción et al., 2017; Yu et al., 2021). For example, Chen et al. (2014) demonstrated that the increase in mean annual temperature over the past half-century in Harbin, China, caused a decrease in temperate species and increased in tropical species over the years.

One of the best bioindicators for anthropogenic climate change is phenology. Studies on urban phenology helped to detect UHIs. There is a strong relationship between changes in the timing of natural events, such as leaf unfolding, flowering, fruit ripening, or leaf coloring and fall and changes in regional temperatures (Jochner and Menzel, 2015). Studies at a spatial scale detected advanced and more extended phenological events (Cochard et al., 2019; Davis et al., 2016; Fisogni et al., 2020; Kondratyeva et al., 2020; Massetti et al., 2015; Oliveira et al., 2019; Su et al., 2019; Yakub and Tiffin, 2017). Long-term studies that focused on more prolonged periods of

observations (Fitchett and Raik, 2021; Lee, 2017; Lindh et al., 2018; Neil et al., 2010; van Vliet et al., 2014; Xingyuan et al., 2016), as well as those that combined both temporal and spatial analyses also detected earlier phenology events (Comber and Brunson, 2015; Jeong et al., 2011; Li et al., 2017; Qiu et al., 2017). Analyses involving a large time scale associated with data between urban and non-urban populations can be useful for comparing the period in which there were changes in phenology and the events of expansion of urbanization in cities.

In contrast, some studies did not find significant changes in phenology in urban gradients (Jochner et al., 2013, 2012; Zipper et al., 2016). The authors suggest that other specific characteristics of the regions where the cities are located, such as altitude, humidity and vegetation type, can influence climatic conditions, making it difficult to analyze and interpret urban phenology. Santangelo et al. (2020a) reported later phenology in *Trifolium repens*. However, they suggest that changes in the biotic community (e.g., insects) or other components of the abiotic environment (e.g., soil moisture) were responsible for this observed pattern. Other factors that interact with temperature changes can make it challenging to analyze results. Therefore, detailed investigations of the system studied are needed to fully understand the effect of urban environmental conditions on plant phenology (Jochner and Menzel, 2015).

Little is known regarding vegetation changes in phenology affecting plant-animal interactions. Changes in flowering phenology lead to a mismatch between the flowering period and pollinators' activity (Fisogni et al., 2020), leading to a possible reduction of pollination services in urban areas and a reduction in reproductive success. Plants may respond differently from pollinators to climatic conditions; therefore, it is suggested that phenological studies focusing on specific species should consider the behavior of pollinators and how they respond to climate change. On the other side, Davis et al. (2016) described increased flower productivity in *Angophora costata*, *Eucalyptus pilularis*, and *Corymbia gummifera* within urban landscapes due to more extended flowering periods, leading to a higher abundance of nectarivorous parrots in Sydney, Australia. More extended periods of phenological events in urban vegetation result in more food resources for associated animals in the form of nectar and pollen (Jochner and Menzel, 2015). This shows that cities can maintain species that have good productivity in warmer habitats, providing resources that attract local animals and increasing the productivity of the habitat.

In addition to higher temperatures attributable to UHI, climate change can lead to increased carbon dioxide and ozone levels in urban areas and greater drought stress experienced by plants (Barradas and Esperon-Rodriguez, 2021; Calfapietra et al., 2015). Zipper et al. (2017) demonstrated that UHIs significantly increase evapotranspiration demand associated with variability in impervious cover, with consistent relationships from year to year in Madison, United States. Lahr et al., (2018, 2015) demonstrated direct negative effects of temperature and water availability on photosynthesis.

Conversely, Searle et al. (2012) did not find changes in the photosynthetic capacity of foliage in *Quercus rubra* driven by urbanization in New York, United States. Climate change is a constant threat to biodiversity, increasing species' vulnerability. Knowing the vulnerabilities of species can help decision-makers plan conservation actions that minimize the effects of global warming on plant productivity.

4.2.3. Pollution

High levels of soil and atmospheric pollution have potentially adverse impacts on the growth and development of plants (Rai, 2016). Different consequences were found when analyzing the effects of pollution in urban areas. Contaminated soils also have been described as the cause of reduced species richness and structural injuries (Bouraoui et al., 2019; Huang et al., 2013; King and Hovick, 2020). The high concentration of soil contaminants (Cadmium, Copper, and Zinc) and salts presented in the cited studies above are detrimental to plant development, causing a reduction in growth by accumulating in roots, stems, and leaves (Kabata-Pendias, 2004). Air pollution was associated with a decrease in the quality of seeds (Turmukhametova and Shadrina, 2020) and affected plant growth, seen through changes in the size and shape of the plant parts studied by Su et al. (2021) and Vujić et al. (2015). Jochner et al. (2015) found an association between delays in phenology and the presence of air pollutants. The authors indicate that this association might be attributable to other environmental conditions statistically correlated with pollution. Because they excluded the influence of air temperature in their analyses, other factors altered by pollution in urban areas, such as radiation and soil nutrients, may be related to the delay in phenology (Jochner et al., 2015).

Chlorophyll measurement is an important tool for evaluating the effect of air pollutants on plants, as it plays an essential role in plant metabolism. Reductions in chlorophyll concentration are usually associated with air pollution (Rai, 2016). Molnár et al. (2018) demonstrated lower chlorophyll-a content in *Celtis occidentalis* leaves, proving that this species is an effective indicator of anthropogenic emission of air pollutants. In the same line, Xiao et al. (2021) showed decreased photosynthetic rate and total chlorophyll contents in the canopies in Guangzhou, China. Still, herbs and shrubs responded with an increase to the same parameter (Xiao et al., 2021).

Roadside plantations are expected to combat air pollution since trees can act as a sink for CO₂ by fixing carbon during photosynthesis (Singh, 2021). The deposition of particulate matter on the leaves interrupted stomatal leaf exchanges by

reduced CO₂ assimilation rate (photosynthesis) and the exchange of water (transpiration) in *Alstonia scholaris*, *Grevillea robusta*, and *Mangifera indica* (Singh, 2021; Singh et al., 2020). However, these species presented modulations in physiological and biochemical processes for acclimatizing or adapting to the altered environment, contributing to future species selection to combat air pollution in cities (Singh et al., 2020).

Pollution was the least cited urban driver among the studies evaluated. The rapid growth of cities has dramatically increased emissions of pollutants with heavy metals in the soil and toxic gases in the air, decreasing the quality of habitat in urban centers. More studies need to be carried out using pollution as one of the parameters of comparison between communities and plant species, since pollution is very present in cities, especially those in developing countries.

4.2.4. Biotic invasion

Apart from the higher similarity in native species composition among cities, seen through the reduction of species richness, studies described a spread of non-native species in urban habitats (Bigirimana et al., 2011; Blouin et al., 2019; Knapp et al., 2017; Lososová et al., 2016; Oliveira et al., 2020). This process of replacing localized native species with increasingly widespread non-native species promotes biotic homogenization, beyond habitat homogenization. Non-native species may enrich local biodiversity, but global diversity is decreased by the extinction of local species that are lost to the global species pool (McKinney, 2006).

The invasion of non-native species into new regions provokes researchers' concern because of perceived threats to agricultural productivity, native biodiversity and ecosystem functioning, and human aesthetics and wellbeing. Cadotte et al. (2017) observed that the alterations of the physical environment in urban habitats offer unique opportunities for these invasions. They create a unique combination of environmental conditions that do not exist in unmodified landscapes. Here, we found that land cover change is one of the most significant opportunities for the gain of non-native species, as seen through their increase in proximity of urban centers (Atasoy et al., 2018; Blood et al., 2016; Chimaimba et al., 2020; Dallimer et al., 2012; Fornal-Pieniak et al., 2020; Greene and Blossey, 2014; Kalusová et al., 2019; Kühn et al., 2017; Landis and Leopold, 2014; Malkinson et al., 2018; Paquin et al., 2020; Park et al., 2021; Pellegrini et al., 2021; Pennington et al., 2010; Schmiedel et al., 2015; Tew et al., 2021; Tordoni et al., 2017; Vakhlamova et al., 2014; Yan et al., 2019), and with the urbanization process over the years (Celesti-Grapow and Ricotta, 2021; Kopel et al., 2015; Wirth et al., 2020; Yu et al., 2021). Furthermore, climate change is crucial for establishing non-native thermophilic species favored by warm conditions typical of urban habitats (Géron et al., 2021; Schmidt et al., 2014; Soltysiak, 2020). Similarly, soil modification by higher quantities of nutrients and pollutants was related to an increase of non-native species (Grella et al., 2018; Lopez et al., 2018).

Cadotte et al. (2017) also infer that cities are islands of reduced competition or offer an escape from natural enemies. Moreover, other authors describe higher competitive skills in non-native species depending on their inserted context (Fukano et al., 2020). Ruderal species that use the competitive ruderal (CR) strategy allocate most of their nutrient supply to growth and reproduction to better compete for space and achieve wide distribution (Chen et al., 2014). Disturbed surfaces support the establishment of non-native species because other species have low competitive ability (Deak et al., 2016). Nitrophilic species have a more remarkable competitive ability due to the high presence of nitrogen in urban soils and thus can exclude less nitrophilic species (Küng and Hovick, 2020). Zeeman et al. (2017) demonstrated a significant shift in the composition of urban grasslands towards taller plants within non-native species, which is correlated with competitive vigor. In a temporal analysis, Cui et al. (2019) suggest that similar ecological niches between native and invasive species lead to a decrease in the competitive power of native species due to the lack of natural enemies for invasives in the local urban ecosystem.

Furthermore, Cadotte et al. (2017) observe that high immigration rates of non-native species are facilitated by humans (see Section 4.2.5). For example, *Carpobrotus edulis*, a succulent plant native to South Africa, has been intentionally introduced globally as an ornamental to prevent soil erosion in coastal areas in Galicia, Spain. The higher presence of *C. edulis* in urban coastal dunes increases soil impacts, allowing for the establishment of the native but ruderal, *Scolymus hispanicus*, which is not adapted to the typically limiting conditions of coastal dunes (Lechuga-Lago et al., 2017).

The performance of these non-native species in the novel habitats will define their persistence in becoming invasive species. They need to deal with a suite of biotic interactions beyond just competition. In particular, they must interact with consumers, pathogens, and mutualists (Cadotte et al., 2017); therefore, we should pay attention to possible changes in the communities' dynamics in urban habitats. For example, in Florida, *Ficus microcarpa* trees were planted as ornamentals as early as 1912. Today, adults are seed sources for fig-eating birds that disperse this invasive species and make it difficult to control the species' abundance (Caughlin et al., 2012). Non-native trees in urban habitats shelter fewer invertebrates, being a possible stronger driver of invertebrate declines in urban areas in Sweden (Jensen et al., 2021). The invasive shrub *Cytisus scoparius* (Scotch broom) is under natural selection by pollinators for increased flower size, but only in urban populations, in Lacey-Olympia, United States. This natural selection by pollinators could result in an invading species' adaptive evolution into a new pollination niche (Bode and Tong, 2018).

We can see the biotic invasion as an urban driver by itself, but it is strongly influenced by the other drivers described. The adverse conditions provided by the urban habitat are very favorable for the spread of non-native species and are one of the greatest threats to local biodiversity. This makes biotic invasion one of the priorities for continuously monitoring populations of exotic species already present in cities and efforts to reduce the spread of new exotic species.

4.2.5. Human activities

Human-assisted "intentional" migration is a major conduit for non-native species that become invasive, and the impact of invaders on native biodiversity remains an area of intense research (Van Kleunen et al., 2015). People move among cities and introduce organisms for a variety of reasons. During the European colonization of Burundi and Brazil, for example, many European and tropical ornamental species of different biomes from local species were introduced for landscaping purposes (Bigirimana et al., 2011; Oliveira et al., 2020). In the contemporary world, the use of species for horticultural interest (Dolan et al., 2011; Greene and Blossey, 2014) and ornamental and gardening practices (Dolan et al., 2017; dos Santos et al., 2020; Gaggini et al., 2017; Löki et al., 2019; Ranta and Viljanen, 2011) are other forms of human activities that introduce exotic species. Human activities facilitate dispersion by roads and railways (Concepción et al., 2016; Gaggini et al., 2017; Rivkin et al., 2021; Skultety and Matthews, 2017; Štajerová et al., 2017; Vakhlamova et al., 2016). Vehicles are an important vector for plant dispersal; thus, rails, roads, rivers, or canals can play as corridors for the spread of plants, resulting in high propagule pressure of exotic species (Ricotta et al., 2014).

Environmental education works involving the dissemination of knowledge of local species should be implemented to prevent the entry of new exotic ornamental species. In addition, encouraging the use of native species for ornamentation is important to restore the productivity of the local ecosystem, increasing resources for the animal community associated with plant species.

4.3. Does urbanization lead to phenotypic plasticity or adaptation in plants?

The drivers that impact fitness in plant communities can be challenging to discern. Urbanization includes environmental change along multiple interacting dimensions that can dramatically increase the complexity of environments to which populations must adapt. Understanding how traits may diverge with urbanization in response to Urban Drivers is necessary to understand the evolution of organisms in urban environments (Rivkin et al., 2019; Santangelo et al., 2022). Here, we have demonstrated that the number of studies describing how Urban Drivers are responsible for changes in plant species and communities has increased in recent years.

Species have evolved phenotypic traits in their historic ranges that might confer an ecological advantage allowing for colonization and establishment in urban environments (Rivkin et al., 2019). For example, five of the six studies with graminoid communities showed positive responses to urban environments. These studies confirmed that this group of plants might be highly adapted to this habitat type. Graminoids have assured insect pollination and can persist in disturbed soils by producing small, durable seeds (Albrecht and Haider, 2013; Beal-Neves et al., 2020; Cochard et al., 2017). Other traits, such as the capacity to grow taller individuals and increase vegetative reproduction, facilitate access to more resources and allow a species to spread (Cochard et al., 2019; Zeeman et al., 2017). Grassland ecosystems are evolutionarily related to disturbance regimes that maintain the high species richness of these systems under appropriate intensity and frequency (Overbeck et al., 2005). Another group that can take advantage of urbanization's new conditions, as Duffy and Chown (2016) observe, are the C₄ plants. Because C₄ plants are organisms adapted to warm environments, through the increase of photosynthetic activity, it is possible that native plants of this group will not be harmed by the global phenomenon of Urban Heat Islands.

Environmental changes induced by urbanization often select plants with specific traits that enhance plant persistence, competition, or resource retention (Ilyas et al., 2021; Murray-Stoker and Johnson, 2021; Song et al., 2019; Vallet et al., 2010b). These authors reported that plants in the urban forests presented an acquisitive strategy through a higher specific leaf area. Higher leaf nitrogen was also related to urban plants (Nikula et al., 2010; Song et al., 2019). Vasconcellos et al. (2019) demonstrated through dendrochronological characteristics of *Ceiba speciosa* growing in urban areas of Rio de Janeiro, Brazil, that this species is plastic and stress-tolerant under polluted conditions. Pollutant levels are lower during the rainy season, and microclimatic conditions may influence radial growth relationships. The authors showed that urban trees have a more immediate growth response to rain than rural ones.

Little is known about the phenotypic changes induced by pollinator and mate limitations on reproductive traits in disturbed urban plant populations (Eckert et al., 2010). For example, *Commelina communis*, an annual species in the metropolitan area of Osaka-Kobe, Japan, showed increased reductions in traits promoting outcrossing under pollen-limited conditions induced by urbanization (Ushimaru et al., 2014). The authors argue that the observed floral diversity across the urbanization gradient may not be driven by urbanization itself but by urbanization-induced pollinator-limited conditions. Larger flowers were described by Santangelo et al. (2020a) in *Trifolium repens*, associated with near-complete turnover of pollinator morphological groups along the urbanization gradient in Toronto, Canada. Hou et al. (2019) described shifts in flower structures in *Gentiana dahurica*, which demonstrated plasticity in producing longer flowers as urbanization intensified. These shifts may have enhanced the floral display and pollinator attraction to ensure reproductive success. However, pollinator visits to the urban area were insufficient to ensure species' reproductive success. Irwin et al. (2018) showed that pollination was associated with the selection for larger floral display sizes in *Gelsemium sempervirens*. However, there is little difference in phenotypes between urban and non-urban sites. Together, these results provide important insights into the possible adaptive evolution of reproductive traits in response to pollinators' limitations in urban areas.

Rivkin et al. (2021) showed how urbanization has the potential to lead to novel selection pressures on ecological interactions by analyzing Darwin's finches and its essential food resource, *Tribulus cistoides*, in the Galápagos Islands. *T. cistoides* presents a mericarp defended by sharp spines with variations in their morphology. Rivkin et al. (2021) found that urbanization imposes phenotypic selection against small mericarps, potentially leading to the evolution of larger fruits.

A recent study has used the globally distributed plant white clover (*Trifolium repens*) as a model for examining evolutionary responses to urbanization (Santangelo et al., 2020b). This species exhibits a Mendelian polymorphism that produces hydrogen cyanide (HCN), an antiherbivore defense trait. This trait has been shown to exhibit adaptive evolution to winter temperature gradients (Santangelo et al., 2020b; Thompson et al., 2016), selecting against cyanogenesis due to reduced snow cover in cities. Thompson et al. (2016) showed no evidence that herbivory is likely to explain the observed urban-rural clines in cyanogenesis. Johnson et al. (2018) also demonstrated that populations did not exhibit changes in genetic diversity with increasing urbanization, indicating that genetic drift is unlikely to explain urban-rural clines in HCN frequency. Analyzing changes in the frequency of genotypes that produce HCN and the frequency of the alleles at genes that epistatically interact to produce HCN, Santangelo et al. (2020b) demonstrated that urban environments often select for similar phenotypes. However, different selective agents and targets underlie the evolutionary response in different cities.

Another model species that has received attention with descriptions of different patterns of natural selection is *Crepis sancta*, a common ruderal winter annual in southern France. The species can produce both dispersing and non-dispersing seeds (Imbert, 1999). Dubois and Cheptou (2017) demonstrated that fragmented urban populations of *C. sancta* that occur in small patches surrounded by an unsuitable matrix, such as asphalt and concrete, produce a higher fraction of non-dispersing seeds. This selection pattern had been observed previously (Cheptou et al., 2008) and is consistent with the higher cost of dispersing seeds in more fragmented habitats. Through neutral microsatellite markers, Dubois and Cheptou (2017) accessed the levels of genetic diversity among populations and traits related to plant size. They observed that the substantial quantitative variation among populations for size was independent of fragmentation and urbanization, reflecting the patterns of neutral genetic variation or the role of other selective agents.

Another interesting trait that may be passing through natural selection in *C. sancta* is the pattern of flowering phenology. Delayed phenology was observed by Dubois and Cheptou (2017) and Lambrecht et al. (2016). Both studies suggest that natural selection in

urban habitats selects delayed flowering, allowing slower-growing plants to gain enough energy to reproduce or reflect the lower diversity of flowering plants in fragmented urban habitats. Lambrecht et al. (2016) also observed increased plant size in the urban habitat. They suggest that *Crepis* plants may benefit from growing and developing leaves over a more extended period, accumulating more carbon before the onset of reproductive resource demands, or increased respiration during warmer nights. In contrast, species demonstrated relaxation of selection on reproductive traits linked to attractiveness (Dubois and Cheptou, 2017).

Despite these promising results, clear examples of the effects of urban environments on evolution by natural selection exist in few urban systems. More studies that compare genetically based phenotypic divergence and local adaptation between urban and non-urban areas are needed to build a mechanistic understanding of how natural selection operates in urban systems (Rivkin et al., 2019). For example, genomic data have revealed that urban populations were more closely related to individuals from other urban populations than to geographically proximate rural areas (Yakub and Tiffin, 2017). This result suggests that selection in urban environments favors specific traits that can drive adaptation and shape population structure.

Human beings have appeared as the major selective agent in the process of evolution in urban environments, either indirectly through the expansion and development of cities leading to habitat fragmentation and further consequences, as well as directly through agriculture and gardening practices. It is necessary to list more model species for these studies on a global scale, involving genomic analyses and functional, physiological, and reproductive traits. The integration of this information can provide feedback to help slow the degradation of biodiversity in cities and to understand how urbanization drives evolutionary diversification in plants.

4.4. The role of regional particularities and urbanization in floras worldwide

It is evident that urbanization has many negative consequences for plants and that the environmental changes caused by urbanization are the same worldwide (Niemelä, 2011). Still, the intensity with which organisms suffer from these changes can vary and depend on the context in which cities are inserted. Cities are embedded in varied biogeographical regions and landscape settings. A global viewpoint is necessary to understand the processes that shape urban biodiversity (Werner, 2011).

Megacities are more vulnerable to natural and man-made disasters due to their higher concentrations of people (Kraas, 2008). We found that seven of the nine studies that evaluated how pollution drives changes in plants in megacities showed negative results. In smaller cities, we found five studies that described the effects of pollution, with four of them relating to the consequences of soil pollutants. Overall, we found that the comparisons between smaller cities and megacities do not demonstrate different proportions of negative, neutral, and positive results in general responses of plants to urbanization (Fig. 4). It is essential to consider that even small cities can significantly negatively impact their local biodiversity.

The publications of the last eleven years demonstrate that most studies evaluating the effects of urbanization on biodiversity are still concentrated in the Northern hemisphere, which means our knowledge about the patterns exhibited in plants is biased (Werner, 2011).

Cities are located in different biomes of the world that are likely to have floras differentially pre-adapted to persistence in urban environments. Williams et al. (2009) predicted stronger filtering effects in environments where the natural biome differs more dramatically from that found in cities (e.g., those in tropical forest environments vs. those in temperate grassland environments). Alternatively, they predict that fragmentation effects may be particularly evident in tropical environments where a high fraction of native species heavily depends on biotic interactions for pollination and dispersal, leaving them more vulnerable to isolation. Indeed studies in tropical/subtropical biomes showed communities with fewer species that are dispersed by animals compared with species that have other modes of dispersion, such as dispersion by humans and abiotic dispersion in urban areas (Guerra et al., 2017; Nero, 2019). These findings are consistent with those reported by Oliveira et al. (2019), who stated that the endangered brazilwood tree

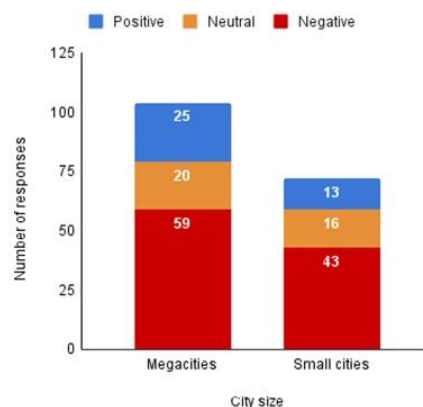


Fig. 4. Number of negative, neutral, and positive responses separated by their occurrences in megacities (more than 1 million habitants - according to the United Nations' World Economic Situation and Prospects) and small cities.

(*Paubrasilia echinata*) demonstrated a reduction in reproductive success in the urban ecosystem in Recife, Brazil, indicating a depletion in the pollination process. Oliveira et al. (2019) also observed changes in the visiting behavior of an effective pollinator that behaved like an occasional pollinator in urban habitats. In contrast, Lobo et al. (2016) found a remarkable diversity and abundance of bee species in the inflorescences of *Tabebuia aurea* in the city of Brasília, Brazil. These authors attributed this result to the conservation of large parks and green zones in Brasília as part of the territorial planning of this recently founded (1960) city. Further studies in cities located in tropical and subtropical biomes are still needed to understand which Urban Drivers may be most important in the urban community assembly in these locations. Also, it is essential to consider the process of forming cities as a factor that will differentiate the consequences of urbanization on local biodiversity.

5. Conclusion

Research on how plants have responded to urbanization has increased in recent years, but many gaps remain to be filled. How each Urban Driver acts separately continues to be challenging to disentangle. This article contributes to the documentation of recent findings on the changes driven by urbanization at two ecological levels: plant species and communities. We found generally negative responses at both levels and a few cases of acclimatization and promising results demonstrating the potential adaptation of species to anthropogenic disturbances. The main weakness in this literature review was the lack of studies on biomes other than temperate, which results in limited knowledge of the patterns exhibited in plant species and communities. Another interesting finding was that even small cities could suffer from megacities' same consequences on their biodiversity. This reinforces the importance of conducting studies on a broad geographic scale and sampling from different cities to predict different forces among Urban Drivers in a variety of urban contexts. More studies are needed to elucidate whether there are different outcomes from the urban flora in other biomes.

It is increasingly necessary to identify which factors put biodiversity at risk, applying the methodologies needed in each area of knowledge to explore how this process can be more fully mitigated. Urban environments are of intrinsic ecological interest, and cities are open laboratories where evolutionary changes occur in real-time. More studies that integrate different aspects of plant communities and species, such as reproductive, physiological, and genetic traits, and monitoring climatic conditions and pollution within cities are vital to establishing priorities for conservation. The establishment of more model species for these large-scale studies is a robust alternative to understand better the processes and patterns of plant responses to urbanization. More broadly, it is essential to outline strategies for continuous monitoring and documenting the progress of species in perpetuating themselves in this new type of environment.

Data Availability

Data will be made available on request.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02243.

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Supplementary Table 1. Methodologies used in the studies to determine plants' responses to urbanization.

Study	Title	DOI	Continent	Country	City/Region
Abd El-Wahab, 2016	Plant assemblage and diversity variation with human disturbances in coastal habitats of the western Arabian Gulf.	https://doi.org/10.1007/s40333-016-0084-x	Asia	Kuwait	Southern coastal area of Kuwait
Albrecht and Häider, 2013	Species diversity and life history traits in calcareous grasslands vary along an urbanization gradient.	https://doi.org/10.1007/s10531-013-0437-0	Europe	Germany	Munich
Anderson et al., 2020	Post-apartheid ecologies in the City of Cape Town: An examination of plant functional traits in relation to urban gradients.	https://doi.org/10.1016/j.landurbplan.2019.103662	Africa	South Africa	Cape Town
Aronson et al., 2015	Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region.	https://doi.org/10.1007/s11252-014-0382-z	North America	United States	New York
Atlasoy et al., 2018	Evaluating the distribution of invasive woody vegetation around riparian corridors in relation to land use.	https://doi.org/10.1007/s11252-017-0729-3	North America	United States	Alabama
Barradas and Esperon-Rodriguez, 2021	Ecophysiological Vulnerability to Climate Change in Mexico City's Urban Forest	https://doi.org/10.3389/fevo.2021.732250	North America	Mexico	Mexico City
Bartlewicz et al., 2015	Population genetic diversity of the clonal self-incompatible herbaceous plant <i>Linaria vulgaris</i> along an urbanization gradient.	https://doi.org/10.1111/bj.12602	Europe	Belgium	Leuven
Beal-Neves et al., 2020	The Influence of Urbanization and Fire Disturbance on Plant-floral Visitor Mutualistic Networks.	https://doi.org/10.3390/d12040141	South America	Brazil	Porto Alegre
Bigirimana et al., 2011	Alien plant species dominate the vegetation in a city of Sub-Saharan Africa.	https://doi.org/10.1016/j.landurbplan.2010.12.012	Africa	Burundi	Bujumbura
Blood et al., 2016	How Do Urban Forests Compare? Tree Diversity in Urban and Periurban Forests of the Southeastern US.	https://doi.org/10.3390/f7060120	North America	United States	Southeastern USA
Blouin et al., 2019	Increase in non-native species richness leads to biotic homogenization in vacant lots of a highly urbanized landscape.	https://doi.org/10.1007/s11252-019-00863-9	North America	Canada	Montréal and Quebec

Study	Taxa	Approach	Megacity	Biome	Community traits
Abd El-Wahab, 2016	All vascular plants	Urban - non-urban gradient	-	Deserts & Xeric Shrublands	Species richness and abundance; β -diversity; conservation status; canopy cover, height and diameters
Albrecht and Häider, 2013	Graminoids	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Total number of species; evenness; numbers of endangered and non-native species; canopy height
Anderson et al., 2020	All vascular plants	Urban - non-urban gradient	Yes	Mediterranean Forests, Woodlands & Scrub	Species richness; cover contribution; total cover
Aronson et al., 2015	Woody plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness; proportion of non-native species; β -diversity
Atasoy et al., 2018	<i>Ligustrum sinense</i> , <i>Elaeagnus pungens</i> , <i>Triadica sebifera</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Forest community form; cover by strata; canopy cover; species total cover; growth stage
Barradas and Esperon-Rodriguez, 2021	<i>Acacia longifolia</i> , <i>Acer negundo</i> , <i>Ahies acuminata</i> , <i>Buddleia cordata</i> , <i>Celtis occidentalis</i> , <i>Dodonaea viscosa</i> , <i>Eucalyptus camaldulensis</i> , <i>Erythrina americana</i> , <i>Fraxinus uhdei</i> , <i>Ligustrum lucidum</i> , <i>Liquidambar styraciflua</i> , <i>Populus alba</i> , <i>Populus deltoides</i> , <i>Quercus rugosa</i> , <i>Ulmus parvifolia</i>	Urban - non-urban gradient	Yes	Tropical & Subtropical Coniferous Forests; Deserts & Xeric Shrublands	-
Bartlewicz et al., 2015	<i>Linaria vulgaris</i>	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Beal-Neves et al., 2020	Graminoids	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Londo's scale cover value
Bigirimana et al., 2011	All vascular plants	Urban - non-urban gradient	No	Tropical & Subtropical Grasslands, Savannas & Shrublands	Species abundances; life forms; ecological groups; presence of non-native species
Blood et al., 2016	Woody plants	Urban vs non-urban	-	Temperate Broadleaf & Mixed Forests; Temperate Grasslands, Savannas & Shrublands	Species richness; presence of non-native species
Blouin et al., 2019	All vascular plants	Urban - non-urban gradient	Yes/ No	Temperate Broadleaf & Mixed Forests	Species richness; life form; presence of non-native species; β -diversity

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Abd El-Wahab, 2016	-	-	-	-	-
Albrecht and Haider, 2013	Soil N, P, Soil pH; temperature; soil and vegetation disturbance; proportion of sealed area; habitat size; habitat type	Specific leaf area	Phytomass; Leaf persistence	Start and duration of flowering; Pollination; Seed longevity, mass, shape, dispersal; vegetative dispersal	-
Anderson et al., 2020	-	Leaf type; rooting depth	-	Pollination mechanism; seed dispersal mechanism	-
Aronson et al., 2015	Proportion of urban land cover	-	-	-	-
Atasoy et al., 2018	Surrounding land cover; visual indication of flooding	Diameter at breast height	-	-	-
Barradas and Esperon-Rodriguez, 2021	Temperature; photosynthetically active radiation; vapor pressure deficit; water availability	-	Stomatal conductance, leaf water potential	-	-
Bartlewicz et al., 2015	Percentage of impervious surfaces	-	-	Clonal diversity; seed set	DNA Molecular markers (SSR); genetic variation within and among populations
Beal-Neves et al., 2020	Land cover classes; Time since fire	-	-	Frequency of floral visitors	-
Bigirimana et al., 2011	Habitat type; degree of trampling by man and/or cattle; presence of shade; existence of a permanent source of humidity; soil type	-	-	-	-
Blood et al., 2016	Land use	Height tree; crown width; crown light exposure; diameter at breast height	-	-	-
Blouin et al., 2019	Local level of urbanization	Height	Light requirement; thermal tolerance; wetland occurrence	Seed dispersal; pollination vectors; seed weight and length; vegetative reproduction	-

Study	Title	DOI	Continent	Country	City/Region
Bode and Tong, 2018	Pollinators exert positive selection on flower size on urban, but not on rural Scotch broom (<i>Cytisus scoparius</i> L., Link).	https://doi.org/10.1093/jpe/rtx024	North America	United States	Lacey-Olympia
Bouraoui et al., 2019	Deicing Salt Pollution Affects the Foliar Traits and Arthropods' Biodiversity of Lime Trees in Riga's Street Greeneries.	https://doi.org/10.3389/fevo.2019.00282	Europe	Latvia	Riga
Brice et al., 2016	Environmental filtering and spatial processes in urban riparian forests	https://doi.org/10.1111/jvs.12425	North America	Canada	Montréal
Brice et al., 2017	Does urbanization lead to taxonomic and functional homogenization in riparian forests?	https://doi.org/10.1111/ddi.12565	North America	Canada	Montréal
Caughlin et al., 2012	Urbanized landscapes favored by fig-eating birds increase invasive but not native juvenile strangler fig abundance.	https://doi.org/10.1890/11694.1	North America	United States	South Florida
Celesti-Grapow and Ricotta, 2021	Plant invasion as an emerging challenge for the conservation of heritage sites: the spread of ornamental trees on ancient monuments in Rome, Italy.	https://doi.org/10.1007/s10530-020-02429-9	Europe	Italy	Rome
Chen et al., 2014	Dynamics of ruderal species diversity under the rapid urbanization over the past half century in Harbin, Northeast China.	https://doi.org/10.1007/s11252-013-0338-8	Asia	China	Harbin
Chimainba et al, 2020	Urban tree species composition and diversity in Zomba city, Malawi: Does land use type matter?	https://doi.org/10.1016/j.ufug.2020.126781	Africa	Malawi	Zomba
Cochard et al., 2017	Grassland plant species occurring in extensively managed road verges are filtered by urban environments	https://doi.org/10.1080/17550874.2017.1350764	Europe	France	Nantes, Angers and La Roche-sur-Yon
Cochard et al., 2019	Intraspecific trait variation in grassland plant communities along urban-rural gradients.	https://doi.org/10.1007/s11252-019-0827-5	Europe	France	Nantes and Angers
Comber and Brunsdon, 2015	A spatial analysis of plant phenophase changes and the impact of increases in urban land use.	https://doi.org/10.1002/joc.4030	Europe	United Kingdom	-
Concepción et al., 2015	Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale	https://doi.org/10.1111/oik.02166	Europe	Switzerland	Central Plateau of Switzerland

Study	Taxa	Approach	Megacity	Biome	Community traits
Bode and Tong, 2018	<i>Cytisus scoparius</i>	Urban vs non-urban	No	Temperate Conifer Forest	-
Bouraoui et al., 2019	<i>Tilia x vulgaris</i>	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	Biodiversity of arthropods in the canopy
Brice et al., 2016	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Brice et al., 2017	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness; proportion of non-native species; β -diversity
Caughlin et al., 2012	<i>Ficus microcarpa</i> , <i>Ficus aurea</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Abundance of the non-native species (<i>F. microcarpa</i>) vs the native species (<i>F. aurea</i>); abundance of juvenile and adult plants; canopy cover
Celesti-Grapow and Ricotta, 2021	All vascular plants	Temporal	Yes	Mediterranean Forests, Woodlands & Scrub	Presence of native and non-native species
Chen et al., 2014	All vascular ruderal plants	Urban - non-urban gradient/ Temporal	Yes	Temperate Broadleaf & Mixed Forests	Species occurrence frequency
Chimamba et al, 2020	Trees	Urban - non-urban gradient	No	Montane Grasslands & Shrublands	Presence of native and non-native species
Cochard et al., 2017	Graminoids	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	Abundance of species
Cochard et al., 2019	Graminoids	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	Abundance of species
Comber and Brunsdon, 2015	<i>Crataegus monogyna</i> , <i>Prunus spinosa</i> , <i>Aesculus hippocastanum</i>	Urban vs non-urban/ Temporal	-	Temperate Broadleaf & Mixed Forests	-
Concepción et al., 2015	All vascular plants	Urban - non-urban gradient	-	Temperate Conifer Forests	Species richness

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Bode and Tong, 2018	-	-	-	Pollinators frequency; proportion of flowers tripped; flower size; pollinator selection on floral size	-
Bouraoui et al., 2019	Soil properties	-	Salt accumulation in the foliage; chlorophyll fluorescence; structural injury in the foliage	-	-
Brice et al., 2016	Forest area; seasonal flood intensity; time since the last major disturbance; historical agricultural and human land use; proportion of impervious surfaces; human influence index	Diameter at breast height; height	Shade tolerance; wetness index	Seed weight; seed bank; vegetative reproduction; dispersal vector	-
Brice et al., 2017	-	Height	Shade tolerance; wetness index	Seed weight; seed bank; reproduction; diaspore morphology; seed buoyancy	-
Caughlin et al., 2012	-	Diameter at breast height	-	Seed dispersors	-
Celesti-Grapow and Ricotta, 2021	-	Plant form	-	Dispersal strategies	-
Chen et al., 2014	Climate variation and land cover changes along the years	-	-	-	-
Chimainba et al, 2020	Land cover type	Diameter at breast height	-	-	-
Cochard et al., 2017	Land use	-	-	Pollination syndrome; dispersal mode; speed of a falling diaspore; seed bank longevity; seed mass	-
Cochard et al., 2019	Soil analysis; temperature	Specific leaf area; maximum height	-	Phenology (flowering)	-
Comber and Brunsdon, 2015	Proportions of land use	-	-	Phenology (flowering)	-
Concepción et al., 2015	Proportion of sealed area; climate; topography; variables related to other land-uses; landscape heterogeneity	-	Degree of specialisation	Dispersal modes	-

Study	Title	DOI	Continent	Country	City/Region
Concepción et al., 2016	Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters.	https://doi.org/10.1007/s11215-015-0474-4	Europe	Switzerland	Central Plateau of Switzerland
Concepción et al., 2017	Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced land-use gradients.	https://doi.org/10.1111/ecog.02121	Europe	Switzerland	Central Plateau of Switzerland
Cui et al., 2019	Phylogenetic and functional structures of plant communities along a spatiotemporal urbanization gradient: Effects of colonization and extinction.	https://doi.org/10.1111/jvs.12724	Asia	China	Shanghai/ Harbin
Dallimer et al., 2012	Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape.	https://doi.org/10.1111/j.1472-4642.2012.00891.x	Europe	United Kingdom	Sheffield
Davis et al., 2015	Top-down vs. bottom-up regulation of herbaceous primary production and composition in an arid, urbanizing ecosystem.	https://doi.org/10.1016/j.jaridenv.2015.01.018	North America	United States	Central Arizona-Phoenix
Davis et al., 2016	Do trees flower longer in the city? A comparison of flowering eucalyptus trees in streets, remnants and continuous forest and their association with nectarivorous birds.	https://doi.org/10.1007/s11215-015-0515-z	Oceania	Australia	Sydney
de Araújo et al., 2021	Plant diversity drives responses of gall-inducing insects to anthropization in Neotropical savannas	https://doi.org/10.1007/s42965-021-00148-3	South America	Brazil	Montes Claros
Déak et al., 2016	Grassland vegetation in urban habitats - testing ecological theories.	https://doi.org/10.14471/2016.36.017	Europe	Hungary	Debrecen
Delnevo et al., 2021	Genetic and ecological consequences of recent habitat fragmentation in a narrow endemic plant species within an urban context	https://doi.org/10.1007/s10531-021-02256-x	Oceania	Australia	Western Australia, Perth
Dessegher et al., 2019	How does urbanization affect the reproductive characteristics and ecological affinities of street plant communities?	https://doi.org/10.1002/ecc3.5539	Europe	France	Paris
Dolan et al., 2011	Documenting effects of urbanization on flora using herbarium records.	https://doi.org/10.1111/j.1365-2745.2011.01820.x	North America	United States	Marion County

Study	Taxa	Approach	Megacity	Biome	Community traits
Concepción et al., 2016	All vascular plants	Urban - non-urban gradient	-	Temperate Conifer Forests	Species richness; presence of native and non-native species
Concepción et al., 2017	All vascular plants	Urban - non-urban gradient	-	Temperate Conifer Forests	-
Cui et al., 2019	All vascular ruderal plants	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Dallimer et al., 2012	All vascular plants	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	Species richness; presence of native and non-native species
Davis et al., 2015	Herbs	Urban vs non-urban	-	Deserts & Xeric Shrublands	Species diversity and composition; herbivory
Davis et al., 2016	<i>Angophora costata</i> , <i>Eucalyptus ptilularis</i> , <i>Corymbia gummifera</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	Presence of nectarivores
de Araújo et al., 2021	All vascular plants	Urban vs non-urban	No	Tropical & Subtropical Grasslands, Savannas & Shrublands	Species richness
Déak et al., 2016	Graminoids	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	-
Delnevo et al., 2021	<i>Conospermum undulatum</i>	Temporal	Yes	Mediterranean Forests, Woodlands & Scrub	-
Desaegher et al., 2019	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Dolan et al., 2011	All vascular plants	Temporal	-	Temperate Broadleaf & Mixed Forests	Presence of non-native species

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Concepción et al., 2016	Urban area; average age of urban area; human population density; spatial dispersion of urban areas; climatic, topographic, and land use variables	-	Degree of specialisation; life cycle	Dispersal modes	-
Concepción et al., 2017	Climate; resource availability; disturbance; land use; landscape heterogeneity; climate; topography	Height	Life history; Leaf Dry Matter Content	Dispersal modes; duration of the flowering period	-
Cui et al., 2019	-	Height; vegetation form	Life cycle	Fruiting time	Phylogenetic diversity
Dallimer et al., 2012	Land cover; topography; sealed surface; human population density; habitat diversity	-	-	-	-
Davis et al., 2015	Soil inorganic nitrogen availability	-	Biomass	-	-
Davis et al., 2016	-	Diameter at breast height	-	Phenology (flowering period); number of flowers produced per tree	-
de Araújo et al., 2021	-	-	-	-	-
Déak et al., 2016	Ellenberg ecological indicator values for temperature, water, and nitrogen	-	Behaviour type	-	-
Delnevo et al., 2021	-	-	-	-	DNA, Molecular markers (SSR); genetic diversity; genetic structure; spatial analysis of genetic differentiation
Desaegher et al., 2019	Land cover; proportion of impervious surfaces; Ellenberg indicator values for light, temperature, continentality, atmospheric moisture, soil moisture, soil reaction, soil nutrient content, and soil salt content	-	Affinity indices for soil granulometry and for soil organic matter	Pollinator morphological typology; floral morphotype; level of entomophily, dispersal vector, beginning and end of flowering; vegetative reproduction; self-compatibility; autogamy; presence or absence of tubular corolla and nectar spur	-
Dolan et al., 2011	Wetland classification	-	Physiognomic group; species' fidelity to high-quality habitats and tolerance of disturbance	-	Historical herbarium records

Study	Title	DOI	Continent	Country	City/Region
Dolan et al., 2017	Floristic response to urbanization: Filtering of the bioregional flora in Indianapolis, Indiana, USA.	https://doi.org/10.3732/ajb.1700136	North America	United States	Indianapolis
dos Santos et al., 2020	Are native nectar robbers against the alien? Effects of floral larceny on the reproductive success of the invasive yellow bells (<i>Tecoma stans</i> , Bignoniaceae).	https://doi.org/10.1016/j.actao.2020.103547	South America	Brazil	João Pessoa, Alhandra
du Toit et al., 2020	Quantifying Long-Term Urban Grassland Dynamics: Biotic Homogenization and Extinction Debts	https://doi.org/10.3390/su12051989	Africa	South Africa	Potchefstroom
Dubois and Cheptou, 2017	Effects of fragmentation on plant adaptation to urban environments.	http://dx.doi.org/10.1098/rsob.2016.0038	Europe	France	Montpellier
Duffy and Chown, 2016	Urban warming favours C4 plants in temperate European cities.	https://doi.org/10.1111/1365-2745.12652	Europe	United Kingdom and Germany	-
El-Barougy et al., 2021	Trait-Environment Relationships Reveal the Success of Alien Plants Invasiveness in an Urbanized Landscape	https://doi.org/10.3390/plants10081519	Africa	Egypt	Saint Katherine Protectorate
Ennel et al., 2021	Type and intensity of surrounding human land use, not local environment, shape genetic structure of a native grassland plant.	https://doi.org/10.1111/mec.15753	North America	United States	Chester, Lancaster, Delaware
Everingham et al., 2019	Inverted invasions: Native plants can frequently colonise urban and highly disturbed habitats.	https://doi.org/10.1111/aec.12719	Oceania	Australia	New South Wales
Fekete et al., 2020	Roadsides provide refuge for orchids: characteristic of the surrounding landscape.	https://doi.org/10.1002/ecc3.6920	Europe	Austria, Hungary, Romania, Slovakia, Slovenia	-
Filiz et al., 2015	Assessment of genetic variations of silver lime (<i>Tilia tomentosa</i> Moench.) by RAPD markers in urban and forest ecosystems.	http://dx.doi.org/10.1080/13102818.2015.1042049	Asia	Turkey	Black Sea region

Study	Taxa	Approach	Megacity	Biome	Community traits
Dolan et al., 2017	All vascular plants	Temporal	Yes	Temperate Grasslands, Savannas & Shrublands	-
dos Santos et al., 2020	<i>Tecoma stans</i>	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Robbing in pre-anthesis quantification (herbivory)
du Toit et al., 2020	All vascular plants	Temporal	No	Montane Grasslands & Shrublands	Species richness, abundance, presence of native and exotic species
Dubois and Cheptou, 2017	<i>Crepis sancta</i>	Urban - non-urban gradient	No	Mediterranean Forests, Woodlands & Scrub	-
Duffy and Chown, 2016	C4 plants	Urban vs non-urban	-	Temperate Broadleaf & Mixed Forests	Relative abundance from GBIF data; species richness
El-Barougy et al., 2021	All vascular plants	Urban - non-urban gradient	No	Deserts & Xeric Shrublands	Canopy diameter, cover percentage, presence of native and exotic species
Enel et al., 2021	<i>Sabbatia angularis</i>	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Everingham et al., 2019	All vascular plants	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	Presence of native and non-native species; species composition, identity and cover data; species richness
Fekete et al., 2020	Orchids	Urban vs non-urban	-	Temperate Conifer Forests, Temperate Broadleaf & Mixed Forests	Species richness
Filiz et al., 2015	<i>Tilia tomentosa</i>	Urban vs non-urban	-	Temperate Broadleaf & Mixed Forests	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Dolan et al., 2017	-	Spinescence	Life Form; Life cycle; Leaf Periodicity	Clonality; Dispersal Mode; Pollination	Historical herbarium records; phylogenetic diversity based on genes
dos Santos et al., 2020	-	-	-	Floral visitors; nectar production; fruit set	-
du Toit et al., 2020	Urban index	-	-	-	-
Dubois and Cheptou, 2017	-	Shape; plant and leaf size	-	Seed germination; date of first capitulum emergence; diameter and the length of the first flowering stalk; dispersal index; total number of capitula produced per individual	DNA Molecular markers (SSR); genetic diversity between urban and rural and between fragmented and unfragmented habitats; genetic structure
Duffy and Chown, 2016	Land surface temperature data from remote-sensing approach	-	-	-	-
El-Barougy et al., 2021	Soil features, urban index	Plant height; leaf production; seed weight; specific leaf area	Biomass	Floral production	Phylogenetic distances within native plants, within alien plants, and between alien and native plants
Enel et al., 2021	Soil heavy metal content	-	-	-	Double digest restriction site associated DNA sequencing (ddRADseq), genomic data, genetic structure, isolation by resistance, isolation by environment
Everingham et al., 2019	Microhabitat conditions; historic disturbance level	Height	-	Seed mass	-
Fekete et al., 2020	Land cover variables	-	-	-	-
Filiz et al., 2015	-	-	-	-	DNA Molecular markers (RAPD); genetic diversity and structure

Study	Title	DOI	Continent	Country	City/Region
Fisogni et al., 2020	Urbanization drives an early spring for plants but not for pollinators	https://doi.org/10.1111/oik.07274	Europe	France	Lille
Fitchett and Raik, 2021	Phenological advance of blossoming over the past century in one of the world's largest urban forests, Gauteng City-Region, South Africa.	https://doi.org/10.1016/j.ufug.2021.1.27238	Africa	South Africa	Gauteng City-Region
Formal-Pieniak et al., 2020	Vascular flora of urban forests in a medium-sized city in Poland: comparison with nature reserves in the city's surrounding.	https://doi.org/10.1080/01426397.2020.1850662	Europe	Poland	Tarnów
Freitas et al., 2020	Urbanization alters the composition, but not the diversity and structure, of Neotropical savanna woody plant communities.	https://doi.org/10.1007/s12224-020-09366-4	South America	Brazil	Montes Claros
Fukano et al., 2020	Contemporary adaptive divergence of plant competitive traits in urban and rural populations and its implication for weed management.	https://doi.org/10.1111/1365-2745.13472	Asia	Japan	Tokyo
Gaggioli et al., 2017	Settlements as a source for the spread of non-native plants into Central European suburban forests.	http://dx.doi.org/10.1016/j.actao.2016.12.008	Europe	Switzerland	Basel/ Lugano
Géron et al., 2021	Shielded environments reduce stress in alien Asteraceae species during hot and dry summers along urban-to-rural gradients	https://doi.org/10.1002/eecs3.7872	Europe	Belgium	Flanders, Brussels Capital Region, and the north of Wallonia
Glisić et al., 2021	Influence of Habitat Types on Diversity and Species Composition of Urban Flora—A Case Study in Serbia	https://doi.org/10.3390/plants10122572	Europe	Serbia	-
Greene and Blossey, 2014	Patterns of Privet: Urbanizing Watersheds, Invasive Ligustrum sinense, and Performance of Native Plant Species in Piedmont Floodplain Forests.	https://doi.org/10.1007/s10021-014-9774-4	North America	United States	Piedmont ecoregion
Grella et al., 2018	Invasive weeds in urban riparian zones: the influence of catchment imperviousness and soil chemistry across an urbanization gradient.	https://doi.org/10.1007/s11252-018-0736-z	Oceania	Australia	Sydney
Guerra et al., 2017	Urban or rural areas: which types of surrounding land use induce stronger edge effects on the functional traits of tropical forests plants?	https://doi.org/10.1111/avsc.12315	South America	Brazil	Recife
Grüler, 2020	Plant species diversity and vegetation in urban grasslands depending on disturbance levels.	https://doi.org/10.2478/s11756-020-00484-0	Asia	Turkey	Izmir

Study	Taxa	Approach	Megacity	Biome	Community traits
Fisogni et al., 2020	Herbs	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species abundance; species cover
Fichett and Raik, 2021	<i>Jacaranda mimosifolia</i>	Temporal	Yes	Tropical & Subtropical Grasslands, Savannas & Shrublands	-
Formal-Peniak et al., 2020	All vascular plants	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	Species cover
Freitas et al., 2020	Woody plants	Urban - non-urban gradient	No	Tropical & Subtropical Grasslands, Savannas & Shrublands	Plant abundance; vegetation cover; species richness; diversity index
Fukano et al., 2020	<i>Digitaria ciliaris</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Gaggioli et al., 2017	All vascular plants	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	Richness and abundance of species; presence of native and non-native species
Géron et al., 2021	<i>Artemisia verlotorum</i> , <i>Erigeron canadense</i> , <i>Gaium soga quadriradiata</i> , <i>Marricaria discoidea</i> , <i>Senecio inaequidens</i> , <i>chamaephyte</i> , <i>Solidago gigantea</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Vegetation cover
Glisić et al., 2021	All vascular plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species richness, life form
Greene and Blosssey, 2014	<i>Ligustrum sinense</i> , <i>Acer negundo</i> var. <i>negundo</i> , <i>Chasmanthium latifolium</i> , <i>Alnus canadense</i>	Urban - non-urban gradient	-	Temperate Conifer Forests	Total plot cover; herbivory
Grella et al., 2018	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Percentage cover, presence of native and non-native species
Guerra et al., 2017	Woody plants	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Grüter, 2020	All vascular plants	Urban - non-urban gradient	Yes	Mediterranean Forests, Woodlands & Scrub	Species richness

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Fisogni et al., 2020	Land cover	-	-	Phenology (flowering); flight period of wild pollinators; abundance and diversity of pollinators	-
Fichett and Raik, 2021	Temperature	-	-	Phenology (flowering)	-
Fomal-Preniak et al., 2020	Indicator values of vascular plants for light, temperature, continentality, soil moisture, trophic, soil acidity and	Diameter at breast height	-	Seed dispersal	-
Freitas et al., 2020	-	Diameter at breast height	-	-	-
Fukano et al., 2020	-	Height and width; number of shoots and total number of nodes	Competition; dry weight	-	-
Gaggioli et al., 2017	Soil characteristics; percentage area covered by forests, agriculture land, traffic infrastructure, built-up area and ornamental gardens	-	-	-	-
Géron et al., 2021	Urban index, sky view factor (SVF)	Height, internode space, specific leaf area	Chlorophyll content, anthocyanins, and flavonols indices	-	-
Glisić et al., 2021	Urban index, climatic characteristics	-	-	-	-
Greene and Blossley, 2014	Land use; soil infiltration, soil nutrients, and ground water table depth	Height	-	Seed germination	-
Grella et al., 2018	Soil properties	-	-	-	-
Guerra et al., 2017	-	Height; circumference	Light requirements; regeneration strategy	Seed size, dispersal syndrome	-
Güler, 2020	-	-	-	-	-

Study	Title	DOI	Continent	Country	City/Region
Gulezian et al., 2010	Distribution of invasive plants in urban environment is strongly spatially structured.	https://doi.org/10.1007/s10980-016-0480-9	North America	United States	Chicago
Hals and McDonnell, 2013	Composition of the soil seed bank in remnant patches of grassy woodland along an urbanization gradient in Melbourne, Australia.	https://doi.org/10.1007/s11258-013-0248-0	Oceania	Australia	Melbourne
Heneidy et al., 2021	Pattern of Urban Flora in Intra-City Railway Habitats (Alexandria, Egypt): A Conservation Perspective	https://doi.org/10.3390/biology10080698	Africa	Egypt	Alexandria
Hou et al., 2019	Urbanization threaten the pollination of <i>Gentiana dahurica</i> .	https://doi.org/10.1038/s41598-018-36773-7	Asia	China	Xi'ning
Huang et al., 2013	Effect of urbanization on the structure and functional traits of remnant subtropical evergreen broad-leaved forests in South China.	https://doi.org/10.1007/s10661-012-2921-5	Asia	China	Guangzhou
Ilyas et al., 2021	Adaptation of functional traits and their plasticity of three ornamental trees growing in urban environment.	https://doi.org/10.1016/j.scienta.2021.110248	Asia	China	Wuhan
Irwin et al., 2018	Phenotypic selection on floral traits in an urban landscape.	http://dx.doi.org/10.1098/rspb.2018.1239	North America	United States	Raleigh-Durham
Jensen et al., 2021	Contrasting effects of tree origin and urbanization on invertebrate abundance and tree phenology.	https://doi.org/10.1002/eap.2491	Europe	Sweden	Malmö
Jeong et al., 2011	Impact of urban warming on earlier spring flowering in Korea.	https://doi.org/10.1002/joc.2178	Asia	South Korea	-
Jochner et al., 2012	The influence of altitude and urbanisation on trends and mean dates in phenology (1980–2009).	https://doi.org/10.1007/s00484-011-0444-3	Europe	Germany	Frankfurt, Cologne and Munich

Study	Taxa	Approach	Megacity	Biome	Community traits
Gulezian et al., 2010	<i>Ailanthus altissima</i> , <i>Alliaria petiolata</i> , <i>Arcytum minus</i> , <i>Cirsium vulgare</i> , <i>Dipsacus sivestris</i> , <i>Melilotus alba</i> , <i>Phragmites australis</i> , <i>Rhamnus cathartica</i> , <i>Rosa multiflora</i> , <i>Setaria glauca</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species abundance
Hals and McDonnell, 2013	Woody plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Heneidy et al., 2021	All vascular plants	Urban - non-urban gradient	Yes	Mediterranean Forests, Woodlands & Scrub	Species richness, species covering, evenness
Hou et al., 2019	<i>Gentiana dahurica</i>	Urban - non-urban gradient	Yes	Montane Grasslands & Shrublands	-
Huang et al., 2013	All vascular plants	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Ilyas et al., 2021	<i>Platanus him</i> , <i>Populus euramevicana</i> , <i>Cinnamomum camphora</i>	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Irwin et al., 2018	<i>Gelsemium sempervirens</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Jensen et al., 2021	<i>Acer platanoides</i> , <i>Betula pendula</i> , <i>Crataegus monogyna</i> , <i>Fagus sylvatica</i> , <i>Prunus avium</i> , <i>Quercus robur</i> , <i>Salix caprea</i> , <i>Sorbus intermedia</i> , <i>Tilia x europaea</i> , <i>Ailanthus altissima</i> , <i>Ginkgo biloba</i> , <i>Gleditsia triacanthos</i> , <i>Platanus x hispanica</i> , <i>Pterocarya fraxinifolia</i> , <i>Quercus cerris</i> , <i>Robinia pseudoacacia</i>	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	Presence of non-native species, abundance of invertebrates associated to the host tree
Jeong et al., 2011	<i>Forsythia koreana</i> , <i>Rhododendron mucronulatum</i> , <i>Prunus yedoensis</i> , <i>Prunus persica</i>	Urban vs non-urban/ Temporal	-	Temperate Broadleaf & Mixed Forests	-
Jochner et al., 2012	<i>Corylus avellana</i> , <i>Galanthus nivalis</i> , <i>Salix caprea</i> , <i>Forsythia suspensa</i> , <i>Acer platanoides</i> , <i>Fagus sylvatica</i> , <i>Malus domestica</i> , <i>Picea abies</i> , <i>Syringa vulgaris</i>	Urban - non-urban gradient/ Temporal	No	Temperate Broadleaf & Mixed Forests	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Gulezian et al., 2010	-	Height	-	-	Earliest recorded date of a herbarium
Hals and McDonnell, 2013	-	Diameter at breast height	-	Soil seed bank; germination	-
Heneidy et al., 2021	Human activities and disturbance, climate data	Life forms	-	-	-
Hou et al., 2019	-	-	-	Pollinator observation; length and width of flowers; length of filaments and style; number of flowers; pollen and ovule numbers; pollen/ovule ratio; flower development; reproductive success; pollen limitation	-
Huang et al., 2013	Topography; soil properties; light	Diameter at breast height	-	-	-
Ilyas et al., 2021	-	Single leaf area, leaf length/width, stomatal density, stomatal length/width, stomatal area, leaf thickness	-	-	-
Irwin et al., 2018	-	-	Concentration of the alkaloid gelsemine	Floral morph; floral display size; corolla and petal length and width; robbing; florivory; pollination; number of open flowers	-
Jensen et al., 2021	Temperature	-	Phenology (bud burst)	-	-
Jeong et al., 2011	Temperature	-	-	Phenology (flowering)	-
Jochner et al., 2012	Proportion of built up areas; altitude	-	Phenology (leaf unfolding, sprout)	Phenology (flowering)	-

Study	Title	DOI	Continent	Country	City/Region
Jochner et al., 2013	Using phenology to assess urban heat islands in tropical and temperate regions.	https://doi.org/10.1002/joc.3651	South America/ Europe	Brazil/ Germany	Campinas/ Munich
Jochner et al., 2015	The effects of short- and long-term air pollutants on plant phenology and leaf characteristics.	https://doi.org/10.1016/j.envp.2015.07.040	Europe	Germany	Munich
Johnson et al., 2018	Contrasting the effects of natural selection, genetic drift and gene flow on urban evolution in white clover (<i>Trifolium repens</i>).	http://dx.doi.org/10.1098/rspb.2018.1019	North America	Canada	Ontario
Kalusova et al., 2019	Similar responses of native and alien floras in European cities to climate.	https://doi.org/10.1111/jbi.13591	Europe	Austria, Belgium, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Netherlands, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Switzerland	Western, Central and Southern Europe
King and Hovick, 2020	Wetland plant community variation across replicate urban to rural gradients: non-native species as both drivers and passengers in systems impacted by anthropogenic land-use.	https://doi.org/10.1007/s11252-020-01012-3	North America	United States	Ohio
Knapp et al., 2017	Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization.	https://doi.org/10.1111/1365-2664.12826	Europe	Germany	Halle
Kobayashi et al., 2018	Comparison of visitors and Pollinators of <i>Micuna macrocarpa</i> between Urban and Forest Environments.	https://doi.org/10.3106/ms2018-0029	Asia	Japan/ Taiwan	Okinawa-jima Island
Kolbe et al., 2016	Effects of natural and anthropogenic environmental influences on tree community composition and structure in forests along an urban-wildland gradient in southwestern Ohio.	https://doi.org/10.1007/s11252-016-0531-7	North America	United States	Southwestern Ohio

Study	Taxa	Approach	Megacity	Biome	Community traits
Jochner et al., 2013	<i>Tabebuia chrysotricha</i> , <i>Caesalpinia peltophoroides</i> , <i>Tipuana tipu</i> , <i>Betula pendula</i>	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests; Temperate Broadleaf & Mixed Forests	-
Jochner et al., 2015	<i>Betula pendula</i> , <i>Corylus avellana</i> , <i>Aesculus hippocastanum</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Johnson et al., 2018	<i>Trifolium repens</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Density of populations
Kalusova et al., 2019	All vascular plants	Urban - non-urban gradient	-	Mediterranean Forests, Woodlands & Scrub; Temperate Broadleaf & Mixed Forests; Temperate Conifer Forests; Temperate Grasslands, Savannas & Shrublands	Presence of native and non-native species; species richness
King and Hovick, 2020	Wetland herbs	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species abundance; species richness; abundance of native and non-native species
Knapp et al., 2017	All vascular plants	Temporal	No	Temperate Broadleaf & Mixed Forests	Presence of native and non-native species; extirpated species; species richness; native immigrants; non-native immigrants; today's threatened species; potential future non-native immigrants
Kobayashi et al., 2018	<i>Mucuna macrocarpa</i>	Urban vs non-urban	-	Tropical & Subtropical Moist Broadleaf Forests	-
Kolbe et al., 2016	Woody plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Canopy cover; species richness, diversity and abundance; evenness

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Jochner et al., 2013	Air temperature and humidity; proportion of built up areas	-	Phenology (leaf unfolding)	Phenology (flowering)	-
Jochner et al., 2015	Air temperature; air pollution	Specific leaf area	Phenology (leaf unfolding)	Phenology (flowering)	-
Johnson et al., 2018	Percentage of impervious surfaces	-	Presence or absence of HCN	-	Human population size and human population density of each city; DNA molecular markers (SSR); population genetic variation within and between populations
Kalusova et al., 2019	Macroclimate conditions between cities	-	-	-	Socio-economic characteristics for each city
King and Hovick, 2020	Soil contaminants	-	-	-	-
Knapp et al., 2017	-	-	-	-	Records of spontaneous flora in manuscripts and herbarium; phylogenetic diversity
Kobayashi et al., 2018	-	-	-	Flower visitors; behavior and contribution to pollination of visitors	-
Kolbe et al., 2016	-	-	-	-	-

Study	Title	DOI	Continent	Country	City/Region
Kondratyeva et al., 2020	Urbanization Effects on Biodiversity Revealed by a Two-Scale Analysis of Species Functional Uniqueness vs. Redundancy.	https://doi.org/10.3389/fevo.2020.00073	Europe	France	Paris
Kopel et al., 2015	Characterization of vegetation community dynamics in areas affected by construction waste along the urban fringe.	https://doi.org/10.1007/s11252-014-0396-6	Asia	Israel	Haifa
Kühn et al., 2017	Is there an urban effect in alien plant invasions?	https://doi.org/10.1007/s10530-017-1591-1	Europe	Germany	-
Kunimmi et al., 2021	Vegetation changes in urban grasslands over 25 years in the city of Zurich, Switzerland.	https://doi.org/10.14471/2021.41.018	Europe	Switzerland	Zurich
Lair et al., 2015	Photosynthesis and isoprene emission from trees along an urban-rural gradient in Texas.	https://doi.org/10.1111/gcb.13010	North America	United States	Houston
Lair et al., 2018	Variation in photosynthesis and stomatal conductance among red maple (<i>Acer rubrum</i>) urban planted cultivars and wildtype trees in the southeastern United States.	https://doi.org/10.1371/journal.pone.0197866	North America	United States	Raleigh
Lambrecht et al., 2016	Natural selection on plant physiological traits in an urban environment.	https://doi.org/10.1016/j.acta.2016.09.002	Europe	France	Montpellier
Landis and Leopold, 2014	Natural Plant Establishment along an Urban Stream, Onondaga Creek, New York.	https://doi.org/10.1656/045.021.0211	North America	United States	Syracuse
Lechuga-Lago et al., 2017	Understanding the influence of urbanization on invasibility: <i>Carpobrotus edulis</i> as an exemplar.	https://doi.org/10.1007/s10530-017-1593-z	Europe	Spain	Galicia
Lee, 2017	Global Warming Leading to Phenological Responses in the Process of Urbanization, South Korea.	https://doi.org/10.3390/su9122203	Asia	South Korea	-
Leong et al., 2014	Pollinator Interactions with Yellow Starthistle (<i>Centaurea solstitialis</i>) across Urban, Agricultural, and Natural Landscapes	https://doi.org/10.1371/journal.pone.0086357	North America	United States	Brentwood
Lhotte et al., 2014	Are there contrasted impacts of urbanization and land uses on population persistence? The case of <i>Teucrium pseudochamaepitys</i> , an endangered species in Southern France.	https://doi.org/10.1016/j.flora.2014.05.002	Europe	France	Marseille

Study	Taxa	Approach	Megacity	Biome	Community traits
Kondratyeva et al., 2020	Herbs	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Kopel et al., 2015	All vascular plants	Urban vs non-urban/ Temporal	Yes	Mediterranean Forests, Woodlands & Scrub	Vegetation cover, species richness; presence of native and non-native species
Kühn et al., 2017	All vascular plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species richness
Kuimmi et al., 2021	All vascular plants	Temporal	Yes	Temperate Conifer Forests	Covering, presence of non-native species, species richness
Lair et al., 2015	<i>Quercus stellata</i> , <i>Liquidambar styraciflua</i>	Urban - non-urban gradient	Yes	Tropical & Subtropical Grasslands, Savannas & Shrublands	-
Lair et al., 2018	<i>Acer rubrum</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Lambrecht et al., 2016	<i>Crepis sancta</i>	Urban vs non-urban	No	Mediterranean Forests, Woodlands & Scrub	-
Landis and Leopold, 2014	All vascular plants	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Lechuga-Lago et al., 2017	<i>Carpobrotus edulis</i> , <i>Malcolmia littorea</i> , <i>Scolymus hispanicus</i>	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	-
Lee, 2017	<i>Forsythia koraiana</i> , <i>Rhododendron mucronulatum</i> , <i>Prunus yedoensis</i> , <i>Prunus mume</i>	Temporal	-	Temperate Broadleaf & Mixed Forests	-
Leong et al., 2014	<i>Centaurea solstitialis</i>	Urban - non-urban gradient	No	Temperate Grasslands, Savannas & Shrublands	-
Lhotte et al., 2014	<i>Teucrium pseudochamaejasme</i>	Urban - non-urban gradient	Yes	Mediterranean Forests, Woodlands & Scrub	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Kondratyeva et al., 2020	Land cover	Leaf size; specific leaf area; plant height	Leaf dry matter content	Life span; pollen vector; seed dispersal mode; type of reproduction; phenology (flowering); seed weight	-
Kopel et al., 2015	-	-	-	-	-
Kühn et al., 2017	Climate; geology; land cover; stems	-	-	-	-
Kuummi et al., 2021	-	-	-	-	-
Lair et al., 2015	Temperature; CO2 concentration	-	Gas exchange measurements; basal isoprene emission; rates of photosynthesis	-	-
Lair et al., 2018	Temperature; CO2 concentration	-	Gas exchange measurements; rates of photosynthesis and stomatal conductance	-	-
Lambrecht et al., 2016	Temperature; soil moisture; climate	Number of leaves; diameter of the rosette	Rates of photosynthesis; stomatal conductance; leaf nitrogen content; water-use efficiency; Phenology (senescence)	-	-
Landis and Leopold, 2014	Urban cover	-	-	Seedbank in soil	-
Lechuga-Lago et al., 2017	Soil pH, conductivity, water content, nutrients; soil enzymatic activities	-	-	Germination performances of the invasive vs the native species	-
Lee, 2017	Climate; precipitation	-	-	Phenology (budding and flowering)	-
Leong et al., 2014	-	-	-	Bee visitation; seed set	-
Lhotte et al., 2014	-	-	-	Pollinator activities; number of flowers, fruits, mature seeds; reproductive success	-

Study	Title	DOI	Continent	Country	City/Region
Li et al., 2017	Response of vegetation phenology to urbanization in the conterminous United States.	https://doi.org/10.1111/gcb.13562	North America	United States	-
Lindh et al., 2018	Changes in urban plant phenology in the Pacific Northwest from 1959 to 2016: anthropogenic warming and natural oscillation.	https://doi.org/10.1007/s00484-018-1567-6	North America	United States	Salem
Lobo et al., 2016	Visitation rate of pollinators and nectar robbers to the flowers and inflorescences of <i>Tabebuia aurea</i> (Bignoniaceae): effects of floral display size and habitat fragmentation.	https://doi.org/10.1111/boj.12435	South America	Brazil	Brasília
Löki et al., 2019	Predictors of conservation value of Turkish cemeteries: A case study using orchids.	https://doi.org/10.1016/j.landurbplan.2019.02.016	Asia	Turkey	-
Lopez et al., 2018	Testing the effects of four urbanization filters on forest plant taxonomic, functional, and phylogenetic diversity.	https://doi.org/10.1002/eap.1812	North America	United States	North Carolina
Lososová et al., 2016	Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences.	https://doi.org/10.1111/jvs.12381	Europe	Austria, Belgium, Czech Republic, Germany, Hungary, Netherlands, Poland, Slovakia, Slovenia, Switzerland	-
Lowry et al., 2020	Spatial patterns of presence, abundance, and richness of invasive woody plants in relation to urbanization in a tropical island setting.	https://doi.org/10.1016/j.ufug.2019.126516	Oceania	Fiji	Suva
Malkinson et al., 2018	From rural-urban gradients to patch – matrix frameworks: Plant diversity patterns in urban landscapes.	https://doi.org/10.1016/j.landurbplan.2017.09.021	Asia	Israel	Haifa

Study	Taxa	Approach	Megacity	Biome	Community traits
Li et al., 2017	All vascular plants	Urban - non-urban gradient/ Temporal	-	Temperate Conifer Forests; Deserts & Xeric Shrublands; Mediterranean Forests, Woodlands & Scrub; Temperate Grasslands, Savannas & Shrublands; Temperate Broadleaf & Mixed Forests; Tropical & Subtropical Grasslands, Savannas & Shrublands; Flooded Grasslands & Savannas	-
Lindh et al., 2018	All vascular plants	Temporal	No	Temperate Broadleaf & Mixed Forests	-
Lobo et al., 2016	<i>Tabebuia aurea</i>	Urban vs non-urban	Yes	Tropical & Subtropical Grasslands, Savannas & Shrublands	-
Lóki et al., 2019	Orchids	Urban - non-urban gradient/ Temporal	-	Mediterranean Forests, Woodlands & Scrub; Temperate Broadleaf & Mixed Forests; Temperate Conifer Forests	Species richness; abundance; probability of finding threatened taxa; tree cover; proportion of native trees
Lopez et al., 2018	Herbs	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species abundance
Lososová et al., 2016	All vascular plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests; Temperate Conifer Forests	Presence on native and non-native species; species turnover; species richness
Lowry et al. 2020	<i>Citharexylum spinosum</i> , <i>Psidium guajava</i> , <i>Schefflera actinophylla</i> , <i>Spathodea campanulata</i> , <i>Clerodendrum chinense</i> , <i>Clidemia hirta</i> , <i>Lantana camara</i> , <i>Leucaena leucocephala</i> , <i>Piper aduncum</i> , <i>Solanum torvianum</i> , <i>Coccoloba grandis</i> , <i>Ipomoea cairica</i> , <i>Merremia peltata</i> , <i>Mikania micrantha</i>	Urban - non-urban gradient	No	Tropical & Subtropical Moist Broadleaf Forests	Species richness, abundance
Malkinson et al., 2018	All vascular plants	Urban - non-urban gradient	Yes	Mediterranean Forests, Woodlands & Scrub	Presence on native and non-native species

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Li et al., 2017	Land use	-	Phenology (greenness)	-	Remote sensing
Lindh et al., 2018	Temperature	-	Phenology (Start leaf; defoliation)	Phenology (flowering)	-
Lobo et al., 2016	-	-	-	Floral visitors; flower size; nectar production	-
Lóki et al., 2019	Latitude, longitude, altitude, area of the cemetery; settlement type	-	-	-	Age, density and type of graves in cemeteries
Lopez et al., 2018	Wetland indicator status; area of forest cover; cover of ornamental plant; UHI; urban stream morphology; additions of soil nutrients; pollutants	Specific leaf area	Leaf type (evergreen vs. deciduous); leaf nitrogen content	Dispersal mode; seed mass	Phylogenetic diversity
Lososová et al., 2016	-	-	-	-	-
Lowry et al., 2020	-	-	-	-	-
Malkinson et al., 2018	Habitat type; percentage of sealed surface	-	-	-	-

Study	Title	DOI	Continent	Country	City/Region
Masseti et al., 2015	The effect of urban morphology on <i>Tilia × europaea</i> flowering.	https://doi.org/10.1016/j.ufug.2014.10.005	Europe	Italy	Florence
McCune and Vellend, 2013	Gains in native species promote biotic homogenization over four decades in a human-dominated landscape.	https://doi.org/10.1111/1365-2745.12156	North America	Canada	Saanich Peninsula
Melliger et al., 2018	Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders.	https://doi.org/10.1371/journal.pone.0199245	Europe	Switzerland	Basel-Stadt
Milanović et al., 2021	Functional diversity changes in native and alien urban flora over three centuries.	https://doi.org/10.1007/s11860-021-02509-4	Europe	Germany	Haale
Molnár et al., 2018	Urban tree leaves' chlorophyll-a content as a proxy of urbanization.	https://doi.org/10.1007/s11869-018-0573-5	Europe	Hungary	Debrecen
Murray-Stoker and Johnson, 2021	Ecological consequences of urbanization on a legume-rhizobia mutualism.	https://doi.org/10.1111/oik.08341	North America	Canada	Toronto
Neil et al., 2010	Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: Findings from herbarium records.	https://doi.org/10.1016/j.jaridenv.2009.10.010	North America	United States	Maricopa County
Nero et al., 2019	Woody species and trait diversity-functional relations of green spaces in Kumasi, Ghana.	https://doi.org/10.1007/s11252-019-00835-z	Africa	Ghana	Kumasi
Nikula et al., 2010	Urbanization-related changes in European aspen (<i>Populus tremula</i> L.): Leaf traits and litter decomposition.	https://doi.org/10.1016/j.envp.2010.02.025	Europe	Finland	Helsinki
Nock et al., 2013	Effects of Urbanization on Tree Species Functional Diversity in Eastern North America.	https://doi.org/10.1007/s10021-013-9697-5	North America	United States	Northeastern
Oliveira et al., 2019	Reduced reproductive success of the endangered tree brazilwood (<i>Pau-brasil</i> <i>Leguminosae</i>) in urban ecosystem compared to Atlantic forest remnant: lessons for tropical urban ecology.	https://doi.org/10.1016/j.ufug.2019.04.020	South America	Brazil	Recife
Oliveira et al., 2020	Urban green areas retain just a small fraction of tree reproductive diversity of the Atlantic forest.	https://doi.org/10.1016/j.ufug.2020.126779	South America	Brazil	Recife

Study	Taxa	Approach	Megacity	Biome	Community traits
Massei et al., 2015	<i>Tilia × europaea</i>	Urban vs non-urban	No	Mediterranean Forests, Woodlands & Scrub	-
McCune and Velend, 2013	All vascular plants	Temporal	-	Temperate Conifer Forests	Abundance of species; total diversity; local diversity; β -diversity; species origin
Melliger et al., 2018	All vascular plants	Urban vs non-urban	-	Temperate Broadleaf & Mixed Forests	Ecological strategy; total cover of vegetation; species richness
Milanović et al., 2021	All vascular plants	Temporal	No	Temperate Broadleaf & Mixed Forests	Species richness, presence of non-native species
Molnár et al., 2018	<i>Celtis occidentalis</i> , <i>Acer campestre</i> , <i>Corylus avellana</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	-
Murray-Stoker and Johnson, 2021	<i>Trifolium repens</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Neil et al., 2010	Shrubs	Temporal	-	Deserts & Xeric Shrublands	-
Nero et al., 2019	Trees	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness
Nikula et al., 2010	<i>Populus tremula</i>	Urban - non-urban gradient	Yes	Boreal Forests/Taiga	Leaf litter
Nock et al., 2013	Woody plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	-
Oliveira et al., 2019	<i>Paubrasilia echinata</i>	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Oliveira et al., 2020	Woody plants	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species origin

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Masseti et al., 2015	Temperature; percentage of impervious surfaces; building volume density	-	-	Phenology (flowering)	-
McCune and Vellend, 2013	-	Specific leaf area	Disturbance tolerance; soil nutrient regime preference; shade tolerance	Seed weight; seed dispersal	Palatability
Melliger et al., 2018	Soil moisture, pH, organic matter content, organic nitrogen content	-	Life form	Reproduction type; pollination syndrome; seed dispersal; seed mass	-
Milanović et al., 2021	-	Height, specific leaf area, storage organs, life form, leaf anatomy	Life span	Seed mass, flowering period, clonal growth, pollinators, ploidy,	-
Molnár et al., 2018	-	-	Chlorophyll-a content of leaves	-	-
Murray-Stoker and Johnson, 2021	N content in soil, land use and land cover	-	Nodule density per cm of root per plant, N content in leaves	-	-
Neil et al., 2010	-	-	-	Phenology (flowering)	-
Nero et al., 2019	-	Diameter at breast height	-	Dispersal mechanism	-
Nikula et al., 2010	pH and conductivity of the hummus layer; temperature; precipitation; air quality	Diameter at breast height; amount of epicuticular waxes	Total C and N concentrations in leaves; litter decomposition; palatability of the litter	-	DNA Molecular markers (SSR); clone identification
Nock et al., 2013	Index of Human Influence	Wood density; maximum plant height	Leaf nitrogen per unit mass	Seed mass	-
Oliveira et al., 2019	-	-	-	Phenology (flowering and fruiting); length of calyx, corolla, sepals, petals, flag petal, stamens, anthers, pistil and ovary; diameter of corolla, sepals, petals, flag petal and stigma; pollen viability; number of pollen grains and ovules per flower; floral visitors; fruit and seed set; flowers per inflorescence	-
Oliveira et al., 2020	-	-	-	Pollination system; floral biology; sexual system; reproductive system; floral type; floral size	-

Study	Title	DOI	Continent	Country	City/Region
Paquin et al., 2020	Native plant turnover and limited exotic spread explain swamp biotic differentiation with urbanization	https://doi.org/10.1111/avsc.12550	North America	Canada	Quebec
Park et al., 2021	Spatially Varying Relationships between Alien Plant Distributions and Environmental Factors in South Korea	https://doi.org/10.3390/plants10071377	Asia	South Korea	-
Pellegrini et al., 2021	Agricultural land use curbs exotic invasion but sustains native plant diversity at intermediate levels.	https://doi.org/10.1038/s41598-021-87806-7	Europe	Italy	Friuli Venezia-Giulia region
Peng et al., 2019	Most suitable landscape patterns to preserve indigenous plant diversity affected by increasing urbanization: A case study of Shunyi District of Beijing, China.	https://doi.org/10.1016/j.ufug.2018.11.004	Asia	China	Beijing
Pennington et al., 2010	Urbanization and riparian forest woody communities: Diversity, composition, and structure within a metropolitan landscape.	https://doi.org/10.1016/j.biocon.2009.10.002	North America	United States	Cincinnati
Planchuelo et al., 2020a	Plant traits, biotopes and urbanization dynamics explain the survival of endangered urban plant populations.	https://doi.org/10.1111/1365-2664.13661	Europe	Germany	Berlin
Planchuelo et al., 2020b	Endangered Plants in Novel Urban Ecosystems Are Filtered by Strategy Type and Dispersal Syndrome, Not by Spatial Dependence on Natural Remnants.	https://doi.org/10.3389/fevo.2020.00018	Europe	Germany	Berlin
Qian et al., 2020	Urban growth and topographical factors shape patterns of spontaneous plant community diversity in a mountainous city in southwest China.	https://doi.org/10.1016/j.ufug.2020.126814	Asia	China	Chongqing
Qiu et al., 2017	Impacts of Urbanization on Vegetation Phenology over the Past Three Decades in Shanghai, China.	https://doi.org/10.3390/rs9090970	Asia	China	Shanghai
Ranta and Viijanen, 2011	Vascular plants along an urban-rural gradient in the city of Tampere, Finland.	https://doi.org/10.1007/s11252-011-0164-9	Europe	Finland	Tampere
Ribeiro et al., 2019	Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance.	https://doi.org/10.1111/1365-2745.13177	South America	Brazil	Panamirim
Rivkin et al., 2021	Urbanization alters interactions between Darwin's finches and <i>Tribulus cistoides</i> on the Galápagos Islands.	https://doi.org/10.1002/ecc3.8236	South America	Ecuador	Galápagos Islands
Salgado et al., 2021	Impact of urbanization and landscape changes on the vegetation of coastal dunes along the Cuif of Mexico	https://doi.org/10.1080/11956860.2021.1934299	North America	Mexico	Veraacruz

Study	Taxa	Approach	Megacity	Biome	Community traits
Paquin et al., 2020	All vascular plants	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	Species origin; habitat preference; species richness; β -diversity; species cover
Park et al., 2021	<i>Aster pilosus</i> , <i>Lactuca scariola</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Presence of the non-native species
Pellegrini et al., 2021	All vascular plants	Urban - non-urban gradient	-	Temperate Conifer Forests; Temperate Broadleaf & Mixed Forests	Species richness, presence of non-native species
Peng et al., 2019	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Abundance of native species
Pennington et al., 2010	Woody riparian plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness; species origin; canopy forest structure
Planchuelo et al., 2020a	Endangered species	Urban - non-urban gradient/ Temporal	Yes	Temperate Broadleaf & Mixed Forests	-
Planchuelo et al., 2020b	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness
Qian et al., 2020	All vascular plants	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness, abundance
Qiu et al., 2017	All vascular plants	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Ranta and Viijanen, 2011	All vascular plants	Urban - non-urban gradient	No	Boreal Forests/Taiga	Species richness; species origin
Ribeiro et al., 2019	All vascular plants	Urban - non-urban gradient	No	Deserts & Xeric Shrublands	Species richness
Rivkin et al., 2021	<i>Tribulus cistoides</i>	Urban vs non-urban	No	Deserts & Xeric Shrublands	Variation in fruit removal and phenotypic selection by finches
Salgado et al., 2021	All vascular plants	Temporal	-	Tropical & Subtropical Moist Broadleaf Forests	Species richness, presence of non-native species

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Paquin et al., 2020	Land cover; Soil features	-	-	-	-
Park et al., 2021	Anthropogenic activity, land-use variables, annual mean air temperature, annual temperature range, annual precipitation, topographic properties	-	-	-	-
Pellegrini et al., 2021	Elevation, Monthly mean temperature, Mean rainfall, land use	-	-	-	-
Peng et al., 2019	Complexity, fragmentation, diversity, and urbanization	-	-	-	-
Pennington et al., 2010	Land-cover data	Diameter at breast height	Species moisture requirement	-	-
Planchuelo et al., 2020a	Land use	Specific leaf area, plant height	-	-	-
Planchuelo et al., 2020b	Land use	-	-	Dispersal syndrome, seed mass, length, width, number and terminal velocity	-
Qian et al., 2020	Land use, topography	-	-	-	-
Qiu et al., 2017	-	-	Phenology (growing season)	-	Remote sensing
Ranta and Viihinen, 2011	Land use	-	-	-	Human population
Ribeiro et al., 2019	Chronic anthropogenic disturbance	Diameter at breast height; Specific leaf area; mass per area; dry matter content and thickness; wood density	Deciduousness	Dispersion	-
Rivkin et al., 2021	-	-	-	Seed removal by finches	-
Salgado et al., 2021	Urban index	-	Functional traits: burial resistance, dispersal by ocean water, salinity resistance and type of below-ground structures	-	-

Study	Title	DOI	Continent	Country	City/Region
Santangelo et al., 2020a	Multivariate phenotypic divergence along an urbanization gradient.	http://dx.doi.org/10.1098/rsbl.2020.0511	North America	Canada	Toronto
Santangelo et al., 2020b	Predicting the strength of urban-rural clines in a Mendelian polymorphism along a latitudinal gradient.	https://doi.org/10.1002/evl3.163	North America	United States	Eastern United States
Santos et al., 2016	Composition and richness of woody species in riparian forests in urban areas of Manaus, Amazonas, Brazil.	https://doi.org/10.1016/j.landurbplan.2016.03.004	South America	Brazil	Manaus
Schmidt et al., 2014	Effects of urban structure on plant species richness in a large European city.	https://doi.org/10.1007/s11252-013-0319-y	Europe	Germany	Hamburg
Schmiedel et al., 2015	Plant species richness patterns along a gradient of landscape modification intensity in Lower Saxony, Germany.	https://doi.org/10.1016/j.landurbplan.2015.03.009	Europe	Germany	Lower Saxony
Schwartz et al., 2016	Are plant communities mainly determined by anthropogenic land cover along urban riparian corridors?	https://doi.org/10.1007/s11252-016-0567-8	Europe	France	Strasbourg
Searle et al., 2012	Urban environment of New York City promotes growth in northern red oak seedlings	https://doi.org/10.1093/breephys/tps027	North America	United States	New York
Silva-Junior et al., 2018	Landscape urbanization threatens plant phylogenetic diversity in the Brazilian Atlantic Forest.	https://doi.org/10.1007/s11252-018-0745-y	South America	Brazil	João Pessoa
Singh et al., 2020	Assessing adaptation and mitigation potential of roadside trees under the influence of vehicular emissions: A case study of <i>Grevillea robusta</i> and <i>Mangifera indica</i> planted in an urban city of India.	https://doi.org/10.1371/journal.pone.0227380	Asia	India	Delhradhun
Singh, 2021	An integrated approach considering physiological- and biophysical-based indicators for assessing tolerance of roadside plantations of <i>Alstonia scholaris</i> towards urban roadside air pollution: an assessment of adaptation of plantations for mitigating roadside air pollution	https://doi.org/10.1007/s00468-021-02179-8	Asia	India	Delhradhun

Study	Taxa	Approach	Megacity	Biome	Community traits
Santangelo et al., 2020a	<i>Trifolium repens</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Santangelo et al., 2020b	<i>Trifolium repens</i>	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests; Temperate Grasslands, Savannas & Shrublands	-
Santos et al., 2016	Woody plants	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness; species origin
Schmidt et al., 2014	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness; species origin; threat status
Schmiedel et al., 2015	All vascular plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species richness; species origin; threat status
Schwoertzig et al., 2016	All vascular riparian plants	Urban - non-urban gradient	-	Temperate Broadleaf & Mixed Forests	Species richness
Searle et al., 2012	<i>Quercus rubra</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Silva-Junior et al., 2018	All vascular plants	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species density
Singh et al. 2020	<i>Grevillea robusta</i> , <i>Mangifera indica</i>	Urban vs non-urban	No	Montane Grasslands & Shrublands	-
Singh, 2021	<i>Alstonia scholaris</i>	Urban vs non-urban	No	Montane Grasslands & Shrublands	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Santangelo et al., 2020a	-	Leaf width; leaf length; stolon diameter; petiole length	Defensive phenotype (HCN); vegetative biomass	Phenology (flowering); petal length; petal width; flowers per inflorescence; inflorescences; peduncle length; reproductive biomass; time to germination; pollinators; seed set	-
Santangelo et al., 2020b	Temperature; precipitation; aridity index; evapotranspiration; snow depth and snowfall	-	Defensive phenotype (HCN)	-	DNA sequences of selected loci
Santos et al., 2016	-	Diameter at breast height	-	-	-
Schmidt et al., 2014	Climate; impervious surface; habitat type; soil	-	-	-	-
Schmiedel et al., 2015	Landscape composition; landscape configuration	-	Habitat preferences	-	-
Schwoertzig et al., 2016	Climate; soil; land cover type	-	-	-	-
Searle et al., 2012	Temperature; CO2 concentrations	-	Leaf nitrogen; biomass	-	-
Silva-Junior et al., 2018	Percentage of urbanization	Diameter at breast height	-	-	Phylogenetic diversity
Singh et al. 2020	Local cooling created by canopy	Leaf thickness	CO2 assimilation rate, transpiration rate, stomatal conductance, water use efficiency, air pollution tolerance index, copper and proline accumulation, dust removal efficiency	-	-
Singh, 2021	Local cooling created by canopy	Height, canopy, leaf thickness	CO2 assimilation rate, transpiration, stomatal conductance, water use efficiency, relative water content, proline, soluble sugar, ascorbic acid, leaf pH, total chlorophyll, accumulation of heavy metals	-	Dust load flux

Study	Title	DOI	Continent	Country	City/Region
Skuliey and Matthews, 2017	Urbanization and roads drive non-native plant invasion in the Chicago Metropolitan region.	https://doi.org/10.1007/s10530-017-1464-7	North America	United States	Chicago
Soltysiak, 2020	Does the urban heat island determine the distribution of Fallopia taxa in cities? – preliminary study from Wrocław (Central Europe).	https://doi.org/10.12775/EQ.2020.010	Europe	Poland	Wrocław
Song et al., 2019	Changes in plant functional traits and their relationships with environmental factors along an urban-rural gradient in Guangzhou, China.	https://doi.org/10.1016/j.ecoliand.2019.105558	Asia	China	Guangzhou
Sonti et al, 2021	Chlorophyll fluorescence parameters, leaf traits and foliar chemistry of white oak and red maple trees in urban forest patches	https://doi.org/10.1093/treephys/tpaa121	North America	United States	New York, Philadelphia, Baltimore
Štajerová et al., 2017	Distribution of invasive plants in urban environment is strongly spatially structured.	https://doi.org/10.1007/s10980-016-0480-9	Europe	Czech Republic	Hradec Kralove
Su et al, 2021	Leaf Functional Traits Vary in Urban Environments: Influences of Leaf Age, Land-Use Type, and Urban-Rural Gradient.	https://doi.org/10.3389/fevo.2021.681959	Asia	China	Beijing
Su et al., 2019	Leaf and male cone phenophases of Chinese pine (<i>Pinus tabulaeformis</i> Carr.) along a rural-urban gradient in Beijing, China.	https://doi.org/10.1111/1365-2019.05009	Asia	China	Beijing
Tew et al, 2021	Quantifying nectar production by flowering plants in urban and rural landscapes.	https://doi.org/10.1111/1365-2745.13598	Europe	United Kingdom	-
Thompson et al., 2016	Urbanization drives the evolution of parallel clines in plant populations.	http://dx.doi.org/10.1098/rspb.2016.2180	North America	Canada	Toronto

Study	Taxa	Approach	Megacity	Biome	Community traits
Skuliey and Matthews, 2017	<i>Altharia petiolata</i> , <i>Aster subulatus</i> , <i>Atriplex patula</i> , <i>Bolboschoenus maritimus</i> , <i>Dipsacus fullonum</i> , <i>Dipsacus laciniatus</i> , <i>Hemerocallis filva</i> , <i>Hordeum jubatum</i> , <i>Lysimachia nummularia</i> , <i>Lythrum salicaria</i> , <i>Phragmites australis</i> , <i>Puccinellia distans</i> , <i>Solanum dulcamara</i> , <i>Solidago sempervirens</i> , <i>Spergularia specios</i> , <i>Viburnum recognitum</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Propagule Sources
Soltysiak, 2020	<i>Fallopia japonica</i> , <i>Fallopia sachalinensis</i> , <i>Fallopia × bohemica</i>	Urban - non-urban gradient/ Temporal	No	Temperate Broadleaf & Mixed Forests	Presence of the non-native species
Song et al., 2019	<i>Schima superba</i> , <i>Castanopsis fissa</i> , <i>Acronychia pedunculata</i> , <i>Diplospora dubia</i> , <i>Ardisia quinquegona</i> , <i>Diospyros morrisiana</i> , <i>Castanopsis chinensis</i> , <i>Psychotria rubra</i> , <i>Meneclyon nigrescens</i> , <i>Strygum lancei</i> , <i>Pygeum topengi</i> , <i>Cinnamomum burmanni</i> , <i>Cryptocarya concinna</i> , <i>Endospermum chinense</i> , <i>Artia pycnantha</i> , <i>Microdesmis casearifolia</i> , <i>Machilus suaveolens</i> , <i>Machilus chinensis</i> , <i>Engelhardtia fenzlii</i> , <i>Albizziella leucocarpa</i> , <i>Neolitsea phanerophlebia</i> , <i>Symplocos adenopus</i> , <i>Michelia skimmeriana</i> , <i>Daphniphyllum subverricillatum</i> , <i>Manglietia motoi</i> , <i>Neolitsea chuii</i>	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	Relative frequency, density and dominance of species
Sonti et al., 2021	<i>Quercus alba</i> , <i>Acer rubrum</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Štajerová et al., 2017	<i>Epilobium adenocaulon</i> , <i>Galeobdolon argenteatum</i> , <i>Maltonia aquifolium</i> , <i>Matricaria discocidea</i> , <i>Oenothera biennis</i> , <i>Physocarpus opulifolius</i> , <i>Rhus typhina</i> , <i>Rumex thyrsiflorus</i> , <i>Syringa vulgaris</i>	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Su et al., 2021	<i>Pinus tabulaeformis</i>	Urban - non-urban gradient/ Temporal	Yes	Temperate Broadleaf & Mixed Forests	-
Su et al., 2019	<i>Pinus tabulaeformis</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	-
Tew et al., 2021	Community of specific flowering species	Urban - non-urban gradient/ Temporal	-	Temperate Broadleaf & Mixed Forests	-
Thompson et al., 2016	<i>Trifolium repens</i>	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Herbivory

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Skulley and Matthews, 2017	Land cover; road type	-	-	-	-
Soltysiak, 2020	Temperature	-	-	-	-
Song et al., 2019	Soil properties	Diameter at breast height; leaf area	Leaf carbon, nitrogen and phosphorus; photosynthetic rate	-	-
Sonti et al., 2021	-	Diameter at breast height, stomatal density	Chlorophyll content, foliar nutrients	-	-
Štajerová et al., 2017	Land use type; habitat richness	-	-	-	-
Su et al., 2021	-	Stomatal density, leaf width, leaf length, specific leaf area	Leaf N, P and K concentration	-	-
Su et al., 2019	Impervious cover; temperature	Length of needles	Phenology (leaf and male cones)	-	-
Tew et al., 2021	-	-	-	Floral abundance, nectar sugar production	-
Thompson et al., 2016	Ground temperature; historical weather data	-	Defensive phenotype (HCN); biomass	Reproductive fitness	-

Study	Title	DOI	Continent	Country	City/Region
Tian et al., 2015	Distribution patterns and traits of weed communities along an urban-rural gradient under rapid urbanization in Shanghai, China.	https://doi.org/10.1111/wbm.12062	Asia	China	Shanghai
Toma et al., 2015	Factors affecting the genetic diversity of a perennial herb <i>Viola grypoceras</i> A. Gray var. <i>grypoceras</i> in urban fragmented forests.	https://doi.org/10.1007/s10980-015-0197-1	Asia	Japan	Kyoto
Tordoni et al., 2017	Diversity patterns of alien and native plant species in Trieste port area: exploring the role of urban habitats in biodiversity conservation.	https://doi.org/10.1007/s11252-017-0667-0	Europe	Italy	Trieste
Trautman et al., 2020	Temperate deciduous forests embedded across developed landscapes: Younger forests harbour invasive plants and urban forests maintain native plants.	https://doi.org/10.1111/1365-2745.13400	North America	United States	Northern Delaware and southeastern Pennsylvania
Treitanovi et al., 2013	Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion.	https://doi.org/10.1111/ddi.12028	Europe	Germany	Berlin
Turmukhmetova and Shadrina, 2020	Changes in the Fluctuating Asymmetry of the Leaf and Reproductive Capacity of <i>Betula pendula</i> Roth Reflect Pessimization of Anthropogenically Transformed Environment	https://doi.org/10.3390/sym12121970	Europe	Russia	Yoshkar-Ola
Ushimaru et al., 2014	Data from: Does urbanization promote floral diversification? Implications from changes in heritogamy with pollinator availability in an urban-rural area.	https://doi.org/10.5061/dryad.pd775	Asia	Japan	Ikoma
Vakhlamova et al., 2014	Changes in plant diversity along an urban-rural gradient in an expanding city in Kazakhstan, Western Siberia.	https://doi.org/10.1016/j.landurbplan.2014.08.014	Asia	Kazakhstan	Pavlodar
Vakhlamova et al., 2016	Effects of road type and urbanization on the diversity and abundance of alien species in roadside verges in Western Siberia.	https://doi.org/10.1007/s11258-016-0565-1	Asia	Kazakhstan	Pavlodar
Vallet et al., 2010a	The effects of urban or rural landscape context and distance from the edge on native woodland plant communities.	https://doi.org/10.1007/s10531-010-9901-2	Europe	France	Angers and Nantes
Vallet et al., 2010b	Using biological traits to assess how urbanization filters plant species of small woodlands.	https://doi.org/10.1111/j.1654-109X.2010.01087.x	Europe	France	Angers, Nantes and Rennes
Van Rossum, 2010	Reproductive success and pollen dispersal in urban populations of an insect-pollinated hay-meadow herb	https://doi.org/10.1016/j.ppees.2009.08.002	Europe	Belgium	Brussels

Study	Taxa	Approach	Megacity	Biome	Community traits
Tian et al., 2015	All vascular weedy plants	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species origin; species richness; relative dominance of species
Toma et al., 2015	<i>Viola grypoceras</i> A. Gray var. <i>grypoceras</i>	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	-
Tordoni et al., 2017	All vascular plants	Urban - non-urban gradient	No	Mediterranean Forests, Woodlands & Scrub	Species origin; species richness; abundance
Trautman et al., 2020	Woody plants	Urban - non-urban gradient/ Temporal	-	Temperate Broadleaf & Mixed Forests	Species origin; population density
Treitanovi et al., 2013	All vascular plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Canopy cover; species origin; species richness
Turmukhametova and Shadrina, 2020	<i>Betula pendula</i>	Urban - non-urban gradient/ Temporal	No	Boreal Forests/Taiga	-
Ushimaru et al., 2014	<i>Commelina communis</i>	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Vakhlamova et al., 2014	All vascular plants	Urban - non-urban gradient	No	Temperate Grasslands, Savannas & Shrublands	Species richness; species abundance; canopy cover; Evenness; species origin
Vakhlamova et al., 2016	All vascular plants	Urban - non-urban gradient	No	Temperate Grasslands, Savannas & Shrublands	Species richness; species abundance; canopy cover; species origin
Vallet et al., 2010a	Woody plants	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	Species richness; species abundance; species origin
Vallet et al., 2010b	All vascular plants	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Van Rossum, 2010	<i>Centaurea jacea</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Tian et al., 2015	Land use type; light intensity; soil properties	Height	Life form	-	-
Toma et al., 2015	Area of urban forests; distance between urban forests	-	-	-	DNA Molecular markers (SSR); genetic diversity
Tordoni et al., 2017	-	-	-	-	-
Trautman et al., 2020	Percentage of impervious surface	Diameter at breast height	-	-	Temporal aerial images
Trentanovi et al., 2013	Land use type	-	-	-	-
Turmukhametova and Shadrina, 2020	Average score of anthropogenic impact	-	-	seed quantity; maturation length, width, ratio	-
Ushimaru et al., 2014	Land use type	-	-	Pollinator frequency; flower abundance; reproductive success; heights of the stigma and anther; length of petal; P:O ratio	-
Vakhlamova et al., 2014	Land use type	-	-	-	-
Vakhlamova et al., 2016	-	-	-	Seed bank; dispersal type	-
Vallet et al., 2010a	Ellenberg indicator values for light, soil pH and nitrogen	-	-	-	-
Vallet et al., 2010b	Ellenberg values for light, soil humidity, soil basicity, soil fertility	Canopy height; leaf position; specific leaf area; shoot growth form	Leaf persistence; Plant life span	Aerial vegetative multiplication; underground vegetative multiplication; first flowering; month of flowering period; start month of seed shedding period; length of seed shedding; seed number; mean weight of germinule; seed bank longevity; pollination; fruit dispersal	-
Van Rossum, 2010	-	-	-	Floral display; number of mature seeds; pollen dispersal patterns	-

Study	Title	DOI	Continent	Country	City/Region
van Vliet et al., 2014	Dendrochronology and dendroclimatology of <i>Ceiba speciosa</i> (A. St.-Hil.) Ravenna (Malvaceae) exposed to urban pollution in Rio de Janeiro city, Brazil.	https://doi.org/10.1016/j.dendro.2018.12.004	Europe	Netherlands	-
Vasconcelos et al., 2019	Pollination and seed set of an obligatory outcrossing plant in an urban–peri-urban gradient.	https://doi.org/10.1016/j.ppees.2014.03.002	South America	Brazil	Rio de Janeiro
Verboven et al., 2014	Observed climate-induced changes in plant phenology in the Netherlands.	https://doi.org/10.1007/s10113-013-0493-8	Europe	Belgium	Leuven
Vujić et al., 2015	The effects of traffic-related air pollution on the flower morphology of <i>Iris punila</i> – Comparison of a polluted city area and the unpolluted deliblato sands (Nature reserve).	https://doi.org/10.15666/aeer/1302_405415	Europe	Serbia	Belgrade
Wang et al., 2020	Effects of urban built-up patches on native plants in subtropical landscapes with ecological thresholds – A case study of Chongqing city.	https://doi.org/10.1016/j.ecohyd.2019.105751	Asia	China	Chongqing
Wang et al., 2020	Plant Diversity Along the Urban–Rural Gradient and Its Relationship with Urbanization Degree in Shanghai, China	https://doi.org/10.3390/f11020171	Asia	China	Shanghai
Wirth et al., 2020	Changes of 70 years in the non-native and native flora of a Hungarian county seat (Pécs, Central Europe).	https://doi.org/10.1080/11263504.2020.1829734	Europe	Hungary	Pécs
Wodkiewicz and Gruszczyńska, 2014	Genetic Diversity and Spatial Genetic Structure of <i>Stellaria Holostea</i> Populations from Urban Forest Islands.	https://doi.org/10.2478/abesb-2014-0004	Europe	Poland	Warsaw
Wu et al., 2013	Dynamics of diversity, distribution patterns and interspecific associations of understory herbs in the city-suburb-exurb context of Wuhan city, China	https://doi.org/10.2298/ABSI1304619W	Asia	China	Wuhan
Xiao et al., 2021	Plant Functional Groups Dominate Responses of Plant Adaptive Strategies to Urbanization.	https://doi.org/10.3389/fpls.2021.773676	Asia	China	Guangzhou
Xiao et al., 2016	Urban-rural and temporal differences of woody plants and bird species in Harbin city, northeastern China.	https://doi.org/10.1016/j.ufug.2016.07.013	Asia	China	Harbin
Xingyuan et al., 2016	Effects of climate warming on phenological characteristics of urban forest in Shenyang City, China.	https://doi.org/10.1007/s11769-015-0782-x	Asia	China	Shenyang
Yakub and Tiffin, 2017	Living in the city: urban environments shape the evolution of a native annual plant.	https://doi.org/10.1111/gcb.13528	North America	United States	Minneapolis-St. Paul, Chicago, Detroit, Baltimore and New York
Yan et al., 2019	Impervious surface area is a key predictor for urban plant diversity in a city undergone rapid urbanization.	https://doi.org/10.1016/j.scitotenv.2018.09.025	Asia	China	Wuhan

Study	Taxa	Approach	Megacity	Biome	Community traits
van Vliet et al., 2014	All vascular plants	Temporal	-	Temperate Broadleaf & Mixed Forests	-
Vasconcellos et al., 2019	<i>Ceiba speciosa</i>	Urban vs non-urban	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Verboven et al., 2014	<i>Trifolium repens</i>	Urban - non-urban gradient	No	Temperate Broadleaf & Mixed Forests	-
Vujić et al., 2015	<i>Iris pumila</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Wang et al. 2020	All vascular plants	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness, presence of non-native species, extinction rates
Wang et al., 2020	All vascular plants	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness; species abundance; species origin; evenness
Wirth et al., 2020	All vascular plants	Temporal	No	Temperate Broadleaf & Mixed Forests	Species richness, presence of non-native species
Wodkiewicz and Gruszczyńska, 2014	<i>Stellaria holostea</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Wu et al., 2013	Herbs	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species cover; species richness
Xiao et al., 2021	<i>Lophatherum gracile</i> , <i>Alpinia chinensis</i> , <i>Ardisia quinquegona</i> , <i>Psychotria rubra</i> , <i>Diospyros morrisiana</i> , <i>Cratogeomys cochinchinense</i> , <i>Engelhardtia roxburghiana</i> , <i>Schinus molle</i>	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	-
Xiao et al., 2016	Woody plants	Urban - non-urban gradient/ Temporal	Yes	Temperate Broadleaf & Mixed Forests	Species origin; species richness
Xingyuan et al., 2016	Woody plants	Temporal	Yes	Temperate Broadleaf & Mixed Forests	-
Yakub and Tiffin, 2017	<i>Lepidium virginicum</i>	Urban vs non-urban	Yes	Temperate Broadleaf & Mixed Forests	-
Yan et al., 2019	All vascular plants	Urban - non-urban gradient	Yes	Tropical & Subtropical Moist Broadleaf Forests	Cultivation status; canopy cover; species origin; species richness

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
van Vliet et al., 2014	Temperature	-	Phenology (leaf unfolding; autumn colouring; leaf fall)	Phenology (flowering; fruits ripe)	-
Vasconcellos et al., 2019	Temperature; precipitation	Growth rings	-	-	Ages and rates of growth of the species
Verboven et al., 2014	Land use type	-	-	Flower visitation rates; seed set	-
Vujić et al., 2015	-	-	-	Length, width, centroid size and shape variation of petals	-
Wang et al., 2020	Land use	Life forms	-	-	-
Wang et al., 2020	Land use	-	-	-	-
Wirth et al., 2020	-	Life forms	-	Dispersal type	-
Wodkiewicz and Gmusczyńska, 2014	-	-	-	-	Allozymes; spatial genetic structure; genetic variability; clonal diversity
Wu et al., 2013	-	Height	-	-	-
Xiao et al., 2021	-	Leaf thickness and surface area	C, N and P content in leaves, concentrations of heavy metals, concentrations of starch in the leaves, stomatal conductance, photosynthetic rate, chlorophyll content, Rubisco content, dry biomass	-	-
Xiao et al., 2016	-	-	-	-	-
Xingyuan et al., 2016	Temperature	-	Phenology (germination)	-	-
Yakub and Tiffin, 2017	-	Rosette height; rosette diameter; height and number of branches at the time of senescence	Phenology (germination; bolting)	Phenology (flowering); number of fruits	Genotype-by-sequencing; molecular divergence among populations; structuring of genomic variation
Yan et al., 2019	Percentage of total impervious surface area	-	-	-	-

Study	Title	DOI	Continent	Country	City/Region
Yang et al., 2021	Impacts of the remnant sizes, forest types, and landscape patterns of surrounding areas on woody plant diversity of urban remnant forest patches.	https://doi.org/10.1007/s11252-020-01040-z	Asia	China	Guiyang
Yu et al., 2021	Dynamic change of composition and functions of flora adapting to rapid urbanization: a case study of Hangzhou, China	https://doi.org/10.15666/aeer/1905_40074023	Asia	China	Hangzhou
Zeeman et al., 2017	Biotic homogenization in an increasingly urbanized temperate grassland ecosystem.	https://doi.org/10.1111/jvs.12507	Oceania	Australia	Victoria
Zhang et al., 2020	The Diversity Distribution Pattern of Ruderal Community under the Rapid Urbanization in Hangzhou, East China	https://doi.org/10.3390/d12030116	Asia	China	Hangzhou
Zhang et al., 2016	Effects of forest type and urbanization on species composition and diversity of urban forest in Changchun, Northeast China.	https://doi.org/10.1007/s11252-015-0473-5	Asia	China	Changchun
Zipper et al., 2016	Urban heat island impacts on plant phenology: intra-urban variability and response to land cover.	https://doi.org/10.1088/1748-9326/11/5/054023	North America	United States	Madison
Zipper et al., 2017	Urban heat island-induced increases in evapotranspirative demand.	https://doi.org/10.1002/2016GL072190	North America	United States	Madison

Study	Taxa	Approach	Megacity	Biome	Community traits
Yang et al., 2021	All vascular plants	Urban - non-urban gradient/ Temporal	Yes	Tropical & Subtropical Moist Broadleaf Forests	Species richness
Yu et al., 2021	All vascular plants	Temporal	Yes	Temperate Broadleaf & Mixed Forests	Species richness, presence of non-native species
Zeeman et al., 2017	Graminoids	Urban vs non-urban/ Temporal	-	Temperate Broadleaf & Mixed Forests	Species origin
Zhang et al., 2020	Ruderal plants	Urban - non-urban gradient/ Temporal	Yes	Temperate Broadleaf & Mixed Forests	Species richness, dominance
Zhang et al., 2016	Woody plants	Urban - non-urban gradient	Yes	Temperate Broadleaf & Mixed Forests	Species richness; evenness index; species Importance Value
Zipper et al., 2016	All vascular plants	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	-
Zipper et al., 2017	All vascular plants	Urban vs non-urban	No	Temperate Broadleaf & Mixed Forests	-

Study	Physical environment	Morphological traits	Physio-chemical traits	Reproductive biology	Other traits
Yang et al., 2021	Impervious surface	-	-	-	-
Yu et al., 2021	Light, temperature, moisture, soil reaction, soil fertility	Life forms	-	-	-
Zeeman et al., 2017	-	Height	-	Life span, vegetative reproduction and dormant bud position	Floristic inventory
Zhang et al., 2020	Land cover	Life forms	-	-	-
Zhang et al., 2016	-	-	-	-	-
Zipper et al., 2016	Temperature; impervious cover	-	-	Phenology	Remote sensing
Zipper et al., 2017	Temperature; humidity, wind speed; impervious cover	-	Evapotranspirative demand	Phenology	-

Supplementary Table 2. Plants' responses to urbanization according to the analyzed studies.

Reference	Taxa	Urban drivers	Negative responses
Abd El-Wahab, 2016	All vascular plants	LC	Lower species richness; lower plant cover; lower species diversity
Albrecht and Haider, 2013	Graminoids	CL/LC	Lower native species richness; lower numbers of endangered species; earlier flowering; disfavoring of windpollinated species
Anderson et al., 2020	All vascular plants	HA/LC/UH	Lower species richness; lower plant cover; lower plant trait diversity; grass domination; less species that reward animals through pollination and seed dispersal; poorer communities have limited green space and lower plant and trait diversity
Aronson et al., 2015	Woody plants	BI/LC	Lower native species richness; increase of non-native species
Atasoy et al., 2018	<i>Ligustrum sinense</i> , <i>Elaeagnus pungens</i> , <i>Triadica sebifera</i>	BI/LC	Cover of two of the invasive species tended to increase
Barradas and Esperon-Rodriguez, 2021	<i>Acacia longifolia</i> , <i>Acer negundo</i> , <i>Alnus acuminata</i> , <i>Buddleja cordata</i> , <i>Celtis occidentalis</i> , <i>Dodonaea viscosa</i> , <i>Eucalyptus camaldulensis</i> , <i>Erythrina americana</i> , <i>Fraxinus uhdei</i> , <i>Ligustrum lucidum</i> , <i>Liquidambar styraciflua</i> , <i>Populus alba</i> , <i>Populus deltoides</i> , <i>Quercus rugosa</i> , <i>Ulmus parvifolia</i>	CL	Higher temperatures and vapor pressure deficit limited the stomatal function of all species
Bartlewicz et al., 2015	<i>Linaria vulgaris</i>	LC	Decrease of the clonal diversity; less ability to reproduce sexually
Beal-Neves et al., 2020	Graminoids	HA	-
Bigirimana et al., 2011	All vascular plants	BI/HA/LC	Lower native species richness; ruderal plants with a high abundance of introduced species
Blood et al., 2016	Woody plants	BI	Increase species richness by greater numbers of non-natives
Blouin et al., 2019	All vascular plants	BI/LC	Biotic homogenization occur resulted from non-native species invasion
Bode and Tong, 2018	<i>Cytisus scoparius</i>	BI	Pollinators select increased flower size, but only in urban populations
Bouraoiti et al., 2019	<i>Tilia x vulgaris</i>	PO	De-icing salt accumulation increases leaf injury, cascading up through the trophic chain and negatively affecting also the associated arthropod biota
Brice et al., 2016	All vascular plants	LC	Land transformation act indirectly on hydrological disturbances altering functional composition of riparian plant communities
Brice et al., 2017	All vascular plants	LC	Urbanization induced taxonomic and functional differentiation through its effect on species loss and turnover
Caughlin et al., 2012	<i>Ficus microcarpa</i> , <i>Ficus aurea</i>	BI	Seed-dispersing birds favours juvenile invasive fig abundance
Celesti-Grapow and Ricotta, 2021	All vascular plants	BI	The diversity of the native flora has steadily decreased, while there has been an increase in non-native, larger and more damaging species.
Chen et al., 2014	All vascular ruderal plants	BI/CL	Increase of tropical originated species; decrease in species richness due to urbanization and climate change along the years

Reference	Neutral responses	Positive responses
Abd El-Wahab, 2016	-	-
Albrecht and Haider, 2013	-	Favoring of plants with insect pollination; more plants with small and durable seeds; some of the endangered species exclusively grew at the urban sites
Anderson et al., 2020	-	-
Aronson et al., 2015	Urbanization did not advance the biotic homogenization	-
Atasoy et al., 2018	-	-
Barradas and Esperon-Rodriguez, 2021	-	-
Bartlewicz et al., 2015	-	-
Beal-Neves et al., 2020	-	Higher species richness; higher floral visitor richness; higher network asymmetry
Bigirimana et al., 2011	-	-
Blood et al., 2016	Maintenance of native species richness	-
Blouin et al., 2019	-	-
Bode and Tong, 2018	-	-
Bouraoui et al., 2019	-	-
Brice et al., 2016	-	-
Brice et al., 2017	-	-
Caughlin et al., 2012	-	-
Celesti-Grapow and Ricotta, 2021	-	-
Chen et al., 2014	-	-

Reference	Taxa	Urban drivers	Negative responses
Chimamba et al., 2020	Trees	BI/ HA /LC	Residential areas, roads and institutional land have high proportion of exotic trees
Cochard et al., 2017	Graminoids	LC	Lower species richness
Cochard et al., 2019	Graminoids	CL/ PO	Early flowering for almost all urban populations of each species
Comber and Brunsdon, 2015	<i>Crataegus monogyna</i> , <i>Prunus spinosa</i> , <i>Aesculus hippocastanum</i>	CL/ LC	First flowering date is getting earlier
Concepción et al., 2015	All vascular plants	LC	Urbanization favours highly mobile species with narrow habitat ranges; the positive response of specialist plants to urbanisation was most likely driven by species within this group that prefer eutrophic habitats, such as early successional species
Concepción et al., 2016	All vascular plants	BI/ HA/ LC	Increased proliferating non-native and ruderal plants; species richness of plants inhabiting eutrophic places, annual, highly dispersive, wind- and human dispersed plants are benefitted
Concepción et al., 2017	All vascular plants	CL/ HA/ LC	(Convergence in vegetative plant traits (plant height and leaf dry matter content)
Cui et al., 2019	All vascular ruderal plants	BI/ LC	Phylogenetic clustering of ruderal species with increasing spatial and temporal urbanization gradients
Dallimer et al., 2012	All vascular plants	BI/ LC	Neophyte richness increased closer to the urban core along all rivers
Davis et al., 2015	Herbs	LC	-
Davis et al., 2016	<i>Angophora costata</i> , <i>Eucalyptus ptilularis</i> , <i>Corymbia gummifera</i>	CL	-
de Araújo et al., 2021	All vascular plants	LC	Plant species richness decreased in anthropized plots resulting in responses in species richness and composition of gall-inducing insects
Déak et al., 2016	Graminoids	BI/ LC	Lower species richness; higher ratio of weeds, disturbance-tolerants, drought-tolerant; large proportion of alien and cosmopolitan species
Delnevo et al., 2021	Conospermum undulatum	LC	-
Desaegher et al., 2019	All vascular plants	CL/ LC/ PO	Proportion of autogamous, self-compatible, and nonentomophilous species was significantly higher in urban plant communities; insect-pollinated species with long and narrow tubular corollas were disadvantaged in urban areas

Reference	Neutral responses	Positive responses
Chimainba et al., 2020	-	Tree species are dominated by indigenous species.
Cochard et al., 2017	-	Insect-pollination and high seed production are favoured in grassland communities in urban areas
Cochard et al., 2019	Inconsistent Specific Leaf Area responses	Individuals were taller in cities than in rural areas
Comber and Brunsdon, 2015	-	-
Concepción et al., 2015	-	-
Concepción et al., 2016	-	-
Concepción et al., 2017	-	Divergence in growth forms, dispersal, and reproductive traits
Cui et al., 2019	-	-
Dallimer et al., 2012	Native plant richness showed a weak relationships with the sealed surface cover and human population density	-
Davis et al., 2015	Urbanization did not alter the relative influence of herbivory or soil resources on annual plant growth or composition	-
Davis et al., 2016	-	Three produced more flowers and flowered for longer
de Aratijo et al., 2021	-	-
Déak et al., 2016	-	-
Delnevo et al., 2021	Despite the current intense fragmentation, there are similar levels of genetic diversity across populations and a weak spatial genetic structure.	-
Desaegher et al., 2019	-	More species with higher affinities to higher temperature, light and nutrient soil content, and lower atmospheric moisture

Reference	Taxa	Urban drivers	Negative responses
Dolan et al., 2011	All vascular plants	BI/ HA/ LC	Significant turnover in species presence; lower native species richness; increase in non-native plants
Dolan et al., 2017	All vascular plants	HA/ LC	Natives species are different between the current and historical floras
dos Santos et al., 2020	Tecoma stans	HA	Urban plants faced up to higher resource theft (nectar and pollen) and lower fruit set
du Toit et al., 2020	All vascular plants	LC	Indigenous forb species richness is declining significantly
Dubois and Cheptou, 2017	<i>Crepis sancta</i>	LC	-
Duffy and Chown, 2016	C4 plants	CL	-
El-Barougy et al., 2021	All vascular plants	BI/ LC	Significant relationships of alien species traits with human-made pressures and soil resources in urban areas; functional and phylogenetic distances declined between the aliens and natives in urban areas, indicating biotic homogenization with increasing urbanization
Emel et al., 2021	<i>Sabbatia angularis</i>	LC	High-intensity urbanization presents a major barrier between populations, resisting gene flow 10–200 times more than natural lands
Everingham et al., 2019	All vascular plants	HA/ LC	Native species were disproportionately likely to be generalist species; native species colonising urban habitats tended to have traits associated with a fast life-history, including short stature and small seeds; high number of native plant species are colonising anthropogenic habitats
Fekete et al., 2020	Orchids	LC	There is a significant negative impact of agricultural and urban land covers on orchid diversity and abundance in general.
Filiz et al., 2015	<i>Tilia tomentosa</i>	LC	-
Fisogni et al., 2020	Herbs	LC	Plant flowering showed advancement of the flowering peak in sites at high urbanization; pollinator communities did not show any clear shift of their flight phenology
Fitchett and Raik, 2021	<i>Jacaranda mimosifolia</i>	CL	An advance of flowering in 2.1 days per decade is calculated for the period 1927–2019
Fornal-Pieniak et al., 2020	All vascular plants	BI/ LC	More alien plant species were growing in the urban forests
Freitas et al., 2020	Woody plants	LC	Species turnover

Reference	Neutral responses	Positive responses
Dolan et al., 2011	-	-
Dolan et al., 2017	-	Highly significant shift toward biotic pollination
dos Santos et al., 2020	-	-
du Toit et al., 2020	Urban vegetation is not currently homogenizing	-
Dubois and Cheptou, 2017	Urbanization showed no effect on phenotypic trait variations; relaxing selection on reproductive traits linked to attractiveness	Later flowering phenology; reduction of dispersal ability in all fragmented urban populations, consistent with the higher cost of dispersing seeds in more fragmented habitats
Duffy and Chown, 2016	-	Urbanized areas across temperate Europe have significantly higher abundance and richness of plants using the C4 photosynthetic pathway
El-Barougy et al., 2021	Native plants showed consistency in their trait–environment relationships in urban and non-urban areas	-
Emel et al., 2021	Isolation by environment in relation to heavy metals concentration was not significant	-
Everingham et al., 2019	-	-
Fekete et al., 2020	Species are able to cope and maintain populations in anthropogenically influenced habitats	Roadsides serve as suitable habitats for endangered taxa
Filiz et al., 2015	Members of the urban and forest ecosystems showed high genetic similarity and they did not separate from each other	-
Fisogni et al., 2020	-	-
Fichett and Raik, 2021	-	-
Fornal-Pieniak et al., 2020	-	-
Freitas et al., 2020	The diversity and structure of the plant communities did not vary in response to urbanization	-

Reference	Taxa	Urban drivers	Negative responses
Fukano et al., 2020	<i>Digitaria ciliaris</i>	BI/ LC	Urban populations had less growth rates, since they can occupy more space in less competitive environments
Gaggini et al., 2017	All vascular plants	BI/ HA/ LC	Higher number and larger abundance of non-native plant species in forest sites adjacent to settlements than in control forest sites; non-native plants more frequently recorded close to roads and in sites surrounded by a large percentage cover of garden.
Géron et al., 2021	<i>Artemisia verlotiorum</i> , <i>Erigeron canadense</i> , <i>Galinisoga quadriradiata</i> , <i>Marricaria discoidea</i> , <i>Senecio inaequidens</i> , <i>chamaephyte</i> , <i>Solidago gigantea</i>	BI/ CL/ LC	-
Glišić et al., 2021	All vascular plants	LC	The lowest alpha and gamma diversity and the dominance of therophytes were observed in habitat types with intensive anthropogenic impact
Greene and Blosssey, 2014	<i>Ligustrum sinense</i> , <i>Acer negundo</i> var. <i>negundo</i> , <i>Chasmanthium latifolium</i> , <i>Allium canadense</i>	BI/ HA/ LC	The invasive species cover was positively associated with urban development.
Grella et al., 2017	All vascular plants	BI/ LC/ PO	Urban concrete materials, urban soil and water contaminants were associated with higher weed coverage
Guerra et al., 2017	Woody plants	HA/ LC	Species showing shade intolerance, with smaller maximum heights, producing small seeds and with abiotic dispersion were present in high proportions in forests bordering heavily urbanized areas
Güler, 2020	All vascular plants	LC	Urban roadsides showed the lowest species richness, Shannon and Simpson diversity
Gulezian et al., 2010	<i>Ailanthus altissima</i> , <i>Alliaria petiolata</i> , <i>Arctium minus</i> , <i>Cirsium vulgare</i> , <i>Dipsacus silvestris</i> , <i>Melilotus alba</i> , <i>Phragmites australis</i> , <i>Rhamnus cathartica</i> , <i>Rosa multiflora</i> , <i>Setaria glauca</i>	BI	-
Hahs and McDormell, 2013	Woody plants	BI/ LC	-
Heneidy et al., 2021	All vascular plants	LC	Species richness shows a considerable decrease under the high disturbance levels in the study area
Hou et al., 2019	<i>Gentiana dahurica</i>	LC	Stability of pollinator visit frequency was weaker as urbanization intensified which result in an effective selective pressure for the urbanized plants; drop in seed-set ratio at the populations where more closed to metropolis

Reference	Neutral responses	Positive responses
Fukano et al., 2020	-	-
Gaggini et al., 2017	-	-
Géron et al., 2021	Alien plant phenotypic responses across all species did not strongly correlate with urbanity at local and landscape scale	-
Glišić et al., 2021	-	-
Greene and Blossey, 2014	-	-
Grella et al., 2017	-	-
Guerra et al., 2017	-	-
Güler, 2020	Few alien species were found with only slightly increasing abundances due to disturbances. Considerable biotic homogenisation did not occur.	-
Gulezian et al., 2010	-	Abundance of invasive species was negatively related to percent impervious surface, and presence was negatively related to local income
Hahs and McDonnell, 2013	Species richness per plot of emergent seedlings was best explained by average annual rainfall, rather than the degree of urbanization in the surrounding landscape	Indigenous plant species can coexist with non-indigenous monocot species within urban areas
Heneidy et al., 2021	-	Species richness shows a remarkable increase under moderate disturbance, coinciding with the increase in the numbers of both alien and weed species richness
Hou et al., 2019	Urbanization did not change the pollination mode of the species	As urbanization intensified, plant borne more flowers and the flower size became "longer"; more pollen numbers, higher P/O ratio and longer floral duration at more urbanization-intensified populations

Reference	Taxa	Urban drivers	Negative responses
Huang et al., 2013	All vascular plants	LC/ PO	Native herb diversity was lower in urban forests; soil heavy metal concentrations were negatively correlated with herb diversity; pioneer species and stress-tolerant species can survive and vigorously establish their population dominance in the urban environment
Ilyas et al., 2021	<i>Platanus linn</i> , <i>Populus euramevicana</i> , <i>Cinnamomum camphora</i>	PO	-
Irwin et al., 2018	<i>Gelsemium sempervirens</i>	LC	Urban landscape had increased florivory and decreased pollen receipt
Jensen et al., 2021	<i>Acer platanoides</i> , <i>Betula pendula</i> , <i>Crataegus monogyna</i> , <i>Fagus sylvatica</i> , <i>Prunus avium</i> , <i>Quercus robur</i> , <i>Salix caprea</i> , <i>Sorbus intermedia</i> , <i>Tilia x europaea</i> , <i>Ailanthus altissima</i> , <i>Ginkgo biloba</i> , <i>Gleditsia triacanthos</i> , <i>Platanus x hispanica</i> , <i>Pterocarya fraxinifolia</i> , <i>Quercus cerris</i> , <i>Robinia pseudoacacia</i>	BI/ CL	In the urban environment, nonnative trees hosted significantly fewer invertebrates compared to native trees. Furthermore, the nonnative trees had a delayed phenology compared to native species
Jeong et al., 2011	<i>Forsythia koreana</i> , <i>Rhododendron mucronulatum</i> , <i>Prunus yedoensis</i> , <i>Prunus persica</i>	CL	Urban warming has led to an advance in the timing of first-flowering of several days to weeks during recent decades, while the intrinsic physiology of plants to sense thermal energy has not been changed
Jochner et al., 2012	<i>Corylus avellana</i> , <i>Galanthus nivalis</i> , <i>Salix caprea</i> , <i>Forsythia suspensa</i> , <i>Acer platanoides</i> , <i>Fagus sylvatica</i> , <i>Malus domestica</i> , <i>Picea abies</i> , <i>Syringa vulgaris</i>	CL/ LC	-
Jochner et al., 2013	<i>Tabebuia chrysostricha</i> , <i>Caesalpinia peltophoroides</i> , <i>Tipuana tipu</i> , <i>Betula pendula</i>	CL/ LC	Phenological onset dates of <i>Betula pendula</i> were able to describe local temperature variations in Munich; phenology of <i>Tipuana</i> was sufficiently sensitive to detect urban heat island effects in Campinas
Jochner et al., 2015	<i>Betula pendula</i> , <i>Corylus avellana</i> , <i>Aesculus hippocastanum</i>	CL/ LC/ PO	Increased ozone, NO ₂ , NO _x and PM levels were significantly related to delays in phenology.
Johnson et al., 2018	<i>Trifolium repens</i>	LC/ UH	-
Kaltsova et al., 2019	All vascular plants	BI/ LC	The proportion of alien species increased in highly urbanized habitats; native species richness decreased with increasing disturbance

Reference	Neutral responses	Positive responses
Huang et al., 2013	-	-
Ilyas et al., 2021	-	The trees at different locations (urban - exurban) indicate a highly significant increase in functional traits analysed, proving that plasticity has a major role in plant adaptation to environmental changes
Irwin et al., 2018	Pollination was associated with selection for larger floral display size, but there is little difference in phenotypes between urban and non-urban sites; the lack of strong difference between urban and non-urban sites in reproduction suggests no extreme maladaptation to the urban landscape in the year of study.	-
Jensen et al., 2021	-	-
Jeong et al., 2011	-	-
Jochner et al., 2012	Trends in phenology did not change significantly with higher altitudes or urbanised areas.	-
Jochner et al., 2013	There were no significant correlations with flowering phenophases of <i>Tabebuia</i> and <i>Caesalpinia</i> ;	-
Jochner et al., 2015	Measurements of foliar characteristics of birch were not suitable for bio-monitoring pollution	-
Johnson et al., 2018	Populations did not exhibit changes in genetic diversity with increasing urbanization; populations frequently exhibited isolation-by-distance and extensive gene flow along most urban-rural transects	HCN frequency increased for every kilometre from an urban centre - urbanization repeatedly drives parallel evolution of an ecologically important trait across many cities that vary in size
Kalishova et al., 2019	-	-

Reference	Taxa	Urban drivers	Negative responses
King and Hovick, 2020	Wetland herbs	BI/ PO	Non-native richness and relative abundance was greater; high non-native relative abundance caused reductions in native plant richness; reduction of native Shannon diversity was related to high concentrations of urban-associated soil contaminants such as cadmium and sodium.
Knapp et al., 2017	All vascular plants	BI/ LC	Increase in species richness, but phylogenetic richness and divergence decreased; extirpations of phylogenetically distinct native species and immigrations of phylogenetically common native and non-native species caused a non-random loss of phylogenetic diversity.
Kobayashi et al., 2018	<i>Mucuna macrocarpa</i>	LC	-
Kolbe et al., 2016	Woody plants	HA/ LC	Tree communities are experiencing reduced richness, abundance, and evenness, and changes in composition
Kondratyeva et al., 2020	Herbs	LC	-
Kopel et al., 2015	All vascular plants	BI/ LC	As time passes, the number of exotic species increased
Kuhn et al., 2017	All vascular plants	BI	-
Kummli et al., 2021	All vascular plants	LC	15 % of the original grasslands had been lost due to changes in land use in 25 years
Lahr et al., 2015	<i>Quercus stellata</i> , <i>Liquidambar styraciflua</i>	CL/ PO	Trees experienced lower stomatal conductance and photosynthesis and higher isoprene emission; urban trees experienced relatively higher isoprene emission at high CO ₂ concentrations, while isoprene emission was suppressed at the other sites.
Lahr et al., 2018	<i>Acer rubrum</i>	CL/ HA	Urban wildtype trees had minor water use efficiency as air temperatures increased
Lambrecht et al., 2016	<i>Crepis sancta</i>	CL	-
Landis and Leopold, 2014	All vascular plants	BI	Numbers of alien species increased at more urban sites
Lechuga-Lago et al., 2017	<i>Carpobrotus edulis</i> , <i>Malcolmia littorea</i> , <i>Scolymus hispanicus</i>	BI/ LC	Changes in soil characteristics due to urbanization allow for the establishment of the native, but ruderal, <i>Scolymus hispanicus</i> and non-native <i>C. edulis</i>

Reference	Neutral responses	Positive responses
King and Hovick, 2020	-	-
Knapp et al., 2017	-	-
Kobayashi et al., 2018	The species successfully attracts local pollinators	-
Kolbe et al., 2016	-	-
Kondratyeva et al., 2020	-	Urban conditions allows the persistence of species with unique traits not observed, or observed less frequently in other land cover types, increasing functional diversity within urban communities
Kopel et al., 2015	-	-
Kuhn et al., 2017	The environmental covariates explaining richness as well as proportions of neophytes remain largely the same across the rural–urban gradient	-
Kummli et al., 2021	Alpha diversity had not changed significantly, alien species were rare in both periods	-
Lahr et al., 2015	Higher isoprene emission from urban trees was not associated with improved photosynthesis as temperatures increased	-
Lahr et al., 2018	-	-
Lambrecht et al., 2016	-	Urban plants flowered and senesced later than rural plants, and natural selection favored later phenology in the urban habitat; natural selection also favored larger plants with more leaves, and increased photosynthesis and leaf nitrogen concentration
Landis and Leopold, 2014	Seedlings of native riparian trees nonetheless germinated along the gradient.	-
Lechuga-Lago et al., 2017	The coastal dune endemic, <i>Malcolmia littorea</i> , showed no fitness effects in response to urbanization or the presence of <i>C. edulis</i> .	-

Reference	Taxa	Urban drivers	Negative responses
Lee, 2017	<i>Forsythia koreana</i> , <i>Rhododendron mucronulatum</i> , <i>Prunus yedoensis</i> , <i>Prunus mume</i>	CL	The species have advancements in phenology due changes in temperature
Leong et al., 2014	<i>Centaurea solstitialis</i>	LC	Bee visitation was highest in urban and agricultural land use contexts, but in contrast, seed set rates in these human-altered landscapes were lower than in natural sites
Lhotte et al., 2014	<i>Teucrium pseudochamaepitys</i>	LC	Reproductive success is low in each site despite an effective insect pollination; diversity of pollinators is lower in urban sites
Li et al., 2017	All vascular plants	CL	Phenology cycle in urban areas starts earlier and ends later resulting in a longer growing season length when compared to the respective surrounding urban areas
Lindh et al., 2018	All vascular plants	CL	In general, phenological events starts earlier in recent years.
Lobo et al., 2016	<i>Tabebuia aurea</i>	LC	Increase in floral displays among remnant individuals, probably reflecting an absence of lateral competition, were not sufficient to maintain high visitation rates to the flowers
Löki et al., 2019	Orchids	HA	Conservation value was smaller in urban cemeteries
Lopez et al., 2018	Herbs	BU/ HA/ LC/ PO	Native species, and species richness overall, declined in sites with less surrounding forest cover; decrease in taxonomic, phylogenetic, and functional richness in sites with higher ornamental species cover; Soil zinc influenced the composition, but not diversity, of plant communities, with more non-native plant species found in sites with higher zinc concentrations.
Lososová et al., 2016	All vascular plants	BI	Changes in β -diversity of urban plant communities induced by the establishment of alien species
Lowry et al, 2020	<i>Citharexylum spinosum</i> , <i>Psidium guajava</i> , <i>Schefflera actinophylla</i> , <i>Spathodea campamilata</i> , <i>Clerodendrum chinense</i> , <i>Clidemia hirta</i> , <i>Lantana camara</i> , <i>Leucaena leucocephala</i> , <i>Piper aduncum</i> , <i>Solanum torvum</i> , <i>Coccinia grandis</i> , <i>Ipomoea cairica</i> , <i>Merremia peltata</i> , <i>Mikania micrantha</i>	LC	Richness of species and overall abundance significantly lower in the urban sector
Malkinson et al., 2018	All vascular plants	BI	Rare and native species are negatively associated with degree of urbanization; non-native species are positively associated with urbanization
Massetti et al., 2015	<i>Tilia</i> × <i>europaea</i>	CL/ LC	Flowering occurred first in the areas with a higher percentage of impervious surfaces

Reference	Neutral responses	Positive responses
Lee, 2017	-	-
Leong et al., 2014	-	-
Lhotte et al., 2014	-	-
Li et al., 2017	-	-
Lindh et al., 2018	-	-
Lobo et al., 2016	-	-
Löki et al., 2019	-	-
Lopez et al., 2018	-	-
Lososová et al., 2016	-	-
Lowry et al., 2020	-	-
Malkinson et al., 2018	-	-
Massetti et al., 2015	-	-

Reference	Taxa	Urban drivers	Negative responses
McCune and Vellend, 2013	All vascular plants	BI/ LC	Most successful species tended to be exotic; biotic homogenization was correlated with the colonization of common, disturbance-tolerant natives
Melliger et al., 2018	All vascular plants	LC	Species richness decreased with degree of urbanisation; functional dispersion of plants decreased with increasing degrees of urbanization
Milanović et al., 2021	All vascular plants	LC	Functional diversity significantly increased for neophytes and invasive species compared to native species, Functional diversity of multiple functional traits combined decreased over time.
Molnár et al., 2018	<i>Celtis occidentalis</i> , <i>Acer campestre</i> , <i>Corylus avellana</i>	PO	Chlorophyll-a content of <i>C. occidentalis</i> leaves was the lowest in the urban area
Murray-Stoker and Johnson, 2021	<i>Trifolium repens</i>	LC	-
Neil et al., 2010	Shrubs	LC	Urbanization may have a significant effect on the flowering phenology of a small but substantial proportion of plants
Nero, 2019	Trees	LC	Native species richness was lowest in the core urban area; pioneers and anthropochory dispersed species were the most abundant in urban landscape
Nikula et al., 2010	<i>Populus tremula</i>	CL/ LC	-
Nock et al., 2013	Woody plants	LC	Tree density is often low and results in low diversity at local scales
Oliveira et al., 2019	<i>Paubrasilia echinata</i>	LC	Brazilwood trees in urban areas had smaller inflorescences, fewer flowers/inflorescences, larger flowers, less pollen/flower, lower richness of floral visitors and lower fruit and seed set when compared to natural ecosystem.
Oliveira et al., 2020	Woody plants	BI/ HA/ LC	Small portion of tree species inhabiting urban green areas is native; squares and parks were impoverished in number of species and individuals with specialized pollination systems; urban green areas were dominated by generalist-pollinated trees with reproductive traits associated with easily accessible floral resources and an increase of hermaphrodites; squares and parks had similarly low functional diversity of reproductive traits
Paquin et al., 2020	All vascular plants	BI/ LC	The richness of exotics increased with urbanization intensity

Reference	Neutral responses	Positive responses
McCune and Vellend, 2013	-	-
Melliger et al., 2018	-	-
Milanović et al., 2021	Overall functional diversity remained constant despite species turnover	-
Molnár et al., 2018	-	-
Murray-Stoker and Johnson, 2021	-	White clover has lower investment in rhizobia with greater N availability in the soil in urban areas
Neil et al., 2010	-	-
Nero, 2019	-	-
Nikula et al., 2010	Specific leaf area showed no differences between habitats	Urbanization resulted in foliar acclimatization, exhibiting a higher amount of epicuticular waxes and N concentration, and a lower C:N ratio; litter decay was faster at the urban site and for urban litter
Nock et al., 2013	-	-
Oliveira et al., 2019	-	-
Oliveira et al., 2020	-	-
Paquin et al., 2020	The richness of natives remained stable with urbanization	Biotic differentiation, rather than homogenization, characterized the response of swamp plant communities to urbanization.

Reference	Taxa	Urban drivers	Negative responses
Park et al., 2021	<i>Aster pilosus</i> , <i>Lactuca scariola</i>	BI/ CL/ LC	The invasiveness of the two alien plants was strongly associated with anthropogenic effects such as human population density, residential area, and road density
Pellegrini et al., 2021	All vascular plants	BI/ CL/ LC	The success of plant invasion at the landscape scale is mainly due to the spread of urban land use
Peng et al., 2019	All vascular plants	LC	Urbanization intensity negatively influenced plant diversity
Pennington et al., 2010	Woody riparian plants	BI/ LC	Exotic canopy species and native early-successional species increased with the level of urbanization while native canopy and understory species declined.
Pianchuelo et al., 2020a	Endangered species	LC	More than one-third of populations went extinct during the observation period, population survival was inversely correlated to the increase in impervious surfaces
Pianchuelo et al., 2020b	All vascular plants	LC	Endangered plant species in novel ecosystems are filtered for ruderal strategy type and wind dispersal syndrome
Qian et al., 2020	All vascular plants	LC	-
Qiu et al., 2017	All vascular plants	LC	Vegetation phenology in the urban area is significantly different from its rural surroundings, with growing seasons during longer
Ranta and Viiljanen, 2011	All vascular plants	BI/ HA/ LC	Non-natives showed the highest values in suburban areas
Ribeiro et al., 2019	All vascular plants	LC	CAD effects were stronger in adult communities by negatively affecting functional richness, dispersion and their effect sizes; CAD also altered the functional composition of leaf mass per area, woody density and leaf area of adult assemblages
Ryvkin et al., 2021	<i>Tribulus cistoides</i>	HA /LC	Predation was higher in towns than natural habitats

Reference	Neutral responses	Positive responses
Park et al., 2021	-	-
Pellegrini et al., 2021	-	-
Peng et al., 2019	-	-
Pennington et al., 2010	-	-
Planchuelo et al., 2020a	-	-
Planchuelo et al., 2020b	-	Novel urban ecosystems can support many populations of endangered plant species beyond the adjacency to natural remnants, with hybrid ecosystems likely acting as stepping stones
Qian et al., 2020	-	A diverse number of plant species can grow spontaneously in urban environments; the magnitude of urban growth was an important driver positively correlated with γ -diversity patterns; native species accounted for most of the urban spontaneous plants observed
Qiu et al., 2017	-	-
Ranta and Viljanen, 2011	-	-
Ribeiro et al., 2019	-	-
Rivkin et al., 2021	-	Mericarps are longer in towns, imposing phenotypic selection against small mericarps, potentially leading to the evolution of larger fruits

Reference	Taxa	Urban drivers	Negative responses
Salgado et al., 2021	All vascular plants	LC	Plant species richness decreased with urban expansion and the proportion of plant functional types was altered; plants typical of inland ecosystems, not tolerant to the beach-dune environment, became more abundant in those locations where the number of human settlements increased the most; the structure of plant communities changed in terms of species dominance, which was the result of the local loss of native species and/or a decreased plant cover
Santangelo et al., 2020a	<i>Trifolium repens</i>	CL	-
Santangelo et al., 2020b	<i>Trifolium repens</i>	LC	-
Santos et al., 2016	Woody plants	LC	-
Schmidt et al., 2014	All vascular plants	BI/ CL/ LC	Proportion of non-native species increased with mean annual temperature
Schmiedel et al., 2015	All vascular plants	BI/ LC	Species richness of neophytes are higher
Schwoertzig et al., 2016	All vascular riparian plants	LC	-
Seattle et al., 2012	<i>Quercus rubra</i>	CL	-
Silva-Junior et al., 2018	All vascular plants	LC	Species density and phylogenetic richness decreased with the increase in urbanization
Singh et al., 2020	<i>Grevillea robusta</i> , <i>Mangifera indica</i>	PO	CO ₂ assimilation, water loss through transpiration rate and stomatal opening and closing in the form of stomatal conductance was reduced for the trees near roadside species due to the deposition of particulate matters on the leaves

Reference	Neutral responses	Positive responses
Salgado et al., 2021	Invasive species were relatively scarce and did not increase with land cover change.	-
Santangelo et al., 2020a	Clines in HCN production did not evolve in cities with the lowest temperatures and greatest snowfall	Strongest clines occurred in the warmest cities where snow and frost are rare, suggesting that alternative selective agents are maintaining clines in warmer cities
Santangelo et al., 2020b	-	Families from urban sites had evolved later phenology and germination, larger flowers, thinner stolons, reduced cyanogenesis, greater biomass and greater seed set. Pollinator observations revealed near-complete turnover of pollinator morphological groups along the urbanization gradient, which may explain some of the observed divergences in floral traits and phenology.
Santos et al., 2016	Absence of significant differences in species richness and diversity between urban and rural basins	-
Schmidt et al., 2014	Species richness differed only slightly between the urbanization zones and increased with habitat diversity	High proportions of endangered species were found in urban areas
Schmiedel et al., 2015	-	In urban areas, species richness of neophytes and high-nutrient indicators are bigger; number of native, threatened and even low-nutrient species is high in urban areas
Schwoertzig et al., 2016	Similar compositional patterns were found within the most urbanized sites with the establishment of ubiquitous species	-
Seattle et al., 2012	Increase in biomass in seedlings; urban seedlings allocated more growth to leaves; no difference in photosynthetic capacity of foliage per unit area.	-
Silva-Junior et al., 2018	Phylogenetic divergence and structure did not respond to urbanization	-
Singh et al., 2020	-	Water use efficiency of trees was enhanced at roadside trees compared to control sites; The leaf thickness of both the species has been found to be more in the trees growing along the roadside

Reference	Taxa	Urban drivers	Negative responses
Singh, 2021	<i>Alstonia scholaris</i>	PO	Urban vehicular emissions hampered the carbon assimilation due to the deposition of heavy dust loads over the foliage surface.
Skultety e Matthews, 2017	<i>Alharia petiolata</i> , <i>Aster subulatus</i> , <i>Atriplex patula</i> , <i>Bolboschoenus maritimus</i> , <i>Dipsacus fullonum</i> , <i>Dipsacus laciniatus</i> , <i>Hemerocallis fulva</i> , <i>Hordeum jubatum</i> , <i>Lysimachia nummularia</i> , <i>Lytirum salicaria</i> , <i>Phragmites australis</i> , <i>Puccinellia distans</i> , <i>Solanum dulcamara</i> , <i>Solidago sempervirens</i> , <i>Spergularia species</i> , <i>Viburnum recognitum</i>	BI/ HA/ LC	Urbanization and roads are drivers in the spread of non-native plant species
Soltysiak, 2020	<i>Fallopia japonica</i> , <i>Fallopia sachalinensis</i> , <i>Fallopia × bohemica</i>	CL	The phenomenon of the urban heat island promotes the spread of foreign species in the city centre
Song et al., 2019	<i>Schima superba</i> , <i>Castanopsis fissa</i> , <i>Acronychia pedunculata</i> , <i>Diplospora dubia</i> , <i>Ardisia quinquegona</i> , <i>Diospyros morrisiana</i> , <i>Castanopsis chinensis</i> , <i>Psychotria rubra</i> , <i>Memecylon nigrescens</i> , <i>Syzygium hancei</i> , <i>Pygeum topengii</i> , <i>Cinnamomum burmanni</i> , <i>Cryptocarya concinna</i> , <i>Endospermum chinense</i> , <i>Aidia pycnantha</i> , <i>Microdesmis casearifolia</i> , <i>Machilus suaveolens</i> , <i>Machilus chinensis</i> , <i>Engelhardtia fenzlii</i> , <i>Allettetella leucocarpa</i> , <i>Neolitsea phanerophlebia</i> , <i>Symplocos adenopus</i> , <i>Michelia skinneriana</i> , <i>Daphniphyllum subverticillatum</i> , <i>Mangifera indica</i> , <i>Neolitsea chunii</i>	LC	-
Sonti et al, 2021	<i>Quercus alba</i> , <i>Acer rubrum</i>	LC	-
Štajerová et al., 2017	<i>Epilobium adenocaulon</i> , <i>Galeobdolon argentatum</i> , <i>Maltonia aquifolium</i> , <i>Matricaria discoidea</i> , <i>Oenothera biennis</i> , <i>Physocarpus opulifolius</i> , <i>Rhus typhina</i> , <i>Rumex thyrsiflorus</i> , <i>Syringa vulgaris</i>	BI/ HA/ LC	Species cover of invasive species increased; road margins, ruderal sites, and railway sites were richest in invasive species
Su et al. 2021	<i>Pinus tabulaeformis</i>	LC	Plants growing on roadsides had traits (lower levels of stomatal density, and smaller leaf length, width and area) representative of a reduced capacity to acquire resources

Reference	Neutral responses	Positive responses
Singh, 2021	-	Increase in leaf thickness was witnessed under traffic emissions, minimizing water loss from foliage; stomatal conductance was diminished while improved water use efficiency under the influence of traffic emissions; accumulation of heavy metals in plants without killing the plants indicates the mitigation capabilities
Skultety e Matthews, 2017	-	-
Softysiak, 2020	-	-
Song et al., 2019	-	Plant species in the urban forests had larger specific leaf area, higher leaf nitrogen content, and lower leaf carbon/nitrogen ratio
Sonti et al., 2021	-	The ecophysiological results suggest that the urban environment is not inherently stressful for native trees, and may allow for greater physiological function
Štajerová et al., 2017	-	-
Su et al., 2021	-	-

Reference	Taxa	Urban drivers	Negative responses
Su et al., 2019	<i>Pinus tabulaeformis</i>	CL/ LC	The increased percentage of impervious cover could advance the timing of leaf and male cone phenophases.
Tew et al., 2021	Community of specific flowering species	BI/ HA /LC	-
Thompson et al., 2016	<i>Trifolium repens</i>	CL/ LC	-
Tian et al., 2015	All vascular weedy plants	LC	The number of weed communities in urban areas was less than the number found in suburban and rural areas
Toma et al., 2015	<i>Viola grypoceras</i> A. Gray var. <i>grypoceras</i>	LC	-
Tordoni et al., 2017	All vascular plants	BI/ LC	Urban plots account for most of the alien species in the sampling
Trammel et al., 2020	Woody plants	BI/ LC	-
Trentanovi et al., 2013	All vascular plants	BI/ LC	Urbanity proved to homogenize the native species pool
Turnukhametova and Shadrina, 2020	<i>Betula pendula</i>	PO	An increase in seed production and variety of fruit-producing organs in size and shape indicates poor quality of the environment and of the seeds themselves. Anthropogenic impact also impairs the quality of seeds, decreases their germination energy and germination capacity.
Ushimaru et al., 2014	<i>Commelina communis</i>	LC	Pollinator and mate availability decreased significantly with developed land area; most urbanized populations suffered from significant pollinator-limited male and/or female reproductive success
Vakhlamova et al., 2014	All vascular plants	BI/ LC	Plant diversity decreased with near to the city centre and was also influenced by the type of land use; the percentage of alien species increase
Vakhlamova et al., 2016	All vascular plants	BI/ HA	More alien species were found in the road verges at the city edge than in the rural surroundings along both road types
Vallet et al., 2010a	Woody plants	LC	Urban woodland edges were not as rich in forest specialists as rural edges
Vallet et al., 2010b	All vascular plants	LC	-

Reference	Neutral responses	Positive responses
Su et al., 2019	-	-
Tew et al., 2021	In urban areas the nectar supply was more diverse in origin and predominantly delivered by non-native flowering plants, but the non-native plants are evolved in the natural range of UK pollinators	-
Thompson et al., 2016	-	Frequency of cyanogenic plants within populations decreased towards the urban centre in three of four cities
Tian et al., 2015	-	-
Toma et al., 2015	There was no significant difference in allelic richness between the urban fragmented and suburban forests.	-
Tordoni et al., 2017	-	-
Trammel et al., 2020	The invasion gradient was not related to the urban gradient across our forests	Greater native species richness in forest canopies and understories with increasing urbanization supports the conclusion that urban forests maintain native species and are not inherently degraded ecosystems.
Trentanovi et al., 2013	-	-
Turmukhametova and Shadrina, 2020	-	-
Ushimaru et al., 2014	-	High fruit set in urbanized populations may suggest the presence of high reproductive assurance by selfing
Vakhlamova et al., 2014	-	-
Vakhlamova et al., 2016	-	-
Vallet et al., 2010a	Total species richness, richness of forest generalists and of non-forest species decreased from edge to interior in both urban and rural woodland;	-
Vallet et al., 2010b	Dispersion traits were not related to the distribution of species along the urban-rural gradient	Species have different persistence traits, resource requirements and regeneration traits to persist in urban habitats

Reference	Taxa	Urban drivers	Negative responses
Van Rossum, 2010	<i>Centaurea jacea</i>	LC	-
van Vliet et al., 2014	All vascular plants	CL	Changes in climate explain variation in timing of phenological events from year to year
Vasconcellos et al., 2019	<i>Ceiba speciosa</i>	CL/ PO	-
Verboven et al., 2014	<i>Trifolium repens</i>	LC	-
Vujić et al., 2015	<i>Iris pumila</i>	PO	Decrease of standard length and centroid size in the polluted environment was detected, as well as a change in the shape; the standards were shorter and wider in the polluted area when compared to those in the unpolluted environment.
Wang et al., 2020	All vascular plants	LC	Extinction of native plants is directly related to the sizes and landscape configurations of urban construction lands
Wang et al., 2020	All vascular plants	LC	The richness of annual herbs exhibited a negative relationship to urbanization degree; the richness of the all plants, woody plants and perennial herbs presented significant positive relationship with urbanization degree, maybe due to the increase of exotic and ruderal species
Wirth et al., 2020	All vascular plants	BI/ LC	The number of woody species neophytes and short-lived alien plants increased
Wodkiewicz and Gruszczyńska, 2014	<i>Stellaria holostea</i>	HA/ LC	-
Wu et al., 2013	Herbs	LC	The composition, diversity indices, mean and total richness gradually decreased
Xiao et al., 2021	<i>Lophatherum gracile</i> , <i>Alpinia chinensis</i> , <i>Ardisia quinquegona</i> , <i>Psychotria rubra</i> , <i>Diospyros morristana</i> , <i>Cratogeomys cochinchinense</i> , <i>Engelhardtia roxburghiana</i> , <i>Schinus molle</i>	CL/ PO	Negative correlations between heavy metal concentrations and maximum photosynthetic rates were all detected in the canopies
Xiao et al., 2016	Woody plants	BI/ CL/ LC	Urbanization had the function of species conservations with sharp increases of alien species and tropical type plants.

Reference	Neutral responses	Positive responses
Van Rossum, 2010	-	Urban park populations showed a higher reproductive success than those in urban semi-natural sites; pollinator movements and a potential gene flow by pollen over relatively long distances.
van Vliet et al., 2014	-	-
Vasconcellos et al., 2019	-	There is an immediate response of urban trees in relation to the rains and, a late response of forest trees to the same factor - the species is stress-tolerant, able to survive and adapt to polluted urban conditions
Verboven et al., 2014	-	Flower visitation rates by bumblebees responded positively to urban land use resulting in higher visitation rates and increased seed set in the more urban sites
Vujić et al., 2015	-	-
Wang et al., 2020	-	-
Wang et al., 2020	The native plant species richness showed no significant relationship to urbanization degree	-
Wirth et al., 2020	-	There is a significant increase in the number of plant species in Pécs
Wodkiewicz and Gruszczyńska, 2014	High clonal diversity indices indicate that the studied populations did not lose the ability to reproduce sexually; the lack of correlation between genetic and geographic distance between the studied populations indicate limited gene flow	-
Wu et al., 2013	-	-
Xiao et al., 2021	-	Urbanization had positive effects on the total chlorophyll contents of the herbs and shrubs, namely, herbs and shrubs changed in their physiologies to adapt to stimulating roles of urbanization
Xiao et al., 2016	-	-

Reference	Taxa	Urban drivers	Negative responses
Xingyuan et al., 2016	Woody plants	CL	Influenced by climate warming, the germination, leafing, and flowering phenologies of this urban forest advanced
Yakub and Tiffin, 2017	<i>Lepidium virginicum</i>	LC	-
Yan et al., 2019	All vascular plants	LC	An increase in percentage of total impervious surface area reduced plant diversity; the ratio of exotic to endemic plant species increased as percentage of total impervious surface area increased.
Yang et al., 2021	All vascular plants	LC	The $\beta 2$ -diversity of adult trees was higher than that of sapling/seedlings. It is believed that species found in the sampling/seedling layer are more likely to be generalists and have high urban tolerance.
Yu et al., 2021	All vascular plants	BI/ CL/ LC	Invasive and ornamental species increased; a significant increase in the number of thermophilous plant species was observed, which is closely related to global warming and the heat island effect in cities
Zeeman et al., 2017	Graminoids	BI/ LC	The most urbanized sites had the highest number of non-native species in both the current and historical data sets; exotic species with an annual life span increased in frequency
Zhang et al., 2020	Ruderal plants	LC	Ruderal diversity decreased from the rural region to central urban area; species with shorter life span and smaller size become more dominant in high urbanized areas
Zhang et al., 2016	Woody plants	LC	Species richness and diversity were the lowest in the urban core
Zipper et al., 2016	All vascular plants	CL/ LC	-
Zipper et al., 2017	All vascular plants	CL/ LC	Plant water requirements are significantly higher in urban areas compared to rural areas, driven by increased air temperature with minimal effects of decreased air moisture content

Reference	Neutral responses	Positive responses
Xingyuan et al., 2016	-	-
Yakub and Tiffin, 2017	Genomic data revealed that the majority of individuals in each of the urban populations were more closely related to individuals from other urban populations than they were to geographically proximate rural areas	Plants grown from seeds collected from urban areas bolted sooner, grew larger, had fewer leaves, had an extended time between bolting and flowering, and produced more seeds than plants grown from seeds collected from rural areas
Yan et al., 2019	-	-
Yang et al., 2021	-	-
Yu et al., 2021	-	-
Zeeman et al., 2017	-	The overall composition of urban grasslands shifted to taller plant species; native species capable of vegetative reproduction increased
Zhang et al., 2020	-	Ruderal communities in Hangzhou are rich due to heterogeneous urban habitats forming a diverse regional micro-habitat for species with different ecological habits
Zhang et al., 2016	-	-
Zipper et al., 2016	Median urban growing season length (GSL) longer than surrounding rural areas, and UHI impacts on GSL are relatively consistent from year-to-year	-
Zipper et al., 2017	-	-

Capítulo IV

*A bromeliad living in the city: a case of a native species resilient to
urbanization in South Brazil*

Artigo a ser submetido na revista American Journal of Botany

Capítulo V

Effects of urbanization on the production and seed viability of

Tillandsia aeranthos (Bromeliaceae)

Artigo a ser submetido na revista Flora

Capítulo VI
Considerações finais

Considerações finais

Nesta tese foram apresentadas as consequências da crescente urbanização e como espécies de plantas estão respondendo à essas mudanças drásticas no ambiente. Apesar do aumento considerável no número de estudos na área da Ecologia Urbana, o impacto da urbanização em plantas ainda é pouco compreendido, especialmente em seus aspectos evolutivos. Revisões anteriores apontaram como aspectos específicos (por exemplo, traços de história de vida, fisiologia, biologia reprodutiva – Alberti et al. (2017); Aronson et al. (2016); Cadotte et al. (2017); Eckert et al. (2010); Harrison & Winfree (2015); Jochner & Menzel (2015); Johnson et al. (2015); Rai (2016); Williams et al. (2015)) de grupos de plantas podem ser prejudicados com a urbanização. Porém, uma compilação compreendendo vários desses aspectos avaliados em escala global, assim como quais fatores específicos levaram à diferentes respostas das plantas frente à urbanização, ainda não havia sido feita. A proposta desta tese foi abordar diferentes aspectos da urbanização como causadores de mudanças em espécies e comunidades de plantas, assim como contribuir com estudos genéticos e evolutivos de uma espécie nativa de bromélia (*Tillandsia aeranthos*) que ocorre em ambientes urbanos no sul do Brasil.

O **Capítulo III** consiste de um artigo de revisão sistemática global integrando várias áreas da Ecologia Urbana para sumarizar como as espécies e comunidades de plantas estão respondendo a urbanização e quais os principais agentes dessas respostas (aqui chamados de *Urban Drivers*). Após avaliar 171 estudos publicados nos últimos onze anos, foi revelado que a maioria dos estudos foi realizada na Europa e na América do Norte, sendo o bioma mais representado o de Florestas Temperadas e Florestas Mistas. Além disso, a maioria dos estudos relatou consequências negativas da urbanização. Os *Urban Drivers* mais citados como responsáveis pelas mudanças nas espécies e comunidades vegetais foram “mudança da cobertura do solo” (alteração das paisagens de vegetação nativa, transformando-as em áreas cobertas por superfícies impermeáveis) e “invasão biótica” (introdução de espécies não nativas no habitat). De forma resumida, os estudos analisados mostraram que a urbanização reduz a riqueza de espécies vegetais e a disponibilidade de polinizadores. Além disso, ela também homogeneiza o ambiente, promove a invasão de espécies não nativas, causa alterações nos tempos dos eventos fenológicos e impõe dificuldades para o crescimento das plantas. No entanto, foi avaliado que algumas espécies apresentam evidências de adaptação

a essas adversidades por meio de sua plasticidade fenotípica e também pela evolução de características que tornam os indivíduos resilientes ao ambiente urbano. Embora tenha sido estabelecido que a urbanização impõe novas pressões seletivas resultando em adaptações únicas à vida da cidade, os padrões de mudanças na biodiversidade em resposta à urbanização podem variar por região, bioma, história da cidade e especialmente de acordo com a espécie ou grupo taxonômico. Os *Urban Drivers* responsáveis pelas respostas da vegetação atuam simultaneamente modificando o ambiente, portanto, é um desafio prever os padrões de resposta das plantas sob o crescimento rápido da urbanização.

Surge então uma grande necessidade de realizar mais estudos na área da Ecologia Urbana com espécies de plantas, principalmente em locais com uma menor representatividade de estudos, como os biomas tropicais e em países em desenvolvimento. Portanto, o **Capítulo IV** desta tese trata dos efeitos da urbanização na diversidade genética, estrutura genética e adaptação local em *T. aeranthes*, uma epífita auto incompatível com alta capacidade de colonizar habitats urbanos no sul do Brasil. Esta espécie, pertencente à família Bromeliaceae, possui capacidade de colonizar com sucesso uma ampla gama de habitats devido a inúmeras adaptações morfológicas e fisiológicas, como suculência foliar, metabolismo ácido das crassuláceas (CAM) e tricomas especializados de absorção de água (Benzing, 2000). Portanto, seu metabolismo CAM é vantajoso para colonizar com sucesso as áreas urbanas, geralmente mais secas, tornando esta espécie um excelente modelo para o estudo de como as plantas podem se adaptar a estes ambientes (Judith *et al.*, 2013).

Este estudo foi realizado utilizando uma amostragem na forma de dois transectos, distribuídos ao longo de um gradiente de urbanização, para testar se haveria diferenças nos padrões genéticos entre populações que ocorrem em ambientes urbanos e não-urbanos. Encontramos uma maior proporção de variação genética dentro das populações, confirmando o padrão esperado para uma espécie que é auto incompatível. Além disso, a fecundação cruzada obrigatória permitiu que esta espécie mantivesse altos níveis de diversidade genética, permitindo que suas populações tolerem uma maior variedade de regimes ambientais, como climas extremos, poluentes, degradação e fragmentação do habitat, que caracterizam o ambiente urbano. De fato, não encontramos uma diminuição na diversidade genética com o aumento da urbanização, como seria esperado se os efeitos da deriva genética fossem maiores nesses habitats fragmentados. Em concordância com este resultado, a fragmentação causada pela urbanização não foi suficiente para separar as

populações urbanas e não-urbanas através das análises de estrutura genética. Em uma espécie com ampla capacidade de dispersão pelo vento, como *T. aeranthos*, a modificação humana na paisagem pode aumentar indiretamente as taxas de dispersão entre populações, removendo barreiras ao fluxo gênico. Por exemplo, estradas com alto tráfego de veículos podem ajudar na dispersão de sementes que se dispersam com o vento, diminuindo o impacto da fragmentação do habitat. A falta de correlação entre os *outlier loci* detectados através do escaneamento genômico e o índice de urbanização encontrado em nosso estudo corrobora com os demais índices de diversidade genética não sendo afetados pela urbanização. Portanto, pode-se supor que a dispersão pode ocorrer por pólen ou sementes entre populações urbanas e não-urbanas, sendo estes os principais determinantes da manutenção da diversidade genética nas populações de *T. aeranthos*.

Seguindo esta linha de raciocínio, no **Capítulo V** desta tese, foi apresentado um estudo sobre a produção e a viabilidade de sementes de *T. aeranthos*, como forma de comparar um dos aspectos de seu sucesso reprodutivo em ambientes urbanos e não-urbanos. A reprodução por sementes desempenha um papel fundamental na adaptação, migração, adaptação e persistência populacional das espécies vegetais (Fenner & Thompson, 2005). Espécies auto incompatíveis só produzem sementes através da fecundação cruzada, portanto elas são altamente dependentes de polinizadores para sua reprodução (Richards, 1997). Assim, espera-se que espécies de plantas auto incompatíveis sejam mais suscetíveis a mudanças nas comunidades de polinizadores (mudanças na abundância, composição e/ou comportamento de forrageamento) como resultado da fragmentação dos habitats urbanos. Consequentemente, seu sucesso reprodutivo deve ser mais afetado pela urbanização do que o sucesso reprodutivo de plantas auto compatíveis (Aguilar *et al.*, 2006).

A produção de sementes não apresentou diferença estatisticamente significativa em relação ao gradiente de urbanização. Por outro lado, a taxa de germinação das sementes variou de 0% a 69%, com diferença estatisticamente significativa em relação ao gradiente de urbanização. Como o desenvolvimento da semente depende estritamente da fertilização cruzada bem-sucedida, é provável que tenha ocorrido uma falha no desenvolvimento da semente posterior à fertilização. Novos estudos com observações mais detalhadas do sistema reprodutivo de *T. aeranthos* replicados em diferentes paisagens urbanizadas devem ser realizados para avaliar as consequências da urbanização para esta espécie.

A Ecologia Urbana fornece cada vez mais evidências de como as mudanças ambientais afetam a ecologia populacional das espécies, a estrutura da comunidade e os processos ecossistêmicos (Rivkin *et al.*, 2019), porém sabemos muito menos sobre os impactos ecológicos da urbanização na evolução das populações de plantas que vivem nas cidades. Desta forma, os resultados obtidos na presente tese contribuirão com os estudos avaliando os efeitos da urbanização em espécies vegetais, especialmente em ambientes tropicais, que ainda são menos representados em escala global. Estudar a ecologia e a evolução das plantas em áreas urbanas nos leva a uma melhor compreensão sobre problemas relacionados à conservação e a estabilidade ambiental em um planeta cada vez mais urbanizado. Logo, estudos ecológicos e evolutivos em áreas urbanas se tornam cada vez mais urgentes para a conservação da biodiversidade.

Capítulo VII
Referências bibliográficas
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- Zotz G, Weigelt P, Kessler M, Kreft H & Taylor A. 2021.** EpiList 1.0: a global checklist of vascular epiphytes. *Ecology* **102**.

Apêndices

Apêndice 1

Artigo publicado durante o período do doutorado fora do escopo da tese

Ruas RB, Paggi GM, Aguiar-Melo C, Hirsch LD, Bered F. 2020. Strong genetic structure in *Dyckia excelsa* (Bromeliaceae), an endangered species found on ironstone outcrops in Pantanal, Brazil. **Botanical Journal of Linnean Society**, <https://doi.org/10.1093/botlinnean/boz099>

Apêndice 2

Prêmio de produtividade do PPGBM-UFRGS

3º Lugar na categoria Área Vegetal/Microrganismo – Nível Doutorado – ano de 2019



Apêndice 3

Fotos de *Tillandsia aeranthos*

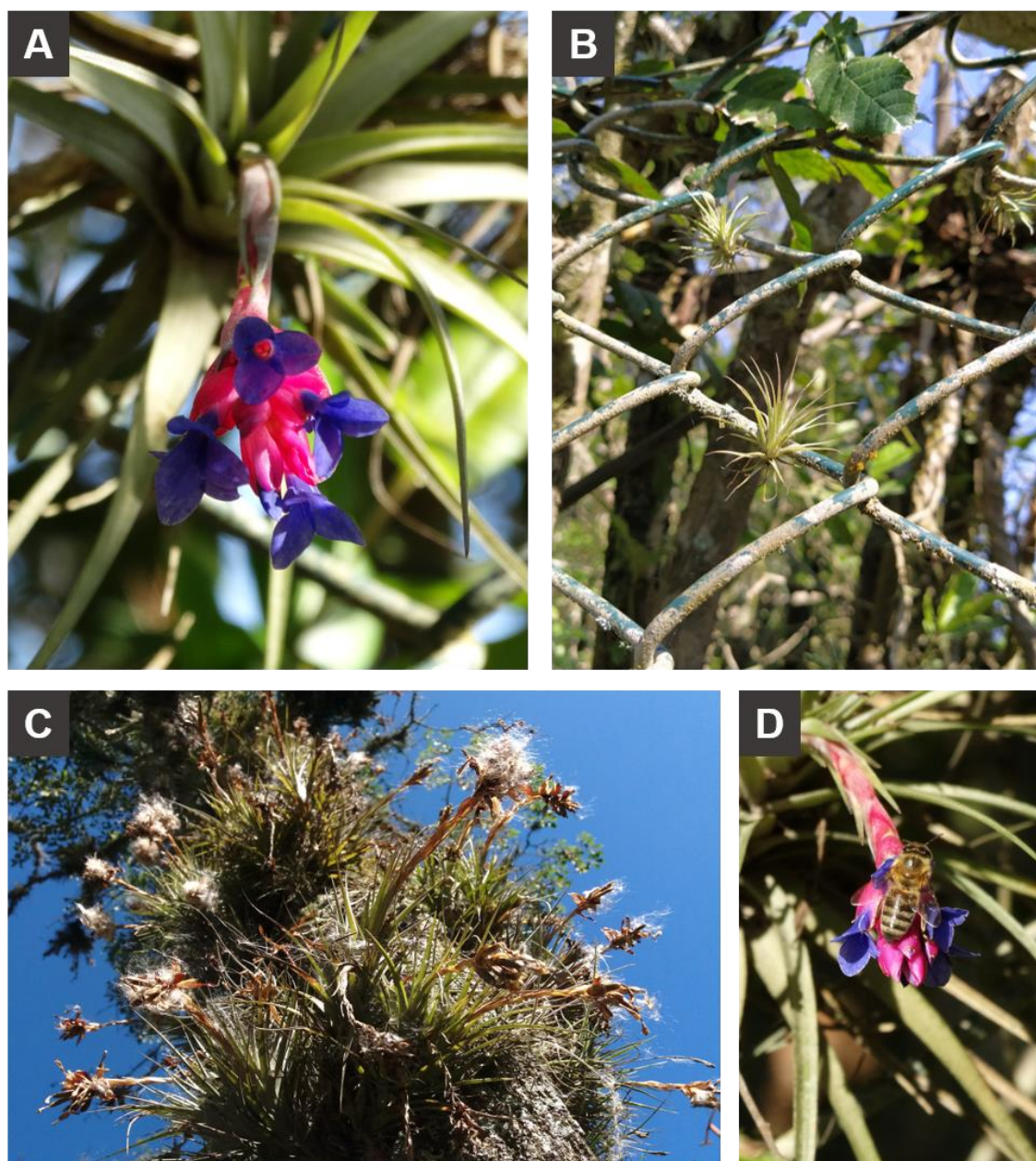


Figura 1. A – Detalhe da inflorescência; B – Indivíduos jovens estabelecidos em substrato artificial; C – Aglomerados de *T. aeranthos* em época de dispersão de sementes; D – Visitante floral avistado em observações preliminares de polinizadores.