Urban forest invertebrates : how they shape and respond to the urban environment

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Abstract

Invertebrates comprise the most diversified animal group on Earth. Due to their long evolutionary history and small size, invertebrates occupy a remarkable range of ecological niches, and play an important role as "ecosystem engineers" by structuring networks of mutualistic and antagonistic ecological interactions in almost all terrestrial ecosystems. Urban forests provide critical ecosystem services to humans, and, as in other systems, invertebrates are central to structuring and maintaining the functioning of urban forests. Identifying the role of invertebrates in urban forests can help elucidate their importance to practitioners and the public, not only to preserve biodiversity in urban environments, but also to make the public aware of their functional importance in maintaining healthy greenspaces. In this review, we examine the multiple functional roles that invertebrates play in urban forests that contribute to ecosystem service provisioning, including pollination, predation, herbivory, seed and microorganism dispersal and organic matter decomposition, but also those that lead to disservices, primarily from a public health perspective, e.g., transmission of invertebrate-borne diseases. We then identify a number of ecological filters that structure urban forest invertebrate communities, such as changes in habitat structure, increased landscape imperviousness, microclimatic changes and pollution. We also discuss the complexity of ways that forest invertebrates respond to urbanisation, including acclimation, local extinction and evolution. Finally, we present management recommendations to support and conserve viable and diverse urban forest invertebrate populations into the future.

Introduction

Terrestrial invertebrates, including insects, mites, spiders, millipedes, centipedes, snails and earthworms amongst many others, comprise the most diversified animal group on Earth, accounting for as much as 80% of all known terrestrial animal species (Zhang 2011). They are characterised by the lack of an internal bone skeleton, instead showing a remarkable breadth in body plans ranging from hard exoskeletons (e.g., insects, particularly beetles) to hydrostatic skeletons (e.g., earthworms). Invertebrates occupy a vast range of ecological niches and microhabitats across terrestrial ecosystems and play an important role in structuring networks of mutualistic and antagonistic ecological interactions in almost all terrestrial ecosystems (Ings et al. 2009), thus contributing to key ecosystem services including pollination, nutrient recycling and pest control (Noriega et al. 2018). For these reasons alone, terrestrial invertebrates have long been recognised as 'the little things that run the world' (Wilson 1987).

Given their role in physically shaping the environment in which they live, and their capacity to change the availability of resources for other species, invertebrates can be considered as "ecosystem engineers" (Jones et al. 1994). While some invertebrates are intentional engineers that directly alter their environment (e.g., ants and termites who create a network of above- and belowground nests), other species are accidental engineers that modify habitat indirectly or as a by-product of their activities (e.g., earthworms that create

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temporary tunnels as they move through the soil and provide additional nutrients in the form of excretions).

Here we focus on the role of invertebrates in shaping urban forests and in providing key ecosystem functions and underlying services. We define urban forests as self-regenerating communities with a tree canopy that exist as remnant patches of formerly contiguous habitat now surrounded by urban areas, as well as communities composed of planted trees, such as those in gardens, parks and along streets (see Alvey 2006). Urban forests in their most complex form are composed of an upper tree canopy, one or more understory layers, a ground-cover layer and soil layers (Jim 2017). They are also one of the dominant types of natural areas in cities − by one estimate, remnant forests account for 68% of parkland area across the most populous cities in the USA (Pregitzer et al. 2021). There is a large amount of variation in the structure and species composition of urban forests, ranging from structurally complex native forest patches to highly simplified systems dominated by a few exotic species (Threlfall et al. 2016). In many contexts, urban forests constitute novel ecosystems (sensu Hobbs et al. 2006), where plants and animals that do not share an evolutionary history now co-exist, including many invasive species. Urban forests provide a plethora of benefits to citizens, including environmental ecosystem services, i.e., the regulation of air, water, soil and climate, the provision of habitat and other goods and services (Roeland et al. 2019) and cultural ecosystem services, including physical, psychological and social health benefits and economic development (Nesbitt et al. 2017). Invertebrates play a critical role in the functioning of urban forests and therefore in providing these benefits to urban inhabitants.

In this review, we describe the many roles invertebrates play in structuring and maintaining the functioning of urban forests and argue for the conservation of urban forests and their invertebrates in the Anthropocene, the current epoch characterised by climate change, urban densification and habitat loss, and the apparent mass loss of invertebrate biomass worldwide (see Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019; Cardoso et al. 2020; Harvey et al. 2020, but see Macgregor et al. 2019; Crossley et al. 2020). The review covers four broad subject areas related to urban forest invertebrates, with the aim of generating a compendium of evidence to be used in the study, planning and management of urban forests. The subject areas are: 1) the diversity and complexity of invertebrate communities in urban forests with a focus on their roles in the provisioning of various ecosystem services and their contributions to people (Díaz et al. 2018); 2) the major ecological filters affecting species assemblages in urban areas; 3) our current understanding of how urban forest invertebrates respond to these filters and the consequences of these responses for ecosystem service provisioning; and 4) how we can incorporate invertebrates into urban design and management to deliver

healthier and more taxonomically and functionally resilient urban forests for the future. This review focuses on evidence in the literature of forest invertebrate community composition and change in human-modified landscapes.

Functional roles of invertebrates in urban forests

Urban forests contain terrestrial and aquatic systems that support invertebrates and their complex and varied life cycle requirements (Wilbur 1980). Our focus is primarily on terrestrial and semi-aquatic invertebrates that occupy the different strata within urban forests, from belowground, to ground level, to understory, sub-canopy and canopy. Terrestrial invertebrates contribute to an array of ecosystem functions (Scudder 2009), which translate into a multitude of services for humans (Prather et al. 2013), but also disservices (Dunn 2010), collectively termed nature's contribution to people (NCP) (Díaz et al. 2018). In this section, we explore the contributions of invertebrates to urban forests and how these forests support invertebrates performing diverse functional roles, recognising that some species may perform different and multiple functions depending on life cycle stage and that their functions in an ecosystem may change over the course of their life. For instance, both holometabolous (complete metamorphosis) and hemimetabolous (partial metamorphosis) insects can experience remarkable ecological niche shifts while transitioning between larval/nymph and adult life stages, e.g., from herbivorous caterpillars to pollinating butterfly and moth adults, or from predacious aquatic nymph to predacious aerial dragonflies.

Pollination

Pollination refers to the exchange of genetic material between plants via reproduction and is a critical process in the ongoing recruitment of new generations for many plant species. Urban forests are a significant habitat resource for pollinators, which primarily include bees (Anthophila), flies (Diptera), and butterflies and moths (Lepidoptera). For example, wild bee communities in remnant forests are stratified vertically in the forest canopy (Urban-Mead et al. 2021) and contain unique species unable to persist in surrounding built-up areas (Harrison et al. 2018; Landsman et al. 2019). Similarly, urban parks that contain patches of remnant forest host more butterfly species, including woodland specialist species, than parks that contain only planted vegetation (e.g., Kitahara and Fujii 1997). However, planted trees (including exotics) can also be important to pollinators (Buchholz and Kowarik 2019), confirmed by the barcoding of pollen sampled from four bee species in five different EU cities (Müller 2021). Additionally, pollinators supported by urban forests provide

pollination services both within these forests and to surrounding urban and rural habitats.

Urban forests provide significant nesting resources for social and solitary wild bees. For instance, social bumblebees will forage in private or community gardens, but queens construct nests in the less-disturbed soils of urban parks and forest edges (McFrederick and LeBuhn 2006). Many cavity-nesting solitary bees nest in logs, snags and stumps, and some, for instance leaf-cutting bees, collect leaves from a variety of trees and shrubs to partition their brood cells in the nest (MacIvor 2016). Many bees, such as species of the genus *Xylocopa*, depend on dead wood for nesting and are potentially limited by these resources in cities, which are found nearly exclusively in remnant urban forests. More generally, many pollinators rely on a variety of urban land covers to complete their complex life cycles, depending on remnant forest for nesting and flower-rich urban greenspaces for foraging. Consequently, ensuring adequate nesting resources in urban forests will improve pollination in nearby urban greenspaces where it is valued (e.g., in residential and community gardens).

In degraded urban forests, many weedy herbaceous species may be present, which often provide foraging resources for generalist pollinators, including non-native honeybees (Threlfall et al. 2015) that might interact with native bees of conservation concern (Colla and MacIvor 2017). However, weeds can have extended flowering periods, or flower at different times than native plants, expanding the foraging season for many groups of pollinators or potentially 'filling the gap' brought about by climate warming if flowering and fruiting phenologies shift and thereby create periods of low resource availability (Sherry et al. 2007). It is therefore important to value and appropriately manage a range of urban forest types, even those perceived as lower quality.

Urban forests also contain many tree and shrub species required by moths and butterflies for oviposition and subsequent offspring development, and the structure of the forest resource in the landscape is important for these taxa. Hardy and Dennis (1999) showed that the proportion of forest in the urban matrix was positively correlated with butterfly diversity. Similarly, Kurylo et al. (2020) found that butterfly species richness increased with tree cover across the urban matrix, and Lintott et al. (2014) found that moth diversity in urban forests increased in larger, older, and less fragmented patches.

Predation

Predation is the mechanisms through which populations of more abundant species are regulated by complex top-down trophic interactions. Invertebrate predator–prey interactions are ubiquitous on the forest floor (epigaeic stratum), with the main taxa involved including carabid and rove beetles (Carabidae, Staphylinidae), ants (Formicidae) and spiders (Araneae). These predators exert top-down control on the epigaeic and edaphic (soil) invertebrate communities, including members of their own guild (i.e., intra-guild predation), thus contributing an important top-down ecological process (predation) that structures communities (Niemelä 1993; Vidal and Murphy 2018). Invertebrate community structure in urban landscapes is, however, different from that in rural landscapes, with a general trend of predacious groups shifting towards smaller-sized species (see Merckx et al. 2018), species capable of flight (Niemelä and Kotze 2009) and thermophilic species (Piano et al. 2017). These differences are in line with the general processes operating in urban landscapes, including habitat fragmentation and degradation and the urban heat-island effect. Furthermore, for the largely predacious carabid beetle taxon, Kotze et al. (2012) argued that due to a long history of urban forest fragmentation, forest specialist species have all but disappeared from boreal cities, like Helsinki, although some remain in highly specialized habitats in the city, such as bogs (Noreika et al. 2015).

Research on the effects of the apparent decoupling of interactions between different trophic levels in urban forests (see Samways et al. 2010) is needed to evaluate the functional importance of this dominant epigaeic predatory guild. A non-urban example illustrates the complex effects of epigaeic predators on ecosystem processes: Lawrence and Wise (2000) showed that the removal of spiders from the forest floor in a secondary oak-hickory-maple forest in Madison County, Kentucky, USA, resulted in increased densities of springtails (Collembola). Yet, rather than an increase in the rate of litter decomposition due to a greater number of springtails, the authors later reported lower decomposition rates in the absence of spiders due, in part, to the release of mesopredators of other potentially important decomposer groups, such as mites (Acari) or flies (Diptera) (Lawrence and Wise 2004).

Urban pest populations often flourish when resources such as food or habitat are increased or novel community structures result in decreases in competition and/or predation (Robinson 1996). Changes in the climate of urban areas – as well as a lack of natural enemies in the case of exotic species – can facilitate pest outbreaks (Meineke et al. 2013) and associated economic consequences (Kovacs et al. 2010), such as the northward expansion by the emerald ash borer (*Agrilus planipennis*) into Canadian cities and towns (Herms and McCullough 2014) and the hemlock woolly adelgid (*Adelges tsugae*) across the Northeastern USA (Paradis et al. 2008). Arthropod pests such as some species of mosquitoes (Culicidae), cockroaches and termites (Blattodea) and beetles (Coleoptera) require extensive management in cities because they threaten stored products, public health or building structures (Rust 2009). In urban parks and forests,

arthropod pests can damage native vegetation (Ciceoi et al. 2017) through elevated levels of herbivory (Christie and Hochuli 2005), or negatively affect native animals through predation or competition. However, arthropod pests may be subject to top-down control in urban areas, as evidenced by decreased foliage loss in large cities across Europe as a result of elevated bird predation (Kozlov et al. 2017). Increases in urban forest pests are also of concern as they can spread to nearby, more natural landscapes, as was shown for the Asian long-horned beetle, *Anoplophora glabripennis* (Dodds and Orwig 2011).

As indicated above, biological control has the potential to regulate arthropod pests in urban forests, thereby reducing the need for pesticides or other control agents and potentially lowering monetary costs in the long term (Olkowski et al. 1976; Kenis et al. 2017). The success of biological control in urban areas relies on diverse source populations of natural enemies, resource accessibility and the ability of these organisms to permeate through and persist in the urban matrix (Shrewsbury and Leather 2012; Frey et al. 2018). For example, urban vegetation fragments can be an important source for biological control agents such as spiders (Lowe et al. 2018) and parasitoids (Fenoglio et al. 2013), and can increase the diversity of predator communities in nearby urban gardens (Vergnes et al. 2012). Increasing supplementary resources for natural enemies within the urban matrix can also increase biological control services (Ellis et al. 2005; Egerer et al. 2018). However, biological control can be hard to achieve in urban areas as arthropod predator communities are often disrupted, limiting their ability to counter pest populations (Meineke et al. 2014; Gardiner and Harwood 2017).

Herbivory

Herbivory is the process through which the energy plants capture from the sun is transferred to the next level of organisms, and is therefore an essential process for life on Earth. Invertebrate herbivores are a taxonomically diverse and speciose ecological group, dominated by juvenile and adult stages of moths and butterflies (Lepidoptera), beetles (Coleoptera), bugs (Hemiptera), flies (Diptera) and grasshoppers and crickets (Orthoptera). Some are specialist feeders on certain host plants, while others have the capacity to feed on a wide array of hosts (Forister et al. 2019). The sheer diversity and abundance of insect herbivores in urban forests make the interactions between plants and insects a key driver in productivity and nutrient cycling (Hawlena et al. 2012).

Collectively, invertebrate herbivores in urban forests are not a homogenous functional group as they employ an extraordinary array of strategies to consume plant material (Strong et al. 1984). This variation in foraging strategy has equally varied impacts on plants. For example, herbivory

can result in substantial reductions in photosynthetic area, the destruction of reproductive structures such as flowers or seeds and, in some instances, can promote disease if invertebrates themselves are disease vectors (e.g., Dutch Elm Disease, *Ophiostoma ulmi* and *O. novo-ulmi*), or if their herbivory creates entry points for pathogens. In an urban context, herbivory, when out of control (e.g., gypsy moth infestations in Eastern North America [Moeller et al. 1977; Schultz and Baldwin 1982]), defoliates trees and impacts recreation and the overall appreciation of urban forests (see also the "Disservices" section). Therefore, overabundant invertebrate herbivores in urban forests are typically perceived as pests, particularly when the extent of defoliation is severe and the health of the urban forest is compromised (Raupp et al. 2010).

The engineering role of herbivorous insects is most apparent during population outbreaks that threaten the persistence of key plant species, especially when outbreaks interact with other disturbances such as fire (Parker et al. 2006; Halofsky et al. 2020). A range of factors may contribute to elevated levels of herbivorous insects and thus herbivory in urban forests, such as loss of key predators (Hochuli and Threlfall 2018) or parasitoids (Peralta et al. 2011; Nelson and Forbes 2014), changes in landscape structure and configuration (Fenoglio et al. 2012; Rossetti et al. 2017) and microclimate (Meineke et al. 2013; Dale and Frank 2017). Mechanisms driving the population ecology of insect herbivores remain a key frontier in identifying how their impacts in urban forests can be assessed (see "Invertebrate responses to urban environments" section) and managed (see "Managing urban forests for invertebrates" section).

Dispersal of seeds and microorganisms

As plants and microbes are sessile, their main mechanism for movement into new locations is through the dispersal of seeds, spores and other propagules. While some ant species are known for playing an important role in seed dispersal in urban forests (Thompson and Mclachlan 2007), there is emerging evidence that seeds are also dispersed by other insect taxa such as hornets (*Vespa* spp.) (Chen et al. 2017), crickets (Grylloidea) (Suetsugu 2020) and dung beetles (Scarabaeoidea) (Milotić et al. 2019). Indeed, there are many examples where plants have co-evolved with invertebrates to such an extent that plants develop specialised structures that enable dispersal by specific taxa (e.g., the elaiosomes on seeds of *Acacia* spp. that enable dispersal by ants). Yet, such ant-seed dispersal relationships can be disrupted in urban areas, as evidenced by elevated rates of seed dispersal after the restoration of ant communities via urban forest restoration efforts in Sydney, Australia (Lomov et al. 2009). Additionally, invertebrates assist with the movement of fungal spores, bacteria and other microorganisms through

intentional (e.g., transporting fruiting bodies of fungi) or incidental means (e.g., through digestion and excretion or via surface adhesion) (Bray and Wickings 2019). For instance, some beetles act as transport for fungi, moving and injecting significant quantities and diversity of spores into dead wood and thus improving decomposition and accelerating the creation of hollows that provide habitat for other organisms (Seibold et al. 2019). The movement and foraging of invertebrate taxa such as earthworms (Grant 1983; Milcu et al. 2006), ants (Beattie and Culver 1982; Christian and Stanton 2004; Rowles and O'Dowd 2009) and dung beetles (deCastro-Arrazola et al. 2020) not only facilitate seed dispersal (and fungal dispersal, see next section) but may be important mediators of germination success and seedling recruitment by protecting seeds from predation and locating seeds in nutrient-rich microsites. Although seed dispersal in urban areas can be a significant driver of urban plant community composition, this interaction remains poorly understood (Cheptou et al. 2008; Johnson et al. 2018). Supporting urban forest invertebrate communities that provide seed and microorganism dispersal could be critical for the species and genetic diversity of urban organisms.

Organic matter decomposition and soil development

The decomposition of organic matter closes the nutrient cycle loop in urban forests by reducing the accumulation of dead material and returning nutrients back to the soil to become available to plants once again. There are many soil- and litter-dwelling invertebrates who perform these important functions. Macro-detritivores (e.g., earthworms, woodlice and millipedes) break down leaf litter into smaller pieces (comminution) making it accessible to micro-detritivores (e.g., springtails, oribatid mites) and bacteria and fungi (David and Handa 2010; Ossola et al. 2017). Estimates across various biomes and ecosystems (not including urban forests) show that the presence of complex decomposer communities, including macro-detritivores and their predators, can accelerate both carbon and nitrogen loss on average by 11% (Handa et al. 2014). Studies in urban habitats remain scarce and are much needed, but recent studies have confirmed the importance of soil faunal community complexity for litter decomposition in both urban gardens (Tresch et al. 2019a) and urban forests (Meyer et al. 2020).

Some invertebrates burrow into the soil but feed on the forest floor (e.g., anecic earthworms), which allows for the incorporation of organic detritus and nutrients from the surface deep into the soil profile, while promoting soil gas exchange and water infiltration (Ossola et al. 2015a). In fire-prone urban ecosystems, the removal of large quantities of plant litter from forests by detritivorous invertebrates can decrease fuel loads and fire risk for neighbouring

communities (Buckingham et al. 2015). An increase in detritivore species richness significantly enhances the process of decomposition in urban greenspaces and urban forests, as shown in urban gardens in Switzerland (Tresch et al. 2019a, b) and in urban forests in Melbourne, Australia (Ossola et al. 2016), despite the latter being dominated by exotic species from Europe. The dominance of exotic detritivore species, however, is not uncommon and numerous species are now ubiquitous in cities worldwide due to trade and the movement of soil and plant material (Tóth et al. 2020). For example, historic anthropogenic disturbance, over a century old, best explained the intensity of exotic earthworm invasion in a north-eastern North American peri-urban forest (Beauséjour et al. 2014). Exotic detritivorous earthworms in North American forests change plant species composition by favouring non-native plants and reducing the cover of native species (Craven et al. 2017) and by reducing the diversity and density of soil invertebrates (Ferlian et al. 2017).

Decomposing dead wood, including snags/stags (standing dead trees), old roots and fallen branches, is another important forest resource (e.g., Thorn et al. 2020), but not always assessed in urban forest management (Korhonen et al. 2020). Wood decomposition is a long process occurring in different parts of a tree and at different stages of its life, thus providing nursery and refuge resources (i.e., a habitat tree, see Bauerle and Nothdurft 2011) to many taxa and from different trophic levels. For example, dead wood can provide important habitat to springtail (Collembola) communities (Raymond-Leonard et al. 2020). Habitat trees and tree related microhabitats are also particularly important to saproxylic invertebrates, especially jewel beetles (Buprestidae), long-horned beetles (Cerambycidae) and bark beetles (Scolytinae) (Speight 1989; Grove 2002; Kraus et al. 2016) whose larval stage can last up to five years. A specific example is the European stag beetle (*Lucanus cervus*), which often occurs in warm urban deciduous forests (Harvey et al. 2011). Saproxylic beetles are key actors in ecosystem processes such as wood decomposition and nutrient cycling (Dajoz 2000), and their richness, community composition and genetic diversity depend mainly on tree species identity, decay stage, wood size and volume (Schiegg 2000; Brin et al. 2011) and distribution (Horák 2011, 2018), as well as on the connectivity and management regime of old trees and woody debris (Vandekerkhove et al. 2013). Old trees and woody debris are a critical resource for this group of invertebrates, however these elements are often missing from urban forests due to public safety concerns and aesthetical preferences (Hauru et al. 2014; Le Roux et al. 2014), threatening the persistence of these animals and the functions they perform.

Many saproxylic invertebrates feed on nectar and pollen as adults, thus the distribution and configuration of floral feeding resources (meadows, flowering bushes and trees) outside urban forests are complementary (e.g., Colding

2007) to maintain viable populations within urban forests (Matteson and Langellotto 2010). Since saproxylic invertebrates are generally not highly mobile, such floral resources should be in close proximity to decaying wood in urban forests, or should be well connected through green corridors providing feeding resources and resting places (see also the "Pollination" section).

Disservices

While biodiversity and nature offer many benefits to people, they can also give rise to negative interactions or consequences that can be considered "disservices". Some examples include property damage by termites or other wood boring insects (e.g., *Xylocopa*), entomophobia (fear of insects) and major outbreaks of pests, both medical and economic. One of the disservices with the most direct consequences for humans occurs when invertebrates transmit diseases that pose a significant risk to public health (Lyytimäki et al. 2008). Arthropod-borne diseases are of significant concern in urban landscapes (LaDeau et al. 2015), with key groups being mosquitoes (Culicidae) (Lourenço-de-Oliviera et al. 2004; Rochlin et al. 2016; Murdock et al. 2017; Goodman et al. 2018) and ticks (Acari) (Maupin et al. 1991; Stafford and Magnarelli 1993; Frank et al. 1998; Uspensky 2017). The latter rely on vertebrate hosts also being present in forests; therefore, understanding how the interactions between host, tick, and pathogen are affected by characteristics of the urban environment is essential for reducing public health risk (Ostfeld and Keesing 2017). For example, Krystosik et al. (2020) conducted a systematic review and found that solid waste associated with urban landscapes provided a breeding ground for zoonotic disease hosts (often mammals) and invertebrate transmission vectors. Given the potential of public health risks to shape perceptions and management of urban forests, it is vital that risks be assessed and compared against the benefits that these forests provide to nature and humans alike.

Filters acting on urban forest invertebrates

To understand community assembly of urban forest invertebrates and associated ecosystem functions, we must consider how the urban environment acts as an ecological filter of invertebrate traits (Brousseau et al. 2018; Fournier et al. 2020). Filters determining urban pools of species act at different temporal and spatial scales. They include both biophysical and biogeographical constraints, as well as broad-scale human factors such as human-mediated species dispersal at a global scale (Swan et al. 2011; Aronson et al. 2016). Beyond such regional considerations, once a species arrives, they must initially survive the local urban environment to become established. Survival will depend on traits that influence morphology, phenology, physiology and behaviour, enabling individuals to overcome the range of dispersal, abiotic and biotic filters at play in urban landscapes (Brousseau et al. 2018). These include urban landscape configuration, development history and human activity and decision-making, as well as interactions among multiple species (Aronson et al. 2016). For example, invertebrates in urban forests face abiotic filters such as higher temperatures resulting from heat islands (Arnfield 2003; but see Ziter et al. 2019) or pollutants such as noise, light or chemicals (Halfwerk and Slabbekoorn 2015) compared to non-urban forests.

At the bottom strata, soil-dwelling invertebrates in cities are confronted with a soil matrix of diverse origins that may include rubble or other non-native parent material (Pickett et al. 2011). These soils may also exhibit alkaline conditions associated with cement, may be compacted and sealed under impervious surfaces, have contaminants such as salt and heavy metals and be subject to major disruptions such as litter removal (Pickett et al. 2011; Szlavecz et al. 2018). Such soils are associated with changes in the abundance and composition of belowground invertebrate communities (Santorufo et al. 2012) and the composition of aboveground communities (e.g. Do et al. 2014). Altered soil conditions may also lead to invertebrate communities with particular traits that enable survival. For example, in a study of Collembola under urban trees in Italy, species most tolerant to filters such as low organic matter and high heavy metal concentrations were smaller, pigmented, sexually reproducing and had a well-developed jumping apparatus (Santorufo et al. 2014).

Biotic filters may have equally important, if not greater effects on invertebrate communities (see Kraft et al. 2015). The high proportion of non-native plant species in urban areas results in novel resources available to urban forest invertebrates and may influence trophic and non-trophic interactions in these ecosystems (Valentine et al. 2020). For instance, non-native trees as sources of organic matter for invertebrates have the potential to influence the community assembly of collembolans (Raymond-Leonard et al. 2018) and mites (Malloch et al. 2020), and ultimately, litter decomposition rates (Makkonen et al. 2012; but see Finerty et al. 2016).

Cities are thus home to novel community assemblages, including non-native organisms introduced by humans. Indeed, urban areas can be entry points for invasions, for instance for carabid beetles (Spence and Spence 1988) and earthworms (Hendrix et al. 2008). Introduced plants may be intentionally selected for the purposes of urban planning, landscaping or other cultural activities by which they provide ecosystem services or disservices; but plant and invertebrate species may also arrive in cities unintentionally (Padayachee et al. 2017). For example, the harlequin

ladybird (*Harmonia axyridis*) was introduced outside of its native range as a biological control agent, but has now spread to urban areas over several continents (Brown et al. 2011). The following paragraphs explore in further detail how various filters may shape invertebrate communities and their associated ecosystem functions.

Changes in habitat structure and vegetation simplification

Invertebrates inhabiting urban forests can be highly sensitive to changes in habitat structure and composition. For instance, leaf litter and wood detritus are both habitat and trophic resources for detritivores and saproxylic organisms, respectively. As such, the removal of leaf litter and dead wood from urban forests can obliterate communities of these specialised invertebrates (Siitonen 2001; Vandekerkhove et al. 2013; Ossola et al. 2016). In highly frequented forests, soil trampling by humans can cause the reduction of burrows and suitable microhabitats on the forest floor, which negatively affects the cover of understorey forest vegetation (Hamberg et al. 2008). This alters carabid beetle assemblages compared to less trampled areas, yet the responses of individual species may vary, as many forest specialist species have already been lost from urban forests (Kotze et al. 2012). Similarly, when soil becomes compacted or sealed with impervious surfaces, this limits nesting resources for burrowing organisms.

Vegetation structure simplification can lead to a more simplified invertebrate community (Threlfall et al. 2017; Mata et al. 2021). Often, changes in vegetation structure occur as a result of development, management (e.g., mowing), or through invasive species proliferation in city parks (Kühn and Klotz 2006; Cadotte et al. 2017). The latter has been shown to result in a decline in soil micro-invertebrate richness and abundance along an urbanization gradient in Toronto, Canada (Malloch et al. 2020). However, the invasion of urban forests by exotic tree species can accelerate species turnover without decreasing invertebrate richness or abundance (Buchholz et al. 2015). Taxa most affected by the simplification of vegetation structure are phytophagous insects dependent on host plants; for example, butterfly caterpillars feeding on leaves, or bees feeding on pollen and nectar (Bernays and Chapman 1994). Particularly vulnerable are those species that form obligate associations and mutualistic relationships with plants or other invertebrates. For instance, in some urban forests in eastern Australia, the larvae of the imperial hairstreak butterfly (*Jalmenus evagoras*) feed on a limited set of tree species within the genus *Acacia* and form a mutualistic relationship with a few ant species of the genus *Iridomyrmex* that receive nutrient-rich secretions from the larvae in exchange for the protection they provide.

Urban forests often have a history of management that includes the planting of trees that resist urban pollutants and other anthropogenic stressors (Roy et al. 2012). Urban afforestation efforts are typically accompanied by the management of herbaceous, often invasive, plants, including by mowing, herbicide application and physical removal (Oldfield et al. 2013). Management interventions such as these, or their absence, influence the type and number of invertebrates in urban forests, which have both positive and negative impacts on the particular ecosystem services invertebrates provide. For example, some ant and butterfly species that are adapted to sparse and more open forests might be impacted by changes in plant communities that occur through plant succession, shrub encroachment or plant invasion (Ossola et al. 2015b). On the other hand, excessive mowing drastically reduces the number of flowers, reducing invertebrate diversity (Watson et al. 2020), while mown parks and urban grasslands result in lower invertebrate abundance compared to un-mown vegetation (Garbuzov et al. 2015; Norton et al. 2019).

Microclimatic changes

Changes in urban habitat structure can affect microclimatic conditions, and thus invertebrate diversity and ecological processes (Ossola et al. 2016). Microclimates available to urban forest invertebrates are influenced by landscape-level changes (e.g., temperature and windflow; Arnfield 2003) as well as the structure and composition of the forest itself. The interior areas of larger forests are buffered against higher temperatures and drier conditions (and edge effects in general) in the surrounding built-up environment (Chang et al. 2007; Chow et al. 2011) and potentially serve as a refuge for edge-sensitive species. However, edge environments and their associated increases in solar radiation, wind and lower moisture levels are common given the very fragmented nature of urban greenspaces. Habitats close to urban forest edges typically support different communities compared to areas away from edges (Kotze et al. 2012). The extent to which the composition and richness of invertebrate communities change is related to the contrast of the forest edge compared to built infrastructure or non-forest vegetation (Noreika and Kotze 2012; Soga et al. 2013; Davis and Gagné 2018). The interior areas of urban forests are also subject to disturbance, such as trampling, that can lead to dramatic changes in habitat structure and microclimatic conditions similar to those at edges. Notably, forest paths have very different conditions from adjacent vegetation, with trails and roadways leading to more open vegetation cover (Lehvävirta et al. 2006) that create movement corridors (or 'flyways') for some aerial insects (e.g., *Papilio* butterflies; Esaki 1949) and compressed leaf litter and soils (Duffey 1975) that can reduce abundances of carabid beetles adapted to more humid conditions (Lehvävirta et al. 2006; Kotze et al. 2012).

Forest management can also have important effects on microclimate. Many urban tree stands, e.g., along roadsides or in parks with mown lawns, are actively managed to avoid an understory from developing (Jorgensen et al. 2002) leading to very dry and sun-exposed conditions similar to those in grasslands, and subsequent changes in species composition (Norton 2011). Urban forest management can also have the opposite effect. For instance, the suppression of fire in built-up areas (Kareiva et al. 2007) and a reduction in historical coppicing (Rackham 2008) that result in a more closed canopy, change the composition of spider communities where species that are dependent on open vegetation decline in number (Košulič et al. 2016). Additionally, the loss of dead wood, leaf litter and tree hollows in urban forests, particularly those managed for public amenity, reduces microclimates available to invertebrates. These are habitats that provide moist and cooler refuge from higher temperatures (Scheffers et al. 2014) and their loss in urban environments might be detrimental to taxa that depend on these conditions (Sebek et al. 2013).

Pollution

Anthropogenic sensory pollution mainly comes in three forms: acoustic noise, artificial light and chemical substances (Halfwerk and Slabbekoorn 2015), all of which may have varied effects on organisms and communities, including the exclusion of maladapted traits, the alteration of acoustic and visual communication or an increase in fitness through adaptation (Swaddle et al. 2015; Henneken and Jones 2017). The effects of light pollution on invertebrates are the most obvious, ranging from a few insects circling a light in the home, to hundreds stuck in the grille or windshield of an automobile and even thousands or more at street lamps, e.g., during termite nuptial flights. However, while light pollution attracts some insects, it also repels other more photophobic species (see examples in Firebaugh and Haynes 2019). Larger urban forest patches may buffer against the effects of light pollution, but this becomes compromised as fragmentation creates ever smaller forest patches in urban environments (Villarroya-Villalba et al. 2021). Consequently, photophobic invertebrates may become locally extinct, while those attracted to light may disperse to a suboptimal environment where they are exposed to elevated predation, physical harm (automobile collisions) and unfavourable habitat conditions.

Artificial light can also have behavioural effects on invertebrates that use light for communication, like fireflies (Lampyridae). Fireflies inhabit ecologically diverse habitats, from wetlands, grasslands, forests to urban parks, but have lost much of this habitat due to urbanisation (Lewis et al. 2020). Owens et al. (2018) showed that male *Aquatica ficta* fireflies emit brighter signals with decreased frequency when exposed to artificial light at wavelengths below 533 nm, demonstrating light signal plasticity in these fireflies. Firebaugh and Haynes

(2019) showed that fireflies lured to artificial light were less likely to engage in courtship dialogues, arguing that these light-polluted areas act as demographic traps. Recent evidence on moths also suggests that artificial light has the potential to disrupt chemical communication resulting in reduced mating opportunities (van Geffen et al. 2015a). The increasing global presence of artificial light at night is linked to shifts and declines in invertebrate diversity (Knop et al. 2017; Grubisic et al. 2018) and related ecosystem processes (e.g., pollination), which may spill over into diurnal insect communities active during the day (Knop et al. 2017).

Little is known about the effects of anthropogenic noise on invertebrates, and even less so in urban forests. In their review, Morley et al. (2014) identified two studies on invertebrates and noise that found: 1) positive correlations between noise levels and both call frequency and chorusing in the cicada *Cryptotympana takasagona* in urban parks, and 2) a greater low-frequency component in the songs of male grasshoppers (*Chorthippus biguttulus*) from noisy roadsides compared to paired quiet areas. In addition, a study by Davis et al. (2018) showed that monarch butterfly (*Danaus plexippus*) larvae exposed to roadside noise for two hours experienced a significant increase in heart rate, which was interpreted as a stress response. Yet, longer exposure to continuous traffic noise did not elevate heart rates at the end of larval development, suggesting desensitisation. Anthropogenic noise (here compressor noise at a natural gas field in New Mexico, USA) has been shown to decrease the abundances of various arthropod taxa collected with pitfall traps (velvet ants and wolf spiders), while some taxa showed no effect and leafhoppers increased (Bunkley et al. 2017).

Chemical disturbances in urban landscapes arise from both indirect sources (e.g., microplastics and heavy metals) and deliberate applications (e.g., pesticides). The effects of active ingredients in some pesticides (e.g., neonicotinoids) have been well documented (Chagnon et al. 2015; van der Sluijs et al. 2015) and led to their ban in areas such as the European Union. In an urban forest context, chemical contamination is likely to be present either as a legacy from past land-uses (e.g., asbestos or heavy metals), current practices (e.g., the direct spraying of or unintentional drift from pesticides, as well as industrial and vehicular emissions), or from novel sources such as microplastics and nanoparticles. While the effects of these first two sources on invertebrates have been relatively well studied (Eggleton 2020), the impacts of novel sources of chemical pollution (e.g., per- and polyfluoroalkyl substances, PFAS) are still largely unknown. Yet regardless of the source, the overwhelming picture is that the presence of chemical contaminants has played a major role in contributing to the massive declines in insect abundance and diversity over the past 20 years (Forister et al. 2019), and even in interfering with the cognitive ability, i.e., learning and memory of honeybees that may have significant

consequences for the vital ecosystem service of pollination (Leonard et al. 2019).

Invertebrate responses to urban environments

In the following section, we look at some of the consequences of the filters discussed above for urban forest invertebrates.

Persistence vs. local extinction

Habitat destruction, reduction, fragmentation and transformation act synergistically with urbanisation-derived threats (New 2009; Kotze et al. 2011), such as the heat island and wind tunnel effects and light, noise and chemical pollution (New 2015). Indeed, many studies have shown the negative relationship between urbanisation and invertebrate species richness (McKinney 2008; Faeth et al. 2011; Mata et al. 2014; Fenoglio et al. 2020; Piano et al. 2020) and trait composition change (Merckx et al. 2018; Fournier et al. 2020). While these studies explored response patterns at the community level, recent studies are increasingly highlighting that the response of invertebrates to urbanisation processes and filters are species- and trait-specific – that is, some species and trait values tend to be absent in extreme environmental conditions, whereas others are present across a wider environmental gradient (Magura et al. 2013; Mata et al. 2014, 2017; Threlfall et al. 2017). Species-specific mechanisms driving the responses of invertebrates to urban filters are poorly understood. Specialist species interact with a narrow subset of mutualistic and prey species, and may be acutely susceptible to local extinctions (Dunn 2005; Kotze et al. 2011). For example, specialist insect herbivores, such as the weevil *Cydmaea dorsalis*, the leafhopper *Pogonella bispinus*, the lacebug *Radinacantha tasmanica* and the plant louse *Acizzia keithi* that depend on specific plant species are unlikely to persist if one or more urban filters result in the local extirpation of their host plant (Moir et al. 2011).

Adaptation and rapid evolution

The urban filters discussed above have the capacity to drive evolutionary as well as phenotypic change in urban-dwelling populations (Johnson and Munshi-South 2017; Alberti 2015; Alberti et al. 2017a, b; Hopkins et al. 2018). To date, the majority of studies assessing adaptation to urban environments are vertebrate and plant focussed (e.g., Kark et al. 2007; McDonnell and Hahs 2015), with little research on invertebrates in urban forests. However, increasing evidence indicates that invertebrates may show comparable biological responses along an urban–rural cline (Altermatt and Ebert 2016; Kotze et al. 2011; Eggenberger et al. 2019). For instance, arthropods in urban environments exhibit increased intraspecific variation in morphology (Weller and Ganzhorn 2004; Magura et al. 2006; Lowe et al. 2014; Eggenberger et al. 2019), key life history traits (Miyashita 1990; Lowe et al. 2016) and behaviour (Kralj-Fišer and Schneider 2012) compared to their rural counterparts. In addition, chemical analyses reveal the presence of human food in the diet of urban ants (Penick et al. 2015).

More recently, the focus has been on exploring the impact of specific anthropogenic stressors on physiological tolerance and behaviour within urban environments, but findings linked to urban forests are scarce. Such studies reveal an increased tolerance for heat in urban ants (Angilletta et al. 2007; Diamond et al. 2018) and carabid beetles (Piano et al. 2017), and higher frequencies in the courtship signals of grasshoppers inhabiting roadside verges (Lampe et al. 2012). Light at night disrupts physiological processes and biological timing (Hopkins et al. 2018), as well as ecosystem functions, such as pollination, carried out by nocturnal and diurnal communities (Knop et al. 2017). Experimental laboratory studies reveal dramatic ecological variation in invertebrates linked directly to the presence of light at night (Durrant et al. 2018; Willmott et al. 2018; van Geffen et al. 2015a, b; van Geffen et al. 2014). The impact of light at night is species-specific and the observed patterns may not reveal the true nature of the ecological trade-offs faced. For example, in spiders, the presence of artificial light at night may disrupt biological timing, affecting growth and development under a resource-controlled laboratory environment (Willmott et al. 2018), but this may be offset by increased nocturnal prey capture rates, as measured in natural environments (Lowe et al. 2014, 2016; Willmott et al. 2019).

Although there are examples of invertebrates that have undergone contemporary evolution to adapt to human activity, there are few documented examples of invertebrate evolution being a direct effect of landscape change (Johnson and Munshi-South 2017). Van't Hof et al. (2016) demonstrated that industrial pollution accumulating on urban trees in nineteenth century Britain led to greater predation on light-coloured peppered moths (*Biston betularia*), and so populations underwent mutation for greater melanism. In another study, Jha (2015) showed that gene flow in a bumblebee species (*Bombus vosnesenskii*) was inhibited by impervious surfaces that replaced natural areas. Reduced flight-to-light behaviour of individuals of the small ermine moth (*Yponomeuta cagnagella*) from urban (artificial light at night) compared to rural (natural light at night) regions suggests adaptation (Altermatt and Ebert 2016). However, there is limited understanding of how fragmentation via the alteration or removal of urban forests and other greenspaces restricts gene flow and genetic variability in invertebrate species, and whether affected populations are more susceptible to future urbanisation and global change (Santangelo et al. 2018). Novel habitats generated as a result of urbanisation may also increase gene flow for some ubiquitous

urban species and pests (Miles et al. 2018), including those that exploit and further damage urban forests. In general, more work is needed to understand how landscape changes in urban areas impact the evolution of urban invertebrates (Miles et al. 2019), both to mitigate evolutionary resistance in pests and foster gene flow within native species populations.

Acknowledging the complexity of responses

There are some general patterns and trends in the responses of urban forest invertebrates to increasing urbanisation that are consistently observed across the diversity of taxa and species. However, there is also an equally diverse array of complex responses that are highly influenced by local context and the specific components of a particular system (see Fournier et al. 2020). For example, at the local scale, insectivorous birds, as well as invertebrate predators, parasites and pathogenic fungi, play an important top-down role in regulating insect numbers in urban tree canopies. Within remnant forests in Sydney, Australia, where small insectivorous birds have been lost from the urban environment, herbivorous insects have been released from predation resulting in higher levels of herbivory (Hochuli et al. 2004). In contrast, recent work from multiple cities in Eastern Europe has found that insectivorous birds are more likely to move into cities, resulting in declines in the density of insects and reduced levels of herbivory (Kozlov et al. 2017). As such, in some cities, urban forests in highly urbanised settings may show enhanced defoliation, whereas in others the impacts of herbivorous insects are diminished through antagonistic trophic interactions. However, changes in bottom-up interactions may be equally at play. Around the world, urban forests are overwhelmingly dominated by very few species (Paquette et al. 2021). Such a simplification of leaf litter traits may lead to a simplification of associated invertebrate consumers. Recent studies in natural forests or plantations have shown a consistent covariation of leaf litter traits and detritivore feeding traits ranging from mesofauna such as springtails (Raymond-Leonard et al. 2019) to detritivorous macrofauna such as millipedes and isopods (Brousseau et al. 2019).

The diversity of invertebrates themselves, and their complex life cycles that include reliance on multiple terrestrial and aquatic habitat types, also mean that it is challenging to identify a common framework that applies across all cities and contexts, and as such, idiosyncratic responses to urbanisation are likely to be common.

Managing urban forests for invertebrates

Based on what we have learned from the responses of invertebrates to the urban environment in general, here we make a series of recommendations aimed at maintaining and enhancing invertebrates in urban forests. We believe that the evidence of impacts in urban environments, even if not specific to forests, is sufficient to formulate measures to mitigate the impacts described above. We recommend that the protection and promotion of urban forest invertebrate diversity be a two-pronged approach that seeks to 1) enhance resources for invertebrates, whilst 2) reducing exposure to urban threats (Fig. 1).

Enhancing resources for invertebrates requires actions such as:

- *Maintaining leaf litter cover and dead and decaying wood* to promote a speciose detritivore and saproxylic community (Siitonen 2001; Ossola et al. 2016). Dead wood is a limiting resource in urban environments (Harper et al. 2005; Sebek et al. 2013; Le Roux et al. 2014; Korhonen et al. 2020) but an important refuge from, for instance, increased temperatures (Scheffers et al. 2014). These resources can be reintroduced by actively adding piles of dead wood of different species, sizes and decay stages (Gaston et al. 2005) and in certain configurations to show intent (the 'cues to care' concept by Nassauer 1995; Li and Nassauer 2020) together with information posts to explain the benefits of dead wood, changing management to support natural regeneration of dead wood features (Sebek et al. 2013), or introducing artificial structures that mimic these features (Goldingay and Stevens 2009). However, it should be noted that the latter strategy is limited in its benefit as it does not provide feeding resources for target taxa.

- *Maintain areas of exposed soils* and soils that have not been overly compacted or otherwise altered by human activities to provide habitat for invertebrates with a soil-dwelling (e.g., earthworms, ants or beetles) or soil-nesting (e.g., some bees and wasps) life stage. Additionally, limiting the sealing and compaction of soils by reducing human use to a small number of trails or areas will benefit ground beetles, ground-nesting bees, and other epigeic and endogeic groups (Cane et al. 2006; Lehvävirta et al. 2006; Galli et al. 2015).

- *Protect, restore and create water bodies*, including natural and human-made permanent or semi-permanent standing or running sources of water, for invertebrates with aquatic life stages. These species can be further supported through the presence of vegetation and natural surfaces (e.g., sand or mud) and minimal macro, micro and chemical pollutants (Forister et al. 2019).

- *Promote indigenous plant species* (Mata et al. 2021), and undertake management practices that support them, to ensure that food resources are provided in a form that is accessible to co-evolved native invertebrates. For example, open cup flowers are an essential resource if we wish to support short-tongued native bee species in south-
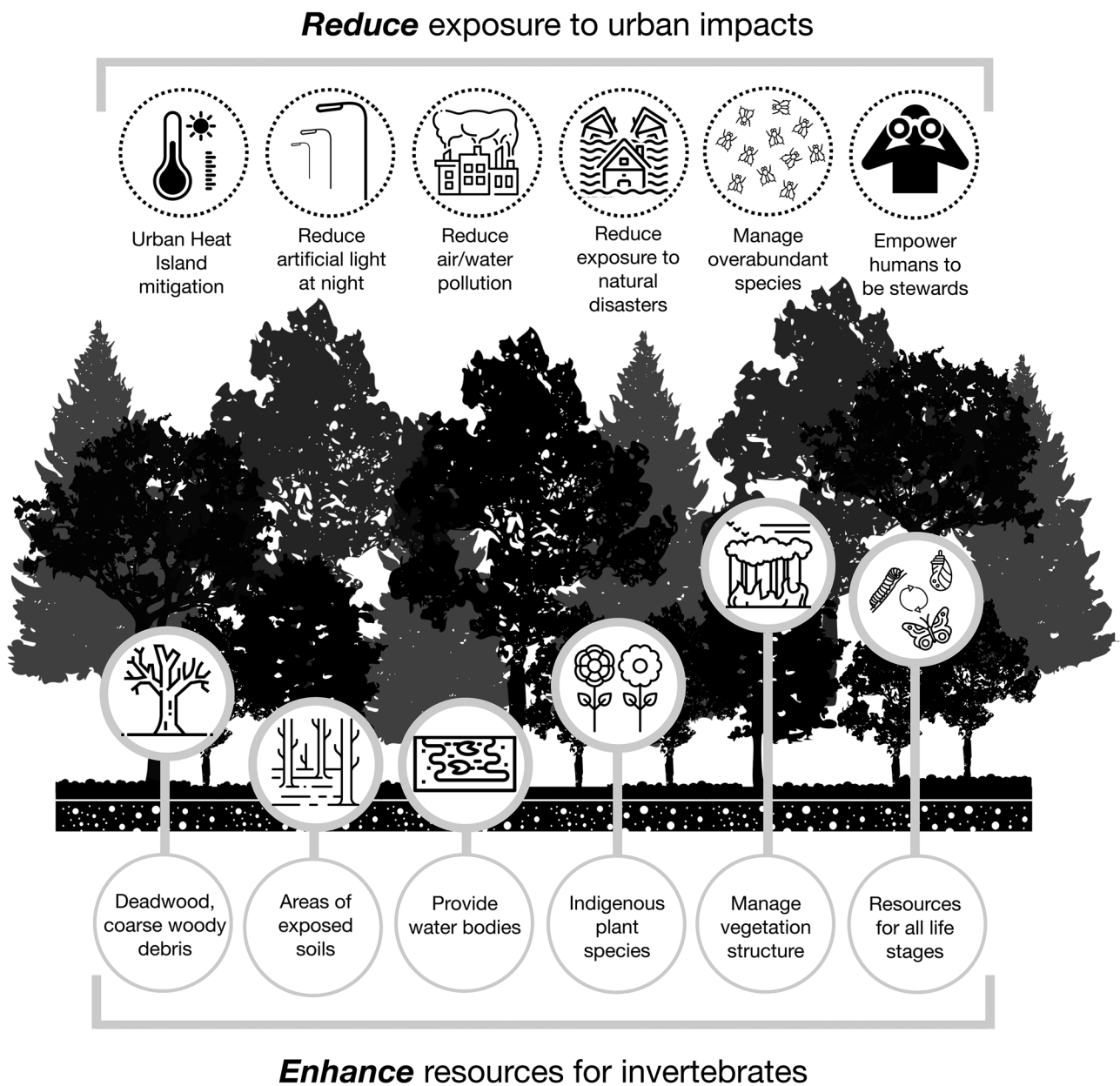
Reduce exposure to urban impacts

Fig. 1 Actions to promote the presence and diversity of invertebrates in urban forests. Invertebrate communities are enhanced by maintaining or increasing habitat complexity through the addition of dead and decaying wood, providing areas of exposed soil and clean water bodies, promoting native and indigenous plant species across all strata of the forest and ensuring resources for all life stages. At the same time, actions that reduce deleterious effects of the city include mitigating the urban heat island effect, reducing light, air, water and soil pollution, and managing overabundant, often pest, species. By involving the public in these actions, people are empowered to be stewards of urban forests and the invertebrates they contain

eastern Australia's urban forests (Threlfall et al. 2015), while the maintenance or establishment of a native forest understory layer will benefit the detritivore community, as well as provide habitat and resources for bees, beetles, and wasps among others (Ossola et al. 2016; Threlfall et al. 2017; Mata et al. 2021). Note that we are not advocating for the exclusion of exotic, ornamental plant species, which also provide important resources for many

urban forest invertebrates, but do promote native plant species that are important for co-evolved invertebrate-plant relationships.

- *Provide resources for all life stages* to support a complex assemblage of invertebrates (see Hauck and Weisser 2015) that require a diversity of habitat types (e.g., dragonflies depend on aquatic and terrestrial habitats to complete their life cycle and aerial moths develop from soil-dwelling

larvae) and food sources (e.g., herbivorous caterpillars or xylophagous beetle larvae become nectar-feeding butterflies and beetles, respectively). It is also important to consider that threats and degrading processes may change as organisms proceed through their life cycle, and to manage habitat accordingly. Furthermore, the length of different life stages should be considered when managing dead wood — saproxylic beetles such as the European stag beetle (*Lucanus cervus*) spend up to five years in decaying roots.

- *Maintain or increase vegetation structural complexity* to provide a wide range of food, shelter and other resources that support the invertebrates that feed directly on plant leaves, nectar, flowers, seeds and fruits, and the predatory invertebrates that feed on them. For public managers, the benefits of increasing vegetation structural complexity in urban forests may be public preference for the resulting naturalistic character this creates (Heyman 2012; Harris et al. 2018), although this may not be a universal phenomenon. Public support for increasing the complexity of an urban forest may be enhanced by co-management programmes that engage with stakeholders to collaboratively achieve common management goals (Tsuchiya et al. 2013), as illustrated by the co-management approach to woodlands in the neighbourhood of Sletten, Denmark (Fors et al. 2018).

While the previous recommendations highlight the positive actions than can enhance urban forests for invertebrates, the following mitigation actions will additionally benefit them by reducing the impact of broader threats and disturbances (Fig. 1). These actions include:

- *Reduce chemical pollutants* by reducing inputs at the source, and by prioritising non-chemical control of pests (e.g., biological control (Kenis et al. 2017)) through Integrated Pest Management.
- *Reduce the urban heat island* effect *and detrimental disturbances* through landscape-scale planning, site-scale design, and appropriate management practices. For example, large greenspaces provide cooling benefits and offer a refuge where invertebrates can reduce their exposure to the urban heat island effect (Ziter et al. 2019). Site and landscape design can also provide local refuges where invertebrates can shelter during disturbances, as can management practices such as creating mosaics of different age stands.
- *Reduce light pollution* by: (i) maintaining unlit areas; (ii) reducing the duration of lighting; (iii) minimising the 'trespass' of light through improved design; (iv) changing the intensity of lighting; (v) adjusting the spectral composition of lighting (Gaston et al. 2012); and (vi) use new technology and lighting systems (Goddard et al. 2021). While night lighting is an important amenity for people, including for their perceived safety, there is also strong evidence that the associated loss of darkness interrupts natural circadian rhythms with negative consequences for human physical and mental health (Cho et al. 2015).

- *Reduce exposure to natural disasters* such as catastrophic bushfires or destructive flooding by distributing areas of urban forest across the landscape, and providing areas where invertebrates can retreat to safety (or repopulate landscapes) such as upland areas in floodplains, or reducing the risk of catastrophic fire through cultural burning and Indigenous land management practices (McKemey et al. 2019).
- *Manage overabundant invasive species and pests* to help prevent completely disrupting urban forest ecosystems by altering invertebrate, vertebrate and plant communities and ecological processes, as has happened with extremely successful invaders, such as Argentine and yellow crazy ants (*Linepithema humile*, *Anoplolepis gracilipes*) (Silverman and Brightwell 2008). As urban areas are also often primary sites for biological invasions, monitoring invertebrates can complement biosecurity efforts and allow a more rapid response to emerging pests (Hendrix et al. 2008). Supporting diverse invertebrate communities can help reduce the incidence and rate of invasions by providing a broader range of potential natural enemies (Jones and Leather 2012; Gaudon and Smith 2020).
- *Empower humans to become stewards* of ecosystems, through actions such as engaging citizens and other urban stakeholders in the sustainable management of pest species (Lowe et al. 2019) and the conservation of wild, forested land in cities. Creative ways to engage and empower people to uphold conservation could include public demonstrations, art installations, guided walks, or education programmes. This, in turn, will help reduce the growing disconnect between people and nature, and generate stronger support for the other actions outlined in this section.

Research gaps and future research

While we know quite a lot about invertebrates in urban environments, several gaps still remain in our knowledge of these organisms in urban forests. To effectively manage and conserve diverse communities of urban forest invertebrates, we need to build a stronger understanding of how they survive, persist and respond to densifying urban landscapes. For a broader perspective on a research agenda for urban biodiversity, see Knapp et al. (2021).

Some of the important questions for future research on invertebrates in urban forests, but also in urban environments in general, include:

i. At what rate are forest invertebrate numbers, biomass and species declining and how strong is the evidence for a sliding baseline of invertebrate numbers based

on the experiences of the people who are doing the assessments? This requires long-term research on population sizes, biomass and species richness in multiple cities and biogeographic areas (Hallmann et al. 2017; Macgregor et al. 2019; Sánchez-Bayo and Wyckhuys 2019), and an understanding of the pitfalls in these long-term studies (Didham et al. 2020).

ii. What are the implications of current and future actions on forest invertebrates and the ability of urban areas to support them under climate extremes (e.g., intensified storm events, droughts and heatwaves) and intentional, e.g., the planting of street trees, and unintentional changes in vegetation (Ossola et al. 2020)?

iii. How do forest invertebrates respond to different types of disturbance events (e.g., catastrophic wildfires versus Indigenous cultural burning practices) and what are the underlying mechanisms behind these responses (Erenler et al. 2020; Filazzola et al. 2021)?

iv. What are the metapopulation and metacommunity structures and dynamics present in urban forest invertebrate communities? What can highly fragmented, isolated and dynamic patches of forests in cities reveal with respect to theories on species and community occupancy (Turrini and Knop 2015)?

v. What are the effects of city history and historical landscapes (legacy effects) on contemporary invertebrate communities (e.g., Lindborg and Eriksson 2004; du Toit et al. 2016 for plants; Ossola et al. 2021)? Furthermore, how do invertebrate communities change over time in different urban spatial contexts and are priority effects, i.e., the impacts on a community based on the order or timing of species arrival (Fukami 2015), important in this process?

vi. What are the pre-existing adaptations that enable invertebrates to persist in cities now and in the future, and what are the eco-evolutionary responses that are emerging in invertebrates in response to current and future urban filters and pressures (Alberti 2015)? What are the potential consequences of these changes on future urban forest invertebrate assemblages and their ability to deliver critical ecosystem services?

vii. To what extent do cities act as a conservation refuge for endangered and vulnerable species that might struggle to survive in human-dominated peri-urban landscapes, such as those affected by intensive agriculture, forest logging, or desertification (Hall et al. 2017)?

Conclusion

Invertebrates play a key role in supporting healthy urban environments for people, as reflected in their diverse and varied contributions to the functioning of urban forest ecosystems.

While many environmental filters are similar in the urban milieu across the globe, individual responses to these filters are highly variable, reflecting the diversity and complexity of invertebrate ecology and life cycles. Given the current concern of an acute loss of invertebrate biomass, abundance and diversity, the conservation of forests in urban environments, and the invertebrates that support key ecosystem processes and underlying services, is even more critical. Delivering healthier and more resilient urban systems into the future requires urgent action to enhance the role of invertebrates as ecosystem engineers of urban forests. This can be achieved by actively promoting access to essential urban forest resources for a broad variety of organisms, combined with management actions to reduce the negative impacts of urban environments, such as habitat loss and air, noise and light pollution. Our success in safeguarding ecosystem functions and processes in the face of an ever-densifying human population truly does rely on 'the little things that run the world'.

Declarations

Ethics approval NA.

Consent to participate NA.

Consent for publication The authors give concent to publish this work in Urban Ecosystems.

Conflicts of interest/Competing interests The authors declare that they have no conflict of interest.

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