ECOGRAPHY

Review

Biodiversity promotes urban ecosystem functioning

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Ecography
2024: e07366
doi: 10.1111/ecog.07366
Subject Editor: Dominique Gravel
Editor-in-Chief: Miguel Araújo
Accepted 29 May 2024

The proportion of people living in urban areas is growing globally. Understanding how to manage urban biodiversity, ecosystem functions, and ecosystem services is becoming more important. Biodiversity can increase ecosystem functioning in non-urban systems. However, few studies have reviewed the relationship between biodiversity and ecosystem functioning in urban areas, which differ in species compositions, abiotic environments, food webs, and turnover rates. We reviewed evidence of biodiversity–ecosystem functioning relationships in urban environments and assessed factors that influence the relationship direction. Based on 70 studies, relationships between biodiversity and ecosystem functioning were more positive than negative in urban areas, especially for pollination and nutrient cycling and retention. Surprisingly, positive and negative relationships between biodiversity and biomass production and storage were equally not statistically different, perhaps due to extensive plant management in urban areas. The number of studies and geographic coverage of our review was still insufficient to provide a general predictive framework for when biodiversity positively impacts ecosystem functioning. We identify gaps and opportunities to improve urban biodiversity–ecosystem functioning research and discuss how our findings can improve urban green space management.

Keywords: biodiversity, city, complementarity, ecosystem functioning, green space management, selection effects, urban

Introduction

Human activities are leading to declines in biodiversity that are unprecedented in human history (Díaz et al. 2019). The effects of biodiversity on ecological processes can be substantial, and are expected to grow stronger at large spatial and temporal scales (Cardinale et al. 2011, Isbell et al. 2017, O'Connor et al. 2017, Loreau et al. 2022). In fact, the loss of biological diversity is a leading driver of ecosystem functioning

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change (ecosystem functions include the flow of energy and materials through the biotic and abiotic components of an ecosystem (IPBES 2019)), especially at high levels of species loss (Hooper et al. 2012). Biodiversity loss decreases ecosystem functions like productivity and nutrient recycling across ecosystems, although the relationship is generally nonlinear and decelerates at high diversity levels (Schmid et al. 2009, Cardinale et al. 2012, Reich et al. 2012). Much of the research on how biodiversity influences ecosystem functioning has focused on forests and grasslands. Studies of the role of biodiversity in promoting ecosystem functioning in urban areas has been limited; a recent review of biodiversity–ecosystem functioning (BEF) relationships included only three urban studies (van der Plas 2019).

Improved understanding of how biodiversity supports ecosystem functioning in urban areas could provide information on preferred practices for sustainable cities. While urban planners often consider locations and users of green spaces and other ecological amenities, they do not often consider ecosystem functioning (Pickett et al. 2011). This could be due to the origin of the urban ecology discipline, which was heavily influenced by the social sciences and urban planning and is only more recently emerging as a mainstream ecological research field (Grimm et al. 2000, Young 2009, Ramalho and Hobbs 2012). With most people now living in cities and the percentage of people living in urban areas increasing globally (United Nations 2018), understanding how to manage urban biodiversity, ecosystem functioning, and ecosystem services is especially important and can increase human well-being (Taylor and Hochuli 2015).

BEF relationships could differ between non-urban and urban ecosystems

Urban ecosystems are often viewed as coupled socio-ecological systems, where human decisions and ecological processes interact to drive the distribution and composition of species (Pickett et al. 2017). Urban landscapes are highly altered ecosystems, with species compositions, abiotic environments, food webs, and turnover rates that differ from natural environments (Lepczyk et al. 2017, El-Sabaawi 2018, Behm 2020). Many species are not adapted to the highly altered conditions in urban ecosystems, yet some thrive (Aronson et al. 2014, Lerman et al. 2021).

Urban biodiversity is influenced by local climate, time since development, land use histories, social inequities, and human activities and management practices (Hope et al. 2003, Walker et al. 2009, Avolio et al. 2018, Schell et al. 2020, Lerman et al. 2021). Plant diversity is especially influenced by landowner planting preferences, neighborhood characteristics, and the composition of plants sold locally, which are often non-native ornamentals (Avolio et al. 2018). Urban animal assemblages often have more generalist species that tolerate and thrive in urban conditions (Nielsen et al. 2013, Lerman et al. 2021). Moving from non-urban areas to more urbanized areas, overall species richness decreases and the abundance of certain species increases, leading to reduced evenness (Chace and Walsh 2006, Shochat et al. 2010). The effect of urbanization on species richness is dependent on taxa, with moderate levels of urbanization decreasing species richness more for vertebrates and invertebrates than for plants; plants can have increased species richness with urbanization due to the addition of non-native species (McKinney 2006, 2008).

Cities can contribute positively to overall biodiversity. For instance, some species do well in urban environments and can act as source populations for colonization of natural areas during stressful conditions (Spotswood et al. 2021). Green spaces in cities can provide resource-rich stopover sites on migration routes, and contribute genetic diversity that may be able to help species adapt to climate change (Spotswood et al. 2021). Indeed, urban areas can harbor species with unique traits that are not found in other land cover types (Kondratyeva et al. 2020). For example, urban and non-urban ponds in the UK had similar invertebrate species richness and contained different species (Hill et al. 2017). These differences in biological communities between urban and natural ecosystems could alter BEF relationships in urban areas.

Complementarity and selection effects (Box 1) are common drivers of positive BEF relationships in non-urban ecosystems. Dominance by one or a few species can reduce complementarity (Hillebrand et al. 2008). Dominance can also affect selection effects, depending on whether the dominant species is better or worse at providing particular ecosystem functions (Hillebrand et al. 2008). Because a small number of urban-adapted species can dominate urban ecosystems, species dominance could more likely affect the relationship between biodiversity and ecosystem functioning in urban areas than in non-urban ecosystems. This could reduce the strength of complementarity, and also increase or reduce selection effects if dominant species are or are not the highest function-providing species (Tilman et al. 2014). Furthermore, native species assemblages show greater complementarity than non-native species assemblages, likely because they share a longer coevolutionary history (Wilsey et al. 2009). Indeed, negative relationships between biodiversity and functioning often involve invasive species (Harrison et al. 2014).

The benefits of diverse assemblages through time and space, temporal and spatial selection effects (Box 1), have also been clearly documented in urban settings. For example, street trees provide a diversity of ecosystem functions, such as regulating local climate and air quality, reducing stormwater runoff, capturing nutrients, and storing carbon (Livesley et al. 2016). High levels of street tree diversity can increase the stability of ecosystem functions over time; Dutch elm disease killed millions of dominant city street trees throughout the eastern USA and resulted in significant loss of ecosystem services (Santamour 1990).

Considering entire ecosystems, more species are needed to maintain multiple ecosystem functions, i.e. multifunctionality (Box 1) (Hector and Bagchi 2007, Lefcheck et al. 2015). For example, a grassland experiment found that the minimum number of species needed to maintain ecosystem function thresholds increased as the number of ecosystem functions considered increased (Zavaleta et al. 2010). They

Box 1. What is biodiversity?

Biodiversity is a broad term that captures multiple facets of the variability among living organisms. Some aspects of biodiversity, such as species richness and functional diversity, are particularly important for ecosystem functioning (Díaz and Cabido 2001, Harrison et al. 2014). Although species richness and functional diversity are related, high species richness does not always correspond to high functional diversity (Díaz and Cabido 2001, Aguirre-Gutiérrez et al. 2017). Species richness and functional diversity may respond differently to drivers of change; therefore, it may be important to examine both for consequences to ecosystem functioning. Despite the importance of these different metrics, assessments of biodiversity and ecosystem service relationships in urban areas have most often assessed species richness, and few studies have looked at more than one metric of diversity (Ziter 2016, Schwarz et al. 2017).

Definitions used in this paper

Biodiversity – The variability among living organisms from all sources, including diversity within species, between species and of ecosystems (United Nations Convention on Biological Diversity 1992).
Ecosystem function – The flow of energy and materials through the biotic and abiotic components of an ecosystem. Common processes include biomass production, trophic relationships, nutrient cycling, water dynamics, and heat transfer (IPBES 2019).
Ecosystem services – Ecosystem services directly link ecosystem components or functions to benefits that people receive (Haase et al. 2014), with the amount of services related to the quantity and quality of various ecosystem components (Daily et al. 2009). In some cases, ecosystem functions directly benefit people (e.g. pollination), and can also be considered ecosystem services.
Species richness – The total number of species in an area of interest.
Species evenness – The equity of relative abundance of species in an area of interest (Wilsey and Polley 2004).
Functional or trait diversity – The range, values, relative abundance, and distribution of functional traits in a given community or ecosystem (IPBES 2019).
Species composition/identity – The array of species present in an ecosystem or study area (IPBES 2022).
Complementarity – An effect of biodiversity where greater species richness or functional diversity increases ecosystem functioning through niche differentiation and resource partitioning, facilitation (i.e. some species alter their environment in ways that benefit other species), or biotic feedbacks (Tilman et al. 1997, Díaz and Cabido 2001, Loreau and Hector 2001, Hooper et al. 2005, Barry et al. 2019).
Selection effects – An effect of biodiversity where more diverse assemblages are more likely to contain the best function-providing species, which can increase overall functioning when these species are dominant (Aarssen 1997, Hooper 1998).
Temporal and spatial selection effects – An effect of biodiversity where because there is selection for different 'best' species at different times and places, increased temporal and spatial beta diversity can increase ecosystem functioning (Yachi and Loreau 1999, Isbell et al. 2018, Loreau et al. 2021).
Multifunctionality – When more species are needed to maintain multiple ecosystem functions and services (Hector and Bagchi 2007, Lefcheck et al. 2015). This is especially true over time because different species support different functions in different contexts (Isbell et al. 2011).

also found that increasing species richness could reduce tradeoffs between some ecosystem functions (e.g. total plant nitrogen and resistance to invasive species) (Zavaleta et al. 2010). Multifunctionality has not yet been extensively studied in urban systems (Schwarz et al. 2017), even though ecosystems are often managed or valued for multiple functions and services. Multifunctionality likely plays an important role in urban areas. For example, increasing soil taxonomic and functional diversity increased ecosystem multifunctionality in urban green spaces (Fan et al. 2023).

Because urban environments can differ so dramatically from the surrounding non-urban environment, the same relationships between biodiversity and ecosystem functioning may not hold. Two major factors could disrupt the relationship. First, in non-urban environments, stable coexistence between species occurs when interspecific competition is weaker than intraspecific competition. In other words, niche differentiation lowers interspecific competition and increases complementary use of resources (Vandermeer 1981, Loreau 2004). In managed urban environments, people maintain plant mixtures that would not coexist in the wild, i.e. novel communities (Kendal et al. 2012, Andrade et al. 2021). In general, management practices and human behaviors have a significant influence on biodiversity, and this is particularly pronounced in urban environments. Second, chemical inputs like fertilizers and pesticides can disrupt the biodiversity and ecosystem functioning relationship, leading to negative observed relationships between biodiversity and function, at least across space. For example, in non-urban grasslands, chemical fertilization increases productivity, but decreases biodiversity, which can lead to loss of productivity over time (Isbell et al. 2013). Thus, when the relationship

between biodiversity and productivity is measured only across space and not across time, the most productive places may be less diverse, even when biodiversity loss leads to an eventual loss of productivity within the fertilized locations (Isbell et al. 2013). Fertilizer use in urban areas is quite common, although an increasing number of cities have banned or are in the process of banning pesticide and fertilizer use (Groffman et al. 2016, Shiffler 2024).

Ecosystem functioning promotes ecosystem services

Although a focus on the relationship between biodiversity and ecosystem functioning in urban areas has been uncommon (Rega-Brodsky et al. 2022), assessments of urban ecosystem services have grown in recent years (Haase et al. 2014, Luederitz et al. 2015). Ecosystem services directly link ecosystem components or functions to benefits that people receive (Haase et al. 2014; Box 1). Many studies only consider the extent or location of green spaces (Osborne and Alvares-Sanches 2019, Peng et al. 2021), and few studies consider species composition in urban green spaces or the role of biodiversity in supporting ecosystem services (Haase et al. 2014, Cameron and Blanuša 2016, Stroud et al. 2022). While some studies do consider which species or species traits might provide the greatest level of ecosystem services, these studies do not incorporate the role of biological diversity itself. A recent review found that this was quite common; most studies did not quantitatively link the magnitude of a biodiversity metric with ecosystem service provision, but instead described the service as dependent on a particular composition of species, functional traits, or structures, or used biodiversity as an indicator of the service itself (Ziter 2016). Moreover, relationships between biodiversity and ecosystem services in urban areas are often assumed rather than explicitly tested (Schwarz et al. 2017). A better understanding of the links between urban biodiversity and ecosystem services, and the mechanisms that drive them (especially through studying species traits), has been identified as a key research gap (Knapp et al. 2021, Pinho et al. 2021).

In this study, our goal was to fill the gap in our understanding of the links between urban biodiversity and ecosystem functioning and to spur additional research on improving urban ecosystem functioning and regulating ecosystem services that support human well-being. Specifically, we 1) review documented evidence of the relationship between BEF in urban environments, and 2) build on previous review papers (Ziter 2016, Schwarz et al. 2017) by examining factors that may influence the direction of BEF relationships such as habitat type, and the spatial and temporal scale of the study. We focus on BEF relationships given that ecosystem functions underpin several urban ecosystem services. This allows us to consider the underlying conceptual relationships between biodiversity and ecosystem functioning as described in the ecological literature and to test whether these theories apply in urban environments where abiotic and biotic conditions have been significantly altered. We also include regulating ecosystem services, given that these services directly relate to ecosystem functioning (e.g. pollination is considered an ecosystem function and a regulating ecosystem service). Given the generally positive BEF relationships found in non-urban ecosystems, we expected increasing biodiversity in urban ecosystems will also increase ecosystem functioning.

Review methods

Article search and screening

For our literature review, we ran a repeatable Web of Science search using the search terms 'TS = ((biodiversity) AND ('ecosystem function*' OR 'ecosystem service') AND (urban OR city OR cities))' and TS = (('functional diversity' OR 'species richness') AND ('ecosystem function*' OR 'ecosystem service') AND (urban OR city OR cities)) on 6 June 2023. This is a rapidly growing field, and it is unlikely that we would capture all relevant articles. Thus, our goal was to capture a representative subset, and we did not conduct searches using individual ecosystem functions as search terms. The search yielded 861 unique results. To be included in our analysis (Table 1), studies needed to fulfill two conditions.

1. Explicitly assess how at least one metric of biodiversity (Box 1) related to at least one ecosystem function or regulating ecosystem services that directly related to ecosystem functioning (e.g. water capture or filtration, air pollution reduction). We only included studies that explicitly assessed correlations between biodiversity and ecosystem functioning or tested cause/effect models or experiments. We included both experimental and observational studies.
2. Have been conducted in an urban setting (as defined by the study author). There are many definitions of 'urban', but common components include demography and structural attributes such as the amount of impervious surface (Mcintyre et al. 2000, Moll et al. 2019).

After our initial full text review, 44 papers met all of our inclusion criteria. We then conducted a snowball search (i.e. we reviewed the citation lists of all initially included papers

Table 1. Inclusion criteria for this review using the population, exposure, comparator, and outcome (PECO) framework.

PECO element	Include	Exclude
Population	Urban ecosystems	
Exposure	Level of biodiversity	
Comparator	Used observations to assess correlations between level of biodiversity and ecosystem functioning or tested cause/effect with models or experiments	Only conceptual link was made between biodiversity and ecosystem functioning
Outcome	Level of ecosystem functioning or regulating ecosystem service	Cultural ecosystem services

for relevant titles). This process yielded an additional 26 papers for a total of 70 papers included in our review.

Data extraction

We extracted data related to basic study information and methodology, including study location, ecosystem and habitat type, spatial scale (grain and extent), study type (i.e. observational experimental, or modeled), sample size, and length of study (see the Supporting information for complete description). Next, we extracted information regarding the BEF relationship. This included the ecosystem function assessed, focal taxonomic group, biodiversity metric, whether the study also considered species identity (and, if so, was species identity important), direction of BEF relationship (i.e. positive, negative, neutral or mixed), and whether the study assessed the impact of invasive species. Data extraction was conducted by a single reviewer to ensure consistency.

We split observations into separate rows by focal taxonomic group, ecosystem type, and biodiversity metric, such that a single paper could have multiple rows in the analysis. Hereafter, we refer to each row, which is a unique relationship between a taxonomic group, ecosystem type, biodiversity metric, and ecosystem function, as a 'relationship' (n = 220).

Data analysis

Distribution of evidence

We calculated summary statistics on the characteristics of studies looking at BEF relationships in urban systems. This included study locations, study size, and study length; and which taxa, biodiversity metrics, ecosystems, and ecosystem functions were assessed. We also looked at the percentage of relationships that were positive, negative, neutral, and mixed.

Direction of BEF relationships

Given that studies measured a variety of response variables and interventions, sample sizes for comparable studies were too small to conduct a formal meta-analysis of effect sizes. Therefore, we focused on the direction of BEF relationships so that we could compare across all relationships. We assessed whether positive BEF relationships were more likely than negative or neutral ones (i.e. did biodiversity increase, decrease, or have no effect on ecosystem functioning) using χ^2-goodness of fit tests. We removed mixed responses for this analysis because there were so few (n = 1) and because mixed responses include both positive and negative impacts of biodiversity. We ran the tests with all relationships combined, and individually for functions that had at least fifteen positive, negative, or neutral responses (or at least ten if a study found only two directions of responses). We corrected p-values for multiple post hoc comparisons using the Holm method in the 'RVAideMemoire' package and considered p-values < 0.05 as significant (Holm 1979, Herve 2023).

Comparison to non-urban ecosystems

To see how the distribution of evidence and direction of BEF relationships in urban systems compared to non-urban systems, we used the data from van der Plas (2019, n = 1232 relationships), removing any observations that came from urban/suburban study areas (n = 13, resulting in a total of 1219 relationships for comparison). We used the direction of relationships between ecosystem function and each specific biodiversity indicator (i.e. the 'Relationship' column in the data). In some cases, we re-categorized the data to match our ecosystem function and/or taxonomic classifications (e.g. we combined terrestrial, aquatic, and belowground invertebrates into one 'invertebrates' category, see the Supporting information for details).

Factors influencing the direction of BEF relationships

We used random forest classification to assess whether any of the study methodology, diversity metric, or ecosystem function variables could predict the direction of BEF relationships. Specifically, we used conditional inference trees to select the values of the covariates that best differentiate the dependent variable (in this case, direction of BEF relationships) using significance tests. Response variables only included positive, negative, or no effect of biodiversity on ecosystem functioning. We excluded mixed responses and the ecosystem stability function because there were so few observations. We used the conditional tree function *ctree* (Hothorn et al. 2006) in the package 'partykit' (Hothorn and Zeileis 2015) to run 10 000 iterations using the variables' taxonomic group, ecosystem type, ecosystem function category, biodiversity metric, spatial scale of the data, study type, sample size, and study years as predictors. We set the significance level for tree splits to $\alpha = 0.05$. We then used the 'ggparty' package (Borkovec and Madin 2019) to visualize the significant tree splits. We conducted all analyses in R ver. 4.0.4 (www.r-project.org).

Results

Distribution of evidence

The 70 papers included in our review contained 220 unique relationships and studied 20 ecosystem functions in urban systems, which we grouped into eight major categories (Supporting information). Biomass included biomass production and biomass stock (commonly used as a proxy for production), although we note that in some cases these metrics may not be tightly linked (TerHorst and Munguia 2008).

The most studied urban ecosystem functions were nutrient cycling and retention, and biomass/carbon storage (Fig. 1). Study length averaged approximately two years, with only one study conducted for longer than five years. Study area plot sizes were small: 30% of relationships came from study plots covering < 1 m^2, and only 4% covering areas > 1 km^2. Most relationships came from terrestrial ecosystems (n = 191), with a few from freshwater ecosystems (especially streams; n = 23), and only six relationships from marine/coastal ecosystems. Study locations were highly skewed, with 79% of papers in North America, Europe or Australia (although one study that

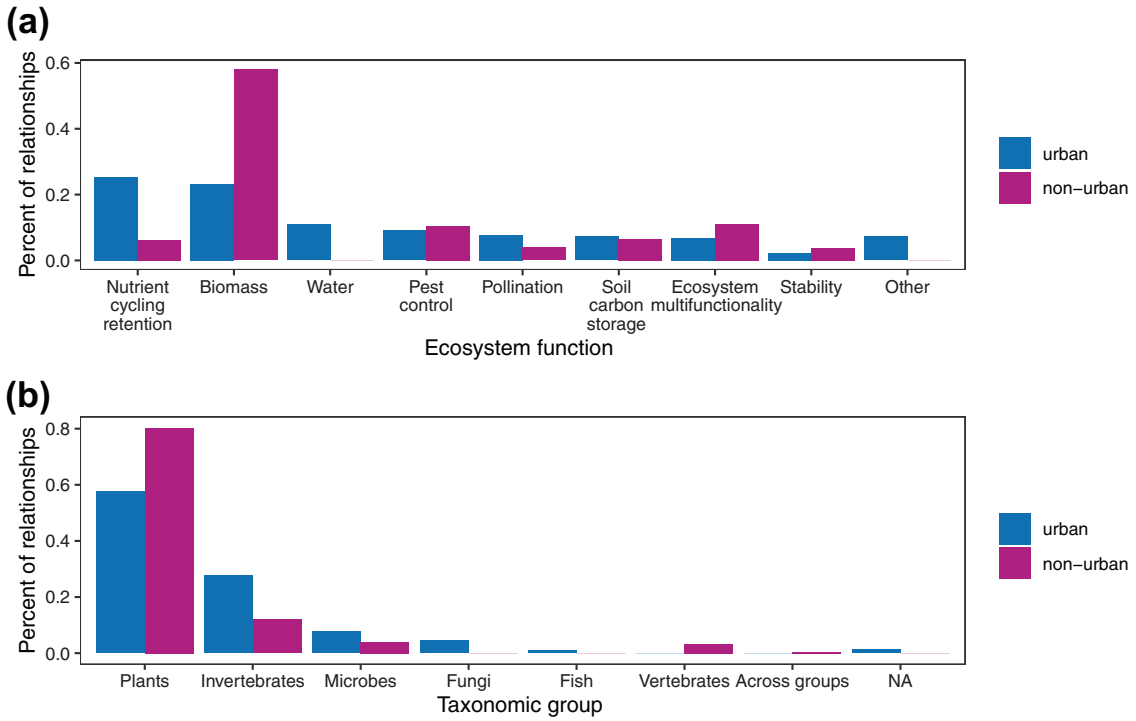

Figure 1. Spread of evidence on biodiversity–ecosystem functioning relationships by ecosystem function (a) and taxonomic group (b) for urban areas (this study, n = 220 relationships) compared to non-urban areas (data drawn from van der Plas 2019, n = 1219 relationships).

included data from 17 countries across six continents did not list the countries, so this paper is excluded from this analysis (Fan et al. 2023, Fig. 2).

Like non-urban system studies, plants were by far the most studied taxonomic group, followed by invertebrates (O'Connor et al. 2017; Fig. 1). The effects of plant diversity were assessed on all ecosystem function categories, while the effects of invertebrate diversity were assessed predominately for nutrient cycling and retention, and pollination (Fig. 3). No studies assessed how the diversity of vertebrates affected urban ecosystem functions (Fig. 1). Species richness was the most common biodiversity metric (n = 133), compared to functional trait diversity (n = 38), evenness (n = 16), or another diversity metric (n = 33). Twenty six percent of the relationships included also assessed whether species identity had an impact on ecosystem functioning, and of those nearly all (98%) found that species identity affected ecosystem functioning. Only 13% of the relationships in our study considered the impact of invasive or non-native species on BEF relationships. Of those, the majority found negative (37%) or neutral impacts (26%) of non-native species, while only 7% found positive impacts, and 23% were unclear.

Direction of BEF relationships

Biodiversity increased ecosystem functioning in 51.8% of the relationships assessed (Supporting information). Urban ecosystem functioning was significantly more likely to have a positive than a negative relationship with biodiversity (8.2% negative). Positive relationships were more common than neutral relationships (39.5% neutral), but the differences were not statistically significant (Supporting information). Positive relationships were more common than negative relationships for all individual ecosystem functions. This difference was significant for nutrient cycling and retention (51.8% positive versus 5.4% negative), and pollination (82.4% positive versus 5.9% negative), but not for biomass (41.2% positive versus 23.5% negative) or pest control (50.0% positive versus 10% negative). Positive relationships were significantly more common than neutral relationships for pollination (82.4% positive versus 11.8% neutral). Positive relationships were more common than neutral relationships for nutrient cycling and retention (51.8% positive versus 42.9% neutral), ecosystem multifunctionality (73.3% positive versus 26.7% neutral), and pest control (50.0% positive versus 40.0% neutral), but these differences were not statistically significant (Supporting information). For soil carbon storage and water-related functions, neutral relationships were the most common (62.5% neutral versus 37.5% positive for soil carbon storage and 58.3% neutral versus 41.7% positive for water-related functions), but again these differences were not statistically significant. No negative relationships were observed for these functions.

Compared to non-urban systems, pollination, pest control, stability, and nutrient cycling and retention had a higher proportion of positive relationships between biodiversity and function in urban systems, while biomass had a higher proportion of negative relationships (Fig. 4).

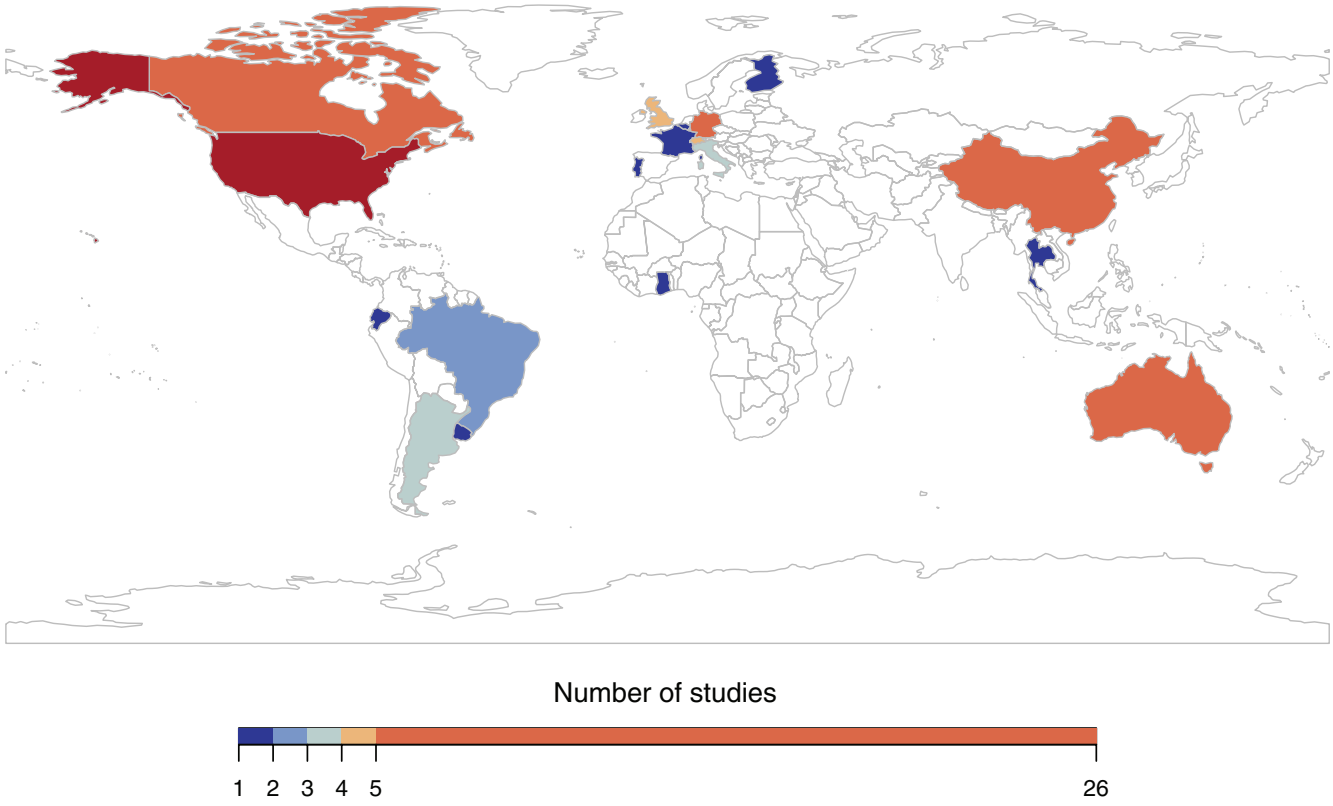

Figure 2. Study area locations for urban biodiversity–ecosystem functioning studies. Scale represents number of studies.

Factors influencing the direction of BEF relationships

Our random forest model did not identify any study factors that affected the direction of BEF relationships in urban areas, but biomass had more negative biodiversity–ecosystem function relationships than other ecosystem functions (Supporting information).

Discussion

Given the generally positive BEF relationships found in non-urban ecosystems, we expected increasing biodiversity in urban ecosystems to also increase ecosystem functioning. We found that biodiversity increased ecosystem functioning in urban areas significantly and more frequently than it decreased ecosystem functioning. However, similar to findings for urban biodiversity–ecosystem service relationships, neutral relationships were also quite common (Ziter 2016, Schwarz et al. 2017). Although positive relationships occurred more frequently than neutral relationships, the difference was not statistically significant. Thus, increases in ecosystem functioning with biodiversity can be context specific, but enhancing biodiversity in urban areas is more likely to have a positive or no effect than a negative effect. Increasing biodiversity in cities can therefore be important for both conservation and ecosystem functioning, and considering biodiversity in urban planning could improve management outcomes.

Pollination

Studies that explored floral resource diversity and pollinator diversity found a positive relationship between plant and pollinator biodiversity and insect pollination. Complementarity between pollinator species could drive this relationship. For example, in a Chicago urban garden experiment, different plant species benefited from a different suite of pollinators so, at the plant community level, pollinator species diversity increased overall yield (Lowenstein et al. 2015). Further, most of the common pollinator species in urban areas are generalists (Lerman and Milam 2016). Thus, each additional pollinator species might increase overall pollination rates. Multiple studies reported higher pollinator abundance, richness, and/or pollination rates in higher population density neighborhoods or urban compared to rural areas (Lowenstein et al. 2014, Theodorou et al. 2016, Hall et al. 2017). Many bees and other pollinators can benefit from native and non-native plants, and urban yards can have high plant diversity that provides nectar and pollen throughout the growing season (Frankie et al. 2009, Hall et al. 2017, Lerman et al. 2018). This could explain why biodiversity was more likely to increase pollination in urban compared to non-urban systems.

Nutrient cycling and retention

Multiple studies found greater invertebrate species richness increased leaf litter decomposition (Tresch et al. 2019,

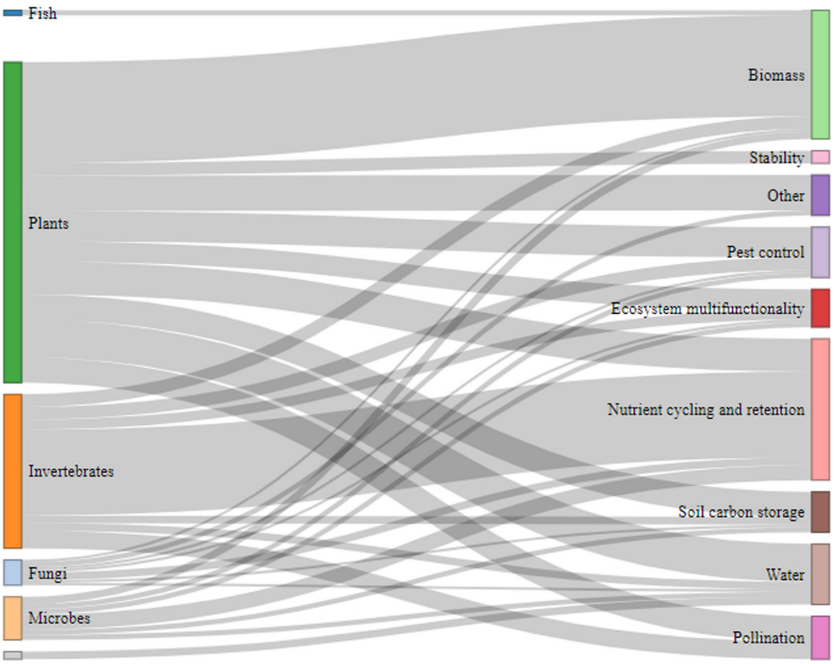

Figure 3. Breakdown of which taxonomic groups were used to assess which ecosystem functions (i.e. the group of organisms whose biodiversity levels are related to ecosystem functioning).

Lemes da Silva et al. 2020). However, one study found a negative relationship; in this case, the presence of a highly efficient invasive ant species (*Tetramorium* sp. *E*) overpowered any effect of arthropod diversity on decomposition (Youngsteadt et al. 2015). Plant diversity also increased the rate of decomposition in non-urban systems (Mori et al. 2020), but most urban studies focused on decomposer diversity only. Increased plant and arthropod species diversity increased nitrogen retention in soils, including in urban grasslands and green roofs (Johnson et al. 2016, Thompson and Kao-Kniffin 2016). This may be driven by complementarity and greater nitrogen uptake by plants in diverse mixtures (Thompson and Kao-Kniffin 2016). In some cases, other site factors like impervious surface

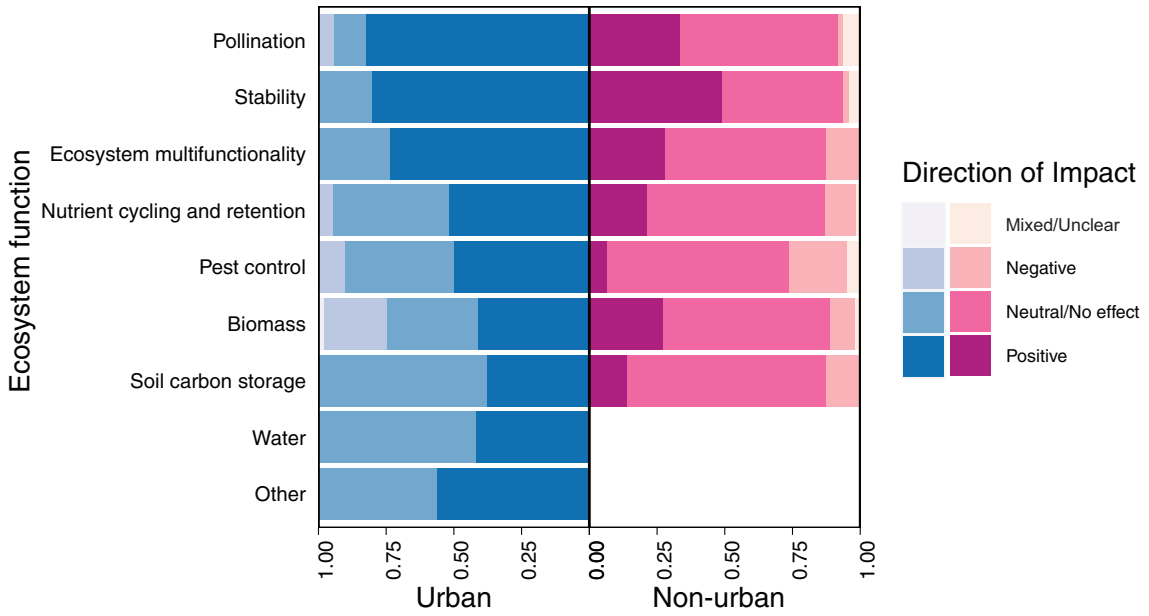

Figure 4. A comparison of proportion of positive, negative, neutral and mixed responses of biodiversity–ecosystem functioning relationships by ecosystem function in urban (this study, n = 220 relationships) versus non-urban systems (data drawn from van der Plas 2019, n = 1219 relationships).

and land use had stronger effects on nitrogen cycling than biodiversity effects (Onandia et al. 2019). In particular, high percentages of impervious surfaces can lead to more runoff and greater nitrogen leaching (Kaye et al. 2006, Grimm et al. 2008), rendering urbanized areas as sources of nutrient pollution.

Biomass

The lack of a strong biodiversity effect on biomass is surprising given the strong evidence for increased biomass with increased diversity in non-urban systems (Cardinale et al. 2011, 2012, Hooper et al. 2012, O'Connor et al. 2017, Loreau et al. 2022). One explanation for a weak effect of biodiversity on biomass may be the high level of plant species manipulation in urban environments, which happens via planting and maintenance of trees, shrubs, and other vegetation. Urban residents plant high numbers of ornamental exotic species, leading to distinctive plant communities (Avolio et al. 2020, Padullés Cubino et al. 2020). Human manipulation of the plant community can alter the patterns of succession and disrupt coexistence mechanisms (Vandermeer 1981, Loreau 2004) that typically take place in non-urban systems. This could lead to lower niche differentiation and less complementary use of resources, which could weaken BEF relationships. We might therefore expect places planted with similar-functioning species to have weaker BEF relationships than more functionally diverse assemblages. Selection effects occur when the highest performing species becomes dominant, but the effect on biomass could be dampened if humans artificially select for less productive species, perhaps to gain other desirable benefits unrelated to biomass production. Pesola et al. (2017) compared biodiversity and aboveground biomass in urban forest plots of varying ages in Milan, Italy. Selective silvicultural thinning over time reduced competition and resulted in a few dominant species in the oldest, highest biomass plots, thus leading to a negative relationship between biodiversity and biomass (Pesola et al. 2017).

On a theoretical level, positive relationships between biodiversity and function are not always expected from observational field data that measure realized diversity (i.e. diversity at the time of the survey) (Loreau 1998, Hagan et al. 2021). Studies can be designed to look at two different questions: 1) within a place, how will a change in biodiversity over time cause a change in ecosystem functioning (i.e. causal relationship between biodiversity and ecosystem functioning)? or 2) at a given time, are the most diverse places also those with the highest levels of ecosystem functioning or services (i.e. spatial correlation between biodiversity and ecosystem functioning)? We included both types of studies in our review. As noted earlier, fertilizer use can cause the most productive places to be the least diverse, even when biodiversity loss leads to loss of productivity over time within the fertilized locations (Isbell et al. 2013). Additionally, if complementarity is the main driver of positive BEF relationships, then we would expect increased realized diversity to increase ecosystem functioning. For example, an experimental urban green roof study found that increasing plant diversity increased plant biomass, and that this effect was due to complementarity (Johnson et al. 2016). However, if selection effects are the main driver of positive BEF relationships, then biodiversity leads to the increases in function when initial diversity is high. Over time, the highest functioning species outcompete other species, leading to lower realized diversity. Therefore, using observational field data to measure BEF relationships may underestimate the importance biodiversity has to ecosystem functioning (Hagan et al. 2021). This may have played a role in the lack of an effect of plant species diversity on biomass in urban forests in San Juan, Puerto Rico, where tree and shrub species identity influenced aboveground carbon storage, while overall species diversity (measured in a single year) did not (Timilsina et al. 2014).

Pest control

Some studies found that increasing parasitoid or natural enemy richness increased parasitism or predation rates on pest species (Bennett and Gratton 2012, Fenoglio et al. 2013), but in some cases defoliation of crop species was more related to abundance of natural enemies than their diversity (Lowenstein and Minor 2018). Positive predator–diversity effects can be driven by niche complementarity, functional facilitation, or sampling effects, while neutral or negative effects can be driven by intraguild predation (i.e. predators may feed on other predators) or non-consumptive effects (e.g. interference competition) (Finke and Snyder 2010). The effects of plant species diversity on pest control were also mixed. While increasing plant species richness sometimes increased predation, this was not always the case. Increasing plant species richness sometimes decreased predation, possibly due to interference competition or intraguild predation between predator species (Bennett and Gratton 2012, Philpott and Bichier 2017).

Soil carbon storage

Biodiversity frequently did not affect soil carbon storage over the time scales considered. Although the number of relationships was small (n = 3), studies investigating arthropod or earthworm diversity found positive effects of biodiversity, whereas those looking at plant diversity were more mixed. Plant biodiversity may increase soil carbon storage indirectly by increasing soil organism diversity (Schittko et al. 2022). In urban systems, plant management and greater presence of non-native species may reduce the beneficial effects of plant diversity if the species present did not co-evolve with the soil communities (Fan et al. 2023).

Water dynamics

Most studies found that biodiversity did not affect water dynamics, despite expectations from non-urban studies that diverse communities capture more resources, including

water (Cardinale et al. 2012). One green roof study found that diverse plant species mixtures had higher water capture rates than nearly all monocultures (Lundholm et al. 2010). This may be due to complementarity of growth phenology; because different species used water at different times, species mixtures were able to provide more stable water uptake over time (Lundholm et al. 2010). In contrast, a different green roof experiment did not find an effect of diversity on water capture, possibly due to the shorter length of the study or lower overall vegetation density (Johnson et al. 2016). Similarly, an afforestation experiment in New York City did not find significant effects of plant diversity on water-holding capacity after one year, which may not have been enough time for trees and shrubs to establish (Oldfield et al. 2014).

Research gaps and future directions

Our random forest model identified ecosystem function category as the only significant metric to predict how biodiversity might affect ecosystem functioning in urban areas. It is not surprising that ecosystem function would influence the relationship, given the variation observed across functions in both urban and non-urban systems (Fig. 4). This highlights that, overall, the number of studies and geographic coverage of our study was too low to create a general predictive framework for how study metrics might lead to differential BEF relationships. Therefore, to better understand urban BEF relationships, we use our results to identify limitations of existing studies, research gaps, and directions for future research which are summarized in Table 2 and described below.

Temporal and spatial scales

Similar to previous urban ecosystem services reviews (Stroud et al. 2022), most studies included in our review occurred over very short time frames (almost all under five years, and many less than one year). BEF relationships grow stronger over time (Isbell et al. 2011, Reich et al. 2012), and longer studies would provide an opportunity to assess whether biodiversity leads to more stable functioning in urban areas. In addition to temporal scales, studies at greater spatial scales are needed to understand the effects of larger-scale processes like dispersal and the influence of beta diversity. Eighty nine percent of relationships in our study were measured at scales of < 1 km^2, while 75% covered only one urban area. In addition, designing studies that align with management scales (i.e. parcel boundaries) and distinguishing between studies on public versus private spaces could be useful, since these land uses can have different management goals. Further, urban areas included in our study were highly skewed towards North America, although we did have studies from six continents.

Assess more ecosystem functions and multifunctionality

Similar to previous work on urban ecosystem services, most studies assessed single ecosystem functions (Ziter 2016). Since higher diversity is needed to maintain multiple functions (Hector and Bagchi 2007, Cardinale et al. 2012, Tilman et al. 2014), single-function studies may underestimate the importance of biodiversity for ecosystem functioning in urban areas. It is also important to measure ecosystem

Table 2. Future research directions for understanding urban BEF relationships.

Future research direction	Rationale
Conduct studies over longer timescales	BEF relationships grow stronger over time. Longer studies can better assess the impacts of diversity on ecosystem function stability
Increase diversity of urban areas where BEF relationships are measured	BEF relationships may differ depending on urban area characteristics such as time since development, level of urbanization/urban density, amount of biodiversity in the area, and climate. More data are needed to parse these differences
Increase taxonomic coverage of biodiversity metrics	Most studies assessed BEF relationships for plants or invertebrates. While plant diversity is easier to measure, other taxonomic groups (e.g. mammals, birds) also provide important functions that have yet to be assessed
Assess BEF relationships across trophic levels	Most studies assessed the impact of horizontal (i.e. within trophic level) diversity but did not assess vertical (i.e. across trophic level) diversity. Loss of diversity across trophic levels can impact ecosystem functioning by altering food webs, leading to trophic cascades
Assess multiple metrics of diversity	Most studies investigated the impact of species richness on ecosystem functioning. However, species richness and other diversity metrics may not respond the same way to environmental changes. In addition, species evenness may be an especially important metric in urban areas where a few species dominate
Assess more functions and multifunctionality	A greater diversity of species are needed to provide multiple services. Single function studies may underestimate the level of diversity required
Investigate the impact of invasive species	Urban areas can have high numbers of invasive species. Native species assemblages often show greater complementarity than exotic species assemblages, but few studies included an assessment of the impact of invasive species on BEF relationships
Assess mechanisms behind BEF relationships rather than only correlations	Understanding whether BEF relationships are driven by complementarity or selection effects, and how spatial and temporal beta diversity within urban areas affects temporal and spatial selection effects, can change management strategies. Controlled experiments can be especially helpful to disentangle causal effects of biodiversity on ecosystem functioning

functions directly; changes in the composition of species traits or abundances do not always result in changes to ecosystem functioning, thus inferences between functional traits and function cannot be assumed (Mayer-Pinto et al. 2018).

Taxonomic diversity and multiple trophic levels

We found that most studies assessed how plant diversity affected ecosystem functioning, while animal, fungi, and microbes were rarely assessed (Fig. 1, 3). Additionally, most studies assessed horizontal diversity (i.e. diversity within a trophic level), while few considered vertical diversity (i.e. diversity across trophic levels). Loss of diversity across trophic levels can impact ecosystem functioning by altering food webs, leading to trophic cascades (Hooper et al. 2005, Dirzo et al. 2014). Feedbacks across trophic levels remain an important gap in our understanding of BEF relationships (Eisenhauer et al. 2019).

Assess multiple metrics of diversity

The majority of relationships in our study assessed species richness as the diversity metric. However, species richness, functional diversity, and evenness are not always correlated (Díaz and Cabido 2001, Stirling and Wilsey 2001, Wilsey et al. 2005, Hillebrand et al. 2008, Aguirre-Gutiérrez et al. 2017), and all metrics of community composition can be affected by global change (Avolio et al. 2021). Lack of attention to functional diversity in urban ecosystem services has been noted before (Schwarz et al. 2017). Additionally, most studies in our review measured alpha diversity, but did not account for important large-scale processes like species dispersal or species turnover (beta diversity) that may be important for maintaining diversity and ecosystem functioning at larger scales.

Impact of non-native species

Non-native invasive species can disrupt BEF relationships (Pejchar and Mooney 2009). Non-native species assemblages may have lower complementarity than native species assemblages (Wilsey et al. 2009). Given that urban areas can have high non-native species richness, especially for plants (Aronson et al. 2014), greater consideration of how non-native plants influence ecosystem functioning is warranted to better understand how invasive species might disrupt BEF relationships. This gap was identified for urban ecosystem services as well (Ziter 2016, Schwarz et al. 2017).

Mechanisms for BEF relationships

Most studies did not explicitly test mechanisms behind observed BEF relationships. Controlled experiments can be especially useful to understand causal effects of biodiversity on ecosystem functioning, but are currently underutilized in urban areas. Only 23% of the relationships assessed in this review came from experimental studies (compared to 75% observational and 2% modeled), and more than half of these focused on enhancing ecosystem functioning on green roofs. Understanding mechanisms can help inform management decisions (Pinho et al. 2021). For example, if complementarity was the main driver of positive BEF relationships, then planting diverse assemblages in urban managed ecosystems could increase functioning. If, however, selection effects were a stronger driver, then managers might instead choose to manage for species that are 'best' at providing desired functions (Ranalli and Lundholm 2008). Even so, different species are the 'best' at different times and places (including through time as the climate changes), making it challenging to correctly identify these species.

Management implications

Landscape planners often consider the extent and location of green spaces without considering the role of species diversity for providing important ecosystem functions or services (Pickett et al. 2011, Haase et al. 2014). However, as we have shown, biodiversity can increase functioning in urban areas and warrants consideration in management plans. A recent review of urban planning documents from 40 cities around the world found that most plans included some goals related to biodiversity or ecosystem services, but few comprehensively included both (Nilon et al. 2017), which means they may be missing opportunities to synergistically achieve both goals. Managers may wish to consider more integrated metrics of diversity rather than only species richness by also considering species evenness, dominance, and functional trait diversity that are important for providing functioning ecosystems over time (Schmitt-Harsh et al. 2013). For example, including a mixture of small and large tree species could increase overall carbon storage by increasing overall resource use (Schmitt-Harsh et al. 2013). Moreover, considering the distribution of biodiversity and who benefits from biodiversity within cities is important. Low income and minoritized communities often have lower access to green space and biodiversity (Astell-Burt et al. 2014, Haaland and van den Bosch 2015, Schell et al. 2020), which translates to lower access to important ecosystem functions and services.

In practice, management for biodiversity in urban areas can be complicated because managers also consider economic, social, and cultural factors (Aronson et al. 2017). Urban plants are often selected because of aesthetics, what will survive, and what is affordable and available for sale in local stores (Cameron and Blanuša 2016, Avolio et al. 2018, 2020). For example, residents in Salt Lake City, Utah, ranked beauty and shade as the two most important services provided by street trees (Avolio et al. 2018). Ease of maintenance is also a major consideration for local landowners and urban greenspace managers (Larson et al. 2009, Avolio et al. 2020). However, having a diversity of street trees can increase maintenance costs and even overall CO_2 emissions if pruning and other life cycle care need to be performed at different time intervals (Strohbach et al. 2012). As a way to balance these considerations, managers in Santa Monica, California, have been planting a single species

along some streets, and different tree species along other streets to increase city-wide diversity (Morgenroth et al. 2016). Although such a strategy may not promote complementarity, it could allow for increased stability of functions across the city over time. Another major consideration for urban planners is how to manage for non-native invasive species. Invasive species removal can be costly, and it is still unclear how to strike a balance between invasive species removal and tolerance by people (Aronson et al. 2017). Improved understanding of the role of invasive species in BEF relationships could help us understand this balance. For example, if fast-growing invasive species are likely to take over before species-rich mixes can establish, then it may be advisable to restore urban areas with a few native cover crops first to limit invasion before adding additional species (Doherty and Zedler 2014).

Conclusion

As urban areas continue to develop and grow, understanding how to manage urban biodiversity, ecosystem functioning, and associated ecosystem services is especially important. One major challenge for urban biodiversity management is that urban green spaces are managed by millions of individuals spanning public and private land. Thus collectively managing urban green spaces can be challenging, and might hinder biodiversity goals (Aronson et al. 2017). In this review, we have shown positive or neutral relationships between biodiversity and ecosystem functioning are more common than negative relationships. Although more work is needed to understand factors that influence the direction of BEF relationships, increasing biodiversity in cities, even in small areas, can be a win–win strategy for both biodiversity conservation and enhancing ecosystem functioning.

Acknowledgements – We thank Mia Wavrek and the Morelli and Lerman/Warren labs for their useful feedback on the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.
Permits – This article does not present research with ethical considerations.

Author contributions

Sarah R. Weiskopf: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Susannah B. Lerman**: Conceptualization (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal). **Forest Isbell**: Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Toni Lyn Morelli**: Conceptualization (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available at the USGS digital repository: https://doi.org/10.5066/P1XSSVXE (Weiskopf et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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