The State of the World's Urban Ecosystems: what can we learn from trees, fungi and bees?

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Summary

1. Trees are a foundation for biodiversity in urban ecosystems and therefore must be able to withstand global change and biological challenges over decades and even centuries to prevent urban ecosystems from deteriorating. Tree quality and diversity should be prioritised over simply numbers to optimise resilience to these challenges.

Successful establishment and renewal of trees in cities must also consider belowground (e.g., mycorrhizas) and aboveground (e.g., bees) interactions to ensure urban ecosystem longevity, biodiversity conservation and continued provision of the full range of ecosystem services provided by trees.

2. Positive interactions with nature inspire people to live more sustainable lifestyles that are consistent with stopping biodiversity loss and to participate in conservation actions such as tree-planting and supporting pollinators. Interacting with nature simultaneously provides mental and physical health benefits to people. Since most people live in cities, here we argue that urban ecosystems provide important opportunities for increasing engagement with nature and educating people about biodiversity conservation.
3. While advocacy on biodiversity must communicate in language that is relevant to a diverse audience, over-simplified messaging, may result in unintended negative outcomes. For example, tree planting actions typically focus on numbers rather than diversity while the call to save bees has inspired unsustainable proliferation of urban beekeeping that may damage wild bee conservation through increased competition for limited forage in cities and disease spread.
4. Ultimately multiple ecosystem services must be considered (and measured) to optimise their delivery in urban ecosystems and messaging to promote the value of nature in cities must be made widely available and more clearly defined.

Key words, Urban Ecosystems, City Trees, Mycorrhizas, Nature's Contribution to People, Urban beekeeping, Regulating Ecosystem Services.

Societal Impact statement:

Positive interactions between people and nature inspire behaviours that are in harmony with biodiversity conservation and also afford physical and mental health benefits. Since most people live in towns and cities urban greenspaces are key points of influence for conservation but also provide diverse ecosystem services. City trees are a foundation for biodiversity in urban ecosystems, and their belowground interactions with mycorrhizal fungi and aboveground interactions with pollinators must be central to urban ecosystem planning. Messaging about biodiversity must be clearer to avoid unintended negative outcomes from conservation actions such as low diversity tree planting and unsustainable levels of urban beekeeping.

1.0 Introduction:

Human activity has deleterious impacts for life on earth (IPBES, 2019) yet the welfare of people and nature are mutually dependent so transformative change in human activity is required to stop biodiversity loss (Diaz et al., 2019). Conservation of biodiversity can be achieved through more sustainable behaviours that recognise and respond to the consequences of contemporary lifestyles (Duffy et al., 2017; Watson and Venter, 2017; Allan et al., 2019). One way to do this is to optimise positive interactions with nature as these inspire more sustainable activities with beneficial outcomes for the environment (Alcock et al., 2020). Interactions with nature also improve human mental and physical well-being (Richardson and McEwen, 2018; Lawton et al., 2017; Bratman et al., 2015). Therefore there is much to be gained from enhancing urban ecosystems to change behaviours and inform the public about conservation and their regulating ecosystems services such as cleaner air and water (Smith et al., 2006; Sandström et al., 2006, Somme et al., 2016; Hausmann et al., 2016). Here we focus on urban ecosystems, defined as the built infrastructure, or as those in which people live at high densities (Pickett et al. 2001). In particular we refer to urban areas of vegetation when using the term urban ecosystems such as parks, gardens, railway sidings, allotments and waste ground.

Urban ecosystems can be managed to deliver many services, such as provisioning food, inspiring cultural development, regulating local environment (e.g., clean air) or supporting wildlife (Figure 1a). We have a better understanding of some services than others which is a challenge for optimising their delivery in cities. A global meta-analysis of urban ecosystem service assessments revealed that benefits to air quality, carbon storage, local climate and wildlife were the most frequently evaluated, whilst others were rarely considered (Figure 1b). The spiritual benefits were evaluated in only 2% of cases, biological pest control in 1% of cases and tourism in just 0.2% of cases (Haase et al, 2014). Furthermore, ecosystem services are not independent; there are synergies and trade-offs between services as well as uncertainties in their measurement (Hou et al, 2013). The net effect of some management interventions can be negative if there are unintended declines in other ecosystem services. This disparity and complexity may explain why some ecosystem services are more regularly included in urban ecosystem management plans.

In this paper we argue that greenspaces in cities should be a key focus of attention in improving human-nature interactions, because this is where most people live (Sanderson et al., 2015) and cities have a disproportionate impact on the environment beyond the city limits and at local to global scales (Grimm et al. 2000, 2008; Seto et al. 2012a and b). Ensuring these urban greenspaces endure is in large part dependent on healthy trees and in turn their belowground (e.g., mycorrhizas) and aboveground (e.g., pollinators) interactions. Fungi are overlooked in some assessments of biodiversity decline (e.g., in Diaz et al., 2018; 2019; Field et al., 2020) so here we highlight their essential function for trees and importance for urban ecosystems. Pollinators, on the other hand, have captured the public imagination and their ecological function is well understood by non-experts. Public enthusiasm for saving bees, however, is almost entirely focussed on honey bees with an unsustainable proliferation of urban beekeeping that may actually do more harm to bee conservation than good (Ropars et al., 2019). Furthermore, bee conservation has overlooked the critical contributions of trees through provision of pollen, nectar and nesting sites (Baldock et al., 2015; 2019). Advocacy on biodiversity in urban ecosystems and more widely should seek to communicate in language and methods suitable to a diverse target audience but should avoid over-simplified messaging.

Here we review the role of trees in urban ecosystems to optimise delivery of services, and human well-being. We assess how green spaces in cities support biodiversity and provide opportunities for people to interact with and learn about nature and inspire behavioural changes that reduce or eliminate negative impacts on biodiversity. We highlight the importance of tree diversity in maintenance and renewal of urban ecosystems and the importance of below and above ground interactions identifying a) where more research is needed; b) where additional benefits could be sought; and c) highlight the multiple benefits of urban ecosystems.

2.0 Future challenges of urban trees

2.1 Diversity underpins the ecosystem services provided by trees

Trees provide structure, resilience and sustainability in cities (Morgenroth et al., 2016; Pauleit et al., 2017) and numerous ecosystem services (Figure 1a) which are critical to sustainable urban development and human well-being (Akbari et al., 2001; Costanza et al., 1997; Gill et al., 2007; Grahn and Stigsdötter, 2003; Morgenroth et al., 2016; Tyrväinen et al., 2005; Xiao and McPherson, 2002; Deak Sjöman, 2016). Larger and healthier trees have the capacity to provide more effective ecosystem services (Xiao and McPherson, 2002; Gratani and Varone, 2006; Gómez-Muñoz et al., 2010; Vos et al., 2013) thus, the biotic and abiotic stresses that limit tree growth impact their capacity to deliver them. The use of site adapted trees is therefore crucial, especially in a future global climate where drier and warmer temperatures or heavy rainfall are predicted that will lead to increased tree mortality (Allen et al., 2010; Teskey et al., 2015). Yet, tree species diversity in urban environments typically low (Raupp et al. 2006; Yang et al., 2012; Cowett and Bassuk, 2014; McPherson et al., 2016). For example, in Scandinavia, common lime or linden (*Tilia* x *europaea*) and silver birch (*Betula pendula*) dominate in cities while in Lhasa, China, poplar (*Populus*) and willow (*Salix*) are the most common genera, and cities in USA are dominated by maple (*Acer*) (Sjöman et al., 2019; Cowett and Bassuk, 2014; Yang et al., 2012).

Urban trees are challenged by pests and pathogens potentially causing large-scale losses that will take years to replace and where low species diversity increases risk. These tree loss scenarios intensify concern about biosecurity when shipping plants globally and where a future scenario might promote in-country nursery production to reduce proliferation of pests and diseases. For example, elms (*Ulmus* spp.) were common urban trees in Europe from the late 1960s, until Dutch elm disease (*Ophiostoma novo-ulmi*) decimated the population (Sinclair and Lyon, 2005) and the tree canopy loss is still recovering. Today, the fungus *Ceratocystis platani* is infecting and killing plane trees (*Platanus* spp.) within 3–7 years of infection (Tsopelas et al., 2017). Since London plane (*Platanus* x *hispanica*) is very common in European cities (Saebo et al., 2005) devastating losses of another large urban tree loom with influences on biodiversity, carbon sequestration and other benefits. Asian and citrus long-horned beetles (*Anoplophora glabripennis* (ALB) and *A. chinensis*) have wide host ranges presenting an even greater potential threat (Sjöman et al., 2014). Losses from ALB in nine cities in the USA were estimated at 1.2 billion trees, or $669 billion (Nowak et al., 2001). The most effective mitigation is increased tree diversity, especially with pest and disease resistant species (Hooper et al. 2005; Alvey 2006). Such targeted tree selection can also reduce peaks of allergenic pollen and biogenic volatile organic compounds produced by some trees that have negative impacts on ozone production and can outweigh their value in mitigating pollution (Asam et al., 2015; Willis and Petrokovsky, 2017; Churkina et al., 2015 & 2017). Urban tree inventories in the northern hemisphere are dominated by a handful of species from moist, cool forests making them less suitable for warmer and drier cities (e.g. Raupp et al. 2006; Yang et al., 2012; Cowett and Bassuk, 2014; McPherson et al., 2016, Sjöman & Östberg 2019). Urban trees globally comprise just a handful of genera including *Acer* (maple), *Fraxinus* (ash), *Platanus* (plane), *Ulmus* (elm), *Picea* (pine), *Quercus* (oak), *Gleditsia* (honeylocust) and *Tilia* (lime, basswood or linden) for example (Figure 2). To create resilience towards future global challenges such as changing climates or diseases, higher diversity and tree tolerance for site conditions such as flooding, or drought are critical.

2.2 Which tree will we use in cities in the future?

Long-term sustainable urban tree populations must comprise large, high quality and healthy trees that can withstand shocks and challenges such as pest and disease outbreaks, climate change and tolerance of urban growing conditions, as well as maintaining the capacity to deliver a wide range of ecosystem services. This demands increased diversity of trees with resilience to local climate and growing conditions (Sjöman et al., 2018). Selection of site-adapted species and high genera/species diversity is challenging and may require the inclusion of exotic species. For example, in Scandinavia, urban green infrastructure based on native trees is not feasible due to limited native woody flora, where the majority of the native species are challenged by numerous serious pests and diseases and have limited capacity to grow well in inner-city environments (Sjöman et al., 2015). Regions with a large native species pool exist where climatic or environmental factors permit higher native tree species diversity on urban sites, e.g., Central China (Ying and Boufford, 1998), and Brazil (Freire Moro et al., 2014). Evidence about the use of non-native trees in urban environments – which ecosystem services they deliver, their capacity to grow in future urban environments/scenarios and which species or genotypes pose an invasive threat – are required. Use of less traditional city tree species will become increasingly important, therefore tree collections such as arboreta and botanical gardens will have a central role in the development of this knowledge. The three main challenges for research to creating sustainable urban environments and human health are summarised in Box 1.

2.3 Quality rather than quantity is the priority

Quality is the priority for urban trees, but quantity drives current policy. Shanghai, Los Angeles, New York and Sacramento have established planting goals of 1 to 5 million trees (Young, 2011; Shanghai 1.2 Million Tree Planting Project, 2020) while London has committed to increasing tree canopy cover by 10 per cent by 2050 (Transportxtra, 2020). However, provenance matching to site, pest or pathogen vulnerability and natural pest regulation is critical to ensure development to mature trees and maximize ecosystem service delivery; increasing tree numbers is no guarantee to enhancing the services they provide. Capacity for carbon sequestration or storm water management is dependent on species (e.g. Nowak & Crane, 2002; Xiao and McPherson, 2002) and their mycorrhizal associations (see below) while other species may create disbenefits e.g., from casting cold shade wintertime (Deak Sjöman et al., 2015) which means selection by site and function specificity is paramount.

Furthermore, tree suppliers must have detailed and qualitative knowledge of the plant material in stock considering for example, that tolerance of warmer and drier climate varies among ecotypes within a species – especially for those with large natural distribution where significant variation occurs. Maples (*Acer* spp.), American ash (*Fraxinus americana*) and northern red oak (*Quercus rubra*), for example, differ across environmental gradients relating to habitat type and precipitation (Kubiske and Abrams, 1992; Alder et al., 1996; Bauerle et al., 2003; Marchin et al., 2008; Sjöman et al., 2015; Schuldt et al., 2016) and diversity in these traits are key to ensuring longevity in urban tree planting and replacement schemes.

The ideal trees for resilient urban landscapes require optimal genetic architecture but this may not yet be present in existing collections and cultivars. Plant hunting to date has been driven by botanical interest such as new species or horticultural appeal (Musgrave et al., 1998; Lancaster, 2008; Kilpatrick, 2014). But botanic gardens still have significant influence in the future selection of urban trees (Cavender and Donnelly, 2019). Evidence-based selection of key traits such as drought tolerance are required to build resilience into urban ecosystems and this needs to be integrated with horticultural and botanical interests in future plant-hunting. We need to study and identify the diversity of species and their benefits to humanity under changing climate or land-use change and species eradication (Antonelli et al., 2019).

3.0 Mycorrhizal fungi in the city

3.1 How do mycorrhizal fungi contribute to nature in urban landscapes?

Ninety percent of known terrestrial plant species engage in symbiotic interactions with fungi via their roots (Brundrett & Tedersoo, 2018) forming different mycorrhizas (meaning 'fungus-roots'). Even rootless non-vascular plants can form mycorrhiza-like symbioses (Rimington et al., 2020). Plants invest up to 20% of their carbon to support fungi in exchange for up to 80% of their nitrogen and 100% of their phosphorus requirement (Smith & Read, 2008). Globally, the most abundant mycorrhizas are arbuscular mycorrhizas (AM), ectomycorrhizas (EM), ericoid and orchid mycorrhizas. Non-mycorrhizal plants are typically weedy herbs (e.g., *Brassicaceae*) or habitat specialists (e.g., *Proteaceae*). Arbuscular mycorrhizal plants (e.g., London plane – *Platanus x hispanica*, sycamore – *Acer pseudoplatanus*, holly – *Ilex aquifolium*, grass – Poaceae) and ectomycorrhizal plants (e.g., oak – *Quercus* spp., spruce – *Picea* spp., lime – *Tilia* spp., birch - *Betula* spp., pine – *Pinus* spp, hazel – *Corylus* spp.) are common in urban areas. Mycorrhizal fungi occur naturally in soils, increasing the volume of explored soil and accessing smaller soil pores far beyond where roots and root hairs can reach (Johnson & Gehring, 2007) leading to increased plant biomass, productivity, and defenses against pests and diseases (Gianinazzi et al., 2010; Rewald et al., 2015). Moreover, many mycorrhizal fungi are host generalists and able to interconnect the roots of different plants, creating belowground networks (van der Heijden & Horton, 2009; Simard et al., 2012; Molina & Horton, 2015) that control seedling establishment and regulate nutrient flow and competition (Tedersoo et al., 2020).

3.2 The contribution of mycorrhizal fungi to urban ecosystem services

Fungi play multiple roles in urban landscapes providing a wide range of ecosystem services (reviewed in Newbound et al. 2010). They are food for many organisms (Bertolino et al., 2004; Lilleskov & Bruns, 2005) including humans (provisioning services), they hold educational, inspirational and aesthetic value (cultural services) and are involved in supporting services such as soil formation, primary production, nutrient, water and carbon cycling (Smith & Read 2008). Globally, mycorrhizal fungi drive ecosystem processes (as defined by Potschin-Young and Haines-Young, 2011) such as carbon sequestration, mineral weathering and soil structure and aggregation (van der Heijden et al., 2015; Tedersoo et al., Bahram, 2019) which are negatively impacted by low mycorrhizal diversity (Bakker et al., 2019). Over time, trees sequester much more carbon belowground via their roots than aboveground. They pump carbon to the mycorrhizal fungi which extend into the soil via their filaments. Mycorrhizal fungi therefore act as carbon sinks, representing up to one third of the soil microbial biomass (Leake et al., 2004). Moreover, ectomycorrhizal fungi compete with decomposers for the limited resources in the soil organic matter suppressing decomposition rates and resulting in greater carbon sequestration in soil (Fernandez and Kennedy, 2016). Mycorrhizal fungi are also involved in soil formation, water uptake and transport and nutrient cycling (Johnson & Gehring, 2007; Fernandez & Kennedy, 2016), ecosystem processes that are of particular relevance in urban soils, where fertility, water content and erosion are often key challenges (Bowles et al., 2016). Tree roots and mycorrhizal mycelia increase the soil porosity enhancing water retention and reduce erosion by holding the soil in place. Mycorrhizal fungi influence tree growth and survival and they affect soil aggregation through changes in the root architecture, the production of hydrophobins that enhance adherence to soil surfaces, enmeshing and entangling soil particles and forming aggregates through the oxidation of the soil organic matter (Tagu et al. 2001; Rillig & Mummey, 2006; Smith & Read 2008; Lehman & Rilling 2015). All of these have a decelerating effect on water flows preventing floods.

Richness and composition of both EM and AM fungi are strongly influenced by host and environmental factors including both atmospheric pollution and soil eutrophication (van der Linde et al., 2018; Ceulemans et al., 2019). Urban habitats are unique and often harsh environments for plants, due to disturbance, pollution, drought, radiation, heat and microclimate extremes, but also due to reduced soil mycorrhizal inoculum and colonization. Comparisons across wild, rural and urban habitats reveal dramatic differences, with the lowest diversity of fungi in urban environments (Bills & Stutz, 2009). In fact, lack of mycorrhizal relationships compromises plant establishment and growth in a variety of urban, agricultural and industrial landscapes (Vosátka et al., 2008). Moreover, non-native plants in urban landscapes can harbour non-native fungi that may replace native species, causing imbalances in urban ecosystems (Lothamer et al., 2014; Nuñez & Dickie, 2014).

Urban reforestation typically requires intensive management using chemicals and fertilizers (Newbound et al., 2010; Pataki et al., 2011). As a sustainable alternative to avoid and/or reduce these, the inoculation of soils and plants with mycorrhizal fungi could enhance plant survival, growth, stress tolerance and promote soil restoration (Stabler et al., 2001; Pavao-Zuckerman, 2008; Fini et al., 2011; Szabó et al., 2014; Rewald et al., 2015; John et al., 2016; Chaudhary et al., 2019). Unfortunately, so far, the application of mycorrhizal fungal inoculum has not always led to significant differences in tree growth or establishment (Gilman, 2001; Ferrini & Nicese, 2002). Therefore, the application of mycorrhizal fungi able to support long-term establishment of urban plants, a careful selection of plant species, and appropriate management will be required in the future for the establishment of urban ecosystems (Szabó et al., 2014; Bowles et al., 2016; Chaudhary et al., 2019).

Mycorrhizal fungi therefore provide not only recreational, human health and economic benefits in urban greenspaces, but also environmental benefits by decreasing the need for fertilizers and pesticides and intercepting nutrients, thus reducing nutrient leaching into groundwater and waterways and the risk of eutrophication (van der Heijden et al, 2015; Tedersoo & Bahram, 2019).

4.0 Urban trees and bees

4.1 The value of bees in cities

While trees form mutualistic relationships with mycorrhizas below ground, above ground many tree species depend on animal pollination, including urban trees (Hausmann et al. 2016). Pollinators, in turn, collect pollen or nectar as food. Arguably the most important group of pollinators globally are bees (Potts et al. 2016) with around 20,000 species worldwide (Ascher & Pickering 2020). Most are solitary, ground, or cavity-nesting species. Even though urbanization threatens global biodiversity (Seto et al., 2012a; Hall et al., 2017;

Cardoso & Gonçalves, 2018), many bee species, thrive in cities with significant green spaces (Beninde et al., 2015) with urban centres often harbouring a diverse and abundant bee fauna (Saure, 1996; Matteson et al., 2008; Baldock et al., 2015, 2019; Threlfall et al., 2015; Mazzeo & Torretta, 2015; Geslin et al., 2015). Some cities may even support more bee individuals and species than intensively farmed countryside (Sirohi et al., 2015; Hall et al., 2017; Theodorou et al., 2016; Theodorou et al., 2020; Wenzel et al., 2019).

Bees provide a range of ecosystem services in cities. Beyond the production of apicultural products like honey, bees pollinate a range of crops in cities (e.g., apples, strawberries, tomatoes, beans) that supplement the diets of city dwellers and increase food security (Lowenstein et al., 2015; Lin et al., 2013). Urban landscapes with high bee diversity and abundance may also benefit pollination services in surrounding agricultural landscapes, by acting as refugia and a source of pollinators (Hall et al., 2017; Senapathi et al., 2015). Ensuring healthy urban bee populations may underpin regulating ecosystem services where the plants providing clean air or flood protection depend on pollinators (see discussion in Klein et al., 2018). Bees furthermore have a positive public profile (Sumner et al., 2018) enabling people in cities to connect with nature (Klein et al., 2018).

4.2 To bee-keep or not to bee-keep.

Bee conservation for landowners, stakeholders and mass media is often focused on the western honey bee (*Apis mellifera*) (Smith & Saunders, 2016). While honey bees make a significant contribution to food production, wild bee species are also critical pollinators (Garibaldi et al., 2014) and often more important than honey bees (Garibaldi et al., 2013). So, while there is a willingness to respond to pollinator declines (Potts et al., 2016; Hallmann et al., 2017; Powney et al., 2019; Wagner, 2020), the outcome has often simply been honey bee hive installation in parks, or on city rooftops (Lorenz & Stark 2015, Alton & Ratnieks 2016a, Colla & MacIvor 2018). Many urban beekeepers see these activities as environmentally important and reducing deficits of pollinators (Alton and Ratnieks, 2016a). However, the number of urban hives has increased dramatically in the last two decades, with potential negative outcomes for wild species. In London, for example, the density of honey bee colonies exceeds 10 hives/km² (Alton & Ratnieks, 2016b; with locally more than 30 colonies/km2) -

more than twice the European mean (4.2 hives/km²) and nearly eight times the UK density (1.3 hives/km² - Chauzat et al., 2013).

Besides the potential health risks for humans from higher numbers of bees in cities (e.g., bee venom allergies, Mach & Potter, 2018), our analyses indicate that current bee-hive numbers in London are inadequately supported by available forage in many locations (Figure 3). Alton and Ratnieks (2016b) estimated that 0.83 hectares of lavender are needed for one colony, not taking into account sessional flowering (i.e., a whole season is needed) and that London's green space is not covered in Lavender. We conservatively estimated that x4 the area of lavender would be needed for flowering session (Alton and Ratnieks (2016b) suggest x10) and that less than 1/4 of London's green space was equivalent to lavender. Thus, we estimate that 13.28 hectares (0.13 km^2) of London greenspace is required per colony or 7.5 colonies per km^2. This concurs with the highest densities of feral and domestic honeybee colonies (Ratnieks et al., 1991; Requier et al., 2019). Based on this estimation the map in Figure 3 shows that beekeeping based on current data is unsustainable in most locations in London. This is a serious problem for bee conservation because honey bees can outcompete wild bees by monopolising floral resources (Torné-Noguera et al., 2016; Henry & Rodet, 2018; Herrera, 2020; Ropars et al., 2019, 2020; Geslin et al., 2017; Mallinger et al., 2017). Wild pollinator populations may also be weakened by diseases spilling over from honey bees (Singh et al., 2010; Fürst et al., 2014; Graystock et al., 2016; Alger et al., 2018).

Messaging about "saving bees" should clarify the importance of wild species and beekeeping should be regulated to minimise environmental harm (e.g., see Henry & Rodet, 2020). Urban planning should support bee diversity, and not just promote one highly competitive species (Stevenson, 2019). Practices that support wild bees are easily established: policies need to be implemented that increase floral resources, nesting sites, and reduce chemical pollutants to fulfil the potential of cities as refuges for pollinators. Allotments, urban wastelands and gardens offer nesting and flowering resources and harbour diverse pollinator populations (Lanner et al., 2020; Baldock et al., 2019) while Britain's private gardens provide diverse flora and cover a wider area than all of its national nature reserves put together (Wildlife Trust, 2020), offering prime opportunities to support bees (Baldock et al., 2015; 2019). Trees can play an integral role in this food provision for bees.

4.3 The role of trees in supporting urban bees

Trees provide food and nesting resources for urban bee populations. The high floral density in tree crowns results in trees often producing significantly more nectar and pollen per unit area of land than herbaceous plants (Bentrup et al., 2019; Donkersley, 2019), and trees are especially important food sources when few herbaceous plants are flowering, as in spring and late summer (Koch & Stevenson, 2017; Wood et al., 2018; Sponsler et al., 2020), or the tropical dry season (Aleixo et al., 2014). Pollen and nectar from urban trees also have good nutritional quality for bees (Somme et al., 2016). Sugar-rich honeydew produced by sap-sucking insects on trees is also collected by some bees (Koch et al., 2011; Requier & Leonhardt, 2020). Tree cavities are used as nest sites by social bee colonies, including some honey bees, stingless bees, and bumblebees (Hill and Webster, 1995; Aidar et al., 2013; Bentrup et al., 2019). Many solitary bees, especially in the Megachilidae and Xylocopinae, also nest in dead wood (Potts et al., 2005; Requier & Leonhardt, 2020). Tree resins, leaves and trichomes are additionally important materials for nest construction for some bees (Krombein, 1967; MacIvor, 2016; Requier & Leonhardt, 2020). Shade and cooler microclimates provided by trees can protect bees against heat stress (Bentrup et al., 2019), although excessive shading in urban sites is detrimental for thermophilic species (Matteson & Langellotto, 2010).

Both native and non-native tree species can, in principle, support urban bees well (Mach & Potter, 2018; Wenzel et al., 2020). Importantly, the value of trees for urban bees has to be considered within the context of the regional bee fauna. For example, in the German bee fauna, 137 (32%) of the 428 pollen-collecting (non-parasitic) species are oligolectic (i.e., collect pollen from one family) (Westrich, 2018). However, out of these oligolectic bees, over 90% are restricted to pollen of herbaceous plants, and less than 10% collect pollen of woody plants, mostly from willows (*Salix* spp.) (Westrich, 2018). In this Central European context, urban trees, including non-native species like horse chestnut (*Aesculus hippocastanum*) and black locust (*Robinia pseudoacacia*), can be valuable for generalist bees (Hausmann et al., 2016), but trees alone will not support high bee diversity. Herbaceous plant diversity also needs to be promoted, especially for oligolectic species, for example in urban grasslands (Fischer et al., 2016), wasteland/brownfield sites (Twerd & Banaszak-Cibicka, 2019) and gardens and allotments (Baldock et al., 2019; Baldock, 2020). By contrast, many Australian native bee species, particularly within the Colletidae (the most diverse Australian bee family), are pollen specialists of endemic trees and shrubs in the Myrtaceae and Proteaceae (Houston,

2018) and will only thrive in urban settings if these native woody plants are present (Threlfall et al., 2015), and planting non-native ornamental trees in this scenario mostly favours non-native honey bees (Threlfall et al., 2015). Cities in the Neotropics present yet another case. The dominant bee taxa in the tropics, including honey bees (*Apis* spp.), stingless bees (Meliponini), orchid bees (Euglossini), leafcutter bees (*Megachile* spp.) and carpenter bees (*Xylocopa* spp.), rely heavily on trees both as nesting and food resources (Roubik, 1992, Aleixo et al., 2014; Frankie et al., 2013; López-Uribe et al., 2008; Nemésio et al., 2015), but this bee fauna is dominated by generalist foragers, with a low single digit percentage of oligolectic bees (Michener, 1979; Danforth et al., 2019). A broad range of both native and non-native trees, shrubs and herbaceous plants were accordingly well visited by urban bees in Brazil (Aleixo et al., 2014) and Costa Rica (Frankie et al., 2013), but generally tropical and developing regions remain understudied for urban pollinators (Wenzel et al., 2020).

An abundance of flowering trees throughout the season may offer a good avenue to reduce competition between honey bees and other bee species in cities with problematically high honey bee densities (see 4.2). As flowering trees are highly attractive to honey bees (Hill & Webster, 1995; Donkersley, 2019; Sponsler et al., 2020), their increased availability could reduce honey bee densities on other flowering plants that are essential to more specialized wild bees, facilitating co-existence of beekeepers and wild bee diversity. If honey bee densities could thus be decreased on forage plants of wild bees, this may also reduce disease transmission of viruses on flowers between bees, which is density dependent (Koch et al., 2017; Bailes et al., 2020).

Regrettably, the benefits provided by different tree species for bees are often not considered when assessing ecosystem services of urban trees (e.g., see Willis & Petrokofsky, 2017). Databases used by urban planners either lack any data on tree-pollinator interactions (see database “i-Tree Eco” (USDA Forest Service, 2016, https://www.itreetools.org/tools/i-tree-eco), or only list whether or not a tree species is a honey plant for honey bees, not assessing benefits to other pollinator species more broadly (see database “Citree” (Vogt et al., 2017)). We stress that more detailed research and dissemination of the value of different urban tree species for bees is needed, so that it can be included in urban planning decisions.

5) Urban ecosystems in the global biodiversity crisis and in education and engagement.

5.1 The benefits of plants in urban ecosystems for water purification, pollution and air quality.

Trees and other plants provide various ecosystem services important to urban landscapes including water purification, flood prevention and improved air quality by disrupting the movement and intercepting, trapping and altering the deposition of pollutants (Ugolini et al., 2013; Fig 1). However, wind helps to disperse urban pollution therefore the wrong tree in the wrong place could impede this process leading to higher local pollution levels. Plants also reduce urban temperatures via transpiration and shading (Gilner et al., 2015). Since the volatilization of many pollutants is influenced by temperature (e.g. organic pollutants), the cooling effect of trees may reduce the negative impacts of Biogenic Volatile Organic Compounds (Willis and Petrokofsky, 2019). A lowering of temperatures on hot days in cities reduces the need to cool buildings, giving additional economic and environmental benefits (McPherson and Simpson, 2003). The inclusion of greenspace in cities also encourages more physical activity (Braubach et al., 2017) which could lead to reduced use of polluting vehicles and lower levels of pollutants.

Roadside verges are sites of run off from nitrogenous or heavy metal pollutants, but trees and other plants can assimilate them and reduce impacts (Zhu et al., 2001). Nitrogen is an important pollutant of stormwater in urban areas causing eutrophication and algal blooms but plant-based biofiltration systems can intercept nitrogen before it pollutes waterways (Hatt et al., 2008). Additionally, in urban environments, levels of nutrient inputs (fertilizers on lawn) can be excessive (Sharma et al., 1996), it is important that plants in urban ecosystems are managed carefully to avoid or reduce pollution (e.g., excess fertiliser inputs).

5.2 Capitalising on cultural value of trees, fungi and bees to engage the urban public

Plants and fungi have underpinned the material culture of humanity providing food, shelter, tools, and medicine, but also serving aesthetic and symbolic values and satisfying secular and also spiritual needs (Yotapakdee et al., 2019; Balick & Cox, 1997; RBG Kew, 2016; Schultes, Hofmann, & Rätsch, 1992). Urban forests can contribute to the creation of a local identity, enhance sense of place, increase aesthetic appreciation, inspire artistic expression, foster tourism, and mitigate stress (FAO, 2018; Diaz et al., 2018; Rathmann et al., 2020). For the public, urban forests can positively impact mood and psychological well-being (FAO, 2018; Diaz et al., 2018; Rathmann et al., 2020; Hobhouse, 2004), and forest bathing (Shinrin Yoku) has been reported to afford medical health benefits (Li et al., 2010) while urban trees as oxygen and shade suppliers are also widely appreciated (Camacho-Cervantes et al., 2014). However, tree retention and planting is not universally welcomed in urban areas by all stakeholders who often relate it to safety issues (i.e. accidents, infrastructure damage), health issues (i.e. allergies), economic and mobility issues and possible inadequate long-term management (Camacho-Cervantes et al., 2014; Carmichael & McDonough, 2018; Lyytimäki et al., 2008). Similarly, fungi (especially macrofungi) and bees are not universally welcomed by humans (Boa, 2004; Gerdes et al., 2009).

Urbanization and loss of natural habitats have resulted in less human interaction with nature. Nevertheless, wild products continue to be consumed, and present an important opportunity to engage with and appreciate biodiversity (Poe et al., 2013; Reyes-García et al., 2015). Different public needs are placed on cities' urban trees in different regions of the world, for example in the USA there are movements to make urban forests serve as agroecological landscapes where people can gather, and practice food (including livestock) production (McLain et al., 2012). Wild food foraging is increasingly popular and while there are purported negative consequences for diversity in urban settings, the evidence suggests this is limited (Egli et al., 2006).

Contemporary interest in wild goods is growing and provides an opportunity to engage urban citizens in nature. Bioblitz and other citizen science activities in urban settings are an excellent way to increase the knowledge of trees, fungi and bees among members of the public. These recording activities also provide useful information on fungal and bee distributions (Baker et al., 2014; Falk et al., 2019; Newbound et al., 2010) and tree conditions (Johnson et al., 2018) in urban areas.

Opportunities to interact with nature across seasons and at all times of the day and a range of human-nature relationships must be encouraged (Barnes et al., 2019; Fabjanski and Brymer, 2017; Richardson and McEwan, 2018). Exercising outdoors and in sight of nature has additional benefits for our relationship with the natural world and reducing anxiety (Lawton et al., 2017; Wooller et al. 2016; Hyvönen et al., 2018; and Niedermeier et al., 2017; Bratman, et al., 2015). Even virtual reality interactions can have a positive impact for those with limited access to nature (Nguyen and Brymer, 2018; Calogiuri et al., 2018).

The challenge for urban and peri-urban ecosystems today is to maintain the multiple services benefits and needs of different people from recreation to foraging and even therapy (Li, 2010; Stara et al., 2015; Takayama et al., 2014; Ulrich et al., 1991). Such interactions could help to raise public awareness about nature and to rethink and change behaviours about how we value nature and biodiversity (Alcock et al., 2020; Diaz et al., 2018). Urban trees, fungi and bees are an untapped educational resource for raising public awareness of the importance of biodiversity for ecosystem service provision in both urban and rural habitats.

6.0 Conclusions and recommendations

Urban ecosystems offer opportunities for positive public engagement with nature and provide a platform to optimize human-nature interactions as the health of both are inextricably linked (Diaz et al., 2019). Daily interactions with nature are important and cities must provide greenspace close to homes and work, so that they are encountered easily and frequently. The trees and other plants, on which these urban ecosystems depend, must be selected carefully and considerately, alongside their mutualists including mycorrhizal fungi and invertebrates, to maximise resilience to current and future constraints. People can be informed about the value of diverse fungal communities and their threats in urban ecosystems and a targeted management including this functionally important group could be developed. Intraspecific tree diversity should also be prioritised especially where urban settings present more challenging conditions such as a warmer and periodically drier climate.

While we highlight the importance of good messaging which doesn’t over simplify the challenges or solutions, a stronger focus on management issues is required in future assessments of ecosystems in urban settings looking at how challenges are being addressed and why, but also how approaches differ around the world with a focus on their successes and failures to draw lessons and improve ecosystem management. In particular, ecosystem service assessments must measure as many ecosystem services as possible over multiple timeframes and at different scales so that we can understand the impacts of urban ecosystems and of management interventions on the full spectrum of the services provided. Consideration of uncertainties, synergies and trade-offs is essential in ecosystem management plans to optimise the delivery of ecosystem services and to avoid unwanted negative impacts on non-target ecosystem services.

Habitats that support a diversity of wildlife that is accessible and supplemented with information that fosters understanding and significance for human well-being must be established. Variation across species groups, both native and non-native, can create a bond between people and natural places, enhancing their appreciation of nature (Schebella et al., 2020). This includes honey bees, a key species for engaging the public with nature and ecosystem concepts, but as with all manipulation of nature this needs to be done with care for the consequences. Messaging needs to be clear and we must share the complexity of biodiversity rather than allowing a single issue to dominate. Saving bees is laudable, but if this leads to excessive interest in apiculture in cities and honey bees outcompete wild bee species, rather than saving bees we may be depleting bee diversity (Geldman and González-Varo, 2018). Similar oversimplified public messages could lead to over enthusiasm for tree planting without considering which species and where.

We must provide environments that in themselves are compelling and encourage time spent in nature. Exercising outdoors and in sight of nature has additional benefits of the relationship with the natural world and reducing anxiety (Lawton et al., 2017; Wooller et al. 2016; Hyvönen et al., 2018; and Niedermeier et al., 2017). Even virtual reality interactions can have a positive impact for those with limited access to nature (Nguyen and Brymer, 2018; Calogiuri et al., 2018).

Ultimately the future well-being of the natural world and humanity demands a commitment and an authentic desire to refocus political and practical efforts on effective human nature relationships. With more than half of the world's population living in towns or cities, urban settings are arguably where the majority of influence can be made. Only through this approach with effective engagement of people and nature will efforts to stop biodiversity loss and reverse declines in species be realized.

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Disclaimer

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Box 1. Challenges for the future in selection of urban trees

The three main challenges for research to creating sustainable urban environments and human health (refs see text):

1. Increase our knowledge about different tree species and suitability of different ecotypes for different urban sites and resilience to future change
2. Increase our knowledge about different species and ecotypes capacity delivering ecosystem services and how to use them in order to get most out of them
3. Develop knowledge from 1 and 2, but towards rare and untraditional tree species that do not face serious threats of pests and diseases

Figure Legends

Figure 1. Trees and fungi in towns and cities provide important ecosystem services and help support biodiversity.

Figure 1a: An illustration of some of the ecosystem services delivered by plants and fungi (represented by mycorrhizal "root" fungi) in urban ecosystems.

Figure 1b:

The proportion of published urban ecosystem service assessments which have evaluated the delivery of the stated service.

Figure 2. Data from OpenTrees (2020) showing the genus of the trees most frequent in cities worldwide. The Open trees dataset includes data from 6,896,687 trees in 67 locations around the world. Of these the 10 most frequent species per location ("Most common") account for over 2.7 million trees, of which eight genera; *Acer* (maple)*, Fraxinus* (ash), *Platanus* (plane), *Ulmus* (elm), *Picea* (pine)*, Quercus* (oak), *Gleditsia* (honeylocust) and *Tilia* (lime, basswood or linden) make up almost 80%.

Figure 3. Forage (greenspace) and honeybee colony distribution in London showing the available greenspace within 1 km grids for each colony. London's greenspace is derived from June 2018 Landsat imagery and the bee colony density from colonies registered on Beebase APHA (2020). Using figures from Alton and Ratnieks (2016b), we estimated 13.28 hectares (0.13 km^2) of London greenspace is required per colony or 7.5 colonies per km^2. This concurs with the highest densities of feral and domestic honeybee colonies (Ratnieks et al., 1991; Requier et al., 2019). Based on this estimation the map uses a divergent palette where white to green is 0.133 km^2 to 1 km^2 of forage per colony (i.e. sustainable to surplus) and purple colours <0.133km^2 where it is not sustainable for the numbers of bee colonies let alone other competing bee species.