Understanding biodiversity-ecosystem service relationships in urban areas: a comprehensive literature review

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1. Introduction

Urbanisation is increasing, with more than half the global human population now living in urban areas (United Nations 2015). This conversion of land-cover to urban land-use results in the loss of key habitats (Knapp et al. 2017; Seto et al. 2012). A major transdisciplinary research task, therefore, is to understand how urban expansion may be planned to minimise the loss of biodiversity and maintain urban ecosystem service (UES) delivery (Haase et al. 2014; Luederitz et al. 2015).

Positive relationships between biodiversity and UES are widely implied within both the scientific and policy literatures, along with the tacit suggestion that the enhancement of urban green infrastructure will automatically improve both biodiversity and UES (Kabisch et al. 2016; Ziter 2016). However, it is unclear how much published empirical evidence exists to support these assumptions (Gómez-Baggethun et al. 2013; Kowarik 2011; Ziter 2016) by ascertaining cause and effect, rather than relying on correlative inferences (Shipley 2000). Without such as evidence-base in place, it calls into question whether the implementation of concepts such as Green Infrastructure (GI; European Commission's Directorate-General Environment 2012) and Nature-Based Solutions (NBS; European Commission 2015) in urban areas will promote biodiversity and UES delivery as expected.

Positive biodiversity-ecosystem services (BES) relationships have been found in studies in non-urban contexts and controlled experiments. This research has established that both taxonomic and functional aspects of biodiversity underpin ecosystem functioning and service delivery in grasslands (e.g. Isbell et al. 2011; Lange et al. 2015; Wright et al. 2017), forests (Verheyen et al. 2016), created wetlands (Means et al. 2016) and mesocosms (Bilá et al. 2014). Additionally, habitat structure and area, as proxies for biodiversity, have been shown to be crucial for the delivery of ecosystem services such as fishing, pollination, water purification and pest regulation in non-urban contexts (Harrison et al. 2014). Urban BES relationships may be modified compared to those in non-urban contexts due to three characteristic factors (Aronson et al. 2016). First, urban ecosystems frequently experience altered abiotic and biotic conditions, including higher temperatures and drier soils (Kuttler 2008), elevated levels of artificial light (Russ et al. 2015) and greater habitat fragmentation within a matrix of sealed surface (Alberti 2015). Second, the functional composition of species assemblages may have shifted due to modified abiotic and biotic conditions (e.g. Kowarik 2011; Williams et al. 2009), leading to the dominance of seed-producing, short-lived and non-native plants species (Concepcion et al. 2015; Knapp et al. 2008; Williams et al. 2015). Third, human decisions and socio-economic circumstances act as further selection and facilitation filters for both biodiversity and community structure in emerging ecosystems (e.g. gardens, brownfield sites), giving rise to novel species assemblages (Colding et al. 2006; Kowarik 2011; Swan et al. 2011). Urban areas are therefore unique, challenging our traditional understanding of how species assemblages may influence ecosystem functioning, stability and ecosystem service delivery (Alberti 2015; Kowarik 2011).

A recent review of urban BES relationships examined 77 studies (Ziter 2016). It showed that the majority of papers focused on just a single service, that biodiversity was measured mostly at the taxonomic level (e.g. species richness, species diversity), and that BES relationships were generally described in a non-correlative manner that lacked a numeric metric of biodiversity (Ziter 2016). Due to this lack of nuanced evidence, several crucial questions regarding the mechanisms underpinning urban BES relationships remain unanswered. For example, syntheses of empirical studies conducted in non-urban systems have highlighted that the distribution of species' trait values in a community more often determine ecosystem functioning than taxonomic diversity (Díaz & Cabido 2001; McGill et al. 2006). This has led to the development of trait-based approaches to identify biotic control over ecosystem service delivery within (de Bello et al. 2010; Díaz et al. 2007; Lavorel 2013) and across trophic levels (Lavorel 2013; Moretti et al. 2013), as well as synergies and trade-offs among ecosystem services (Lavorel & Grigulis 2012). However, it is still not clear which functional biodiversity metric chiefly drives ecosystem processes and service delivery (Dias et al. 2013). Two hypotheses have been proposed (Ricotta & Moretti 2011): (1) mass ratio hypothesis (Grime 1998); and, (2) niche complementarity hypothesis (Tilman et al. 1996). The first states that the traits (or functional identity) of the species dominating an ecosystem predominantly control ecosystem functioning. The second suggests that the degree to which trait values differ between species in a community (functional diversity) relates to non-additive community effects and niche complementarity (i.e. more diverse plant communities should use resources more completely and be more productive). Evidence on the relative importance of these mechanisms is lacking for urban areas.

Here we examine new aspects of urban BES relationships, addressing: (1) which biodiversity metrics (i.e. taxonomic or functional) are positively, negatively or not related to UES; (1a) how functional identity (mass ratio hypothesis; Grime 1998) compares to functional diversity (niche complementarity hypothesis; Tilman et al. 1996; Trenbath 1974) in UES delivery; (1b) which species traits relate to UES; (1c) whether taxonomic biodiversity metrics (i.e. single species, species composition, or species diversity) underpin UES; and, (2) whether BES relationships in urban ecosystems have been empirically tested (e.g. by applying an experimental setting or testing assumptions statistically) or are simply assumed.

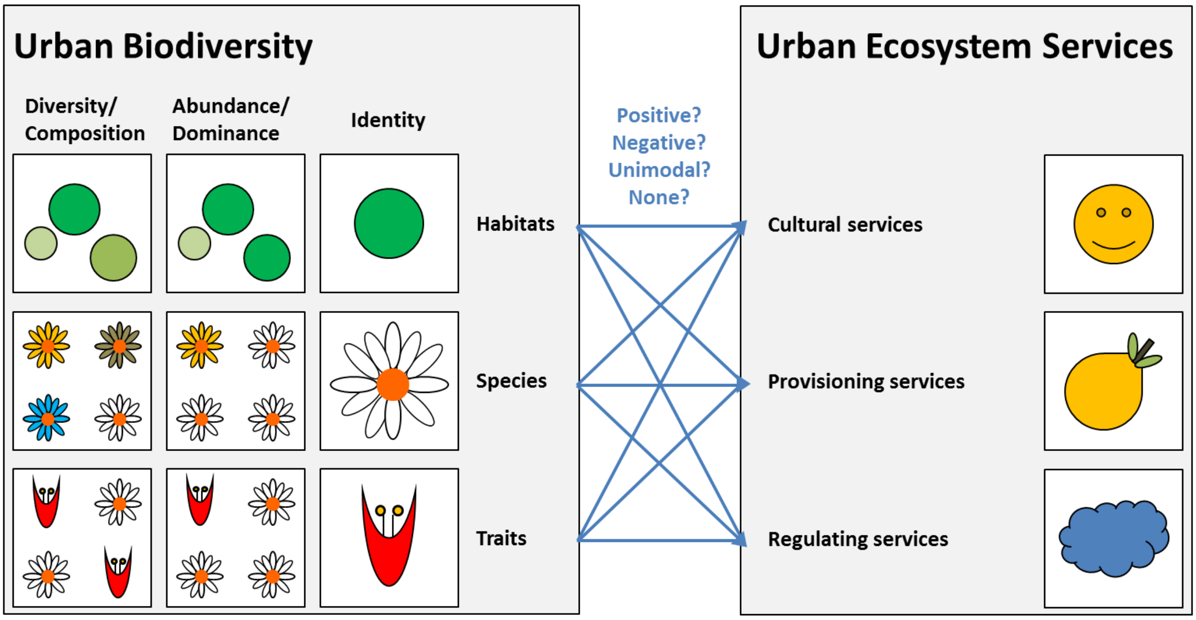

Fig. 1. Conceptual overview of our review, which sought to find empirical evidence of relationships (positive, negative, unimodal, non-significant) between different biodiversity (e.g. measures of diversity, abundance, dominance or identity of habitats, species or traits) and urban ecosystem service metrics (for the broad categories of cultural, provisioning and regulating services).

To address these questions, we conducted a comprehensive literature review on the relationship between specific biodiversity and UES metrics (Fig. 1). We build on Ziter (2016), which reviewed 77 articles, by conducting a wider search for publications examining urban BES relationships and synthesising across the 317 relevant papers we identified. Second, we discuss in detail the ecology behind BES relationships, as this was a clear research gap identified by Ziter (2016). We focus on the role of traits and functional diversity, influence of non-native species and application of empirical research. Furthermore, we investigate the context-dependency (i.e. reliance on factors such as biome, climate or management) of BES relationships (Balvanera et al. 2014; Mace et al. 2012).

2. Methods

The peer-reviewed journal literature was searched systematically using ISI Web of Science (WoS) (Fig. 2). The keywords to be used in our review related to UES were determined after a pilot search conducted in WoS, using the following broad terms: biodiversity AND 'ecosystem service' AND (urban OR city OR cities) AND (important OR importance OR relevant) (the latter being used to specifically find papers that suggested the relevance of a single ecosystem service). This generated 31 papers, from which we collected 107 UES keywords (Appendix S1) to be used in the main WoS search. We then determined 34 keywords for biodiversity, among them the most widely used terms of taxonomic and functional diversity from selected papers such as Wilson (1992), Magurran (2004) and Magurran and Mc Gill (2010) (Appendix S1). Eight keywords were included for urban areas (Appendix S1) and, after another pilot search, 'ecol*' and 'ecos' were also included to limit the material to ecological and ecosystem studies, and exclude psychological articles on human traits. Our final search string thus consisted of four blocks of terms, with at least one keyword needed for each block. To keep the amount of literature manageable and to focus on the asserted positive relationships between biodiversity and desired services, we did not include keywords on ecosystem disservices (Lyytimäki & Sipilä 2009).

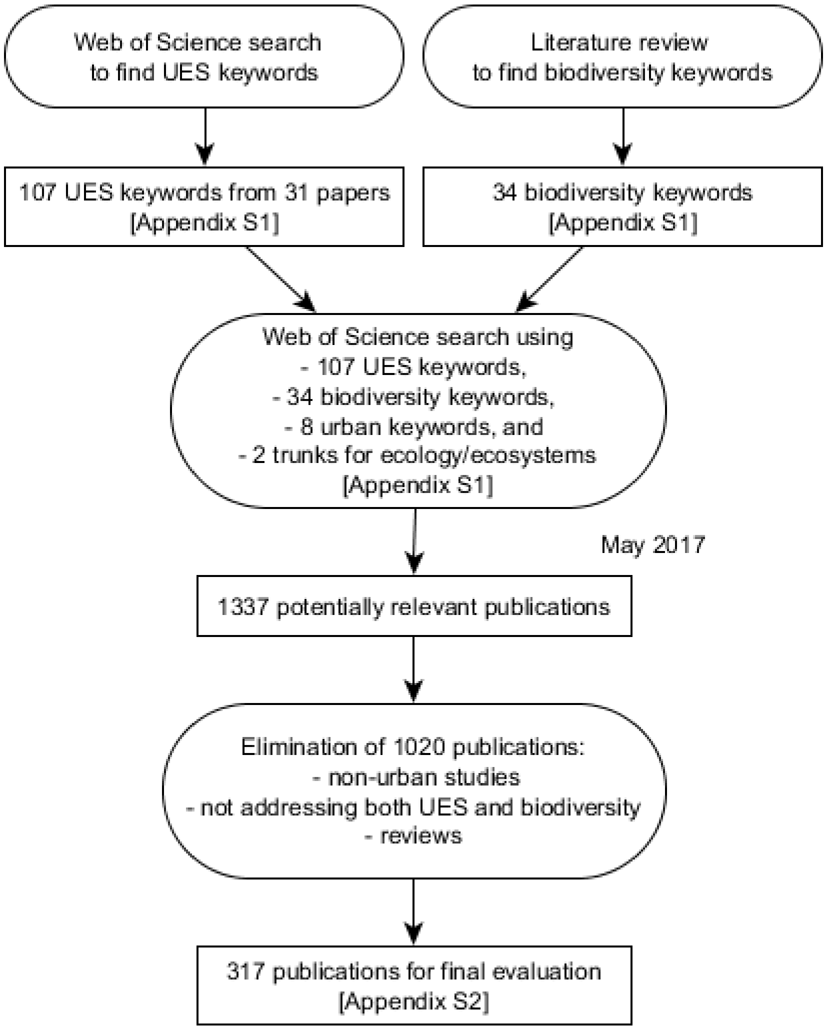

Fig. 2. Overview of the search strategy used to identify relevant papers for our comprehensive literature review.

We conducted the main WoS search in May 2017, restricting it to publications written in English and indexed in one of the WoS Core Collections (Science Citation Index; Social Sciences Citation Index). The search string was applied to title, keywords and abstracts of all papers. Publications prior to 1990 did not analyse UES (Haase et al. 2014).

The search yielded 1337 potentially relevant papers. We eliminated those that were outside of our focus (e.g. non-urban, not addressing biodiversity) by screening the titles and abstracts. As we were looking for primary research reporting BES relationships, we also excluded literature reviews at this stage. This procedure narrowed the relevant material down to 317 articles (Appendix S2) potentially suitable for data extraction (Tab. 1) at full-text review.

Tab. 1: Data extracted on biodiversity-ecosystem service relationships in urban areas from the 317 publications, which were examined at full text after a systematic search of ISI Web of Science.

	Predictor	**Parameters**
Data extracted from all 317 publications	The biodiversity-metrics used	See Tab. 2
	The UES metrics used	See Tab. 3
	Evidence of BES relationships	(i) empirically tested; (ii) only assumed (i.e., only mentioned or suggested)
	Basis of the BES relationship	(i) purely conceptual (e.g., based on theories and concepts only); (ii) tested based on correlative analyses (e.g., simple or multiple regressions); (iii) tested based on cause-effect models (e.g., structural equation models or mechanistic models)
	Statistical significance of BES relationship	(i) significant (positive, negative); (ii) unclear; (iii) non-significant
Data extracted from publications with empirically tested BES-relationships	Research design	(i) controlled/manipulative experiment; (ii) observation experiment
	Type of biodiversity metric delivering UES	(i) taxonomic; (ii) functional
	Taxonomic biodiversity metrics delivering UES	(i) single species; (ii) species diversity; (iii) species composition; (iv) others
	Origin of the species delivering UES	(i) native; (ii) non-native; (iii) unknown/undefined
	Type of non-native species	(i) invasive; (ii) non-invasive; (iii) unknown/undefined
	Functional biodiversity metrics delivering UES	(i) functional identity; (ii) functional diversity; (iii) others
	Functional traits delivering UES, if mentioned	Any trait mentioned

We categorised all extracted biodiversity metrics into one of nine classes (Tab. 2), which were either direct or indirect measures of biodiversity. The latter were included as proxies, which are often used for biodiversity, rather than measures of biodiversity *sensu strictu*. Extracted ecosystem services were classified according to TEEB (The Economics of Ecosystems and Biodiversity; TEEB 2010) and Haase et al. (2014) (Tab. 3). In accordance with Gómez-Baggethun et al. (2013), yet contrary to TEEB (2010) and Haase et al. (2014), we did not consider services such as habitat provision for nursery species or maintenance of genetic diversity, to avoid the circularity associated with biodiversity supporting or providing biodiversity.

From the data extracted, we derived information on the evidence, basis, direction and statistical significance of BES relationships (see Tab. 1). The numbers of studies reporting different categories of BES relationship were examined using descriptive statistics in R (R Core Team 2014). A formal meta-analysis could not be conducted because of the lack of suitable quantitative data.

3. Results

The 317 publications mentioned biodiversity and UES metrics a total of 944 times, as many papers explored multiple measures. In 441 (47%) of these 944 mentions, a BES relationship was asserted (Appendix S5), but not empirically tested. Only 228 mentions (24%) involved the BES relationships being tested empirically (e.g. by applying an experimental setting or testing assumptions statistically). Among these, 119 (52%) demonstrated a positive BES relationship and 25 (11%) a negative relationship, one was unimodal. A further 63 (28%) of all tested BES relationships were not found to be statistically significant, and for 20 (9%) the text was unclear and could not be deciphered reliably.

82 (41%) of the 228 tested BES relationships used taxonomic diversity as a biodiversity metric, rather than presence of green (16%), species abundance or biomass (16%), functional identity (12%) and species composition (7%) (Tab. 2). Half of the 228 tested BES relationships examined regulating services (50%) and 38% cultural services (Tab. 3). When looking at the UES categories suggested by Haase et al. (2014), metrics of recreation, health and wellbeing were assessed most often, followed by erosion prevention or maintenance of soil fertility, pollination, aesthetic appreciation or inspiration, local climate regulation or air quality regulation, and carbon sequestration or storage (Tab. 3). Almost half (55 out of 135%) of all possible BES relationships had

only been tested empirically once (Tab. 4); 27 BES combinations have not been tested yet. For those tested several times, results often showed contrasting patterns, with specific BES relationships found to be positive in one study, but negative or not statistically significant in others (Tab. 4; Fig. 3). The most well-tested BES relationships (≥ 10 times) were taxonomic diversity and metrics of recreation, health and wellbeing, taxonomic diversity and pollination, taxonomic diversity and aesthetic appreciation/inspiration, presence of green and metrics of recreation, health and wellbeing, as well as functional identity and metrics of local climate/air quality regulation (Tab. 4; Fig. 3).

Of the 228 tested BES relationships, 222 (97%) were tested by applying a statistical method. However, just six BES relationships (2.6%) were tested using cause-effect models such as structural equation modelling (Appendix S3). Thirty % of the 228 tested BES relationships were tested in an experimental setting with controlled variables (Appendix S3).

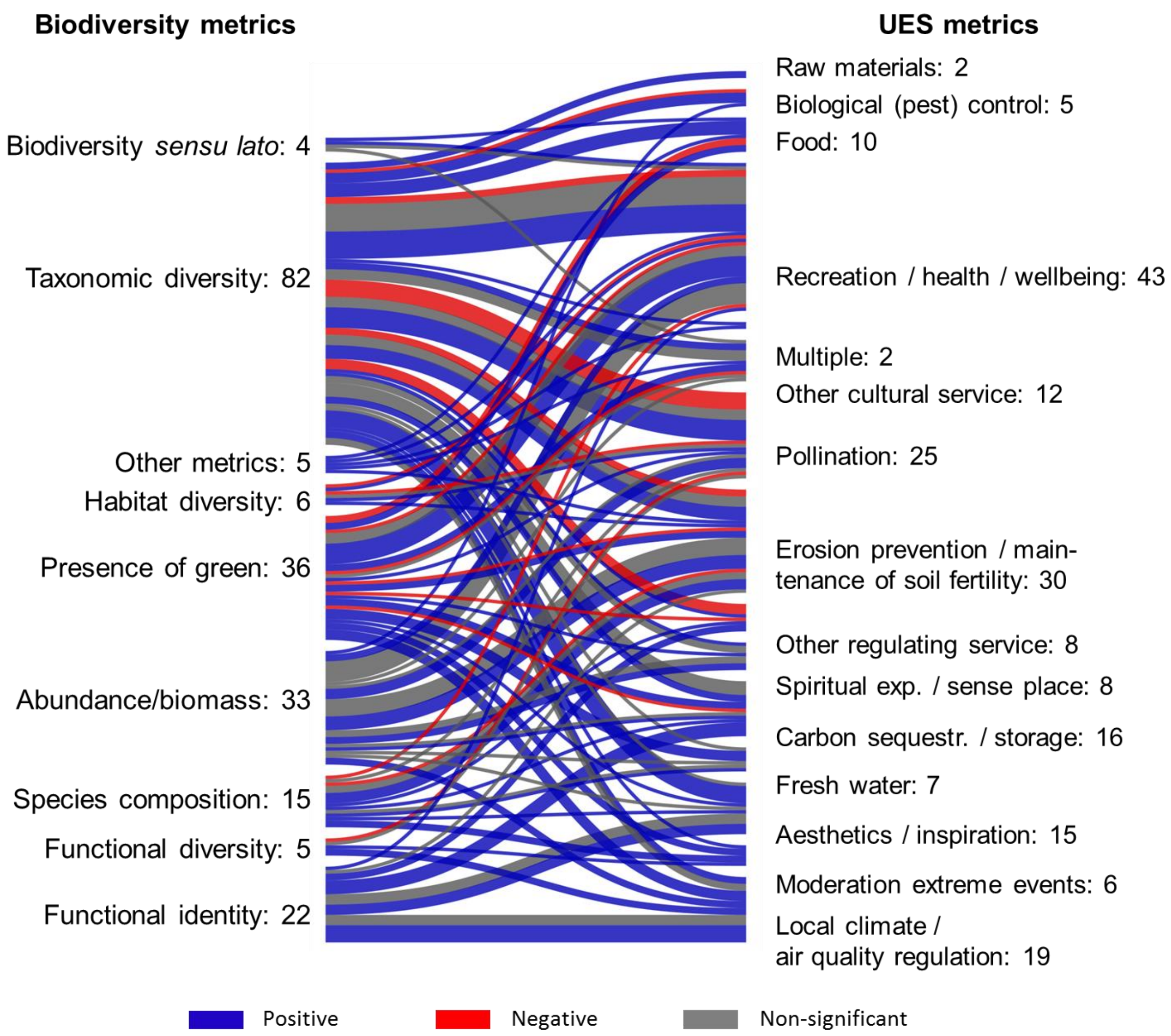

Fig. 3. Number of biodiversity-ecosystem service relationships between biodiversity (left) and urban ecosystem services (right) metrics that have been tested empirically. The width of the lines represents the proportion of tested BES relationships for a specific combination of a biodiversity and an ecosystem service metric. Colours represent the direction of single BES relationships (positive, negative, non-significant) with unclear and unimodal relationships omitted for clarity. The figure was created using SankeyMATIC (http://sankeymatic.com/).

Tab. 2: Biodiversity metrics used in the 317 publications included in our review, plus the number and percentage of empirically tested urban biodiversity-ecosystem service (BES) relationships. The number of studies is smaller than the number of tested BES relationships because papers frequently examined more than one biodiversity metric. 'Type of indicator' states whether a biodiversity metric is a direct or indirect (proxy) measure of biodiversity.

Biodiversity-metrics	**Definition**	**Type of indicator**	**Number of studies**	**Number of tested BES relationships**	**Percentage (%)**
Taxonomic diversity	Any metric of biotic diversity, richness or dissimilarity for any level of organisation (from species to order, and broad taxonomic groups to morpho-species and –types). This included species and taxonomic richness, family density and richness, Simpson, Shannon, evenness, Sorensen, Morisita-Horn, flower and crop diversity and number of broad taxonomic groups (e.g. birds, plants, insects).	direct	35	93	40.8
Biodiversity *sensu lato* (i.e. term 'biodiversity' was used but not further resolved)	Biotic diversity without any further specification.	unclear	2	4	1.8
Functional diversity	Any metric of functional diversity of any level of organisation. This included functional richness, functional evenness, functional divergence and Rao's quadratic entropy.	direct	3	5	2.2
Functional identity	Metrics indicating dominant functional features within communities or species groups. This included community (weighted) mean of trait values (CWM), and abundance or biomass of functional groups (e.g. trophic guilds, vegetation layers).	direct	11	28	12.3
Habitat diversity	Any metric of habitat and landscape diversity, richness and dissimilarity. This included diversity of habitats, land-use and land-cover types or habitat heterogeneity, vegetation structural richness and green space diversity.	direct	5	6	2.6
Species composition	Metrics quantifying the composition or structure of species communities or other levels of organisation. This included proportion of rare and threatened fauna, proportion of native	direct	10	15	96.6

	versus non-native species, proportion of vegetation types or strata.				
Abundance/biomass	Metrics quantifying the number, abundance, biomass or density of any biotic element and level of organisation. This included abundance or biomass of species, species or vegetation density, plant, species or canopy cover, proportion plant cover, number of trees or individuals, species' commonness, Berger-Parker index and presence of plants.	direct	20	36	15.8
Presence of green	Presence of any vegetated habitat, such as urban green spaces, protected areas or agricultural land. This included metrics of habitat quality or habitat potential for biodiversity conservation, and metrics of the geometry and connectivity of vegetated areas.	indirect	13	36	15.8
Other	Not classifiable according to the other categories (e.g. one index combining the percentage of vegetation cover and structure with number of plant genera)	direct/ indirect	4	5	2.2
Total			**68**	**228**	**100**

Tab. 3: Ecosystem service categories and metrics used in the 317 publications included in our review, plus the number and percentage of empirically tested urban biodiversity-ecosystem service (BES) relationships. The number of studies is smaller than the number of tested BES relationships because papers frequently examined more than one biodiversity metric.

Main TEEB-ecosystem service categories[a]	Broad ecosystem service categories[b]	Ecosystem service metrics included in categories	Number of underlying studies	Number of tested BES relationships	Percentage of tested BES relationships (%)
Cultural	Aesthetic appreciation/inspiration	Aesthetic; education potential; green space amenity; opportunity to learn; perception of biodiversity	10	23	10.1
	Spiritual experience/sense of place	Connection to nature; cultural identity; sensation; sense of place; spiritual	2	8	3.5
	Recreation/health/wellbeing	Recreation; human health; mental health; physical health; wellbeing	21	43	18.9
	Other cultural service (not included in Haase et al. 2014 categories)	Cultural; gardening: living standard; social equality; social value	9	13	5.7
Provisioning	Fresh water	Drinking water; groundwater recharge; groundwater yield; water quality improvement; water supply	4	6	2.6
	Food	Agricultural production; food production	6	10	4.4
	Raw materials	Biomass; fibre; forest product; natural resources; net ecosystem production; raw materials	2	2	0.9
	Medicinal resources	Medicinal	0	0	0.0
Regulating	Local climate/air quality regulation	Air ammonia regulation; air filtering; air quality regulation; climate regulation; cooling; gas regulation; microclimate regulation; mitigation nitrous oxide emissions; NH4-N uptake; ozone removal; temperature regulation; reduction of electrical energy used by green walls	12	22	9.6
	Carbon sequestration/storage	Carbon balance; carbon sequestration; carbon storage; CO_2assimilation	9	16	7.0
	Moderation extreme events	Extreme event mitigation; flood control/regulation; hydrological regulation; runoff mitigation; stormwater retention/run-off/capture; water filtration capacity; water flow regulation; water regulation/run-off	6	7	3.1

	Waste water treatment	Biofiltration; groundwater quality improvement; waste water treatment	0	0	0.0
	Erosion prevention/maintenance of soil fertility	Ammonification; consumption of littered food waste/food removal; decomposition; geochemical pathways; erosion control; mineralization; nitrification; nitrogen deposition; nitrogen sequestration; N-mineralisation; nutrient cycling; nutrient storage; soil aeration; soil chemistry; soil CO_2 respiration rate; soil conservation; soil fertility; soil formation; soil infiltration capacity; soil surface stability	15	31	13.6
	Pollination	Pollination; pollinator abundance, pollinator conservation	8	26	11.4
	Biological (pest) control	Disease/pest regulation; pest control	2	5	2.2
	Other regulating service (not fitting the Haase et al. categories)	Disturbance regulation; fencing; noise reduction; seed dispersal; seed set; ecosystem self-maintenance; waste treatment; water management; windbreak	4	8	3.5
Multiple	Multiple	Ecosystem multifunctionality; monetary ESS-values of various land uses; cultural response to various ESS; various ESS	3	8	3.5
Total			**68**	**228**	**100**

[a] Ecosystem service categories according to TEEB framework (TEEB 2010).
[b] Ecosystem service categories according to Haase et al. (2014), but excluding habitat for species, biodiversity and maintenance of genetic diversity as we did not classify biodiversity as ecosystem service.

Tab. 4. Matrix illustrating the research effort that has been invested into empirically testing relationships between specific biodiversity and UES metrics. UES metrics were classified into categories according to TEEB and Haase et al. (2014). The number of BES relationships tested in the papers identified by the review are indicated within cells. Empty cells indicate that the BES relationship is yet to be empirically tested.

Main TEEB-ecosystem service categories	Cultural											Provisioning					Regulating																				Multiple	
Ecosystem service categories by Haase et al. (2014)	Aesthetic appreciation/inspiration			Spiritual experience/sense of place		Recreation/health/wellbeing			Other cultural service			Fresh water		Food		Raw materials	Local climate/air quality regulation			Carbon sequestration/storage			Moderation extreme events		Erosion prevention/maintenance of soil fertility				Pollination				Biological (pest) control		Other regulating services		Multiple	
Biodiversity metrics	non-significant	unclear	positive	non-significant	positive	negative	non-significant	positive	positive	negative	non-significant	non-significant	positive	negative	positive	positive	non-significant	unclear	positive	non-significant	positive	negative	Unimodal	positive	negative	non-significant	unclear	positive	negative	non-significant	unclear	positive	negative	positive	negative	positive	unclear	positive
Biodiversity sensu lato							1	1			1				1																							
Taxonomic diversity	1	5	5	2	1	2	8	8	2		3	1			4	2	2		2	4	2		1	1	2	3		4	5	3		6	1	3	3	1	5	1
Functional diversity																			2					1					1	1								
Habitat diversity						1		1																				1	1	1		1						

Species composition			1			1						1	1								1			2	1	2		3		1						1		
Functional identity	3	2	3					1									3	3	5		4					1	1									2		
Abundance/biomass	1	1		2	2		6	2			1	1							2	1	1					5		4		1	1	3		1			1	
Presence of green			1		1	1	3	6	2	1	1		3	2	2				3		2	1		2	1			2				1			1			
Other biodiversity metrics								2	1						1													1										

4. Discussion

The results from our review show that the urban BES relationships tested to date involve primarily taxonomic biodiversity metrics rather than mean traits or functional diversity (Tab. 2 & 4; Fig. 3). Only eight studies tested both taxonomic (abundance/biomass, species composition or taxonomic diversity) and functional biodiversity metrics (functional diversity or mean trait values). Four of these demonstrated the same urban BES relationships for functional and taxonomic metrics (Briguiche & Zidane 2016; Capotorti et al. 2017; Lundholm et al. 2010; Schmitt-Harsh et al. 2013), while the remaining four found diverging trends (Pieper & Weigmann 2008; Theodorou et al. 2017; Timilsina et al. 2014; Vauramo et al. 2011). None of the studies tested mean traits and functional diversity simultaneously.

4.1. Which functional biodiversity metrics underpin UES?

No specific trait was mentioned for 77% of the tested urban BES relationships. The 33 studies that investigated relationships among traits or their diversity and UES mainly focused on plants and, in particular, leaf traits (Appendix S4). This is noteworthy as plant leaf traits may simultaneously respond to urban environmental conditions (e.g. Knapp et al. 2008; Thompson & McCarthy 2008) and affect UES (e.g. Manes et al. 2012). However, the findings regarding how plant leaf traits are influenced by urbanisation are mixed (Williams et al. 2015) and the direction (positive, negative, none) of urban BES relationships may be specific to the service and species trait analysed (Pataki et al. 2013). For example, tree canopy architecture has been shown to affect water capture of urban green roofs (i.e. mitigation of extreme weather events, Lundholm et al. 2010), but leaf traits (e.g. specific leaf area, thickness) do not predict ecosystem service related traits (such as tree crown size and, thus, shading capacity) (Pataki et al. 2013). Less is known about animal traits (Lavorel 2013), and our review only found two studies that considered their impact on a service (isopod body mass and litter decomposition in one case, and flower visitor generality on pollination in the other) (Pieper &

Weigmann 2008; Theodorou et al. 2017); the decomposition paper showed no relationship, and the pollination paper recorded a negative relationship.

We believe that greater research attention should be given to those traits that are known to be both sensitive to urbanisation processes and important in ecosystem service delivery. Based on the ‘response-effect traits’ framework (Lavorel & Garnier 2002), only those traits that fulfil this double role within and across trophic levels (Lavorel et al. 2013) are crucial for maintaining ecosystem services. Thus far, this framework has only been applied successfully in semi-natural ecosystems (Moretti et al. 2013; Suding et al. 2008). We think that its application in urban ecosystems would be valuable, as it would improve our mechanistic understanding of urban BES relationships. Moreover, since urbanisation can cause species and functional homogenisation (Knop 2016; Aronson et al. 2014; Hahs & McDonnell 2016), studies should investigate the range of reactions across different species contributing to the same urban ecosystem function (Elmqvist et al. 2003). A loss of response diversity may reduce the ability of urban ecosystems to adapt to future environmental change and, therefore, its long-term functionality and resilience (Folke et al. 2004; Hooper et al. 2005). For example, Manes et al. (2012) found that urban tree diversity (modelled by plant leaf type) affects the stability of urban air quality, with different tree functional groups showing complementary ozone uptake patterns, thus removing tropospheric ozone throughout the year.

4.2 Which taxonomic biodiversity metrics underpin UES?

The results from our review show that in 99 (43%) out of the 228 tested BES relationships, certain taxonomic groups delivered UES, such as plants, birds, or insects. For instance, when comparing the importance of burying beetles versus scavenging vertebrates for the decomposition of carcasses in urban forests, Sugiura et al. (2013) found taxonomic diversity sustained decomposition in the face of forest loss. Plant species diversity was also reported to increase soil nitrogen retention capacity in the city of Lahti, Finland (Vauramo et al. 2011). Mixed evidence is provided by Lowenstein et al. (2014) in their study on pollination services in Chicago, USA. They showed that 37 bee species vary largely in pollinator performance, with only five performing exceptionally well. Support for the importance of species identity for UES also comes from Youngsteadt et al. (2015), who demonstrated that species identity, rather than diversity, predicted the extent of refuse consumption by urban arthropods. The relevance of species identity for delivering a given service (Lavorel et al. 2015) can be explained by the keystone species concept, which centres on the fact that some species have a disproportionately large effect on their environment relative to their abundance (Paine 1995). However, services that depend on single species will have a low functional redundancy, as the loss of that particular species will cause further extinctions and the loss of other functions.

The role of non-native species in the delivery of ecosystem services may change in the future because of climate change (Riley et al. 2017). For instance, non-native species may be better adapted to future urban climates and thus more appropriate as street trees (Gillner et al. 2016). Nonetheless, some non-native species may be invasive, with the potential to spread beyond urban areas. Negative effects or 'disservices' (Lyytimäki & Sipilä 2009) of invasive trees, such as the suppression of native flora, might only become apparent decades after planting (Kowarik 1995). Case-by-case studies on the influence of non-native species on UES delivery are therefore needed (Kowarik 2011) to inform the ongoing debate (Sjörman et al 2016).

In our review, 94 of the publications that tested BES relationships considered both native and non-native species, but most of them did not tease apart the effects of two types of species on ecosystem services. From those that did, Swan et al. (2008) showed that leaf litter of *Ailanthus altissima* (Mill.) Swingle, an Asian tree species invasive in Europe and North America, decayed much faster than the leaf litter of native species. Szlavecz et al. (2006) stressed that non-native earthworms have the potential to alter soil nutrient dynamics, but the authors were unable to provide a comparison between native and non-native species because their community only contained invasive European earthworms. Leong et al. (2014) investigated plant-pollinator interactions along an urban-rural gradient, finding that a higher diversity of non-native plants in urban areas decreased pollinator efficiency in the form of seed set. Overall, comparisons of UES delivery by native and non-native species are scarce. As urban areas are hotspots for non-native species occurrence (Kühn et al. 2004), it is important for BES research to focus on both services and disservices of non-native species (Kowarik 2011). By doing so, evidence-based recommendations can be given for the design and management of urban green spaces.

As urban ecosystems are increasingly expected to deliver a range of services, another question that arises is how multifunctionality can be secured. The optimisation of biodiversity and ecosystem services has been considered for non-urban areas (e.g. Bugalho et al. 2016) but less is know for UES. Lundholm (2015) investigated a range of ecosystem services delivered by green roofs and showed that plant diversity enhanced multifunctionality. Furthermore, if single UES are dependent on single species, then maximising such UES may lead to reduced biodiversity. For example, modelling the increase of urban trees in an English city showed that short-rotation coppice comprising only two species (*Eucalyptus gunnii* Hook F. and *Populus tremula* L.) would outperform carbon sequestration by the current urban tree stock by a factor 12 (McHugh et al. 2015). However, the authors caution that while this approach would increase carbon sequestration, it would be unlikely to be acceptable from a biodiversity or aesthetic perspective (McHugh et al. 2015).

Finally, BES relationships need to be examined over long time periods. For instance, the positive effects of species richness on UES have been reported to increase over time on green roofs (Lundholm 2015). Likewise, the age of urban green spaces has been shown to be the most important factor when statistically explaining biodiversity in Swiss cities (Sattler et al. 2011).

4.3 Which methods were used to analyse urban BES relationships?

There is a lack of empirical research that uses statistical models (e.g. structural equation modelling) to test cause-effect relationships between biodiversity and UES. Similarly, there is a paucity of experimental studies with controlled variables, with only 37% of the 228 tested BES relationships were tested in this way. Manipulative experiments in urban ecosystems, in which biodiversity metrics could be modelled and tested, could generate knowledge addressing BES relationships, while improving our mechanistic understanding of community assembly rules, ecosystem functioning and functional resilience.

Biodiversity and cultural UES relationships may often be intangible and indirect, compared to those associated with provisioning and regulating services (Clark et al. 2014, Shanahan et al. 2016). An example of this is provided by Dallimer et al. (2012), who found no consistent relationship between psychological well-being and measured species richness, but a positive relationship between psychological well-being and perceived richness by greenspace visitors. This highlights the importance of understanding human perceptions of urban biodiversity, which is a research field where crucial knowledge gaps remain (Botzat et al. 2016). Carefully designed interdisciplinary studies that account for the wide range of both social and biophysical characteristics that may influence the delivery of cultural services is needed (Pett et al. 2016). By limiting the scope of our review to studies that tested urban BES relationships, we might have excluded papers that looked at the indirect effects of biodiversity that are much harder to quantify. Equally, our study was restricted to peer-reviewed journal papers across all UES, not just cultural ones. This might mean that the data we have analysed are subject to bias because statistically significant relationships, negative or positive, are more likely to be published.

5. Conclusions: ways forward in urban BES research

While there is a growing body of evidence from controlled experiments in non-urban ecosystems demonstrating that biodiversity underpins ecosystem service delivery, comparatively little research on the topic has been conducted in urban areas. Our review has shown that where urban BES relationships have been tested, the studies are restricted principally to examination of a single pair of biodiversity and UES metrics that have been investigated just once. Our findings indicate that the majority of BES relationships are positive, but not every UES is supported by biodiversity and not all biodiversity metrics are related to UES delivery. Indeed, some urban BES relationships are negative. This serves to illustrate the complex mechanistic nature of BES relationships, which should not be oversimplified to the assumption that more biodiversity will result in greater UES delivery. Likewise, managing urban green spaces with the aim of improving UES delivery will not automatically lead to increases in biodiversity, as often presumed by urban GI and NBS advocates.

In order to optimise urban biodiversity and ecosystem services, we call for more quantitative empirical urban BES research to increase our mechanistic understanding of these relationships. This should include: (i) assessment of the importance of different biodiversity metrics for UES delivery; (ii) integration of trait-based approaches in social and ecological BES research, paying particular attention to traits that are known to be both sensitive to urbanisation processes and important in UES (‘response-effect traits’ framework; Lavorel & Garnier 2002; Lavorel et al. 2013); (iii) application of standardised trait measurement methodologies (Perez-Harguindeguy et al. 2013; Moretti et al. 2017) to make different (e.g. urban versus non-urban) environmental contexts comparable; (iv) investigation of how urbanisation can impact upon functional redundancy, response diversity (Elmqvist et al. 2003) and UES delivery in the longer-term; and, (v) broadening the scope of urban BES research to encompass fauna, multi-trophic interactions and a wider spectrum of functional traits.

Supporting Information

The methods used for searching Web of Science for literature (Appendix S1), a list of the 317 references identified as potentially relevant and examined at full text (Appendix S2), and an overview of the methods (Appendix S3) and traits tested for BES relationships in the reviewed publications (Appendix S4) are available online.

Note: The first two authors contributed equally to the publication.

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