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## ABSTRACT

Urban ecology is a rapidly growing research field that has to keep pace with the pressing need to tackle the sustainability crisis. As an inherently multi-disciplinary field with close ties to practitioners and administrators, research synthesis and knowledge transfer between those different stakeholders is crucial. Knowledge maps can enhance knowledge transfer and provide orientation to researchers as well as practitioners. A promising option for developing such knowledge maps is to create hypothesis networks, which structure existing hypotheses and aggregate them according to topics and research aims. Combining expert knowledge with information from the literature, we here identify 62 research hypotheses used in urban ecology and link them in such a network. Our network clusters hypotheses into four distinct themes: (i) Urban species traits & evolution, (ii) Urban biotic communities, (iii) Urban habitats and (iv) Urban ecosystems. We discuss the potentials and limitations of this approach. All information is openly provided as part of an extendable *Wikidata* project, and we invite researchers, practitioners and others interested in urban ecology to contribute additional hypotheses, as well as comment and add to the existing ones. The hypothesis network and *Wikidata* project form a first step towards a knowledge base for urban ecology, which can be expanded and curated to benefit both practitioners and researchers.

*Key words:* conceptual network, ecological theory, hypothesis network, knowledge visualisation, map of science, research synthesis, urban biology, Wikidata.

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## I. INTRODUCTION

### (1) Urban ecology

*‘to truly advance the discipline of urban ecology requires the creation of new hypotheses and the identification of confirmed generalizations’* McDonnell & Niemelä (2011, p. 12)

Urban ecology is a multifaceted research field that ties together research traditions and methods from a wide range of backgrounds and disciplines. Over the past century, it has been adopted and expanded by researchers from fields as diverse as the social sciences, natural sciences and engineering (McDonnell & Niemelä, 2011; Weiland & Richter, 2011; Wu, 2014). While urban ecology used to be underrepresented in textbooks and journals of ecology (Forman, 2016), it is now recognised as an important research field for ecologists, evolutionary biologists and others. With urban systems being responsible for 60–80% of natural resource consumption (Peter & Swilling, 2012; UN-Habitat, 2017, 2020), and substantially impacting every other ecosystem on the globe, urban ecology has become a key research field in tackling the sustainability crisis (Rosenzweig *et al.*, 2010; Sachs *et al.*, 2019; Spiliotopoulou & Roseland, 2020; Tanner *et al.*, 2014). A number of journals cover the intersection of ecology with urban planning, urban biodiversity conservation and urban socio-economy, such as *Landscape and Urban Planning* (founded in 1974), *Urban Ecosystems* (1997), *Urban Forestry and Urban Greening* (2002) and the *Journal of Urban Ecology* (2015).

Urban ecology has different meanings to different researchers and stakeholders, a circumstance that is rooted in the history of the field, the unstandardized use of the term ‘urban’ (McIntyre, Knowles-Yanez & Hope, 2008; MacGregor-Fors, 2011; McDonnell & Hahs, 2008; Sukopp, 2008) and different meanings of the term ‘ecology’ (Schwarz & Jax, 2011). For example, Sukopp (1998) divided urban ecology into a solution-oriented branch with a research agenda to make cities more habitable and sustainable

from the perspective of humans, focusing, for example on nature-based solutions and green infrastructure; and a natural-science branch that studies the natural world within cities, including environmental, biological, evolutionary and ecological patterns and processes, and treating human influences as ecological factors. Both branches are interdisciplinary; the first with a focus on urban planning and the second taking the perspective of natural scientists. They have partly been developed in concert, and the Berlin School provides an example for linking ecological studies with approaches to conserve and develop cities for the benefit of humans (see Kowarik, 2020; Popkin, 2022).

A framework introduced by Pickett *et al.* (1997) and put forward by Grimm *et al.* (2000) differentiates between ecology of cities and ecology in cities. Here, ecology in cities focuses on the distribution, abundance and interactions of non-human populations in the context of the diverse influences and impacts that urbanisation poses on them (Grimm *et al.*, 2000). The ecology of cities has a broader scope: it integrates ecology in cities with research from a social and environmental science perspective, with the aim of studying and understanding cities as ecosystems from an interdisciplinary perspective, including how they ‘process energy or matter relative to their surroundings’ (Grimm *et al.*, 2000, p. 574), but also looking at cities as social-ecological systems. Going even further, Des Roches *et al.* (2021) proposed to integrate evolutionary biology into the investigation of urban social-ecological systems, and McPhearson *et al.* (2016b) envisioned a ‘science of cities’ which comprises the ecology in, of and for cities in order to: ‘motivate new and advanced cross-city comparative ecology, to develop more unified conceptual frameworks to advance urban ecology theory, and to synthesise core urban ecology research principles to guide future research in the field’ (McPhearson *et al.*, 2016b, p. 198).

What researchers mean by urban ecology tends to be shaped by their disciplinary background and the research school they come from (Dooling, Graybill & Greve, 2007).

It is a common narrative that urban ecology in Europe focused on what Grimm *et al.* (2000) described as ecology *in* cities, while urban ecology in the anglophone literature was shaped by the sociological adaptation of the term ‘ecology’ to urban settings by the Chicago School of urban ecology in the 1920s (Wu, 2014), adopting an ecosystem-centred perspective with a focus on humans as key agents from the start (ecology *of* cities). Yet, this view is at least in part the result of barriers in communication. For example, there is a vast amount of urban-wildlife literature in the USA (Magle *et al.*, 2012) that even though not explicitly termed urban ecology can be viewed as ecology *in* cities; and there is the holistic ecosystem-centred research in Europe put forward in the late 1960s and culminating in the meticulous analyses of ecosystem flows of the metropolitan region of Brussels (Danneels, 2018; Kowarik, 2020) that can certainly be regarded as ecology *of* cities. International exchange between researchers from different schools of urban ecology grew stronger in the 1990s, along with important research schools arising around the globe, with a particular emphasis on research schools in Asia and Australia. Nowadays, research schools from all continents are collaborating with each other (Breuste & Qureshi, 2011), with collaborations spanning continents [e.g. the Urban Wildlife Information Network (UWIN); the Comparative Urban Research Training (CURT) network; the Global Urban Soil Ecological Education Network (GLUSEEN); and the Urban Biodiversity and Design (Urbio) network] and barriers in communication being less of an issue. Albeit not a new approach (e.g. Stearns & Montag, 1975; Sukopp, Numata & Huber, 1995), researchers all over the world now focus increasingly on combining natural-science urban ecology and solution-focused urban ecology, since a combined, integrative perspective is needed to tackle omnipresent challenges, such as building sustainable cities and conserving biodiversity outside of nature reserves (Collins *et al.*, 2000; Ramadier, 2004; Wolfram, Frantzeskaki & Maschmeyer, 2016).

## (2) Mapping urban ecology

*‘I sense that humans have an urge to map – and that this mapping instinct, like our opposable thumbs, is what makes us human’ – Katharine Harmon, cited in Börner (2010, p. 10)*

Maps of research fields can visually guide us through the complex structure of science. They can guide scientists from both within and outside the field as well as policy makers, practitioners and others interested in the topic. This is particularly important in our current era, which is characterised by a rapid growth in data and publications. It is important to recognise that data and publications do not automatically translate into knowledge and understanding (e.g. Jeschke *et al.*, 2019), and that research in rapidly growing fields can become ‘relatively ineffective and inefficient, as existing evidence is often not found, collaboration opportunities are missed, and research is too often conducted in pursuit of dead ends’ (Jeschke

*et al.*, 2021, p. 6). There is thus a strong need for synthesis tools that can intuitively provide orientation to research fields. Maps can serve as such tools and are becoming increasingly popular to structure active research fields (e.g. Enders *et al.*, 2020; Klavans & Boyack, 2009; Leydesdorff, Carley & Rafols, 2013). As outlined above, urban ecology is a particularly active field (see also Bai *et al.*, 2018; Wolfram *et al.*, 2016), and the pace of urban growth as well as the urgency of acting fast require sound and accessible synthesis tools. Ideally, such tools should enable dynamic, community-based evidence assessment.

Our aim here is to take initial steps towards a community-built knowledge base for urban ecology that can later be expanded and also interlinked with other disciplines. We use hypotheses as focal entities to build a map of urban ecology. Such an approach has the advantage that the mapped hypotheses can be linked with empirical evidence in the future. For the field of invasion biology, conceptual maps based on hypotheses were developed by Enders, Hütt & Jeschke, (2018) and Enders *et al.* (2020) and then combined with empirical evidence (Jeschke & Heger, 2018; Heger *et al.*, 2021) to create interactive maps of this research field (see <http://www.hi-knowledge.org>). When selecting a hypothesis from the map, it is possible to see how well it is supported and to identify research gaps. Ideally, the evidence for each hypothesis in such a map will grow continuously; an idea that has been proposed as community-built ‘evidence revolution’ (Nakagawa *et al.*, 2020).

For the current study, we took the following initial steps towards such a community-built knowledge base. First, we combined expert knowledge with information from the literature to identify key hypotheses in urban ecology; these will be the focal units of our map. Second, we structured the hypotheses in a network based on their attributes, identified important groups of hypotheses (clusters in the network) and propose this clustered network as a preliminary map of hypotheses in urban ecology. Third, we discuss the list and network of hypotheses in urban ecology and propose follow-up steps towards a community-curated knowledge base for urban ecology. To realise this goal, we invite other researchers to join us and contribute other relevant hypotheses, collectively to build a growing and evidence-linked map of urban ecology.

## II. METHODS

### (1) Identifying relevant hypotheses in urban ecology

We compiled hypotheses from urban ecology based on a combination of expert knowledge within our group and literature searches. A challenge for searching in literature databases like the *Web of Science* was that the term ‘hypothesis’ is (i) often not spelled out when hypotheses are formulated or (ii) is used for null-hypotheses and other statistical tests, which meant that this approach was not feasible. Therefore, we

combined literature searches with an expert-based approach. Our goal was not to collect all existing hypotheses in the field of urban ecology, but to identify a set of relevant hypotheses that can serve as a starting point for a community-built knowledge base of urban ecology and can be expanded in the future.

Our approach to identify relevant hypotheses in the field of urban ecology consisted of the following steps. First, 74 hypotheses were identified from textbooks and *via* literature searches in the *Web of Science* and *Google Scholar*, including searching for the key words ‘urban’, ‘city OR cities’, ‘ecology’, ‘hypothes\*’, ‘theory’, ‘prediction’, and back-tracing literature cited within key references (S. L., J. M. J., T. H.). Second, 11 additional experts in the field working on different aspects of urban ecology (M. B.-V., S. B., H.-P. G., F. Ha., Y. I., I. K., S. K.-S., C. L. M., A. P., C. S., T. M. S.) were asked to contribute further hypotheses that they considered relevant to urban ecology. The resulting list included 149 potentially relevant hypotheses (including synonymous hypotheses and concepts that other experts do not consider hypotheses or not relevant to urban ecology). Third, we identified synonymous hypotheses and merged them, agreed on a definition of ‘hypothesis’ (see next paragraph) and on which of the proposed hypotheses are actually relevant for urban ecology. We also cross-compared the identified hypotheses with the studies by Parris (2018), Forman (2016), as well as Cadenasso & Pickett (2008) and Pickett & Cadenasso (2017), who previously provided collections of theories, hypotheses and/or principles in urban ecology. This step resulted in 115 hypotheses. Fourth, we discussed and agreed on which of these hypotheses are overarching hypotheses *versus* lower-level sub-hypotheses. For example, the *Ideal urban dweller* hypothesis is an overarching hypothesis (see online Supporting Information, Data S1). It states that there are specific traits that make species successful in urban ecosystems. Several sub-hypotheses can be specified, depending on the taxonomic focus or type of change (see ‘Sub-hypotheses’ sheet in Data S1). For example, a sub-hypothesis focusing on animals is that urban dwellers have a higher cognitive performance than urban avoiders (Sol, Lapedra & Ducatez, 2020). In this final step, we identified 53 sub-hypotheses and 62 overarching hypotheses; full lists of all sub-hypotheses and overarching hypotheses are provided in Data S1. The overarching hypotheses were mapped as a network (see Section II.2).

A basic methodological question is what exactly is regarded as a ‘hypothesis’. Betts *et al.* (2021) define a hypothesis as ‘an explanation for an observed phenomenon’ (p. 5763), and a research question as ‘a statement about a phenomenon that also includes the potential mechanism or cause of that phenomenon’ (p. 5763). Scientists often tend to use the term ‘hypothesis’ in a broader sense, for ideas or predicted outcomes that can be tested and/or discussed. We here decided to define a hypothesis as an assumption that is based on a formalised or non-formalised theoretical model of the real world and can deliver one or more testable predictions (Heger *et al.*, 2021; after Giere, Bickle & Mauldin, 2005). Further,

an important question is whether the prediction of a pattern is regarded as a hypothesis as well. While Pickett, Kolasa & Jones (2010) argue for regarding predictions of patterns as hypotheses as well, other authors have a much stricter view (Betts *et al.*, 2021). Here, we explicitly include non-explanatory, descriptive hypotheses, and suggest that they also contribute to ecological knowledge about cities. The identification of patterns can lead to valuable predictions and stimulate further research on underlying causal relationships. For example, for the *Earlier phenology* hypothesis, which states that seasonal life cycles tend to start earlier in the urban core than in rural surroundings (Roetzer *et al.*, 2000), several predictions can be formulated on how urbanisation influences phenology, e.g. by increased and/or more constant temperatures or concentrated light pollution.

A summary of the identified hypotheses is provided in Table 1 [the full data file is provided in Data S1 and as an open *Wikidata* project ([https://www.wikidata.org/wiki/Wikidata:WikiProject\\_Ecology/Task\\_Force\\_Urban\\_Ecology](https://www.wikidata.org/wiki/Wikidata:WikiProject_Ecology/Task_Force_Urban_Ecology))]. Where, to our knowledge, no accepted name for a given hypothesis currently exists, we provide a suitable name. The open *Wikidata* file is a ‘living’ project and can be expanded by including additional hypotheses or information, e.g. on additional taxonomic groups that a hypothesis has been applied to, the addition of sub-hypotheses, and empirical support of the hypotheses and respective sub-hypotheses.

We differentiate between (i) hypotheses that are specific to urban environments (i.e. they can only be tested in an urban environment) and have not been derived from more general ecological hypotheses, thus are unique to research in urban ecology; (ii) ‘urbanised’ hypotheses that exist in a more general or analogous form outside of urban ecology, but have been adapted to urban systems; and (iii) general hypotheses from another research field that have not been specifically adapted to urban systems but are nonetheless highly relevant there (e.g. the street barrier effect, as the high density of streets in cities can lead to strong constraints on species’ movement; Mader, 1984).

To structure the hypothesis network, we characterised each hypothesis based on its focal entity or topic (i.e. whether it addresses species traits, trait evolution, niche shift, species abundance, community composition, species interactions, habitat quality, or ecosystem functioning and services), and the hypothesised drivers of change [artificial light at night, anthropogenic noise, climatic change (e.g. heat islands), chemical pollution, nutrients, fragmentation, habitat loss and isolation, invasive alien species and other novel organisms (*sensu* Jeschke, Keesing & Ostfeld, 2013), novel community composition and structure, and human presence and intervention]. A decision about which attribute to assign to each hypothesis was reached by a consensus approach: each hypothesis was assessed by two authors. If there was no agreement, a third author reassessed the respective hypotheses and consensus was reached *via* in-depth discussion among these three authors. The attributes assigned in this way were then shared with all other authors for feedback and final consensus. These assignments are provided for each hypothesis in Data S1.

Table 1. Information on the 62 hypotheses in urban ecology included in this study. Names for hypotheses are either taken from the literature or new names are proposed here (indicated by \*). ‘Label’ refers to the abbreviation for each hypothesis used in Fig. 2. ‘Cluster’ indicates where each hypothesis is located: Cluster I, Urban species traits & evolution; II, Urban biotic communities; III, Urban habitats; IV, Urban ecosystems. ‘Type’ refers to the research field in which a hypothesis was formulated: Urban, urban ecology; Urbanised, hypotheses originally formulated in a related field other than urban ecology, but adapted to urban environments; Related field, research field other than urban ecology (if the hypothesis was originally formulated outside of urban ecology).

Hypothesis	Label	Cluster	Definition	Key reference(s)	Type
Acoustic adaptation*	AA	I	Animals that communicate acoustically adapt their vocalisations to the local conditions to optimise signal transmission.	Morton (1975)	Related field
Biodiverse cities*	BC	II, IV	Cities can sustain and promote biodiversity.	Walters (1970), Kühn <i>et al.</i> (2004)	Urban
Biodiversity-wealth*	BW	III	The socio-economic status of urban residents is positively related to the biodiversity in their neighbourhoods.	Kinzig <i>et al.</i> (2005)	Urban
Cities as entry points	CEP		Cities are entry points for introduced non-native species.	Pyšek <i>et al.</i> (2010); Potgieter & Cadotte (2020)	Urban
Credit card	CC	II	Low variability in resource abundance and reduced predation allow higher population densities in urban areas through the persistence of many weak competitors who remain in poor body condition, are less reproductively successful, and would not otherwise survive.	Shochat (2004)	Urban
Decay paradigm	DP	III	Species richness declines within patches of remnant native habitat isolated within an urban matrix; habitat-dependent (such as ‘forest interior’) species are expected to suffer a progressive series of local extinctions over time.	Catterall <i>et al.</i> (2010)	Urbanised
Earlier phenology	EP	I	Seasonal life cycles tend to start earlier in the urban core than in rural surroundings.	Roetzer <i>et al.</i> (2000)	Urbanised
Ecological trap	ET	I, III	Habitats preferred over other, higher quality habitats that are low in quality for reproduction or survival may not sustain a population.	Schlaepfer <i>et al.</i> (2002); Battin (2004)	Related field
Enemy release	ER	II	The absence of enemies is a cause of invasion success.	Keane & Crawley (2002)	Related field
Environmental filter	EF		Urban habitats filter communities as a function of their traits.	Aronson <i>et al.</i> (2016)	Urbanised
Epigenetic adaptation*	EA	I	Epigenetic mechanisms can explain why some organisms are more successful in urban than non-urban areas.	Isaksson (2015)	Urbanised
Food-web reshaping*	FWR	II	Urban food webs largely lack weak interactions, but the partly disassembled food webs retain a greater density of species interactions (e.g. greater connectance).	Start <i>et al.</i> (2020)	Urban
Generalists <i>vs.</i> specialists*	GVS		Generalist species are more frequent in urban areas than specialist species.	Sorace & Gustin (2009)	Urbanised
Genetic signatures*	GS	I	‘Genetic signatures of urban eco-evolutionary feedback can be detected across multiple taxa and ecosystem functions.’ (Alberti, 2015, p. 116)	Alberti (2015)	Urban
Green roofs	GR	III	Green roofs promote urban biodiversity.	Oberndorfer <i>et al.</i> (2007); Williams <i>et al.</i> (2014)	Urban
Habitat diversity	HD	III	Biodiversity in urban areas is high due to habitat diversity.	Pyšek (1989)	Urbanised
Habitat isolation	HI	III	More isolated habitat islands have lower species richness.	MacArthur & Wilson (1967)	Related field

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Table 1. (Cont.)

Hypothesis	Label	Cluster	Definition	Key reference(s)	Type
Herbivore proliferation*	HP	II	Herbivores may become hyperabundant in urban areas, sometimes leading to pest outbreaks.	Raupp <i>et al.</i> (2010)	Urban
High propagule pressure in cities*	PHC		A higher proportion of alien taxa in captivity and cultivation leads to an increased propagule pressure in cities.	Kühn <i>et al.</i> (2017); Potgieter & Cadotte (2020)	Urbanised
Home range reduction*	HRR	I, III	Many species maintain smaller home ranges in urban areas.	Mannan & Boal (2000); Atwood <i>et al.</i> (2004); Wright <i>et al.</i> (2012)	Urban
Human commensalism	HC	I	Species that live in close proximity to humans are more successful in invading new areas than other species.	Jeschke & Strayer (2006)	Related field
Hyperabundance due to anthropogenic food*	HAF	I, II, III	An increase in the proportion of anthropogenic food with urbanisation leads to an increase in the abundance of prey as well as mid-sized animals (e.g. mesopredators).	Fischer <i>et al.</i> (2012)	Urban
Ideal urban dweller*	IUD	I	There are specific traits that make species successful in urban ecosystems.	Evans <i>et al.</i> (2011); Adler & Tanner (2013, p. 202)	Urban
Increased boldness	IB	I	Animals tend to become bolder in urban than non-urban areas.	Knight <i>et al.</i> (1987); Uchida <i>et al.</i> (2019)	Urban
Intermediate disturbance	ID	III	Biodiversity is high in sites that show intermediate levels of disturbance and decreases with no and high levels of management.	Grime (1973); Connell (1978, p. 1303)	Related field
Landscape of fear	LOF	I, II	Animals adjust their behaviour and activity to avoid humans spatio-temporally.	Brown <i>et al.</i> (1999); Laundré <i>et al.</i> (2010); Bleicher (2017)	Related field
Light at night – social interaction*	LSI	I, II	Light pollution alters the social interactions and group dynamics of animals.	Kurvers & Hoelker (2015)	Related field
Matrix species	MS	II, III	Urban habitat remnants are more sensitive to the penetration of matrix species than less disturbed suburban or rural remnants.	Tóthmérész <i>et al.</i> (2011)	Urban
Microbiota exposure	ME	II, IV	Urbanisation reduces exposure of humans to environmental microbiota, leading to higher allergy risks and negative effects on immune function.	Ruiz-Calderon <i>et al.</i> (2016); Parajuli <i>et al.</i> (2018)	Urban
Non-native species hypothesis* aka Invader species	IS		Non-native species richness increases with urbanisation.	Sukopp (1969); Kunick (1974); Kowarik (1988); Blair (2001)	Urban
Non-native substitution*	NNS	II	Non-native plants in urban areas can sometimes substitute the loss of resources provided by native plants.	Berthon <i>et al.</i> (2021)	Urbanised
Novel communities	NC	II	Urban environments have novel communities that do not exist in natural environments.	Perring <i>et al.</i> (2013a)	Urban
Plant host switching	PHS	I, II	The abundance of alien plants in the urban core encourages native arthropods (herbivores, pollinators) to switch from native to alien host(s).	Shapiro (2002); Raupp <i>et al.</i> (2010)	Urban
Population pressure hypothesis	PPH	III	Urban habitats serve as sinks for rural dispersers. Continuous gene flow between a rural source and an urban sink population prohibits pronounced genetic differentiation.	Gloor <i>et al.</i> (2001)	Urban
Predator proliferation	PP	II	Predator densities and/or predation rates are higher in urban than non-urban areas.	Fischer <i>et al.</i> (2012) based on Sorace (2002); Eötvös <i>et al.</i> (2018)	Urban
Predator relaxation	PR	I, II	Predator density, prey mortality and/or prey fearfulness are lower in urban than non-urban areas.	Tomialojc (1982); Gering & Blair (1999)	Urban

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Table 1. (Cont.)

Hypothesis	Label	Cluster	Definition	Key reference(s)	Type
Prey specialisation	PS	I, II	'The diet of carnivorous mesopredators will be increasingly dominated by a few species with urbanisation. These prey species will be hyperabundant within cities. The predation rate on prey species that are not hyperabundant will decline with urbanisation.' (Fischer <i>et al.</i> , 2012, p p. 816)	Fischer <i>et al.</i> (2012)	Urban
Rapid adaptation	RA	I	Rates of evolutionary change are greater in urban systems.	Alberti <i>et al.</i> (2017b); Johnson & Munshi-South (2017)	Urbanised
Resilience of urban hybrid systems*	RUH	II, IV	'Resilience in urban ecosystems is a function of the patterns of human activities and natural habitats that control and are controlled by both socio-economic and biophysical processes operating at various scales'. (Alberti & Marzluff, 2004, p. 242)	Alberti & Marzluff (2004)	Urban
Shift toward non-migratory species*	SMS	I	Urbanisation favours non-migratory species.	McClure (1989)	Urban
Species richness – HPD*	SRH		Species richness is positively correlated with human population density.	Luck (2007)	Related field
Species-area relationship	SAR	III	Species richness and diversity increase with habitat size.	MacArthur & Wilson (1967)	Related field
Street barrier effect	SBE	III	Streets act as dispersal barriers.	Mader (1984)	Related field
Street corridor effect	SCE	III	Streets act as dispersal corridors.	Seabrook & Dettmann (1996); James & Stuart-Smith (2000); von der Lippe & Kowarik (2007)	Related field
Suburban peak*	SP	III	Species richness is highest in sub-urban areas; it is lower in urban centres and the (rural) periphery.	Blair (2001)	Urban
Synanthropic species	SS		The number of synanthropic species increases along the rural–urban gradient.	Klausnitzer (1987, p. 106); Guetté <i>et al.</i> (2017)	Urban
Thermal tolerance increase	TTI	I	Thermal tolerance increases with urbanisation.	Diamond <i>et al.</i> (2018)	Urban
Urban avoiders	UA	I	Urban avoiders have a reduced ability to adapt, compete and/or reproduce in cities.	Blair (1996)	Urban
Urban biodiversity hot spots*	UHS	II, III, IV	Cities are often located in areas of high biodiversity, and urbanisation is disproportionately higher in areas with high biodiversity.	Kühn <i>et al.</i> (2004); Luck (2007); Ives <i>et al.</i> (2016)	Urban
Urban biotic homogenisation	UBH		Species composition of different cities will become more and more similar as urbanisation increases.	Blair (2001); McKinney (2006); Groffman <i>et al.</i> (2014)	Urbanised
Urban core herbivore decline*	UCH	II	The abundance of alien plants in the urban core tends to reduce the richness and abundance of native herbivore insects incapable of using non-native plants.	Raupp <i>et al.</i> (2010)	Urbanised
Urban density-diversity paradox*	UDD		Diversity typically increases as the number of individuals increases in biological communities. Urban environments, however, tend to be characterised by lower biodiversity than wildlands despite high population densities.	Shochat <i>et al.</i> (2010); Saari <i>et al.</i> (2016)	Urban
Urban eco-evolutionary mechanisms*	UEE	I	'Through urbanisation, humans mediate the interactions and feedbacks between evolution and ecology in subtle ways by introducing changes in habitat, biotic interactions, heterogeneity, novel disturbance, and social interactions.' (Alberti, 2015, p. 116)	Alberti (2015)	Urban

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Table 1. (Cont.)

Hypothesis	Label	Cluster	Definition	Key reference(s)	Type
Urban ecosystem convergence	UEC	II, IV	All ecosystems types respond to urban land use in a convergent manner (in other words: urban ecosystems are convergent regardless of the original ecosystem they replaced).	Pouyat <i>et al.</i> (2002)	Urban
Urban ecosystems as source of innovation*	USI	I	'The hybrid nature of urban ecosystems – resulting from co-evolving human and natural systems – is a source of "innovation" in eco-evolutionary processes.' (Alberti, 2015, p. 117)	Alberti (2015)	Urban
'Urban effect' on invasion	UEI		The number of non-native species moving through each invasion stage (transport, introduction, establishment, spread) is higher in urban areas than in natural environments.	Potgieter & Cadotte (2020)	Urban
Urban fragmentation	UF	I, III	Urbanisation, specifically the fragmentation of habitats, leads to a loss of genetic variation within and increased differentiation between populations.	Miles <i>et al.</i> (2019)	Urbanised
Urban habitat analogues*	UHA	I	Native species can switch to urban habitats.	Thellung (1919); Lundholm & Richardson (2010)	Urbanised
Urban mesopredator release*	UMR	II	'The abundance of large-bodied predators will decline with urbanisation, whereas the abundance of mesopredators will increase.' (Fischer <i>et al.</i> , 2012, p. 816)	Crooks & Soulé (1999); Fischer <i>et al.</i> (2012)	Urbanised
Urban sexual traits*	UST	I	In urban environments, species show shifts in several traits related to sexual selection (particularly in their coloration, acoustic signals including songs and calls, hormones, pheromones, mating behaviour).	Sepp <i>et al.</i> (2020)	Urban
Urbanisation ecosystem functioning*	UEF	II, IV	Urbanisation leads to a reduction in ecosystem functions and services.	Grimm <i>et al.</i> (2008)	Urban
Urbanisation tolerance	UT	III	Biodiversity loss in cities can be explained by a low tolerance of species to urbanisation.	Sol <i>et al.</i> (2014)	Urban

## (2) Network and cluster analysis

The matrix of hypotheses and attributes was used to create a bipartite network; here, every hypothesis is linked to attributes (i.e. focal entities or topic related to a hypothesis, or drivers of change) and *vice versa*. No information is lost, as opposed to monopartite networks that use dissimilarity matrices of the interconnected nodes rather than the connections between hypotheses and attributes themselves, resulting in a network showing presence *versus* absence of links.

Typically, clusters in network analyses are created based on the similarity or connectivity of nodes, here hypotheses and attributes. Nodes are assigned to specific clusters, and each node is attributed to exactly one cluster. Here, we created a set of 24 clusters based on four regularly used node-based algorithms from R iGraph (GN, Fastgreedy, Walktrap and leading eigenvector, R version R 4.1.1). All four algorithms evaluate network partitioning into disjoint node communities or clusters by calculating modularity (see Newman & Girvan, 2004).

In a third step, these clusters were optimised by a memetic algorithm (PsiMinL) that clusters links instead of nodes and

optimises each cluster separately (Havemann, Gläser & Heinz, 2017; Havemann, 2021) by iteratively adding or removing links. By setting the value of the resolution parameter  $r$  ( $r < 1$ ), we can control the resolution of the set of clusters; a small value (closer to 0) results in many poorly distinct clusters, while a value close to 1 will result in few clusters with little overlap. Because the network analysed here is relatively small, we are confident that PsiMinL can find all relevant clusters possible for the chosen value for  $r$  (here  $r = 1/3$ ) after a small number of evolutionary searches. The resulting optimised clusters have the advantage that nodes can be members of more than one cluster (see Enders *et al.*, 2020), and the resulting clusters also will be more robust, as the algorithm does not force nodes into clusters. A detailed description of the network analysis is provided in Appendix S1.

Membership of a hypothesis in a cluster is quantified as the percentage of links between attributes and a hypothesis, e.g. two out of three links leading to a node equals a membership of 67% in the respective cluster. A hypothesis (node) can be included in two clusters with 100% if they overlap one another.



### III. RESULTS AND DISCUSSION

#### (1) Hypotheses in urban ecology

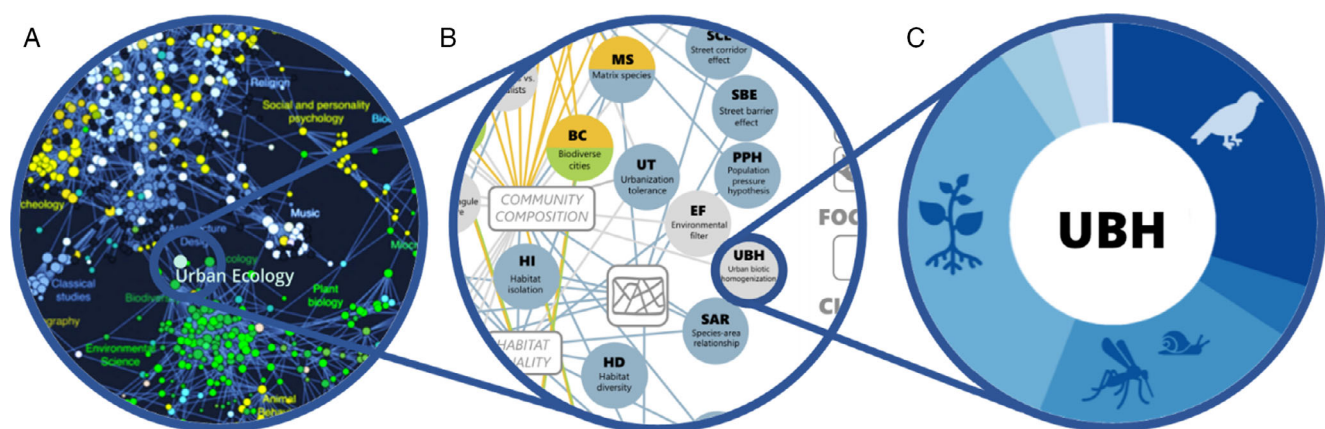
We identified 62 hypotheses in urban ecology (Table 1). Thirty-six hypotheses are uniquely or originally urban; 12 stem from related fields like invasion biology or biogeography, but are highly relevant to urban ecology; and 14 hypotheses exist in a general version and, here, are adapted to an urban setting ('urbanised'). This collection of hypotheses for urban ecology has a different scope and goes beyond previous compilations that have attempted to structure this field. The approach of Cadenasso & Pickett (2008) was theory driven, and their five principles aimed to ground urban ecology within scientific theory and provide suggestions for urban planning and landscape design. These five principles are: (i) 'urban areas are ecosystems', (ii) 'urban ecosystems are diverse', (iii) 'urban ecosystems are dynamic'; (iv) 'human and natural processes interact in cities' and (v) 'ecological processes remain important in cities' (Cadenasso & Pickett, 2008, p. 8). These principles were later extended by the same authors to 13 principles (Pickett & Cadenasso, 2012).

Taking a different approach, Forman (2016) published a compilation of 90 principles, based on six reviews on urban ecology. These contain more detailed and case-specific findings and generalisations from empirical research on urban ecosystems; for example, 'More buildings and tall structures create both more habitats and hazards for organisms.' (Forman, 2016, p. 1657). Parris (2018) recently published a collection of theories, paradigms and hypotheses from general ecology that have been shown to apply in urban systems.

Similar to Forman (2016) and Parris (2018), and unlike Cadenasso & Pickett (2008) and Pickett & Cadenasso (2017), we used a bottom-up approach to structure the field of urban ecology. While there are shared aims between these studies and ours, focusing on hypotheses has two large

benefits: (i) in contrast to principles, hypotheses and hypothetical generalisations imply that what they describe or predict is still under scientific inquiry, and possibly questioned and tested in numerous instances; (ii) hypotheses can be directly linked to empirical evidence in a future step (see Fig. 1), thereby distinguishing between well-supported and highly questioned hypotheses, and allowing the identification of research gaps.

Given the unique nature of urban ecosystems, an interesting question is whether general ecological theory can be directly applied to urban ecology (Parris, 2018). Urban ecosystems differ profoundly from natural ones, and ecologists have identified many differences between urban and non-urban systems, arguing that ecological theory has at least to be adapted (Niemelä, 1999), if not profoundly expanded (Collins *et al.*, 2000; Alberti, 2008; McPhearson *et al.*, 2016a), for urban systems. Still, ecological theory has been repeatedly applied to urban settings (Parris, 2018). Of the 62 hypotheses listed in Table 1, 14 have been adapted from general ecological theory to urban systems (23%), and 12 (19%) are from related fields. These hypotheses from fields like evolutionary biology or general ecology are highly relevant in urban settings, and thus a vital part of urban ecology. Take, for example, the *enemy release* hypothesis which is well known in invasion ecology (Enders *et al.*, 2018) and explains the invasion success of species in the absence of (co-evolved) enemies in novel settings. As urban ecosystems have been shown to be rich in non-native species (e.g. Kowarik, 2008), and even hypothesised to act as distribution hubs for species invasions into rural regions (von der Lippe & Kowarik, 2008) as well as to other cities worldwide (Potgieter & Cadotte, 2020), urban ecology and invasion biology are closely connected research fields. Therefore, hypotheses formulated for invasion biology can often be applied to urban settings. As a wide variety (if not most) of general ecological theory also can be applied in urban settings (see Parris, 2018), our selection here is far from



**Fig. 1.** The network of hypotheses in urban ecology (B) can be interlinked with hypotheses (or other knowledge entities) from other fields and positioned within a broader network of science (A; modified from Bollen *et al.*, 2009). Each hypothesis can be connected with empirical evidence, or with meta-information on the research related to a hypothesis (C; modified from Lokatis & Jeschke, 2022). Here, the proportion of taxonomic groups for which biotic homogenisation has been studied in an urban context is shown.

exhaustive. Accompanying the rapid loss of the untouched, pristine nature (Watson *et al.*, 2016; Potapov *et al.*, 2017) that has been studied by classical ecology (Inkpen, 2017), urban ecosystems are nowadays only one among many strongly transformed ecosystem types, and can even be regarded as trial systems for studying effects of multiple global changes (Lahr, Dunn & Frank, 2018). For Johnson & Munshi-South (2017, p. 1), the global network of cities might even be ‘the best and largest-scale unintended evolution experiment’. So instead of asking if and in what form classical ecological theory can be applied to urban systems, the inverse question might become increasingly important in the future (Forman, 2016): can research from urban ecology help us to understand other anthropogenically shaped ecosystems?

(2) A first map of hypotheses in urban ecology

Maps are a powerful tool to visualise knowledge. Envisioning an ‘atlas of science’ that uses mapping technology to connect the different branches of science, we here propose a first map

of urban ecology. This map can be connected to other fields (Fig. 1A) and serve as a reference point for researchers from urban ecology and other disciplines (Fig. 1B). Using hypotheses as nodes for the network opens the possibility that each hypothesis can be connected with empirical evidence and meta-information about a particular hypothesis (Fig. 1C).

To provide a visualisation of knowledge in urban ecology, we applied a semi-automated approach to map all 62 hypotheses and the 16 assigned attributes listed in Table 1 in a bipartite network (Appendix S1; Fig. 2). Of the seven clusters identified in a network analysis (see Table S1 in Appendix S1), the four best separated clusters were retained (clusters I–IV). These clusters were named according to the hypotheses and attributes they contain (Figs 2, 3), and will be described in detail below. Cluster L0–L1 is the complementary cluster to cluster I and is thus redundant, and three clusters (L5, L6 and L7, see Table S1 in Appendix S1) were not retained because they were rather small and not as well separated as the other clusters (see Appendix S1). Several hypotheses are part of more than

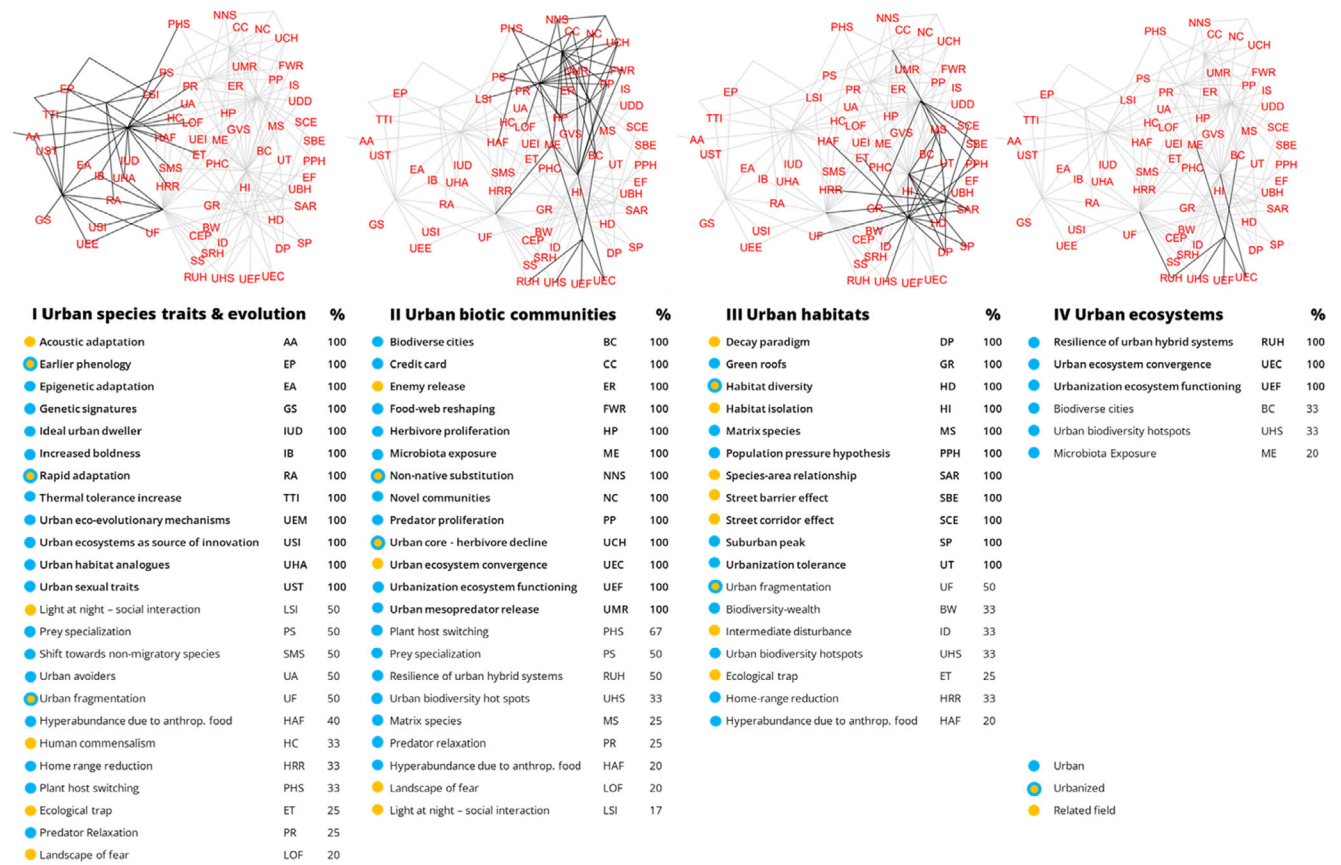
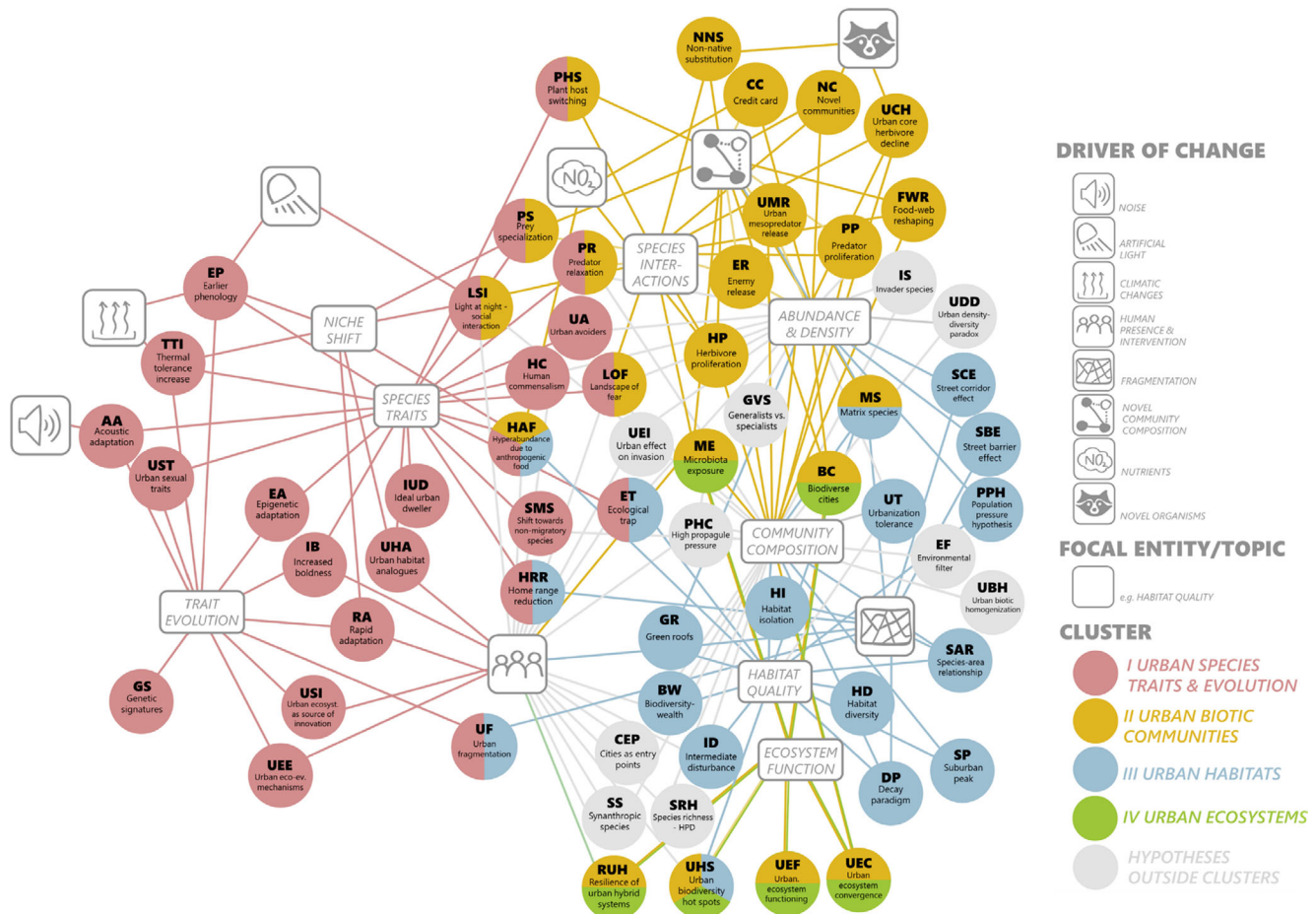


Fig. 2. 62 hypotheses in urban ecology grouped into clusters identified by a link clustering algorithm. The best separated and meaningful clusters are shown here and were subsequently named Urban species traits & evolution, Urban biotic communities, Urban habitats and Urban ecosystems. Cluster membership of all hypotheses attributed to a cluster are listed below each cluster. Cluster membership values indicates the proportion of links leading to a hypothesis that belong to that cluster. Coloured circles indicate whether a hypothesis has been formulated within urban ecology (blue), adapted to urban ecology (‘urbanised’, blue-outlined yellow), or is a general hypothesis from a related field (yellow). Links that belong to a cluster are black, other links are grey. Note that not all hypotheses were allocated into one of the four clusters, and that some appear in more than one cluster.

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**Fig. 3.** Bipartite network of 62 hypotheses (circles) and 16 attributes (grey boxes at the intersection of several links showing focal entities/topics and drivers of change), which were used to characterise and group the hypotheses. Four clusters that emerged when applying a link clustering algorithm (see Appendix S1) are shown: Urban species traits & evolution (red), Urban biotic communities (yellow), Urban habitats (blue) and Urban ecosystems (green). Full circles belong to a single cluster, divided circles indicate that a hypothesis has shared membership between two or more clusters. Hypotheses within a white circle do not belong to any of the clusters.

one cluster, and ten hypotheses are not part of any of the four named clusters (Fig. 3). Cluster IV is nested within cluster II, but was retained as it is well separated and informative. It is a feature of such analyses that clusters share overlapping links and nodes (Fig. 1).

(a) *Cluster I: urban species traits & evolution*

Cluster I (Urban species traits & evolution) comprises 24 hypotheses; 12 hypotheses have 100% membership (i.e. all links leading to a hypothesis belong to that cluster) and 12 hypotheses have a membership of  $\leq 50\%$  (Fig. 2). Attributes of this cluster can be separated into the focal entities or topics: species traits, trait evolution and niche shift (all 100% cluster membership); and into the drivers of change: artificial light, noise, climatic change (all 100% cluster membership) and human presence and intervention (23%) (Fig. 3). Although this cluster has some overlap with Urban biotic

communities (cluster II) and Urban habitats (cluster III), it has the lowest normalised node-cut Psi-value among the identified clusters, indicating that it was the best separated cluster.

A major focus of the hypotheses in this cluster is to predict and explain which traits characterise species that inhabit urban areas, and how they adapt to urban environments. The study of species that live close to human settlements dates back to studies on birds, mammals and blowflies in the 1950s (see Povolný, 1962; Nuorteva, 1963, 1971), and far earlier for plants (Linkola, 1916; reviewed by Sukopp, 2008). A central idea in this cluster is the *Ideal urban dweller* hypothesis, which posits that specific traits make species successful in urban ecosystems. This is a very general statement that we chose to treat as an overarching hypothesis that can be specified into a range of descriptive hypotheses focusing on a specific taxonomic group or urban setting, and which implicitly assumes that there is a set of traits characterising an ideal urban dweller (or other positions on the

urban affinity spectrum; Wolf *et al.*, 2022). This might be higher cognitive performance or increased capability to learn (Sol *et al.*, 2020), an enhanced movement capacity (Santini *et al.*, 2019), or greater dietary flexibility (Palacio, 2020; Scholz *et al.*, 2020; Planillo *et al.*, 2021). Hypotheses like *acoustic adaptation*, *earlier phenology*, *increased boldness*, *thermal tolerance increase* and *shift towards non-migratory species* link evolutionary changes to physical stressors in urban environments or the presence of humans. *Epigenetic adaptation*, *genetic signatures*, *rapid adaptation* and *urban eco-evolutionary mechanisms* are hypotheses about general evolutionary processes that are expected in urban settings.

#### (b) Cluster II: urban biotic communities

The Urban biotic communities cluster includes 13 hypotheses with 100% membership and nine hypotheses with a membership between 17% and 67% (Fig. 2). Drivers of change within this cluster are: nutrients, novel organisms and novel community composition (all 100%) as well as human presence and intervention (5%); focal entities and topics include species interaction (100%), ecosystem functioning (100%) abundance & density (33%), and community composition (30%).

Hypotheses in the Urban biotic communities cluster focus on research questions investigating how urban food webs, communities and species assemblages differ from non-urban ones, and what features characterise urban species interactions (e.g. predation or competition). Four hypotheses that are clearly related to abundance and density, as well as community composition (i.e. *invader species*, *urban density-diversity paradox*, *urban effect on invasion* and *high propagule pressure in cities*) were not grouped within cluster II, but are in the vicinity of this cluster (Fig. 3). Nested completely within the Urban biotic communities cluster is the Urban ecosystems cluster (cluster IV) outlined below.

#### (c) Cluster III: urban habitats

The Urban habitats cluster includes 11 hypotheses with 100% membership and seven hypotheses with  $\leq 50\%$  membership (Fig. 2). The focal entities/topics for this cluster are: habitat quality (100%) as well as abundance & density and community composition (23% and 24%, respectively), and the drivers of change are fragmentation (100%), novel community composition (7%) and human presence and interaction (5% membership).

The central question of this cluster is which habitat characteristics influence populations, species and their interactions, and how urban habitats can be characterised. For example, a high diversity of habitats in urban areas has been linked to high overall biodiversity of cities (Pyšek, 1989; Sattler *et al.*, 2010; Helden & Leather, 2004), a hypothesis that is well known but often only implicitly tested. An example for a pair of contrasting hypotheses included in this cluster is the *street barrier effect*, which predicts that traffic routes reduce the mobility of urban wildlife (Rondinini & Doncaster, 2002;

Riley *et al.*, 2014), and the *street corridor effect* (Seabrook & Dettmann, 1996; von der Lippe & Kowarik, 2007; Riley *et al.*, 2014), which describes the opposite, i.e. species or populations moving more easily along streets. The Urban habitats cluster is characterised by a larger proportion of hypotheses adapted or directly applied to urban systems from other research areas, especially biogeography, population ecology and conservation ecology.

#### (d) Cluster IV: urban ecosystems

Incorporating patterns and processes on the ecosystem level, the Urban ecosystems cluster comprises only six hypotheses, of which only three have a cluster membership of 100% (Fig. 2). These hypotheses focus on ecosystem functions or services. Three other hypotheses have a lower affiliation (20–33%). The attributes of this cluster are: ecosystem functioning (focal topic, 100% membership), human presence and intervention (driver of change, 5% membership) and community composition (focal topic, 3%).

Not all hypotheses dealing with ecosystems are included in this cluster (e.g. *urban ecosystems as source of innovation* belongs to cluster I), but it is still striking that so few of the hypotheses are concerned with ecosystem functions or services. Thus, while we expect that this part of the network will be extended in the future, e.g. by including research on microbial urban ecology, it might be fruitful to consider how work in urban ecosystems that is not hypothesis-oriented could be covered within a community-built knowledge base as proposed here.

### (3) Critical reflections

The network presented here was built by combining expert knowledge with a network algorithm. While there are many possibilities for building networks, we chose to create a bipartite network with the advantage that the information about the assessed hypotheses is directly translated into a network structure, instead of relying on one of numerous possible measures of (dis)similarity. This approach is also flexible and easy to adjust for additions to the underlying data set, which we hope will happen in the near future. The resulting network represents a first step towards a knowledge map for urban ecology (see Fig. 1). It has to be noted, however, that by only building on explicitly formulated hypotheses, certain topics addressed in urban ecology might be underrepresented or even missing. Grogan (2005) found that less than half of a selection of articles from ecological journals explicitly used hypotheses. Nilsen, Bowler & Lind (2020) found this proportion to be only 19% in a random selection of articles from practitioner-orientated journals in conservation biology, applied ecology and wildlife management. We expect that this proportion is equally low in urban ecology, and also will vary profoundly among its sub-disciplines, due to its inherent multidisciplinary nature. For example, we expect the content of the Urban ecosystems cluster to increase once more explicit hypotheses are included, because urban ecosystem models and analyses of material flow and processes in cities

implicitly contain hypotheses. Whether it makes sense to formulate these hypotheses, and add them to our network, or whether it might be more constructive to adapt the network to include models, concepts or research questions remains to be discussed in the future.

As pointed out above, this network builds on a first list of key hypotheses identified by a group of experts that will need to be expanded with the help of the broader community of urban ecologists. Additional hypotheses will then probably also alter the structure of our network. For example, the Urban species traits & evolution cluster is currently well separated from all other clusters, with only a few hypotheses shared with the Urban biotic communities cluster (e.g. *plant host switching*) and the Urban habitats cluster (e.g. *ecological trap*, *urban fragmentation*). We expect that increasing the network resolution (i.e. including additional sub-hypotheses and adding new hypotheses) will probably strengthen the overlap between these clusters, as habitat fragmentation, community composition and novel organisms are also studied as important evolutionary factors (Shochat *et al.*, 2006; Diamond & Martin, 2021; Winchell, Battles & Moore, 2020; Borden & Flory, 2021).

The collection of hypotheses and their clustering are a result of the joint contributions and expertise within our group. Our scientific work is currently predominantly carried out in Berlin (Germany), and even though many of us have close connections or backgrounds with other research schools and scientists around the world, we expect that other researchers would have selected different hypotheses and added their own perspectives to the creation of a hypothesis map in urban ecology. In the next and final section, we therefore discuss how the present selection and map of hypotheses can be expanded to incorporate a more diverse and less biogeographically and culturally biased view on hypotheses in urban ecology.

#### (4) Co-creating a knowledge base of urban hypotheses

The list of hypotheses that we mapped is not exhaustive, but can serve as a basis to formulate other hypotheses, to expand the map with additional (sub-)hypotheses from urban ecology, and to link it to other disciplines from within and outside urban ecology (see Fig. 1). We hope that the network can act as a starting point which other disciplines from urban ecology in the broader sense can expand, and rearrange, where appropriate. Knowledge gaps are known to be especially pronounced in the Global South and in areas with the highest urbanisation pressure, as well as on a global level, with most research still carried out locally (Young & Wolf, 2006; Shackleton *et al.*, 2021). To synthesise existing theory and constantly update new findings, as well as to identify research gaps, it is necessary to compare and communicate between different research disciplines and stakeholders. As a first step, we provide our data file of hypotheses as an open expandable *Wikidata* file, that we envision to grow collaboratively in the future. As part of the *Wikidata* project, well-studied

hypotheses can also be linked to meta-analyses and literature reviews, or to the body of relevant data and literature. Hypotheses can thus be assessed directly, as well as analysed from a meta-perspective, i.e. by generating bibliometric networks, and charts, as well as evidence maps, with the aim to identify gaps and biases in research. A *Wikidata*-based tool – Scholia – is available for such visualisations (Nielsen, Mietchen & Willighagen, 2017) and can provide an introductory overview of research areas like urban ecology. It has been adapted to support geospatial queries (Nielsen, Mietchen & Willighagen, 2018) and is currently being refined further to facilitate hypothesis-centric visualisations (Jeschke *et al.*, 2021). We chose *Wikidata* as a platform, as it is free, open-access, community-run, user-friendly, well established and adheres to the FAIR-principles (Wilkinson *et al.*, 2016, Waagmeester *et al.*, 2020). Entries can be easily linked to entries from other platforms, and existing knowledge (in our case: hypotheses) can be linked to existing literature and data sets (Erxleben *et al.*, 2014; Vrandečić & Krötzsch, 2014).

We advocate for a more frequent use of explicit hypotheses in urban ecology and invite future authors to expand our data file both by adding more or alternative hypotheses and by adding explanations to overarching and descriptive hypotheses. Additionally, this collection and mapping of hypotheses will greatly benefit from information on the validity or generality of the collected hypotheses and from linking of hypotheses with empirical data. In the future, we envision a more extensive knowledge base that includes related fields like urban ecology, restoration ecology (Heger *et al.*, 2022) and invasion biology.

## IV. CONCLUSIONS

- (1) Urban ecology is a growing research field in which there are numerous different hypotheses that could benefit from applying new synthesis tools.
- (2) A map of 62 hypotheses from urban ecology broadly clusters into four main themes: Urban species traits & evolution; Urban biotic communities; Urban habitats; and Urban ecosystems.
- (3) We propose using this network as a basis for a community-built knowledge base of hypotheses in urban ecology, and introduce a *Wikidata* project for this purpose.
- (4) Our map of hypotheses in urban ecology will hopefully foster knowledge exchange, help identify research gaps, and provide orientation and guidance for researchers and practitioners.

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## VI. DATA AVAILABILITY STATEMENT

The dataset compiled for this article is available in the supplementary material of this article. A related wikidata-site can be found at [https://www.wikidata.org/wiki/Wikidata:WikiProject\\_Ecology/Task\\_Force\\_Urban\\_Ecology](https://www.wikidata.org/wiki/Wikidata:WikiProject_Ecology/Task_Force_Urban_Ecology).

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Data S1.** Excel-file containing four sheets: (1) a glossary, (2) the full list of 62 hypotheses included in the network, their attributes and relevant literature, (3) a list of additional sub-hypotheses and (4) cited literature over all sheets.

**Appendix S1.** Detailed description of the network analysis.

**Fig. S1.** Dendrogram of clusters calculated by igraph's Walktrap algorithm.

**Table S1.** Details of seven link communities (resolution  $r = 1/3$ ) ordered by  $\Psi$ ; size is given as number of links and as sum of membership grades of nodes ( $\mu_{\text{total}}$ ).

**Fig. S2.** Paths through the  $\Psi$  landscape for six seed sub-graphs obtained from Walktrap.

**Fig. S3.** Approximative hierarchy of the main clusters we identified.

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