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What are the traits of a social-ecological system: towards a framework in support of urban sustainability

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To ensure that cities and urban ecosystems support human wellbeing and overall quality of life we need conceptual frameworks that can connect different scientific disciplines as well as research and practice. In this perspective, we explore the potential of a traits framework for understanding social-ecological patterns, dynamics, interactions, and tipping points in complex urban systems. To do so, we discuss what kind of framing, and what research, that would allow traits to (1) link the sensitivity of a given environmental entity to different globally relevant pressures, such as land conversion or climate change to its social-ecological consequences; (2) connect to human appraisal and diverse bio-cultural sense-making through the different cues and characteristics people use to detect change or articulate value narratives, and (3) examine how and under what conditions this new approach may trigger, inform, and support decision making in land/resources management at different scales.

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TRAITS AS SOCIAL-ECOLOGICAL BOUNDARY OBJECTS FOR URBAN STUDIES AND GOVERNANCE

Traits are attributes that speak to biophysical limitations, pressure on species, ecological functionality, and interactions. They have found their way to the forefront of many discussions and debates about ecosystem dynamics and, with a slight time lag, social-ecological systems[1–3]. The promise is that a traits framework can further our understanding of patterns, dynamics, interactions, and tipping points within and across complex social-ecological systems. But what will it take to make good on this promise, in particular for our cities, where change is fast and—being the places where the majority of humans live—human perceptions are particularly diverse? What kind of framing, what research, would allow traits—classically understood as a different representation and interpretation of well-established and known properties of the social-ecological system——to fully work as "mediators" for understanding the behavior, functions, and needs of urban systems under pressure?

This perspective aims to contribute to the current wide-ranging discussion about traits in both theoretical and applied ecology, and parallel work on better understanding human connections to nature. To this end, we explore the potential of using an expanded conceptualization of traits as a platform for integrated approaches to understanding the different facets of people-in-nature relationships and dynamics[4,5].

Expanding from the original "characteristics which have demonstrable links to the organism's function"[6], we see traits as a nexus where different theories and conceptualisations about social-ecological systems can connect, intertwine and comprehensively allow us to assess the current state of a system—and even more importantly, evaluate the implications of change (Box 1

and Fig. 1). To make it an integrative and useful framework for urban studies and policy/practice, traits need to be easy to recognise and relevant to decision makers across scales and in different contexts. In addition, information on trait profiles—generic as well as site specific—need to be easily available through monitoring or in databases.

Our argument is threefold: The first dimension focuses on how to assess and anticipate change by establishing chains of interconnected traits that describe and causally connect sensitivity and response to different urban pressures such as heat, soil compaction, environmental toxicants, and stormwater runoff, understood through "response" traits[7–10] to their functional consequences[11], mediated by "effect traits". The second dimension is grounded in human perceptions and appraisal of diversity to highlight the different cues and characteristics people use to detect change or articulate value narratives, and it is linked to the role of traits in ecological literacy. Here, we propose traits be viewed as boundary objects, i.e., features that carry meaning across society (although the meanings might be diverse and sometimes conflicting), and that this second dimension is essential for understanding the role of society and humans in a traits framework. The third dimension outlines how the first two dimensions connect to inform and support decision making and management at different scales, for example in different, multilayer, and multiactor governance processes[12] (Fig. 2).

The first dimension: response and its effect outcomes

Trait-based approaches have been used for descriptive purposes[13] to enable broader global comparisons that transcend the constraints of regional taxonomic diversity (e.g., see refs. [6,14])

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and allow for the types of generalizations sought in ecology[15,16]. Traits offer a way of looking at causality and change, and trait profiles can indicate whether emergent communities are functionally different from historic communities. To this end, traits can be divided into those that determine an organism's sensitivity and response to environmental factors, and those that relate to its effect on the environment[4,17]. When combined, the two categories of traits can be used to detect, identify and monitor the current state of ecosystems, and to anticipate the outcomes of change[8,10,17–19].

An environment described through traits: The urban biophysical environment includes hydrology and soils, as well as biotic elements (flora and fauna), and understanding the relationships among those components is necessary to measure and anticipate the profound effects of urbanisation. Currently, knowledge of plant traits is most developed[4,20], although there is work emerging on traits for animals or other taxonomic groups[8,21] as well as for soil and geodiversity[22]. Animal studies so far tend to

focus on habitat modelling for birds, insects, invertebrates and a few on mammals (e.g., see refs. [3,8,16,23]). Many studies have looked at the impact of different community assemblages on ecological functions through effect traits and, in particular, how altered or dynamically changing communities will affect ecosystem process through changes in representation of effect traits (but e.g., see ref.[23]). However, the link between traits and ecosystem functions has largely been inferred (ibid.), and is, according to Cadotte et al.[24], rudimentary (see also[25] and[26]). As we indicated with our definition of traits (Box 1), we see a value in including soil properties as traits and not to leave them as "environmental filters", as this may offer a more dynamic way of understanding one of the major urban processes of change—soil sealing and compaction—and thus help guide urban development.

Traits at different levels and scales: Traits at the species level are by far the best known and most explored, but there are also studies that use traits from other ecological levels—gene, community, ecosystem and landscape—as indicators for tracking response to stress[27] and calculating functional "performance". A common approach to scale is to aggregate species level information. For example, the average values of aggregations of plant species traits at the ecosystem level provide a basis for calculating overall sensitivity to pressures[28]. This in turn, and drawing on different sets of traits, allows for estimations of changes in ecosystem function (e.g., see ref.[29]). However, there are other characteristics that could also be understood as traits. At the landscape level the mosaic of ecosystems and the location and combination of patches are used to assess flows and exchange across larger areas (e.g., see ref.[30]). A good example is a city in a river valley, where water flows and exact location within the drainage basin affect urban green spaces and their aggregated matter production, CO_2 absorption or carbon subsection[31]. Aggregate, or higher-level traits, such as structural composition and functional diversity of vegetation, matter flows, or species migration, are the most common traits analysed through remote sensing in order to track trends[25]. More work needs to be done to explore relevant traits at different levels of organisation to match the scale and nature of disturbances and the spatial and temporal scale at which different functions are

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Box 1 definitions

Functional trait: A feature of an organism which has demonstrable links to the organism's function[69], and, as such, "determines the organism's response to pressures (response trait), and/or its effects on ecosystem processes or services (effect trait). In plants, functional traits include morphological, ecophysiological, biochemical and regeneration traits, including demographic traits (at population level). In animals, these traits are combined with life history and behavioral traits (e.g., guilds, organisms that use similar resources/habitats)"[70], p. 2779.

Boundary object: "[…] those […] objects which both inhabit several intersecting social worlds and satisfy the information requirements of each of them. Boundary objects are objects, which are both plastic enough to adapt to local needs and the constraints of the several parties involving them, yet robust enough to maintain a common identity across sites. […] They have different meanings in different social worlds [and across cultures] but their structure is common enough to more than one world to make them recognizable, a means of translation."[71] p. 393, see also[72].

Social-ecological traits (expanded definition): An ecologically or socially (inter) active and demonstrable feature of the environment at any level or scale. A social-ecological trait either mediates reactions to selective social-ecological filtering (response trait) or determines effects on ecosystem processes or services (effect trait), or both. The aggregate trait profile of a given entity should ideally speak both to ecological functioning and socio-cultural meaning.
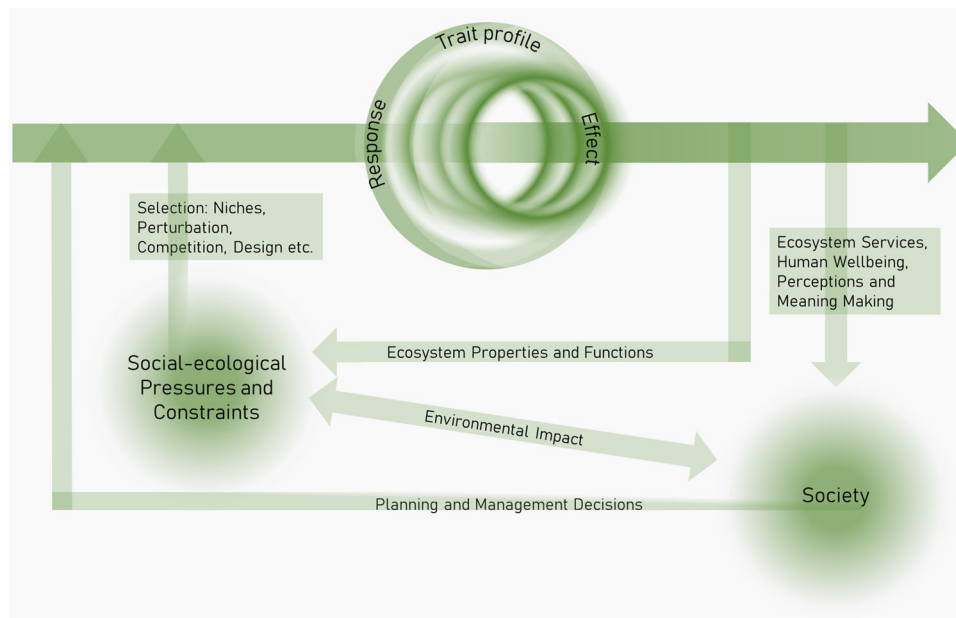

Fig. 1 Traits within social ecological systems. Theoretical flow chart linking the entities of a social-ecological system to its traits, demonstrating how a traits framework—as outlined in this article—might be positioned to support the analysis, interpretation and governance of urban systems.
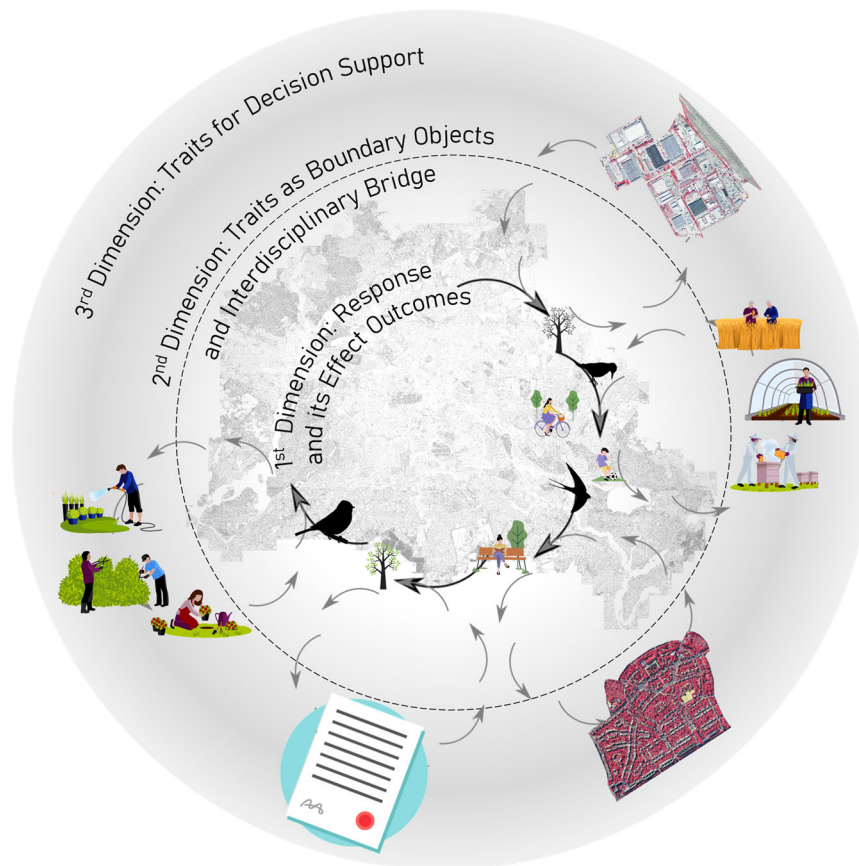
Fig. 2 A traits framework for scientific study and practical application. The three dimensions of a social-ecological traits framework for understanding and governing urban systems. The first dimension is represented by observable traits of the urban environment, e.g., features of humans and other co-inhabiting species and their differing responses to pressures and selection, leading to functional consequences and finally, altered characters of an urban social-ecological system. The second dimension is characterized by feedback loops between those effect outcomes and individual and collective perceptions and decision making. Lastly, the third dimension is represented by urban ecosystem planning and management embedded in governance processes and instruments. Through its ability to connect different spheres and discourses, an expanded traits framework can aim for effective and inclusive decision support that is responsive and place-adapted. By expanding and bridging these three dimensions, we can connect different insights and knowledge about ecosystem function and human perceptions, values and interactions with the environment. This will support the development of a (meta-) theoretically grounded, practically applicable traits framework to interrogate reciprocal feedback linkages and nature-human relationships. The figure includes resources from Freepik.com.

most relevant. Being explicit about scale, and ensuring traits at different levels are nested, allows for tracking of processes across scales.

Individual traits, trait combinations, and interlinked suites of traits: A key promise of traits is to provide mechanistic explanations of observed structure, patterns and functionality, which is usually demonstrated through statistical correlations. Further developing suites of response and effect traits could provide valuable input and indicators for assessment and monitoring frameworks. For example, traits could inform DPSIR (drivers, pressures, state, impact, and response) models by anticipating or measuring response to a pressure and the direct and indirect impact this response could have. At a more fundamental level, traits explain whether impacts may be causing a change in the functional state of the system. Interlinked traits, from those determining sensitivity, to those mediating response elicited by sensitivity, could improve mechanistic understanding by supporting the development of stepwise response-effect pathways[17]. For example, land conversion—like the soil sealing and compaction typical in cities—fundamentally alters soil properties, which in turn affects vegetation. Soil properties influence the growth and composition of plant communities. This translates into trait-mediated effects like reduction of total leaf

area, which leads to cascading effects of early leaf senescence and limitation of stomatal transpiration. This reduces water exchange capacity, which in turn is key for mediating air cooling or shading and other functions/services plants may offer to humans.

For this first dimension, trait databases, classical field inventories, and experiments, remote sensing data, and GIS-based information are crucial[15,32]. We see valuable developments from the past two decades of research towards achieving a traits response-effect library in both the ecology and remote sensing communities[33,34], even if recent advances from remote sensing studies still rarely find entrance into urban planners' work and policy decision-making[35]. In particular, the development in the technical dimensions of detecting traits and trait variation[20,34], and tracking these over time, has recently rapidly developed. The progress in application of high-resolution hyperspectral data, light detection, and ranging (LiDAR) or the possibility of mounting the recently developed sensors on unmanned aerial vehicles (UAVs) equip the researchers with addditional tools that can not only expand the range of measurable traits but also allow easy access to data. This provides a powerful support for urban planning and, ultimately, urban governance. Moreover, applications for tablets or smartphones offer alternative ways to directly involve

citizens in ecosystem monitoring and further develop citizen science (e.g., see refs. [22,36]).

The second dimension: traits as an interdisciplinary bridge

The literature explicitly using the term traits tends to focus on soil, geodiversity, plant, and community trait profiles as an outcome of social-ecological selection through environmental conditions, species interactions, human preferences, management regimes etc. (e.g., see refs. [4,37]). This approach has started to address not just how people filter traits (e.g., see ref. [38]), but the reason(s) behind either individual or group decisions that lead to filtering (e.g., see refs. [39,40]). Here, we propose that the environment, described through traits, could be considered a boundary object (Box 1), allowing for a multiplicity of views, disciplinary connections, engagements, and perceptions, and that speaks to the complexity of social-ecological systems. This will expand the range of functions used to describe a system, and the types of traits required to capture them.

Ecological functions relative to ecosystem services: The plant and animal traits that people respond to may not be the same ones that mediate responses to environmental change. For example, seed mass and specific leaf area are important plant functional traits[41] but are less likely to influence people's preferences for urban vegetation (e.g., see ref. [42]). Indeed, some esthetic traits promoted by human decision-making and management, such as selection for leaf variation and predominantly deciduous plants, may also lead to the predominance of woody plants that are strongly affected by water stress, fungal attack or insect infestation or trimmed canopies, and thus promote reduced fitness of individual organisms and communities[43]. On the other hand, a successful reproductive strategy such as the emission of high quantities of pollen might limit the suitability to human-dominated environments (including cities) due to allergenic potential[44]. Do we need more, or different traits to link ecosystem dynamics more strongly to the lived reality of people? Are traits too simplistic proxies, or perhaps too specific features, to express and understand people–nature interactions? Introducing humans and human appraisal into our trait framework encourages a broader definition of what might be relevant traits. Traits used in this way provide a specific link to interactions and feedback mechanisms between human wellbeing and functional ecology (and respective proxies that serve multiple relational (feedback) purposes).

Traits as relational features: Trait lists already include features which are easy to understand and readily detected by human sensory organs, and thus find traction in society or connect to existing ethno-biological narrations[39]. Traits such as flower colour, leaf shape, and canopy density, which may not necessarily be considered central functional traits, are important drivers of people's preferences[37,39,45,46]. Both size and colour of the flowers are plant traits affecting people's perception[47] and can thus be an important factor for gaining societal approval for more urban greenery[48]. Seasonality is another relevant trait; for example, an extended flowering season[49]. At the same time, there is a growing interest in flowers and blooming meadows among gardeners worldwide also to support insects in urban landscapes to counteract global biodiversity decline[37,39].

In this vein, we argue that traits are a formative force influencing human wellbeing and world views, giving shape to ecological systems and linked human affordances (through, e.g., shade and sensory stimuli), and social systems by shaping the context of human activities and experiences. For example, we know that people recognize and value a wide range of plant traits, and that this has even been identified as a useful way to speak about the state of nature and large scale change[50]. There is evidently a role for traits and trait composition as language for more "functional" ecological literacy[36,50]. This position as a

boundary object needs to be further explored and linked to the responses of social-ecological urban systems, which are subject to a multitude of pressures, including climate change and soil sealing.

Traits as boundary objects and connectors between knowledge systems: What is needed to better position and connect the concept of traits to multiple different literatures and disciplines and enable traits to be used as a useful boundary object? Many disciplines outside the ecological and environmental sciences have an interest in understanding ecosystem function and biodiversity, and how people relate to these ideas. Traits, and deeper meanings of some traits, can be found within environmental psychology, ethno-botany/zoology and environmental anthropology. Trait-based approaches may also be well suited to engage with other ways of knowing, such as traditional ecological knowledge and religious systems. This disciplinary and transdisciplinary knowledge is needed if traits are to connect social-ecological attributes to diverse human values and wellbeing dimensions, and to ensure we do not produce trivial and culturally biased conclusions[51,52]. Based on the diverse use and potential meanings of the word "traits", we argue that a traits framework, and traits-focused interdisciplinary discussions and projects, could support a dual ontological stance where some connections are more universal, while others are inherently interpretational or simply individual. Hence, this may help to effectively connect the social and cultural dimensions of traits to a deep ecological understanding of change and its multiple consequences. This would be an important development that allows for critical engagement with concepts like tipping points and system states and what they actually mean in a complex social–ecological urban system.

The third dimension: traits for decision support

The major purpose of the traits concept, as we present it here, is to develop an ontologically inclusive traits framework capable of addressing both the resilience of ecological functions and the experiential and relational aspects of human interactions with nature. On the applied side, this would be relevant to a wide range of decision-making processes, not least urban planning. Clearly visible and easy-to-map traits are well-suited as indicators to describe the state of urban landscapes relevant for biodiversity and society alike. To this end, there are still many questions that need answers. For example, how can the understanding of trait profiles help improve species selection in times of climate change, to inform management priorities and strengthen cross-community stewardship, especially where the diversity of response traits may be low? And which traits are incompatible and how are they best kept separate, a question particularly relevant in the light of zoonosis like the COVID-19 pandemic in 2020? And finally, what traits could best serve as reasonable proxies or indicators to provide either cues or early signals of species responses to (fundamental) change in urban environments?

Supporting holistic decisions: Already now we see increasing use of traits in modelling and decision support tools like CiTree and iTree[53,54]. As cities strive to adapt to climate change by, for example, revising tree species selection (e.g., see ref. [55]), an improved understanding of the relationship between detectable functional traits and the provision of ecosystem services can help avoid maladaptation[56]. For example, replacing shade trees with fine-foliaged trees may improve adaptation to future climates but would not provide the same levels of climate mitigation[57]. From a decision-making point of view, key traits are those determining the response of ecosystems to human-induced pressures such as air pollution, soil sealing, or urban heat islands, as well as those mediating the effects of these changes on ecosystem services and related benefits as perceived by people[8,58].

A traits framework that uses our social-ecological definition of traits might support informed decisions on trade-offs. For example, invasive or non-native plants are often seen as ecologically problematic, but certain traits such as high leaf coverage or flower colour and shape make them socially desirable[48]. Traits connected to more social-ecological dimensions will allow for a more holistic assessment of options and the potential trade-off implications of different choices. While decisions are often grounded, implicitly or explicitly, in considerations of multiple traits (e.g., see ref. [53]), we need to ensure that traits considered in the plant selection include both traits related to broad and diverse preferences and desires for ecosystem services and traits, that ensure a resilient response to drivers of change that may impact their ability to provide these services (see, e.g., the scoring system for urban vegetation species proposed by Tiwary et al.[59]).

Urban planning informed by an expanded traits framework and spatial-temporal patterns of trait profiles has the promise to be adaptive in the best sense and thus, resilient. More city and regional comparisons are needed to make target setting and threshold discussions grounded and allow for global discussion. This requires a targeted effort at broader inclusion of cases and trait data from different climates, biomes, multiple ecological levels but also cultures, and would move traits studies towards a truly transdisciplinary venture with real impact on how we plan and manage our cities.

Feasible and easy to use: Indicator traits need to be robust, easy to measure and low-cost to assess, and have a causal link to relevant social-ecological processes and patterns (such as ecosystem services for recreation, cooling or food[4,60]). The potential use in planning and decision-making at multiple levels again point to the need to discuss the scales and levels for traits studies to make sure trait levels are nested and logically

Table 1. Research agenda.

	Data	Questions	Urban governance and practice contexts
Traits for monitoring and comparison	Remote sensing data on urban soils and vegetation, surveys and inventories, environmental monitoring	Heterogeneity within and across cities, spatial distribution high/low trait diversity	Urban growth, land conversion, restoration, monitoring changes induced by urbanization and climate change
Response-effect chains	Experimental and longitudinal studies in different urban settings, interactions between soils-vegetation-animals	What are the effect outcomes (and iterative loops) of response to change? What does response diversity really mean?	Design of nature-based solutions, impact assessment of planning actions, offset schemes and compensation mechanisms
Experience and sense-making of diversity and dimensions of diversity	In-depth value and preference studies, self-reported social media, narratives and biocultural/ethno-biological studies	What are the consequences of human perceptions, preferences and dislikes, what are the ES consequences of different responses to pressures?	Ecological literacy, awareness raising, citizen science, participation, stewardship

Research agenda for developing and grounding an extended, interdisciplinary and practically applicable traits framework. The research questions are connected and meant to serve as a basis for integration, and management and decision making will benefit from the integrated framework.

commensurable. Higher-level, larger-scale properties such as landscape morphology and water availability, the profile of pest communities or potential invasions can be further informed by the development of more detailed traits frameworks. This makes traits frameworks highly relevant also from an economic, social and health perspective, especially in intensely managed environments like cities, where combinations of multiple stressors and external factors create small scale heterogeneity and fast temporal change in pressures[61,62].

Trait selection can play that important role for assisting in the planning and design and then evaluation of the functionality of high-biodiversity green spaces[63], and for trait-informed assessment of "performance", e.g., of ecologically protected areas. A relevant example to this point is the ongoing debate about how to evaluate ex-ante, and then monitor, the implementation of nature-based solutions[62,64], which remains a challenge[65]. Could this be done using traits instead of commonly used area-based indicators? Could traits become the basis to design and assess the impacts of offsets and compensation measures, thus increasing their efficacy? From this perspective, we see in a traits framework the potential to support a shift towards more flexible and effective planning approaches, more suitable to address today's urban challenges and to promote greater well-being, sustainability and resilience of present and future cities.

Conclusion and looking ahead
Through their direct relation to ecosystem services such as cooling and fresh air, easy-to-understand traits can be an entry-point for nature awareness and, subsequently, ecological knowledge in decision-making both at the citizen and the societal level[66]. However, to make traits successful indicators of global, regional, or local environmental changes, it is vital that urban society is understood as diverse across characteristics such as cultural background, physical mobility, gender, age, degree of formal or informal education, access to information and communication, purchasing power, and political influence[67]. All these factors affect the needs, preferences, and values of individuals and groups, and the way each interpret human-nature relationships. Only by taking these factors into account, planning for spatial-temporal diversity in traits across an urban landscape will create more inclusive urban systems that foster multiple benefits for both people and biodiversity[68].

The expansion and implementation of a traits-based approach for urban systems is impeded by availability of traits data. For example, trait databases are usually a primary data source in studies on urban ecology, however, these data have mainly been collected in natural areas or controlled environments such as laboratories, where organisms may display different trait values than those in urban environments. Studies have also been concentrated in the global north, and there are major challenges with potentially transferring and adapting thinking mostly developed in the Global North to rapidly urbanising areas in Africa, Asia and South America.

To enable a social-ecological traits framework for interdisciplinary discussion and for guiding urban planning and decision making, we suggest a three-pronged approach for building a social-ecological understanding of trait mediated interactions and their implications, and make this understanding useful to practice (Table 1). Large-scale monitoring needs to be coupled with in-depth understanding of response mechanisms and their impact on ecosystem functions as well as services, and a deeper connection between traits and human perception as well as sense-making of the world we live in. Application to human perception and sense-making requires more data, theory and empirical work, and especially the way people relate to traits will likely vary considerably across cities and contexts across the globe. All branches of investigation need to be embedded in an interdisciplinary discussion about the role that traits play for social-ecological interactions and mutual exchange. Drawing on this broad evidence base, synthesized knowledge will offer a more comprehensive support for urban decision making, not least in anticipation of future change.

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The authors declare no competing interests.

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