npj | urban sustainability

Review article

Published in partnership with RMIT University

https://doi.org/10.1038/s42949-024-00163-y

Engineering blue-green infrastructure for and with biodiversity in cities

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Blue-green infrastructure (BGI), combining semi-natural and engineered elements, offers multifaceted benefits like stormwater management, water purification, heat mitigation, and habitat provision. However, current BGI designs prioritize engineering goals, overlooking its ecological potential. Here we advocate for integrating engineering and ecological objectives into BGI design to enhance performance and biodiversity. Through an interdisciplinary literature review, we emphasize the importance of species diversity, abundance, and ecological processes, to improve engineering performance and resilience, and lower management costs. We emphasize the importance of interdisciplinary collaboration to navigate trade-offs between engineering and ecological objectives, ultimately enabling us to engineer both *for* and *with* biodiversity.

In response to challenges associated with urbanization, such as heat, pollution, and an altered water balance, cities are increasingly implementing a network of semi-natural to engineered elements that can help to restore natural cycles, such as vegetated basins, green roofs, and stormwater ponds. These elements, often called "sustainable urban drainage systems" or "green stormwater infrastructure,"[1,2] have typically been designed to manage stormwater quantity and quality[3]. Yet more recently, design considerations are expanding to include heat mitigation[4], and nomenclature is evolving to "Blue-Green Infrastructure" (BGI)[5], whose definition encompasses a wider scope of functions and elements, such as wetlands, parks, or urban forests[4]. This broader perspective aligns with a growing consensus that BGI should be considered as multifunctional infrastructure that performs multiple ecological, social, and economic functions[6].

Unfortunately, however, the ecological aspects of BGI – the fact that these are interconnected systems composed of living organisms – tend to be overlooked by the engineering community. This is regrettable, as there is evidence that biodiversity provides various ecosystem services (e.g., food provision, pest control[7]) and can enhance the performance and resilience of these engineered systems. For instance, increasing the number of plant species in a given BGI (e.g., rain garden or wetland) can allow for more heterogeneous root structures, which can increase water absorption[8] and improve water quality[9].

Drawing on ecological theories to inform engineering practice is an emerging discipline, referred to as ecological engineering[10], that has successful applications in fields such as flood protection[11] and landslide prevention[12]. With respect to BGI, ecological engineering is typically applied to understand how biodiversity contributes to engineering objectives, including stormwater management[13] and water purification[14]. However, many ecological theories that could be valuable for engineering objectives remain underexplored or restricted to certain BGI elements (e.g., green roofs).

While ecological engineering studies typically explore what nature can do for humans, they often overlook the reciprocal relationship between BGI and biodiversity. As it has been made clear by the urban ecology communitiy[15]—BGI can play a major role in mitigating the biodiversity crisis, in particular in cities[16]. Global biodiversity is declining at a dramatic rate due to numerous threats (e.g., land-use change, climate change, resource exploitation, and invasive species spread[17,18]) and international organizations are calling on cities to contribute to its conservation and restoration[19]. Although urbanization is a main driver of biodiversity loss, urban areas can also provide valuable habitat for species, including those of conservation importance[20]. Cities often overlap with endangered ecosystems and biodiversity hotspots[21], and are sometimes the last remnant of habitat for species[22]. Furthermore, the total area of the built environment also surpasses that of conservation areas in many countries[23], emphasizing the imperative for biodiversity conservation in cities. Engineered BGI systems, even when designed for other purposes (e.g., stormwater ponds[24]), can enhance biodiversity by directly supporting species' needs (e.g., habitat, food, breeding grounds). However, trade-offs are also expected when BGI design cannot accommodate both ecological and engineering goals (e.g., pollutants collected by BGI can accumulate within the food chain[25] or leaf litter necessary for some species can clog drainage pipes and increase flood risk)[26].

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Here we advocate for a much-needed shift towards a holistic perspective on the interconnectedness of ecology and engineering for BGI, not only to account for trade-offs, but also to design more effective and resilient BGI. We must more thoroughly examine the bidirectionality of BGI and biodiversity: how BGI performance is affected by biodiversity, and in turn, how engineered infrastructure such as BGI impacts biodiversity. The objective of this study is to present the value and approach to incorporating principles of ecological engineering into BGI design. We draw on a wide range of literature to substantiate our call to action and to guide the interested reader who wishes to explore specific topics in more depth. We first identify facets of urban biodiversity that pertain to BGI design and illustrate how these aspects can improve stormwater management, water purification, and heat mitigation performance of BGI, while bolstering resilience and reducing maintenance costs – engineering *with* biodiversity. To properly harness these facets, we identify how BGI can be used to conserve and restore biodiversity – engineering *for* biodiversity. Lastly, we discuss potential trade-offs that may arise when the needs of people and of biodiversity are simultaneously addressed.

Synthesis of literature

To substantiate our call for engineering BGI both *for* and *with* biodiversity, we synthesize in the following the rapidly accumulating body of literature on the benefits of ecological engineering. Recognizing the strong linkages between aquatic and terrestrial ecosystems and their influence on biodiversity and system properties[27], we place our focus on terrestrial (e.g., green roofs, rain gardens, urban parks) and freshwater (e.g., detention and retention stormwater ponds, constructed wetlands, urban streams) BGI (hereafter “terrestrial BGI” and “freshwater BGI”, respectively), excluding marine environments. Here, we specifically examine the contributions of deliberately selected and spontaneously occurring plants and animals, excluding microbial diversity (e.g., bacteria, fungi, protists). Given the considerable variability in both BGI and biodiversity, results presented in this study do not promise guaranteed impact but rather represent a compilation of well-established guidelines of best practice. Although most of the research discussed in this study was conducted in urban settings, findings presented in the following sections are also expected to be relevant beyond conventional city boundaries and thus applicable to the broader, built environment.

Findings presented here stem from three Scopus searches conducted in August 2023, investigating the impact of biodiversity on BGI stormwater management, water quality, and heat mitigation. Importantly, our study does not constitute a meta-analysis or systematic review but rather presents a targeted review of both ecological and engineering literature. The three searches sought papers published as of August 24th 2023 (date of the search) that cross-referenced BGI elements (e.g., "green roof*" OR "rain garden*"), biodiversity terms (e.g., biodiversity OR richness), and one of three engineering performance criteria (e.g., stormwater), resilience (e.g., “drought response”), or maintenance costs (e.g., “upkeep expens*”) in their title or indexed keywords. Supplementary Table 1 presents the complete queries, including synonyms for each term. We screened the titles and abstracts of retrieved papers, excluding those not investigating the relationship between species diversity, abundance, ecological processes, and one of the three engineering objectives, infrastructure resilience, or maintenance costs. Only studies related to plants and animals were included, excluding those related to microbial biodiversity (e.g., bacteria, fungi, protists), which are difficult to control for in BGI design but merit a dedicated review. Only research papers written in English were considered, and reviews, opinion papers, and non-academic literature were excluded.

Our Scopus search, which was intended to capture studies at the intersection between engineering and ecology, exclusively identified articles referencing a combination of keywords from both disciplines in the title or indexed keywords, to capture the multifunctionality of BGI. These keywords, selected to capture BGI multifunctionality[28], corresponded to the following three categories: (1) BGI (e.g., “rain garden*”), (2) biodiversity (e.g., “vegetation type”), and (3) engineering performance criteria (e.g., “urban drainage”), resilience (e.g., “drought surviv*”), or maintenance costs (e.g., “manage* cost*”). If the article did not have a combination of keywords in all three areas, the article would not be found in the search. To address this limitation, we further examined the references of selected papers to identify any omitted studies. In total, we reviewed 26 studies on biodiversity and stormwater management, 50 on water purification, 34 on heat mitigation, 26 on infrastructure resilience, and eight on maintenance costs (see Supplementary Table 2).

Engineering with biodiversity

Biodiversity plays a pivotal, often unrecognized, and underexploited role in ensuring that BGI are effective[9,29–32], resilient[33–35], and low-maintenance[36,37]. While some of these facets have been explored only for individual BGI elements[38,39], this section highlights the current scientific evidence across BGI elements. Here we present the facets of biodiversity (see Box 1) that affect BGI performance with regards to stormwater management, water quality and heat mitigation (*Performance* subsection), resilience (*Resilience* subsection), as well as maintenance costs (*Maintenance costs* subsection).

Performance

Although the literature on biodiversity and BGI performance is often restricted to green roofs or wetlands and typically centered around selected plants, it is evident that facets of biodiversity (i.e., diversity, abundance, and ecological processes) can considerably affect the stormwater management[8,30,40], water purification[9,41], and heat mitigation[29,30,42] of BGI. Enhancing species richness and diversity is expected to increase functional diversity, thereby expanding the range of traits that favor water capture and evapotranspiration and thus engineering performance, such as leaf area, stomatal conductance, and root morphology[43,44]. As the number of functionally distinct species increases, complementarity in resource use becomes more likely[30]. Consequently, functionally rich assemblages tend to exhibit higher stormwater retention[30,45], water purification[9,14], and heat mitigation rates[32,46] than assemblages of lower functional diversity (Fig. 2). For instance, diverse tree assemblages are superior at mitigating heat in urban parks[29], while biodiverse rain gardens feature higher stormwater retention rates than their species-poor counterparts[40].

Importantly, increasing species richness is more likely to enhance BGI engineering performance when accompanied by increases in functional and structural diversity[30,42]. Thus, ensuring functional diversity of species traits is more important than sheer species richness, as the variation and multiplicity of traits will likely enhance the provision of multiple engineering objectives[46,47]. For instance, the cooling potential of green roofs is usually greater in functionally diverse assemblages than those of low functional diversity[32].

Unfortunately, assessments of the functional diversity of BGI elements, whether through trait measurement[48] or phylogenetic (i.e., evolutionary history) analysis[46], remain uncommon and should be integrated into future research initiatives[49]. Although the introduction of multiple and possibly less efficient species may, in some cases, decrease the performance of a single engineering objective (e.g., stormwater management), functionally diverse BGI tend to perform better when multiple functions (e.g., including heat mitigation) are considered[30,46] (Fig. 1B). Similarly, while monoculture wetlands may exhibit a higher removal rate of a single pollutant, they tend to be outperformed by biodiverse assemblages when faced with a cocktail of pollutants[9].

In addition to species diversity, much like in natural ecosystems[50] (Fig. 1C), increasing the abundance of plant species has been shown to increase water retention and to lower runoff in BGI[40,45], as vegetation coverage and biomass also play a direct role in water capture and retention[45,51]. High abundance of plants, especially with those with high leaf area and transpiration rates[52], also improves evapotranspiration rates and thus heat mitigation[53]. Increasing plant cover and biomass on green roofs is therefore expected to maximize the provision of various ecosystem services, including enhanced cooling and increased water capture rates[32] (Fig. 2). Plant abundance also improves pollutant removal efficiency[54], but excessive levels of

Box 1 | Facets of biodiversity

Biodiversity can be described in various ways, from the number and abundance of species (taxonomic diversity) to variations in the genetic composition within species (genetic diversity). While ecologists have done considerable work to characterize these facets of biodiversity, the diversity of definitions can also cause confusion, notably on how to conserve biodiversity. Here we present three major facets of biodiversity known to affect the functioning of their ecosystems[74]: the diversity of organisms (Diversity subsection), their abundances (Abundance subsection), and the ecological processes that support key services and shape ecosystem resilience (Ecological processes and resilience subsection).

Diversity

One of the core metrics to describe biodiversity is the number of units (classically species, but can also refer to genetic or habitat diversity), defined as **richness** (e.g., species richness). Diversity can also be used to describe the multitude of morphological and physiological features – called **traits –** in which organisms differ, such as variations in appearance, anatomy, bodily functions (e.g., body size, wing span). Traits affect how species survive, grow, reproduce and interact within and across environments. The more these features differ within a community of species in a given environment, the higher the **functional diversity** of that community[135].

Abundance

The number of individual organisms of a certain species is quantified as **abundance**, while their total weight is the **biomass**. Functional diversity and species abundances are key drivers of the **functioning of ecosystems** (i.e., biotic and abiotic processes in an ecosystem)[74]. A subset of these processes contribute to human well-being and are thus called ecosystem services[136] or nature's contributions to people[7]. On the one hand, functional diversity dictates the effects of a given species or group of species on the ecosystem[135]. On the other hand, the relative and absolute abundance of species and their respective traits play a major role in specific processes (e.g., nutrient cycling[50]). Figure 1A, B, C illustrates how species diversity, functional diversity and species abundance can affect ecosystem functioning, especially after a disturbance (e.g., drought or pest invasion).

Ecological processes and resilience

Ecological processes encompass many phenomena such as **natural succession**, which refers to the temporally dynamics of assemblages of species in an unmanaged ecosystem, or **species interactions**, which pertains to the numerous ways that co-occurring species interact, including predation and competition (negative interaction), as well as facilitation and pollination (positive interaction). These ecological processes shape the **resilience** of an ecosystem[137,138], hereafter defined as the ability of an ecosystem to recover key ecosystem functions after a disturbance[139]. The resilience of an ecosystem is defined by two concepts: **functional redundancy** and **response diversity**[140]. Functional redundancy represents the similar way that different species affect an ecosystem due to the resemblance of their traits. Since multiple species perform similar functions, high functional redundancy can increase the resilience of an ecosystem, but only if these functionally redundant species exhibit high response diversity[140], which is the property of multiple species to respond differently to a given environmental stressor[141]. The importance of both properties to ecosystem resilience is depicted in Fig. 1D and E.

vegetation can also have adverse effects. For instance, evidence suggests that constructed wetlands may experience a decrease in water purification potential if vegetation exceeds a certain maximum threshold[55]. Moderate vegetation cover, complemented with open areas, may therefore result in better water quality in freshwater BGI[55]. Likewise, intermediate vegetation density on green roofs can grant greater resource (i.e., water) accessibility, thereby mitigating drought risks, while providing similar stormwater retention rates as densely vegetated roofs[56].

Finally, ecological processes, such as species interactions and natural succession, should be harnessed rather than controlled through excessive management practices. Although more research is required to determine how species interactions and food web complexity translates to engineering objectives, studies indicate that interactions between vegetation and soil biodiversity can improve water quality[57], nutrient processing[58] and water infiltration[59]. Moreover, recent evidence suggests that interacting animals (e.g., earthworms, fish) can enhance water quality through direct absorption of pollutants or plant consumption[60], underscoring the benefits brought by faunal biodiversity. Alternatively, allowing for the spontaneous emergence of species assemblages (i.e., natural succession) will not only increase species diversity but can also give rise to complementary effects by selecting for species assemblages that efficiently partition their resource use[61]. This could, in turn, enhance functional diversity and ultimately BGI performance (Fig. 2). For instance, unmaintained BGI, such as green roofs, typically performs better than other, frequently maintained BGI elements at mitigating heat[62]. Similarly, natural succession has been shown to maintain or enhance stormwater quality (e.g., of green roofs[63] and constructed wetlands[64]). However, major knowledge gaps prevail on the temporal partitioning of resource use, its response to diverse habitat conditions, and its potential advantages for engineering objectives. Uncertainties also remain about the potential and consequences of non-indigenous species spreading in unmaintained BGI. Non-indigenous species could outcompete local species, form monocultures, and overall hinder BGI performance[65].

Resilience

As in natural ecosystems[66], increasing biodiversity (e.g., through selective planting) will likely enhance infrastructure resilience by ensuring high functional redundancy and response diversity (Fig. 1). High species diversity has been shown to increase BGI resilience to droughts[33,35], heavy rainfall[40], pests[34,67,68] or seasonal variations[69]. For instance, on green roofs, *Sedum* plants can benefit neighboring plants by lowering evapotranspiration and thus increasing resilience during times of water deficit[70]. Further, allowing for self-assembling plant communities on green roofs or in bioswales may also increase functional redundancy and response diversity, and thus ensuring BGI resilience[35] and increasing the multifunctionality of urban ecosystems[38]. However, studies connecting and measuring biodiversity and infrastructure resilience (e.g., testing plant survival between droughts or measuring the rehabilitation of BGI functions after a flood) are very rare. Further research is required to clarify how species diversity, abundance, and natural succession shape the resilience of BGI to multiple stressors, now and in a future marked by increased frequencies and intensities of extreme events (e.g., floods, droughts) due to climate change[17].

Maintenance cost

Embracing natural species and community turnover can lower maintenance costs (e.g., removal of undesired species, leaf litter, or mowing) and benefit biodiversity[36,68]. Though cost savings are rarely reported, some studies have estimated that reduced maintenance (e.g., by decreasing mowing frequency) would lower costs up to 36%[71] and have emphasized the cost-effectiveness of maintaining high levels of biodiversity in the provisioning of engineering objectives[41]. However, reduced maintenance could also facilitate invasive species spread and deteriorate the infrastructure. More research is therefore

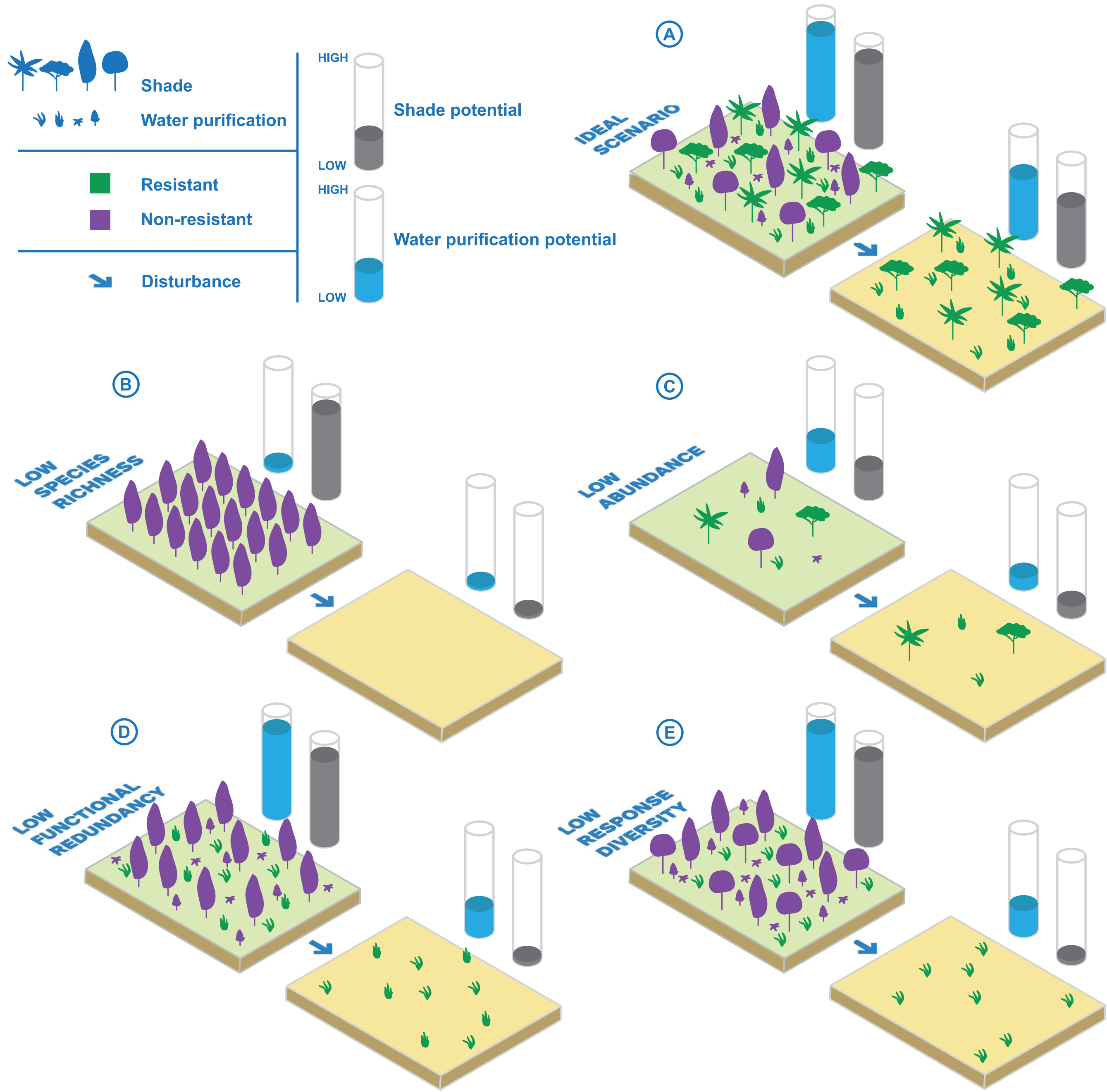


Fig. 1 | Different facets of biodiversity and their influence on ecosystem function and resilience. The arrows represent a shift after a disturbance, while the color of the plants illustrate their sensitivity or resistance to said perturbation. In these hypothetical scenarios, we assume that only trees provide shade and only herbs and grasses contribute to water purification. In an ideal scenario (**A**), species richness, abundance, functional redundancy, and response diversity are high, which results in high functional resilience. The other plots represent variations of each of these characteristics and hypothetical consequences on ecosystem services: (**B**) low species richness, (**C**) low abundance of species, (**D**) low functional redundancy of a community, and (**E**) low response diversity of a community.

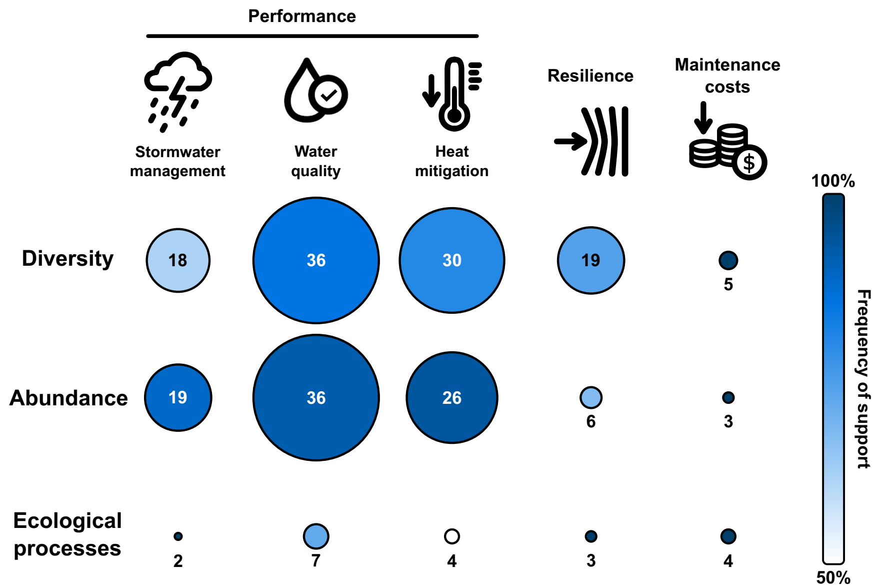
needed to understand the engineering performance and long-term cost savings from reduced maintenance.

Maintenance also implies controlling nuisance species such as mosquitoes and aphids – which typically require costly measures like pond drainage, introduction of mosquito fish or pesticide use. These costs could be reduced by increasing the functional diversity of species assemblages through better infrastructure design (e.g., urban gardens, wetlands)[67,72]. As infrastructure design improves, biodiversity increases and regulating species interactions, such as pest-predator interactions, are more frequent[67,72]. For instance, it has been documented that increasing flower diversity and coverage in urban gardens can lead to further pest-predator interactions, thereby decreasing pest populations[34]. However, the effectiveness and limits of biological pest control in cities merits further research.

Engineering for biodiversity

While increasing biodiversity within BGI can enhance its performance, resilience, and cost-effectiveness, current worldwide biodiversity decline jeopardizes this potential[7,17]. If species disappear or their populations dwindle significantly, it will limit planting options and mixture diversity, impacting BGI performance and resilience[73]. However, biodiversity should not be solely regarded as a tool for improving engineering objectives. Beyond ethical incentives, biodiversity is also a fundamental driver of many

Fig. 2 | The influence of biodiversity on BGI performance, resilience, and maintenance, and their respective levels of support. Results from the targeted literature review. The size of the circle and the number inscribed in the middle reflects the number of papers reviewed in this study, while the color gradient indicates the proportion of studies reporting a positive correlation between the biodiversity indicators and the engineering objectives. The list of articles reviewed for this figure is reported in the Supplementary Table 2.



ecosystem functions and services (e.g., pollination) in urban and non-urban areas alike[74]. Biodiversity conservation should thus be integrated as a BGI design objective alongside stormwater management and heat mitigation.

Urban planning and engineering design affect biodiversity both at the local and landscape scale. Locally, infrastructure design and maintenance choices determine the quality and suitability of urban habitats for biodiversity and therefore the distribution and abundance of species. At the landscape scale, the urban fabric imposes a set of filters that act as barriers to dispersal and survival (e.g., habitat fragmentation and pollution), which negatively affect and homogenize local biodiversity[75]. The ecological needs of a diverse biological community thus has to be considered both at the infrastructure (*Infrastructure scale* subsection) and city-wide scales (*City-wide scale* subsection)[76], as discussed in the following subsections.

Infrastructure scale

At the infrastructure-scale, design factors play a major role in how biological communities assemble within and across BGI elements, such as green roofs[77], rain gardens[78], stormwater ponds[79], and constructed wetlands[80]. For many types of BGI (see Supplementary Table 3 for BGI-specific reviews), it is evident that maximizing surface area[81,82], increasing vegetation diversity[78,83], ensuring sufficient soil and water depth[84,85] and quality[86–88], and providing structural heterogeneity[89,90] can help conserve various biological communities, as summarized in Table 1. For instance, ample evidence indicates that large urban parks with increased vegetation cover and additional habitat structures (e.g., ponds) typically provide habitat to a greater diversity of species[91]. Additionally, ensuring species dispersal and maintaining high levels of habitat quality (e.g., removing polluted sediments[92]) will decrease the probability of BGI (i.e., habitats) functioning as ecological traps, which can cause animals to become unwell, die, or reduce their dispersal ability[93].

City-wide scale

Although city-wide conditions cannot be changed with the implementation of a single BGI, engineers and urban planners should consider the landscape context within the wider urban fabric (e.g., connectivity to other BGI) when deciding where and which type of BGI element to implement (Fig. 3). Implementation of different and complementary habitat types (i.e., different BGI elements such as ponds, and urban forests) will allow more species to access diverse resources and complete their life stages[83,94]. For instance, the biodiversity of urban ponds generally increases with greater vegetation cover in the landscape, as (semi-) aquatic species (e.g., dragonflies) are expected to benefit from the additional resources provided by vegetation, such as increased prey abundance[83]. Well-connected BGI elements will also facilitate species' dispersal throughout the highly fragmented urban fabric. This is especially relevant for low-mobility species, whose dispersal can easily be hindered by barriers such as roads, buildings, or large impervious areas without ecological infrastructures[94]. This connectivity can be achieved by implementing both blue and green corridors (contiguous habitat such as daylighted streams and trails), which should be prioritized during planning due to space requirements[76]. Connectivity can also be supported by so-called stepping-stone habitats (e.g., ponds, green roofs) which address species' needs that are not served by corridors[95]. To optimally conserve biodiversity, high levels of complementarity and connectivity between BGI should be ensured[94] (Fig. 3).

Trade-offs in multifunctional systems

As shown in the previous two sections, ecological and engineering goals can align to achieve synergies in BGI design (e.g., larger surface area and increased vegetation cover advance both objectives in stormwater ponds[24]). However, conflicts between these objectives may arise. Trade-offs in design (*Design trade-offs* subsection) and maintenance (*Maintenance trade-offs* subsection) will ultimately need to be addressed.

Design trade-offs

In some cases, design choices may diverge when designing BGI for either engineering or ecological purposes. For instance, engineers install stormwater ponds primarily to capture stormwater, where dissolved pollutants create an inhospitable environment for pollution-sensitive species[79] and pose bioaccumulation risks[25]. Conversely, plant establishment in wetlands may hinder desilting and sludge excavation processes, potentially obstructing water purification efforts. Accordingly, recognizing that BGI implementation may not consistently achieve concurrent ecological and engineering objectives underscores the necessity for systematic trade-off assessments in decision-making.

Technological advances may mitigate some of these trade-offs. For instance, pre-treatment of polluted water could decrease the potential harm of poor water quality for species in constructed wetlands[96]. Similarly, multiple cell systems with water bodies collecting pollutants upstream, designed to limit colonization by species as much as possible (e.g., with concrete walls, no vegetation) and downstream basins with cleaner water intended to attract wildlife (e.g., increased vegetation cover and diversity) may help reconcile engineering and ecological objectives[97].

Table 1 | An overview of infrastructure parameters known to affect different taxonomic groups in various BGI

Characteristics	Terrestrial BGI	Freshwater BGI	Design considerations
Surface area	Arthropods[81,116,117]	Macroinvertebrates[82,84] Birds[89] Fish[97]	Despite being sometimes challenging or even impossible to modify (e.g., on green roofs), the surface area of BGI should ideally be maximized, such as in the case of tree pits.
Vegetation diversity and structure	Arthropods[81,118,119] Birds[120] Fungi[121]	Macroinvertebrates[82,83,122] Birds[89] Amphibians[123] Fish[97]	Certain taxa exhibit a stronger response to the functional diversity and structural complexity of the vegetation than the sheer number of plant species[103]. Despite the ecological or engineering appeal of non-indigenous plants[124], local plants should be prioritized, as they benefit local specialist species and do not risk becoming invasive.
Soil or water depth	Arthropods[78,81] Plants[125–128]	Macroinvertebrates[84] Plants[129] Fish[130] Amphibians[109,131,132]	In terrestrial BGI, heterogeneous substrate thickness is a cost-efficient alternative that also benefits biodiversity[85]. In freshwater BGI, increasing water level and hydroperiod length (i.e., the duration of inundation) can benefit fish[132], while decreasing them can favor arthropods and amphibians[109].
Soil or water composition	Arthropods[88] Plant[86,126,133]	Macroinvertebrates[82,87,122] Arthropods[83] Fish[97]	On green roofs, fertilizer has been shown to negatively affect plant species richness, but can increase plant biomass[86,126]. Substrate composition is also expected to affect plant and ground-dwelling arthropod diversity[88,134], but its significance for other taxonomic groups remains understudied.
Structural heterogeneity	Plants[85,125] Arthropods[90]	Birds[89]	Diverse and complex vegetation creates such structural heterogeneity, but biodiversity may also benefit from additional artificial (e.g., solar panels on a green roof[94]) or natural structures (e.g., logs or stones on a green roof[90], irregular shoreline around a wetland[89]).

Parameters documented in terrestrial (green roofs, bioretention cells, rain gardens, bioswales, green walls) and freshwater (stormwater ponds, constructed wetlands, urban streams) BGI, including surface area, vegetation diversity and structure, soil or water depth and quality, and structural heterogeneity. References provide examples rather than an exhaustive literature review. Parameters were selected based on their common occurrence in BGI-specific review (see Supplementary Table 3).

An overview of infrastructure parameters known to affect different taxonomic groups in terrestrial (green roofs, bioretention cells, rain gardens, bioswales, green walls) and freshwater (stormwater ponds, constructed wetlands, urban streams) BGI, including surface area, vegetation diversity and structure, soil or water depth and quality, and structural heterogeneity. References provide examples rather than an exhaustive literature review. Parameters were selected based on their common occurrence in BGI-specific review (see Table S3).

Not only will it be important to strike a balance between ecological and engineering needs but engineers and ecologists will also have to incorporate various other considerations moving forwards (e.g., including people's preferences, during planting). Additionally, practitioners are also tasked with reconciling potential drawbacks and societal concerns arising from increasing urban biodiversity, such as plant and animal-induced infrastructure damage or the spread of mosquitoes[98]. Technological solutions may alleviate some disservices of biodiverse systems (e.g., circulating water with a pump or deepening ponds to avoid mosquito colonization[99]), yet triages between engineering objectives, ecosystem disservices, and biodiversity conservation will be required moving forwards. Participatory approaches should also be used to garner public support for biodiversity in urban systems.

Maintenance trade-offs

BGI maintenance is required to ensure public safety (e.g., pruning), avoid disservices (e.g., damage to physical structures), control pests (e.g., mosquitoes or rats[100]), maintain engineering objectives[101], or preserve esthetic preferences[102]. Some maintenance practices can have a positive outcome to biodiversity, such as the desilting of polluted sludge in stormwater ponds[92] or the removal of invasive species. However, systems that are highly maintained have been shown to contain fewer taxonomic groups (e.g., arthropods[42], birds[103], amphibians[79]), as common landscaping practices (e.g., frequent mowing, leaf removal) tend to decrease habitat quality, deplete resources, disrupt ecological processes, and increase pressure on biodiversity, with possible implications for BGI performance and resilience (*Engineering with biodiversity* section).

Moreover, maintenance costs can be substantial, which is why *Sedum* species continue to be globally planted on green roofs due to their low-maintenance requirements[104], despite extensive research on optimizing plant community functional trait combinations for stormwater management, heat mitigation, and ecological benefits[30,46]. As a result, the appropriate maintenance practices are eminently debated and highly context-dependent[36]. For instance, leaf litter can provide resources to several soil organisms and contribute to key ecosystem processes[36] (e.g., nutrient cycling), yet they can also clog sewer drains[26] and deteriorate water quality[105]. As maintenance should ideally fulfill both engineering objectives and biodiversity requirements, it is often unclear which maintenance practices should be embraced in which context[106]. While uncertainties remain, a good practice might be to opt for a spatially and temporally heterogeneous form of maintenance, where maintenance of patches occurs at varying intensities and frequencies throughout different times of the year. Such diverse range of maintenance activities creates a mosaic of ecological niches, which in turn fosters biodiversity[107].

Ecological trade-offs

Similar to the trade-offs between ecological and engineering objectives, purely ecological trade-offs arise when engineering *for* and *with* biodiversity. Essentially, certain species will need to be prioritized over others. For instance, prioritization is evident when plants are selected or removed to meet engineering objectives, such as maximizing stormwater infiltration or preventing infrastructure damage from plant roots. To engineer *for* biodiversity, BGI design and maintenance choices must be adapted to the target species and their environmental tolerance, ecological needs, and mobility[108]. Accordingly, recommendations outlined earlier (*Engineering for biodiversity* section) may align with the needs of some species, but certainly not all. For instance, fish preferring deeper water with longer inundation durations can intensify predation on other organisms, such as amphibians, making the management of water levels and hydroperiods (e.g., for stormwater management purposes) crucial in determining species dominance[109]. Therefore, when available, local ecological knowledge should be integrated into BGI design and maintenance to understand which species should be prioritized in the region[110]. Non-indigenous species, while having the potential to increase species and trait diversity, can also spread uncontrollably and become invasive. Therefore, their use in BGI should undergo critical evaluation.

Future directions

Interdisciplinary collaborations will be increasingly relevant, not only to address challenges related to engineering and ecological trade-offs, but also to cope with the effects of climate change on BGI and urban systems. The magnitude and frequency of heatwaves and storm events are predicted to

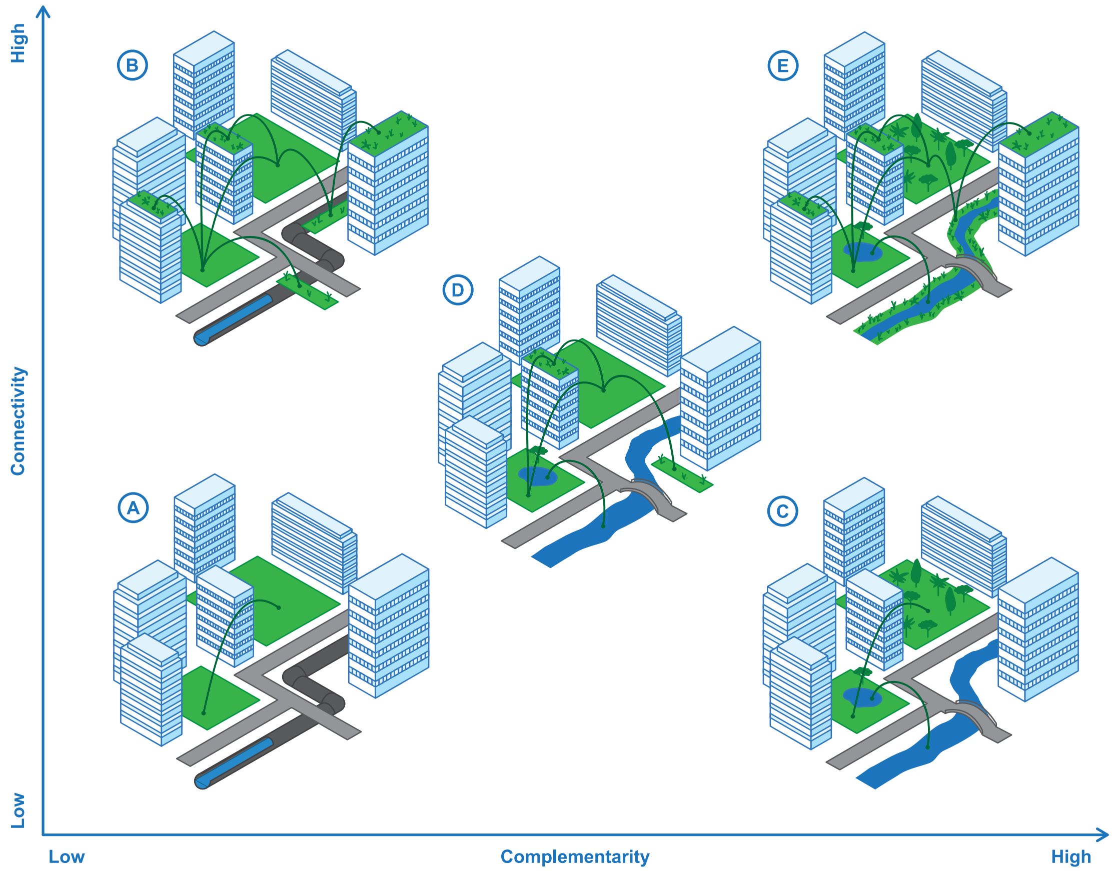


Fig. 3 | BGI connectivity and complementarity. Connectivity and complementarity of BGI can be incorporated to varying degrees during planning (**A**, **D**, **E**). Here, BGI that are close to one another increase the connectivity of biological communities, illustrated by the dark green lines (**B**, **E**). In addition, having diversified types of BGI elements provides more resources to multiple species (**C**, **E**).

increase in the coming decades, as is the number of species threatened by extinction[17]. While more research is needed to evaluate the contribution of BGI and biodiversity to abating these effects on urban systems[111], drawing from highly productive, complex, and resilient ecosystems (e.g., forests) to inform the design of BGI[112] could help ensure their resilience to future climate change. Rather than attempting to control all aspects of BGI design – from substrate depth to the living communities it harbors – biodiversity and its multiple facets can act as potential allies. More integrative research is needed to understand and quantify the capacity of BGI to perform under changing climatic conditions and to address both human and ecological needs while minimizing potential conflicts[113] and indirect effects[114,115].

Although a targeted but not systematic review nor a meta-analysis, this paper is a call to action for designing BGI *for* and *with* biodiversity to help alleviate the ongoing and simultaneous challenges faced by cities and the built environment, such as frequent storms and higher temperatures, as well as water pollution and biodiversity loss. However, it would be reductionist to consider BGI as the sum of its parts – e.g., a simple combination of substrate and plants subject to cycles of installation, deterioration and maintenance. Instead, we should acknowledge and embrace that BGI both shapes and is shaped by biodiversity and the underlying complex ecological processes that influence BGI performance and resilience. By engineering *with* biodiversity, we can enhance BGI performance, reduce costs and create more resilient systems. By engineering *for* biodiversity, we can harness this potential and ensure that BGI provides suitable habitat for a variety of species.

However, ecological engineering studies often do not account for infrastructure-scale and, even less frequently, for city-wide factors that shape biodiversity and the ecological functioning of the engineered systems, with possible implications for the generalizability and scalability of their findings. For instance, BGI surrounded by fragmented habitats are likely to harbor impoverished faunal and floral communities, potentially affecting engineering objectives. Given the significance of city-wide factors (e.g., infrastructure connectivity) for plant and animal colonization rates, reporting BGI position within an urbanization gradient would facilitate the expansion and generalization of a study's findings. Furthermore, instead of reporting on biodiversity benefits at a specific moment (e.g., one year after planting), continuous and simultaneous monitoring of both engineering and ecological outcomes would enhance our understanding of ecological processes (e.g., species interaction, natural succession) in BGI and their implications for engineering performance and infrastructure resilience. While more work is needed to develop standards for monitoring biodiversity, tracking functional or phylogenetic diversity alongside taxonomic diversity is a promising initial step.

Importantly, BGI comes in different sizes and shapes, and constitutes only one approach to engineering urban infrastructure. Yet, it is becoming increasingly evident that a paradigm shift is urgently needed, from the typically highly standardized BGI design towards distributed networks of BGI that consist of a diverse set of locally adapted, flexible, interconnected, functionally redundant and complementary elements. More interdisciplinary collaboration and research, including bold experimentation with innovative BGI designs, is needed to gauge and quantify the conditions under which nature can serve as an ally in BGI design and management. This is especially true for ecological processes, such as natural succession, which are greatly under-investigated in engineering sciences and require further attention. Moving forward, we encourage engineers and ecologists to expand and formalize their collaborations to further innovate the design of effective and resilient BGI systems that can help mitigate accelerating environmental challenges faced within the built environment.

Reporting summary
Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
All studies considered for the reviewing process in *Engineering with biodiversity* section are reported in the Supplementary Tables 2 and 3. No additional datasets were generated.

Received: 26 April 2023; Accepted: 11 April 2024;
Published online: 24 April 2024

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Acknowledgements
This study was funded by ETH Board through the Blue-Green Biodiversity (BGB) Initiative (BGB 2021-2024). The funder played no role in study design, data collection, analysis and interpretation of data, or the writing of this manuscript. We thank the following people for their contribution or constructive feedback during the writing of this manuscript: L. Chaboche, P. Lechevallier, P. Thomas, and the Altermatt research group. We also thank the reviewers for their constructive feedback, which significantly contributed to the improvement of the manuscript.

Author contributions
K.P. did the literature review, conceived the figures, and conceptualized the study with the help of M.M., A.D., L.C. K.P. led the writing of the manuscript, with the help of M.M., A.D., and L.C. F.A. provided additional insights and reviewed the manuscript. All authors read and approved the final manuscript.

Competing interest
The authors declare no competing interests.

Additional information
Supplementary information The online version contains

supplementary material available at
https://doi.org/10.1038/s42949-024-00163-y.

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