Social-ecological networks in urban ecology research

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Preface
Urban ecosystems are complex and dynamic, shaped by feedback loops between social and ecological components. However, urban ecology requires tools to unravel this complexity. Social-ecological networks (SENs) offer a conceptual and analytical framework by integrating network theory to understand the relationships between and within social-ecological systems. Here, we integrate perspectives from urban ecology and SEN research to introduce SENs as a promising, yet underexplored, framework for advancing urban ecology research. With an example from Melbourne, Australia, we demonstrate how SENs can advance our understanding of urban biodiversity conservation. Lastly, we propose nine key themes for future urban biodiversity research that will benefit from exploration through an SEN approach. By adopting and further developing the SEN framework for urban ecology, researchers can gain structural and relational insights into urban social-ecological systems. Importantly, an SEN framework may not only bridge the inter- but also transdisciplinary gap between research and practice.

Introduction

Cities are not just built environments. They are complex systems where interdependencies and feedbacks exist among social (e.g., institutions, individuals) and ecological (e.g., habitat, species) domains [1,2]. Urban ecology investigates the reciprocal relationships among these domains [1,2,3], including place-based studies of relationships between local communities and urban nature [4] or studies of interactions between governmental actors and their nature-related decisions [5]. Urban ecology evolved from biology-based approaches studying ecology *in* cities toward interdisciplinary research viewing cities as social-ecological systems (ecology *of* cities) and lately, bringing a stewardship ethic to bear and engaging diverse stakeholders (ecology *for* cities) [6]. However, urban ecology research has fallen short of understanding human-nature interactions through feedback loops between knowledge and action and identifying key actors and links among actors [7,8]. This gap can be addressed through a social-ecological network framework by unravelling how human-nature interactions shape the resilience, sustainability, and complexities of social and ecological outcomes in urban areas.

Social-ecological networks (SENs) use network theory to provide a conceptual and analytical framework for exploring the complex interactions between human (social) and environmental (ecological) entities within social-ecological systems [9,10,11]. Specifically, SENs aim to disentangle these complex interactions by focusing on the structure and dynamics of social-ecological systems (or their parts), namely their social and ecological actors and links such as flows of, e.g., materials, energy or information between them (Fig. 1). This approach makes it easier to identify patterns, to quantify characteristics (e.g., direction, strength, quality) of the links and to identify key actors or relationships that contribute to the system's resilience and sustainability. For instance, an SEN framework could reveal how urban governmental structures and dynamics influence environmental decision-making, the outcomes of these decision-making processes on urban biodiversity and how these differ across cities (i.e., within the field of comparative urban ecology).

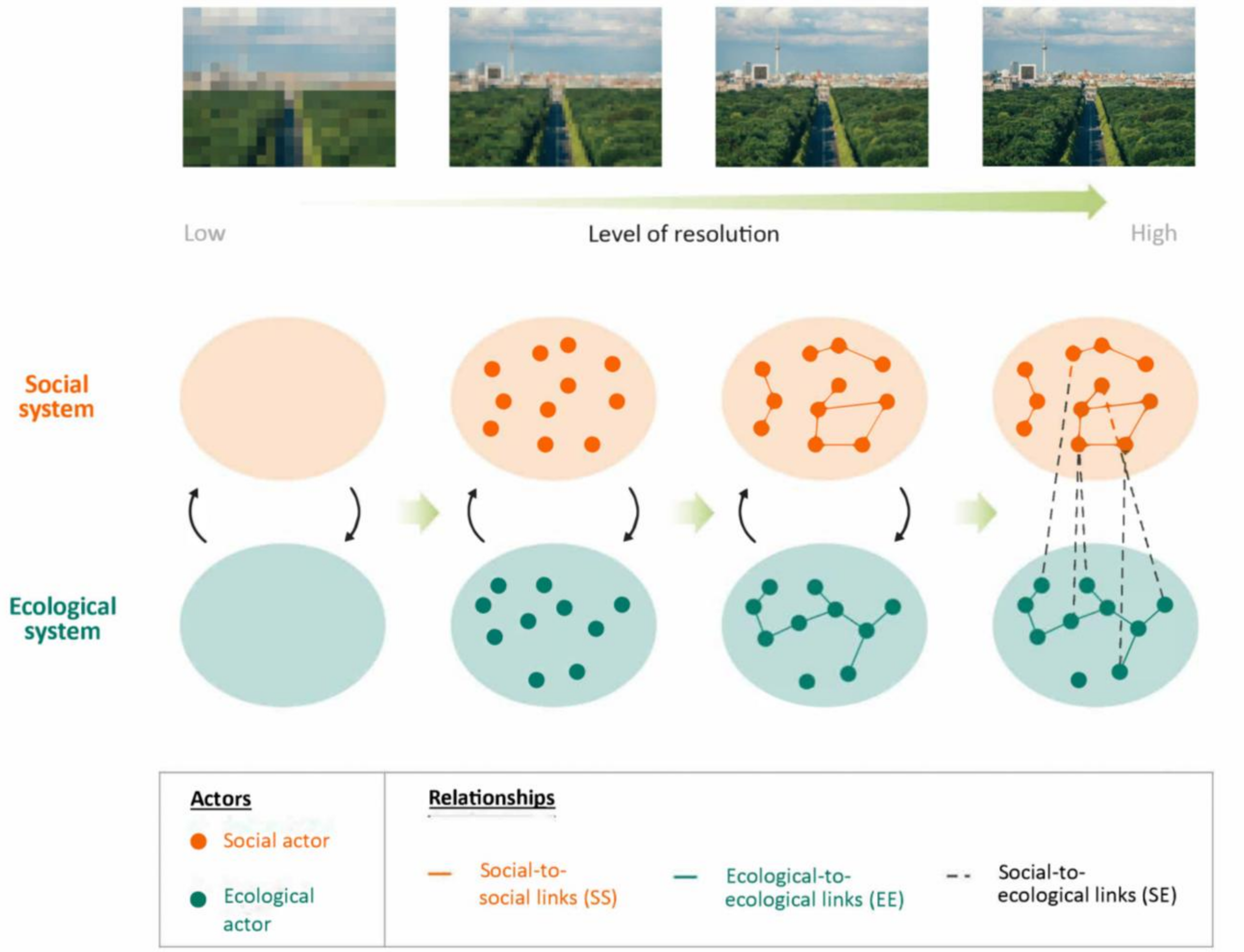


Figure 1. The conceptual social-ecological network framework progressively increases the level of resolution by exploring the interactions between social and ecological systems. Dots represent social and ecological actors, while their relationships are shown as (dashed) lines. The level of resolution can be adapted to the research question and availability of data. At the highest resolution (right), the fully articulated SEN captures a detailed representation of actors, their connections and interrelationships within and between social (orange) and ecological (green) systems (adapted figure [11]).

Over the past two decades, SENs have primarily been developed and applied in research on the governance of common-pool resources, where they have proven effective in disentangling social-ecological interactions and feedback loops [12-14]. They have helped identify effective management regimes and whether social institutions align with the scale of the ecological processes they manage [15-17]. For example, SENs have revealed critical market regulations in marine systems [15] and demonstrated how partnership structures affect wildfire risk management [16].

Despite the SEN approach's promise as a framework for studying social-ecological systems, only few urban ecology studies have applied it (Table S1). These studies primarily focused on landscape-context analyses of urban green spaces, urban water or social-ecological fit. Identifying a social-ecological fit or misfit, that is, the match or mismatch between the scales of ecological (e.g. connectivity) and social (e.g., governance) processes, is one of the strengths of the SEN approach [10], though not without debate [18]. Urban areas are heterogeneous, potentially leading to misfits between the social network structures and ecological processes [19]. For example, biotic interactions such as pollination often occur locally, while social processes operate across much larger spatial scales [10,19], potentially leading to scale mismatches [20]. Similarly, urban water management faces challenges where governance structures are fragmented across municipalities, creating gaps in addressing issues such as river pollution or flood mitigation. The SEN approach can help identify and address such challenges. For example, a study on ecological connectivity between wetlands and intermunicipal collaborations in Stockholm identified misfits between ecological connectivity and stakeholder cooperation efforts [21]. This information made it possible to identify where limited collaborative resources could be most strategically allocated to enhance the social-ecological fit of wetland management in Stockholm. Similarly, subsequent work found that collaborations among decision-makers were more robust in rural terrestrial ("green") and aquatic ("blue") areas than in urban environments, revealing a social-ecological misfit in cities [22].

This perspective piece results from an interdisciplinary collaboration between researchers from urban ecology and SENs. We believe that by capturing the complex and interconnected relationships within and between social and ecological actors, SENs provide a comprehensive, nuanced and actionable understanding of urban biodiversity governance, ecosystem services and human–biodiversity interactions. They offer a way to unpack the often broadly applied urban social-ecological systems framework into manageable and comparable components [9] (Fig. 1), while fostering a shared conceptual and epistemological language across disciplines [9,23]. In the following, we (i) introduce the SEN framework in the context of urban ecology, with a focus on urban biodiversity research, (ii) illustrate its potential application through an example with urban green spaces in Melbourne, Australia, a city with a well-established tradition of integrating ecological and social dimensions in urban research, (iii) outline nine key research themes for future research directions in urban ecology applying the SEN framework, and (iv) discuss the challenges and considerations of the SEN framework in urban ecology research.

Setting the scene: What are social-ecological networks?

The SEN framework is nested within social-ecological systems research, which addresses integrated systems of ecosystems and human societies, highlighting their reciprocal feedback and interdependencies [24,25]. Networks have a rich history across various research fields (e.g., social, natural and complex systems science [10,26]) with partly different terminologies. However, certain terms, such as nodes (or vertices), links (or ties, edges) and attributes, are shared across social and ecological disciplines [9,23]. At its core, an SEN consists of ecological and social actors or entities (*hereafter* nodes) and interactions between them *(hereafter* links). Overviews of potential nodes and links in SENs have been provided in earlier work [10,26,27]. SENs can be modelled spatially (landscape approaches) or abstractly (system approaches) [10].

Nodes, links, current use: Conceptualizing network components for urban ecology research

The definition of a node is flexible and tailored to each study's focus or research question [10,11]. In cities, social nodes can include human individuals, groups (e.g., neighbourhoods, friends), organisations (e.g., non-governmental organisations, government agencies, professional societies) or individuals or groups with shared values. Aggregated forms of social nodes can also include abstract concepts such as human stressors (e.g., climate change, dredging, sewage) that influence social-ecological interactions [28]. Ecological nodes may include biological entities ranging from individual organisms to species, communities, habitat patches (such as green spaces or waterbodies), or geographic entities (e.g., urban districts) and similarly abstract concepts such as biodiversity or ecosystem services [29] or policy issues [30]. There are benefits and drawbacks to aggregation and disaggregation (i.e., larger spatial units into smaller ones, such as small habitat patches), and results at a given resolution will likely resonate more with specific audiences (e.g., local versus regional planners) [10]. For the analysis of a network, one can provide more information and context to nodes by assigning them attributes, which may be categorical (e.g., gender, habitat type) or continuous (e.g., age, population size, species richness) variables. The decision of which attributes are needed depends on the study aim and question [10,11]. For example, different insights derive from characterising a habitat patch by its species richness as opposed to by its type (e.g., forest versus park).

Links represent relationships or interactions between nodes in SENs and can be characterised by different properties. Social-to-social links can represent power dynamics, trust, communication, collaboration, common interests, information or exchange of resources. Ecological-to-ecological links can encompass connectivity between habitat patches through, e.g., seed dispersal or corridors, biotic interactions on the organism level (e.g., predation, parasitism, mutualism, interference competition), movements of species and physical materials (e.g., water, sediment [10]), geographic proximity [32] or information flows between species [33]. Links can be directed or undirected (Fig. 2, upper right). These include the directional flow of the interaction, from social-to-social (SS), ecological-to-ecological (EE), social-to-ecological (SE) or ecological-to-social (ES), as shown in early foundational work on SENs [31]. For example, a directed SE link (i.e., from S to E) might represent a management action or the number of people visiting green spaces, whereas a directed ES link (i.e., from E to S) could indicate an ecosystem service, such as fishing, harvesting fruit, or the impact of green spaces on housing prices. The strength or intensity of the relationship can be represented by its weight, such as the number of interactions (or link attribute, Fig. 2). For simplicity, we refer to both SE and ES links collectively as SE throughout this text. Undirected links can also be represented in SENs, such as mutual friendships where both individuals recognize each other as friends and directionality is not relevant.

Earlier urban ecology studies that applied a network approach (n = 27, Fig. S1, Table S1) primarily focused on urban green spaces (12 studies, i.e., 44.4%), urban waters (9 studies, i.e., 33.3%), or both (3 studies, 11.1%). Four studies explored the urban matrix, and one focused on biodiversity. Across these studies, most social nodes were stakeholders involved in habitat management (10 studies, 37.0%), human inhabitants (3, 11.1%) or socioeconomic factors (3, 11.1%). Ecological nodes were typically green spaces (10, 37.0%) or wetlands (3, 11.1%), waterways (1), green infrastructure (1) or specific tree species (1). Links predominantly addressed landscape connectivity (10 studies, 37.0%, EE links) and stakeholder collaborations (6 studies, 22.2%, SS links). Other SS links included mental models, stakeholder inclusion/exclusion and one undefined link. Only eight of these studies (29.6%) incorporated SE links and only two addressed all three link types (SS, SE, EE; [19, 34]). These findings highlight the underexploration of SENs in urban ecology research, specifically of the links between social and ecological domains.

From concept to analysis: defining the analytical lens for SENs in urban ecology

Social-ecological networks can be conceptualised and analysed in multiple ways, with the choice of approach guided by the research question, the skills of the researcher(s) and available data or resources. Here, we provide an overview of possible options for applying an SEN framework, define core concepts and illustrate how these elements can be used to build and analyse SENs.

Approaches to *conceptualising* SENs range from non-articulated forms, where social and ecological nodes are aggregated without differentiation, to fully articulated SENs, where social-social (SS), ecological-ecological (EE) and social-ecological (SE, including ES) links, are distinct [10] (Fig. 1 most right). A complementary typology has also been proposed, distinguishing between Type I networks, focused on a single dimension (SS or EE links), to Type III networks, which integrate links within and between both dimensions (SS, SE, EE) [26], corresponding to fully articulated SENs [10]. SENs can be conceptualised in four main ways. First, single-layer networks involve one layer of nodes with one type of link (e.g., a stakeholder network linked by information flows, or a food web linked by feeding interactions [35]). Second, multiplex networks involve the same set of nodes replicated across different layers, but each defined by a different type of interaction [16]. Third, multilevel networks involve different types and numbers of nodes across layers, but one kind of link within and between layers [21]. Finally, multidimensional networks combine multiplex and multilevel approaches, with different types and numbers of nodes in different layers and multiple links within and among different node types [19].

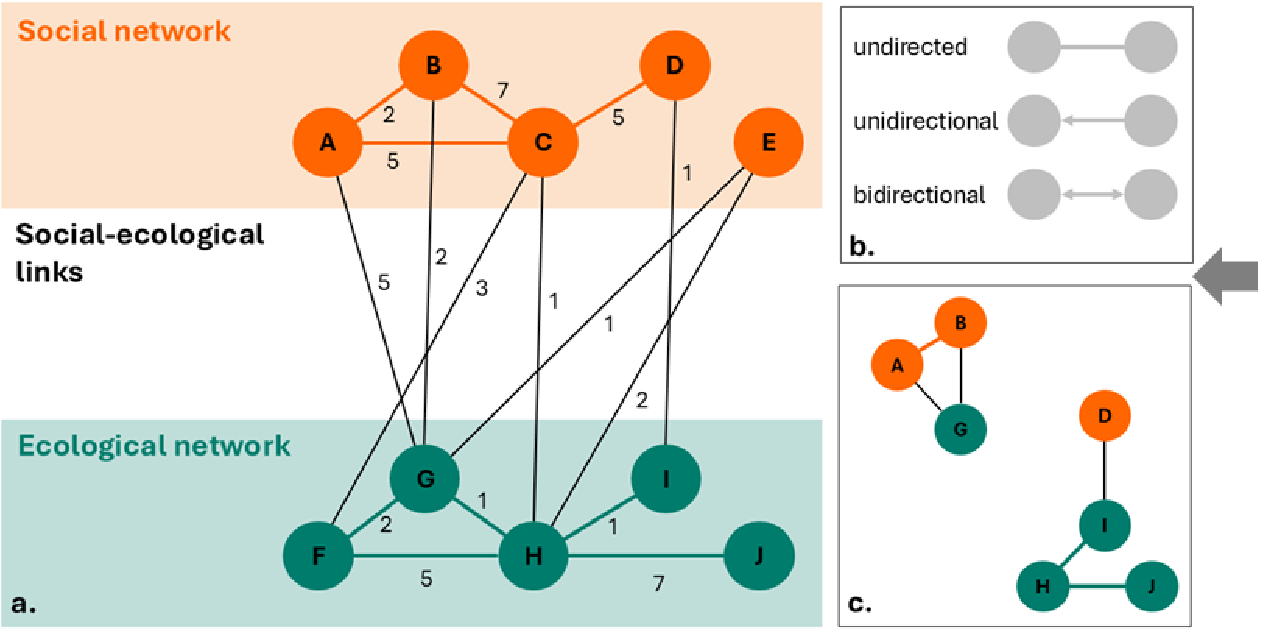
Social-ecological network *data* can be organised in several ways. In adjacency matrices, all nodes are listed in both the first row and column, with entries indicating the links between them (Fig. 2, right panel). Links may be binary (presence or absence of a connection) or weighted (e.g., by connecting strength or distance) [36]. The directionality is captured through the assignment of values. Asymmetric adjacency matrices represent directed networks, where a link from A to B does not imply a link from B to A. Symmetric adjacency matrices represent undirected graphs, where connections are reciprocal. Incidence matrices describe bipartite networks or connections between layers in multilevel networks, with rows representing one type of node and columns another. Alternatively, data can be organised in an edge and node list, where each row represents one link or one node, respectively. The first two columns of an edge list are the nodes that the link connects, and the remaining columns can be attributes. The node list includes the node IDs in the first column and their attributes in the other columns.

Social-ecological network *analysis methods* range from simple descriptive approaches (e.g., tabulating network metrics, or visual representation) to advanced methods such as agent-based modelling, exponential random graph models (ERGMs) or stochastic actor oriented models (SAOM) [10,11,37]. Other analytical methods include motif frequency counts (analysing specific network structures by comparison with a large set of random networks (Conditional Uniform Graphs, which could be seen as a simplified analysis in comparison to ERGM and SOAM)), block modelling (grouping similar nodes) or quadratic assignment procedure (assessing correlations between network matrices; overview in Sayles et al.[10]). While mathematical analyses in ecological and social networks offer strong potential to advance interdisciplinary research [23], integrating SEN analyses remains challenging [17].

Depending on the research question, analyses can target specific nodes and links or apply network-wide indicators. Centrality, a common metric in ecological and social networks [38], assesses a node's relative importance based on its number of links and position relative to other nodes. Centrality metrics include closeness centrality (proximity to others), betweenness centrality (how many paths lead through the node of interest) and degree centrality (number of incoming, outgoing or total links). Centrality helps identify key actors, bottlenecks or dominance structures in urban biodiversity management.

Alternatively, network-level metrics describe the overall structure. Measures such as path length (number of links connecting the nodes in a network), diameter (longest of all the shortest paths in a network), or density (ratio of the actual to the maximum possible number of links) provide insights into connectivity [39]. For instance, in a network where organisations collaborate on urban biodiversity projects, short path lengths indicate rapid information flow, while large diameters may suggest isolated actors. Density reflects how well-connected the organisations are, with high density indicating frequent interactions and low density showing fewer connections (bearing in mind that density does not scale well with network size). Identifying structural patterns supports an understanding of which network forms will most likely enhance biodiversity outcomes. Nevertheless, one metric alone does not provide a full picture of a social-ecological system; multiple measures are typically needed to describe and thus explain the system.

Motif analysis has become central in SEN research, particularly for understanding collaborative governance and environmental problems [12]. Motifs are recurring connectivity patterns between social and ecological nodes [31] (Fig. 2c), such as a triangle linking two social actors to a shared ecological resource (e.g., shared management) or a social actor connected to multiple, interlinked ecological resources (e.g., isolated management). These patterns, also referred to as configurations, have been classified into distinct motif families that vary in their levels of social, ecological and social-ecological connectivity [31]. Motifs are particularly useful for assessing social-ecological fit, or the alignment between ecological and social nodes. Institutional misfits occur when key ecological resources lack any institutional arrangement, while institutional-ecological fit exists when the key ecological resources are accounted for by one or more institutions [28]. Further distinctions have been made between ecological fit, social fit and social-ecological (SES) fit [10]. Although social-ecological fit is generally linked to positive environmental outcomes, empirical research testing this is still lacking [18].



	A	B	C	D	E	F	G	H	I	J
A		2	5				5			
B	2		7				2			
C	5	7		5		3		1		
D			5						1	
E							1	2		
F			3				2	5		
G	5	2			1	2		1		
H			1		2	5	1		1	7
I				1				1		
J								7		

Figure 2. a. Schematic of the example network (cf. Table 1). Circles represent nodes and lines represent links, with social (S) and ecological (E) elements shown in orange and green, respectively; black lines indicate social-ecological links. Numbers indicate weight, a measure of link strength. b. Examples of undirected and directed links. c. Two examples of motifs representing shared (top) and isolated (bottom) management. Right panel: adjacency matrix displaying social and ecological nodes (cf. Table 1). Numbers represent link weight, for instance the frequency of interactions.

Applying social-ecological network theory to urban ecology: a case study from Melbourne

To guide the application of an SEN approach, we developed a checklist for conceptualizing an SEN illustrated with an example from Melbourne, Australia (Table 1). Melbourne was selected for its strong research base in urban ecology research. However, the checklist applies to cities globally, including in contexts with limited data, different SEN research questions or at early stages of research. It is also intended to support the design and data collection process. The checklist draws on existing guidance in the literature on ecological networks [40], social networks [17] and SENs [11].

Between 2010 and 2013, four of this paper's authors (*initials removed for review*) investigated how urban green spaces, including private front yards, public parks, reserves and golf courses, support biodiversity and ecosystem services. The project aimed to measure the biodiversity value of different types of urban green spaces and to determine which habitat attributes and management practices increase biodiversity across multiple taxa. Findings showed how different vegetation attributes (e.g., complexity of different strata, proportion of native plant species, number of large old trees) influenced the habitat value of golf courses, parks and front yards for multiple taxa including birds, bats, bees and true bugs (hemipterans) [41-44]. However, it became evident during the project that ecological data alone captured only part of the picture. For example, vegetation outcomes on golf courses were shaped by the decision-making of managers and influenced by ongoing interactions with golf-course users and the neighbouring community (unpublished data). These social dynamics differed between private (members-only) and public (municipally run and 'open to all') golf courses. In this way, each golf course was a functionally distinct social-ecological system with varying relationships between social nodes and impacts on biodiversity. Although qualitative interviews were conducted to explore these dynamics, the study was not originally designed as an SEN analysis. Explicitly embedding social actors within a network framework would likely have revealed additional drivers of biodiversity outcomes that were not captured. We use this example, even without complete data, to build on these insights and present a checklist (Table 1) to guide the conceptualization of an SEN, including at early stages before data collection.

Table 1. Checklist describing a potential pathway for conceptualizing and analysing social-ecological networks (SENs) involving urban biodiversity, based on literature about ecological networks [40], social networks [17] and SENs [11], demonstrated through the Melbourne case study and visualised in Fig. 2.

Checklist item	Melbourne case study
1. Define a clear research question for social-ecological interdependence related to urban biodiversity (examples in Table 2) and define the **spatial scale** (e.g., single urban green or blue space or whole city).	**Research question**: Among golf course managers* and users, whose opinion is sought and how are decisions made about the vegetation composition and structure on the golf course? * The golf course managers were divided into subgroups in the next step. **Spatial scale**: golf courses within Melbourne.
2. Identify ecological (e.g., species, habitats) **and social** (e.g., individuals, organisations) **nodes** relevant to the research question. **Define network boundaries** (determining what should be inside/outside the analysis). Consider whether it is more appropriate to define individuals as nodes or to aggregate individuals into groups. Define	**Relevant actors (social nodes)** aggregated into groups: (A) superintendents (responsible for on-the-ground management); (B) groundskeepers (golf-course maintenance); (C) golfers; (D) golf-course architects (design course); (E) "owner" (whether private or responsible within the municipality)

attributes that might be relevant for later analysis (e.g., traits, demographics).	**Social nodes** outside the boundary setting of the question: golf-course board members (responsible for governance and administration), professional association (Australian Golf Course Superintendents Association), and also the surrounding community (non-users). **Relevant ecological nodes:** the studied sites within the golf courses (F-J) and, as attributes, their vegetation structure (trees, understory, fairways). **Ecological attributes** outside the boundary setting of the question, e.g., faunal biodiversity.
3. Conceptualise a list of possible SS, SE, and EE links. The starting point can be the identification of interfaces where SE interactions likely occur, and mapping out the potential links and nodes. Select the types of links (e.g., species movement for EE, communication for SS, management for SE).	**SS links:** any type of social interaction between social actors. For instance, communication, measured as the number of contacts per year. **SE links:** any type of interest or influence that exists between a social and ecological actor, for instance, the maintenance by groundskeepers (B) on studied site within the golf course, e.g., irrigation, mowing, fertilisation of certain plants, tree planting, measured as the number of times per year or month). **EE links:** any type of ecological interaction or link between studied sites. For instance, distance measured in meters (although EE links were not part of the example).
4. Organise your data in an adjacency matrix or, if no data are collected yet, construct a preliminary adjacency matrix based on hypotheses, with nodes as columns and rows, and links as entries. This makes the existing information more organised and highlights potential gaps. It may also help to identify the resources needed to build the SEN, e.g., acquire more data.	**Adjacency matrix** where each row and column includes the full list of social and ecological nodes from step 2. Entries can be the presence/absence data for each SS, SE and EE links listed in step 3, or they can be already quantified relationships (e.g., the number of contacts per year).
5. Collect empirical data, if needed, to refine the relationships identified in the adjacency matrix. This may include field observations, surveys, interviews, or remote sensing.	While the researchers have already collected the ecological data, interviews focusing on, e.g., frequency of interactions among social actors and types of exchanges (SS) and how this impacts the maintenance of golf course vegetation (SE) would add a different layer of understanding in this example.
6. Refine the adjacency matrix and construct the network using the collected data. This can also include grouping nodes or refining links based on the collected evidence.	This might involve the integration of new insights from the interviews or additional field observations.
7. Analyse the network quantitatively (e.g., network metrics, exponential random graph model (ERGM)) or qualitatively to address the research question.	Since the research question is on the most influential actor, centrality and path length might be appropriate metrics.

Advancing urban biodiversity research through SENs

To advance urban biodiversity research using SENs, we identified nine research themes (Table 2). These themes emerged from a design thinking workshop held in July 2023 in Berlin, Germany (Fig. S2), and integrate the identified gaps from the scoping review (Table S1). They are intended to guide future SEN applications in urban biodiversity research in both research and practice and to meaningfully inform future conceptual and empirical work:

1. Environmental decision-making: Investigating how SEN interactions emerge, the conditions that enable them, including macro-drivers such as international agreements or municipal strategies, and the impacts of these decision-making processes on urban biodiversity. The opposite scenario is also possible, where emerging biodiversity issues influence decision-making at the macro scale.

2. Barriers and dysfunctions (related to fit and misfit): Studying the dysfunctions in an ecological network (e.g., absence or loss of keystone species) and how they impact ecosystem functions and services. Also, addressing barriers that impede people's access to these services or the “invisible” components of a network that emerge under certain circumstances (e.g., “sleeping” nodes or links that activate when needed, such as during environmental catastrophes like urban flooding or heatwaves).

3. Resilience and resistance to global challenges: Understanding how SENs reveal resilience or resistance to pressures such as climate change, disease outbreaks, invasive species and natural disasters.

4. Ethics, power dynamics, and societal norms: Examining how decision-making processes reflect and reproduce power dynamics, ethical considerations, and identifying misfits (e.g., scale and responsibilities).

5. Human-nature relationships (human perspective): Exploring the positive and negative relationships (e.g., emotions, attitudes) between humans and non-human actors, ecosystem services or disservices, spatial use, and interdependencies between people and other organisms within networks.

6. Nature-human relationships (non-human perspective): Investigating networks from the viewpoint of non-human species, examining how human activities shape, disrupt or support ecological interactions across spatial and temporal scales.

7. Intercity influences: Understanding how urban areas are interconnected through ecological and social processes and how these linkages influence biodiversity across cities.

8. Temporal dimensions: Although temporal dimensions can be part of the previous themes, we highlight them as a distinct theme because they capture dynamic changes in relationships between social and ecological actors that are often missed in static analyses.

9. Distinctiveness of an urban SEN: While all previous themes and questions can be approached comparatively to analyse differences among cities, this theme focuses on broader, general questions that focus on the unique characteristics of urban SENs as opposed to rural SEN.

Table 2. Nine key urban-ecology research themes with a focus on biodiversity where applying a social-ecological network (SEN) approach has great potential. Each theme is accompanied by a definition, sample research questions and possible network metrics, primarily drawn from graph theory (more details and examples on the possible network metrics can be found in Table S2) [45,46]. While a range of network-based approaches can address these questions, this overview provides examples to inspire SEN approaches in urban ecology.

Primary focus	Research themes	Possible questions	Possible network metrics
Urban environmental governance	**1. Environmental decision-making** to inform and improve policies and decisions related to urban biodiversity.	Who is the major actor when it comes to decisions about biodiversity management in urban green and blue spaces? What type of governance (network) structure will likely deliver more effective biodiversity-conservation outcomes? How do emerging biodiversity challenges shape interactions, such as knowledge exchange, trust-building and frequency of meetings, among decision-makers involved in biodiversity-policy and conservation-strategy processes?	Centrality, path length and motif research (including ERGM and SAOM).
	2. Barriers and dysfunctions to identify obstacles to effective urban environmental governance and that support or deliver ecosystem functions and services**.**	What physical barriers exist in urban areas that restrict access for people, and how does infrastructure influence access to ecosystem services? Which “sleeping” nodes or links in an urban social-ecological network can become crucial during specific events or circumstances? What cultural and socio-economic barriers exist for people in urban areas to support or protect biodiversity (e.g., lack of opportunities, minority identities, lack of local knowledge, erosion of cultural values, perceptions of insecurity, or social inequality)? Do these social barriers affect different plant or animal species groups differently?	Temporal dynamics, spatial network analysis, culture and networks
	3. Resilience and resistance to global challenges.	What social and ecological conditions are most likely to absorb shocks and disturbances from climate impacts, natural disasters, disease outbreaks, etc.?	Centrality and network density

		Compared to single cities, how do networks of cities enhance resilience to disturbances particularly through sharing knowledge, values, and strategies? (*also theme 7*) What are the key nodes that promote the resilience of urban systems in the face of [climate change | diseases | invasive species | natural disasters]?	
	4. Ethics, power dynamics, and societal norms related to urban nature.	How is local knowledge and/or traditional ecological knowledge integrated into decision-making processes about urban biodiversity? How does a city address the needs and moral obligations of marginalised people and future generations? How do ethics, power dynamics and societal norms shape decision-making processes about urban biodiversity?	Core-periphery analysis, centrality.
Human-nature and nature-human relationships	**5. Human-nature relationships** from an anthropocentric perspective, examining how different nodes interact and use urban green and blue spaces, as well as species and/or individual organisms.	How does social-ecological connectivity, specifically interactions between humans and green/blue spaces, impact human wellbeing across different urban contexts? How does a person's social network of friends shape their relationship with nature in an urban environment? How do patterns of human-nature interactions affect the composition, structure, and dynamics of ecological communities in urban ecosystems?	Analysis of in-degrees, centrality, ego network analysis, temporal and ecological network analysis, ERGMs, spatial network analysis.
	6. Nature-human relationships from a non-human perspective.	Which non-human species serve as connectors between urban green or blue spaces via, e.g., dispersal, and how do these species also facilitate nature-human connections or enhance social interactions among people? How does one species interact with other human and non-human nodes in its ecosystem, and what are the impacts of these interactions on ecological and social systems?	ERGMs, ego network, temporal networks, ecological network analysis (ENA), Spatial network analysis, temporal and ecological network analysis (see above) to analyse

		What are the key interdependencies and interactions within a network that simultaneously enhance ecological processes, promote biodiversity and improve nature-human relationships? If so, what are they and how do they contribute to win-win outcomes for humans and non-humans?	
Intercity influence	**7. Intercity influence** to understanding how cities affect each other and urban biodiversity.	Are some cities "keystone" nodes in a network of cities, i.e., having a disproportionate influence on other cities? If “keystone cities” exist, how do they impact [biotic homogenisation | functional traits | the loss of biocultural values | environmental political agendas] across a city network? Do shared values among cities influence other cities and, if so, how? How, if at all, does the spread of specific types of information (e.g., technological advancements, public-health knowledge) and innovation (e.g., green technologies, startup ecosystems) differ between cities in the Global North and the Global South, and what factors influence these patterns globally? How are pathogens and invasive species transported between cities through a global supply chain?	Centrality, culture and network, spatial network, temporal network, exponential random graph models and SAOM, trade networks.
Temporal dynamics	**8. Temporal dimensions** to understand how a city’s history influences its social-ecological dynamics.	How does a city’s history (e.g., war, natural disaster) influence the relationships between its human and non-human nodes? Are there temporal patterns in which SENs in cities evolve over time, and what are the implications of these changes for emergent properties such as biodiversity conservation?	Comparing SENs to different historical or seasonal data sets, loop analysis. SAOM. Comparing different networks that exist at different moments in time.

		Are there seasonal variations in SENs, and what are the implications of these variations for emergent properties such as biodiversity conservation?	
Distinctiveness	**9. Distinctiveness of an urban SEN compared to non-urban or other urban SENs** to understand the distinctiveness of urban systems compared to other systems or among urban systems.	Are there common or universal network elements (e.g. nodes, links, motifs) of urban SENs compared to non-urban ones? Do urban SENs differ across cities (also from different sizes, i.e.,metropolises and small and medium-sized cities) and from non-urban areas and, if so, how? What, if any, are the novel nodes, edges and attributes of urban SENs compared to non-urban SENs?	Comparing networks for different cities and between cities and non-urban areas (e.g. studied via network metrics, or motifs)

Challenges and considerations

In this perspective, we argue that an SEN approach allows urban ecology researchers to unpack, define and formalise complex social-ecological systems into tangible components, making them more concrete and easier to understand [31]. We argue that the SEN framework can offer particular value for advancing urban biodiversity studies that account for both biotic interactions and social dynamics. Current key blind spots are, for example, that species-level applications are rare, temporal misfits between urban management and ecological or evolutionary processes remain underexplored, historical data are underused, social relations such as trust and legitimacy are often overlooked and intercity influence is seldom addressed from a network perspective to name a few. However, we also acknowledge challenges to their application.

When and how to apply social-ecological networks in urban ecology?

"There is no such thing as the right way to represent a social-ecological network of a given system, just a useful and not so useful one" [9]. This quote by early SEN scholars captures a central consideration: SENs excel at untangling complexity where relationships between and among social and ecological actors are the focus [10,31]. Yet, SENs are not always necessary, and other approaches might be sufficient for research questions with less of a focus on how entities within a system influence each other through complex webs of interactions [47,48]. The complexity of SENs should be tailored to the research question. While fully articulated SENs (type III) provide valuable insights, simpler networks focusing on selected nodes, links or motifs can often suffice [10,26,31]. Aggregating nodes by similarity or proximity may further simplify analysis. In cases where causality is the primary interest, path analysis or structural equation modelling [49] may be more appropriate. Ultimately, the decision of *when* an SEN is useful and *how* it will be conceptualised depends on the research question [10,29]. Our list of potential research questions (Table 2) aims to inspire and guide future studies in this emerging field.

Conceptual and data challenges

Guerrero et al.[17] highlighted persistent challenges in network analysis, including inadequate handling of incomplete data, statistical dependencies and weak links between theory, research questions and analytical methods. Data scarcity and heterogeneity remain major obstacles for SENs, especially as data are often siloed and costly to collect [11]. Researchers face trade-offs between investing in the collection of new data and using existing data. However, for quantitative analyses, secondary data analysis can be a viable option, especially given the growing availability of large, open datasets. For instance, egocentric networks were derived via random forest models with data from the Socio-Economic Panel in Germany [50]. Further, although any level of network detail is theoretically possible, a descriptive approach can sometimes suffice for initial explorations. Social-ecological networks offer a lens to rethink assumptions and relationships [32], even without a fully quantified data set, as shown in our Melbourne case study. And the impact of missing data depends on the metric used. For example, basic centrality measures are relatively robust to missing data, whereas betweenness centrality is more sensitive [17]. Further, despite limitations, techniques such as Bayesian modelling can address missing data and quantify uncertainties [51]. Starting with smaller, manageable network motifs or drawing from established relationships in the literature can mitigate the risks of overlooking key nodes. Importantly, advancing urban SEN research will also require greater attention to the Global South, where biophysical and socio-economic contexts differ significantly from the Global North and where urban ecology research and secondary data remain less developed [52].

General considerations for future SEN research

First, future urban SEN studies should aim for a balanced integration of social and ecological research. While we found in our scoping review that urban SENs have focused predominantly on ecological analyses, non-urban SEN studies tend to emphasise social network analyses [10]. We echo the growing call for stronger collaborations between social and ecological researchers and highlight the importance of bridging these disciplines to achieve more comprehensive insights.

Second, SENs offer opportunities beyond academia and interdisciplinary collaborations [23]. They can support transdisciplinary collaboration by translating the gained knowledge into actionable insights and bridge the knowledge-action gap for policymakers through, e.g., policy briefs. Similarly, museum exhibitions and signs in urban parks could more effectively visualise human-nature interconnections through SEN-based illustrations. Tailored communication featuring clear and engaging, illustrative or even interactive network visualisations could serve as powerful outreach and educational tools, especially to demonstrate the interconnectedness of humans and nature within urban areas.

Third, while we focused on SENs, there is growing research into social-technological networks (STNs) [53,54]. As interest in social-ecological-technological systems rises within urban ecology[2], a logical progression would be to connect SENs with STNs in social-ecological-technical networks, bridging the three interconnected domains.

Finally, a critical knowledge gap stymies the application of SENs to comparative studies in urban ecology. While cities worldwide face common challenges, such as biodiversity conservation and climate change mitigation, they do so within diverse cultural and governance contexts. Comparative urban ecology (*sensu* McDonnell and Hahs [55]) is instrumental when it comes to identifying these commonalities and differences, potentially leading to universal strategies for sustainable urban development. By focusing on specific actors and links, the SEN framework may facilitate comparisons across social-ecological systems [9]. However, while our identified themes and questions can be addressed comparatively, the methodological approach may still hold its challenges, as widely discussed in comparative network analyses [56]. Integrating SEN research into nationally funded long-term research programs presents a promising path forward [10] and can facilitate the establishment of comparative urban SEN research. Doing so will not only better equip the urban ecologists' toolbox but also facilitate comparisons of complex social-ecological interactions across diverse cities. This approach can reveal how these dynamics shape emergent properties, irrespective of geographical location and contribute to our understanding and vision of socially, ecologically and technologically resilient cities [7].

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Supplementary Material

Scoping literature review

We performed a literature review to identify studies that previously used social-ecological networks in urban ecology. After identifying potentially relevant publications as described in the two boxes in the upper row, we manually screened all papers to remove those that did not specifically address network science. Papers were screened using the abstract or main text. Papers were included in the final review if they met the following criteria: (1) They were empirical or theoretical studies based on primary field or desk research, case-study synthesis, or computational modelling. Review and opinion papers were not included. (2) Papers needed to apply a network approach with a set of social and ecological nodes and links between either the ecological, social or both dimensions.

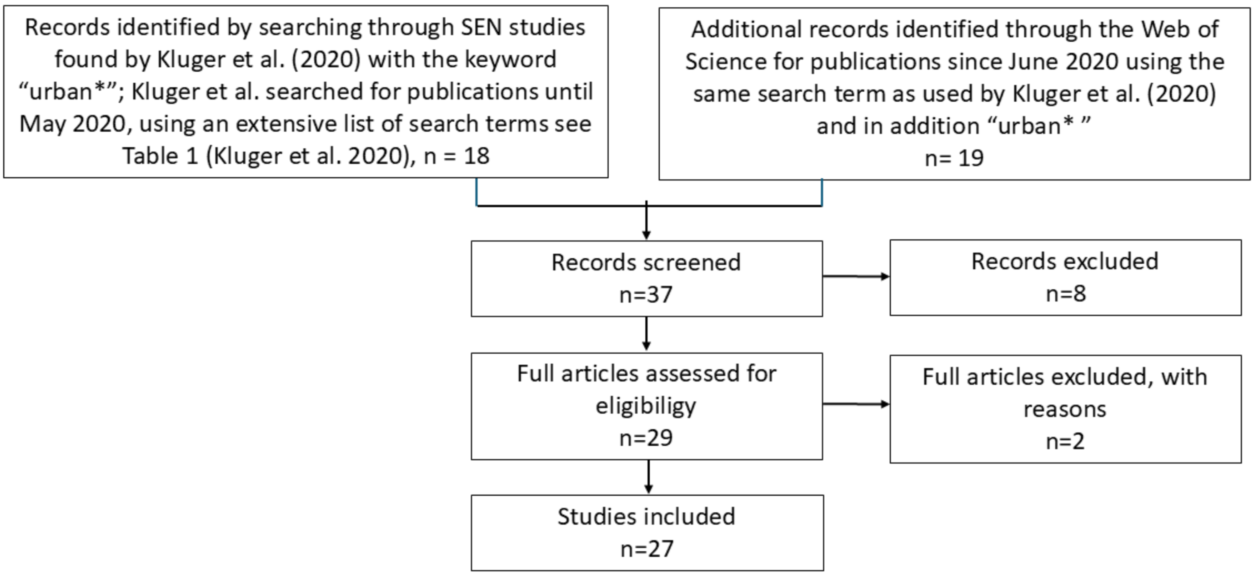

Figure S1. PRISMA flow diagram for the literature review process (diagram adapted from Page et al. 2021).

Table S1. Scoping literature review results consisting of 27 studies that previously applied a network approach in urban ecology.

Publication	**Realm and other concepts**	**Nodes** (E = ecological, S = social)	**Links**	**Type of links** EE = ecological-ecological SS = social-social SE = social-ecological	**Scale match/mismatch**
Aly et al. 2010	Terrestrial	Green patches (E)	Connectivity	EE	
Arnaiz-Schmitz et al. 2023	Urban matrix	Landscape, socioeconomic factor	Influence of socio-economics on land use/change	*not defined*	
Bergstein et al. 2014	Freshwater	Wetlands (E) and stakeholders (S)	collaboration between actors, connection between wetlands	SS, SE	yes
Calder et al. 2015	Freshwater	Wetlands (E)	Connectivity between sites; weaver bird movement	EE	
Djoudi et al. 2022	Terrestrial	Trees (E) and residents (S), focus on single tree species *Parkia biglobosa*	Benefits of trees to residents, interactions among people	SE	
Egerer & Anderson 2020	Terrestrial	Different parcels of land use (E), socio-economics (S)	Connectivity, socio-economics	EE, SE	
Enqvist et al. 2014	Terrestrial and freshwater	Citizen (groups/ networks) (S)	Collaboration	SS	
Ernstson et al. 2008	Terrestrial	Stakeholder (S)	Collaboration	SS	
Ernstson et al. 2010	Theoretical	Allotment gardens (E), urban parks (E), cemeteries (E) and	Collaborations, management of green sites, connectivity	SS, SE, EE	yes

		protected areas (E) stakeholders (S)			
Ernstson et al. 2013	Theoretical	Urban green areas (E), local actors (S)	Value articulation of social actors, ecological flows (water, species movement, etc.)	SE, EE	Yes
Frimpong Boamah 2018	Freshwater	Urban watershed (E), stakeholders (S)	Collaboration, management	SS, SE	yes
Furlan et al. 2022	Terrestrial	Green patches (E)	Connectivity	EE	
Gao et al. 2018	Freshwater	Stakeholders (S)	Collaborations	SS	
Holt et al. 2012	Freshwater	Individuals and groups (S)	Collaborations	SS	
Larson et al. 2013	Freshwater	Stakeholders (S)	Collaboration	SS	
Łaszkiewicz et al. 2022	Terrestrial	Urban green spaces (E)	Connectivity	EE	
LeBrasseur 2022	Urban matrix	Ecological, hydrological, recreational, working lands (E)	Connectivity	EE	
Lishan et al. 2021	Freshwater	Stakeholders (S)	*Not clearly defined*	SS	
Liu et al. 2020	Terrestrial	Green infrastructure (E)	Connectivity	EE	
Mao et al. 2015	Freshwater	Waterways (E)	Water flow	EE	
O'Connor & Levin 2023	Freshwater	Stakeholders (S)	Mental models	SS	

Ossola et al. 2019	Terrestrial	Green patches (forests and yards) (E)	Connectivity	EE	
Sen et al. 2021	Terrestrial and freshwater	Stakeholders (S)	Exclusion and inclusion of stakeholders	SS	
Villaseñor et al. 2018	Biodiversity	Stakeholders (S)	Collaborations	SS	
Wang & Pei 2020	Terrestrial and freshwater	Green patches (E) and wetlands (E)	Connectivity	EE	
Xiu et al. 2017	Terrestrial	Green patches (E) (attributes: tits, toads and humans)	Connectivity between sites	EE	yes, landscape scale
Zhang et al. 2018	Urban matrix	Natural (E) and socioeconomic sectors (S)	Flow within and between social and ecological actors, *not clearly defined*	SS, SE, EE	
Zhang et al. 2016	Urban matrix	ecological compartments (forest, atmosphere etc.) (E) and social (human activities e.g. industries, farms etc.) (S)	Nitrogen flow	SE, EE	

Table S2. Details and examples of possible network metrics from Table 2, primarily drawn from graph theory (Urban and Keitt, 2001, Koutrouli et al. 2020).

Analysis of in-degrees (i.e., number of links from blue/green spaces to human actors) versus perceived individual wellbeing.
Centrality to identify the key nodes (individuals or organisations) with the most power or influence in the network based on the number of direct links (Newman, 2010; Centola, 2023). Popular methods include (1) degree centrality to identify nodes with the most links, (2) betweenness centrality to highlight nodes that act as bridges between others by controlling the flow of information or resources, (3) eigenvector centrality to measure how well the neighbours of a node are connected and (4) closeness centrality to show the distance from one node to all others and thereby identify the central and peripheral nodes and their reach, or influence.
Core-periphery analysis (Borgatti and Everett, 2000) to understand the degree to which local knowledge holders are integrated in decision-making according to their location, e.g., on the periphery vs. within the decision-making network.
Culture and network: In this research discipline, a key concept is the "cultural hole": the gaps in cultural knowledge or understanding between different social groups or networks that can limit the flow of ideas and information across them (Lizardo 2023).
Density: One of the earliest explorations of social-ecological systems through a network approach focused on resilience (Janssen et al., 2006). Approaches here could address **centrality** (see above) or **network density** to explore the hypothesis that more connected networks are more resilient, the same relates to a high density of actors and low centralisation and also considering motifs to better understand patterns (Bodin and Tengö 2012).
Ecological network analyses (ENA), such as degree centrality, to identify species or urban spaces with the most direct links to other ecological elements (showing their significance in maintaining ecosystem services), or betweenness centrality to identify species or urban areas that are critical nodes and facilitate essential interactions between different paths in the ecosystem. Ecological network analyses (e.g., as outlined in Fath et al. 2007 and undertaken by Morris et al. (2021)) in urban-industrial ecosystems can be excellent starting points. Adding the social component can help elucidate potential barriers..
Ego network analysis (Prell and Schaefer, 2023) to understand the influence of social connections on a person’s relationship with nature. For example, having a friend (the “alter”) who frequently visits parks or participates in nature-related activities can make a person (the “ego”) more likely to perform these behaviours. Or to understand one species’ (the “ego”) interactions with its direct connections, including humans and other non-human species (the “alter”).
Exponential random graph models (ERGMs) to statistically model the likelihoods of various network configurations, e.g., considering the influence of human-nature interactions on non-human species. Further, to model how various factors (e.g., city influence, ecological and cultural interactions) affect the likelihood of keystone cities and their impacts
Motifs (Bodin and Tengö, 2012; Bodin, 2017) to identify common governance sub-structures, typical interaction patterns, governance roles and potential mismatches in the network configurations or the analyses of network dynamics to understand feedback processes that are characteristic of networks (Snijders and Steglich 2023).
Path length to address communication questions within the network. The average shortest **path length** (Centola, 2023), i.e., smallest number of “steps” between nodes in a graph measures how efficiently

information spreads through a population. This concept also considers “strong” ties (e.g., inner circles such as friends and family) and “weak” ties (e.g., acquaintances). Alternatively, paths between two nodes of interest can be measured, i.e., how many steps it takes for a governance decision to be enacted on an ecological node.
Spatial network analysis can elucidate how urban infrastructure(e.g. pathways, roads or public transport **system**) influences access to ecosystem services across a city. Here, applying social networks layers in GIS can provide crucial information (Hipp, 2023). Further, to understand social movement patterns and the geographic distribution of services and disservices or to understand how spatial arrangements influence win-win interactions. It can further help to map the spatial distribution of keystone cities and their influence on other cities, followed by an analysis of how spatial patterns affect biodiversity and cultural values.
Temporal dynamics, e.g., longitudinal approaches at two or more moments (Carroll et al., 2024), or **simulations** can help to determine when specific links or nodes become active or when certain links may emerge under varying circumstances.
Trade networks (Prell et al., 2023) could inspire questions about how pathogens and invasive species spread between cities given the focus of commodity trade networks on flows of goods and services from one actor (in this case a city) to another.

Design thinking approach applied for the workshop

A summary of how elements of design thinking were applied to carry out the workshop. Design thinking is an approach to drive meaningful and sustainable transformation processes in business and society (Dorst, 2011). It applies methods, workflows and mindset of design to tackle wicked problems with no clear evident solution (Dorst, 2011). Being an effective tool for fast-paced group work, design thinking is a valuable approach to conduct workshops (Micheli et al., 2019), including in research contexts (Pusca and Northwood, 2018).

Figure S2. Design thinking approach where our nine research themes derived from (Table 2).

In the framework of the organized workshop, two main aims were defined a priori: (1) identify key questions that can be addressed with a social-ecological network (SEN) approach in urban systems across realms (terrestrial, freshwater, marine) and spatiotemporal scales (e.g. geographical regions, future scenarios); (2) identify relevant methods and approaches to (a) construct, inform and analyse social-ecological networks in urban systems (incl. challenges to do so), and (b) compare SENs across realms and spatiotemporal scales.

Participants were divided into four teams, built to maximize professional (early and senior researchers, network experts and urban ecologists) and personal (in terms of sex, age and country of origin) diversity within each group (Micheli et al., 2019). Throughout the workshop, two teams worked on aim 1 and the other two worked on aim 2, supported by variable materials (digital/analogue) and working within variable spaces (indoor/outdoor). Each team tackled their aim going through the canonical steps of the design thinking iterative process (Schwemmle et al., 2018), re-adapted where needed to fit the topic covered. Given the aims of the workshop, the activities were mostly based on the initial phases of the process (namely the so-called “problem space”, divided into the “understand”, “observe” and “define point of view” phases). However, several tools and mindsets of the subsequent “solution space” were utilized, too, such as brainstorming creative approaches to explore potential solutions and cross-sharing sessions to maximize knowledge exchange (Schwemmle et al., 2018).

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