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Urban ecology, stakeholders and the future of ecology

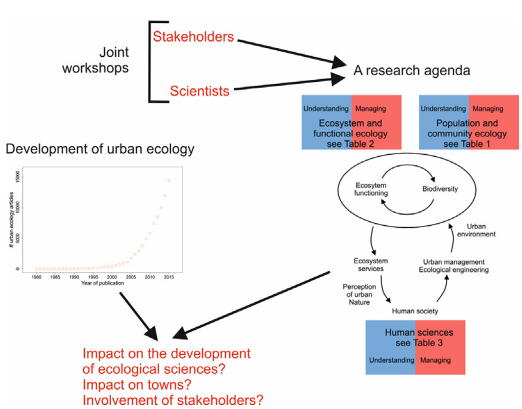
Sébastien Barot [a,*], Luc Abbadie [a], Apolline Auclerc [b], Carole Barthélémy [c], Etienne Bérille [d], Philippe Billet [e], Philippe Clergeau [f], Jean-Noël Consales [g], Magali Deschamp-Cottin [c], Ambre David [a], Cédric Devigne [h], Véronique Dham [i], Yann Dusza [a], Anne Gaillard [j], Emmanuelle Gonzalez [k], Marianne Hédont [l], Dorothée Labarraque [m], Anne-Marie Le Bastard [n], Jean-Louis Morel [b], Yves Petit-Berghem [o], Elisabeth Rémy [p], Emma Rochelle-Newall [a], Marion Veyrières [q]

[a] Institute of Ecology and Environmental Sciences-Paris (IRD, Sorbonne Université, CNRS, INRA, UPEC), 75252 Paris, France
[b] Laboratoire Sols et Environnement (Université de Lorraine, CNRS, INRA, ensaia) F-54000 Nancy, France
[c] LPED (Aix-Marseille Univ., IRD), Marseille, France
[d] Institut de Recherche et d'Innovation pour le Climat et l'Écologie, 13290 Aix-en-Provence, France
[e] Institut de Droit de l'Environnement (Université Lyon 3), 69362 Lyon, France
[f] CESCO (MNHN, Sorbonne Université, CNRS), 75005 Paris, France
[g] TELEMME (CNRS, Aix-Marseille Université), 13094 Aix-en-Provence, France
[h] Laboratoire Ecologie & Biodiversité (Université Catholique de Lille), 59 016 Lille, France
[i] Gondwana Biodiversity Development, 75008 Paris, France
[j] Fédération Française du Paysage, 78000 Versailles, France
[k] CDC Biodiversité, 75002 Paris, France
[l] Plante & cité, 49066 Angers, France
[m] EGIS, 78286 Saint-Quentin-en-Yvelines Paris, France
[n] FRB, 75005 Paris, France
[o] Ecole Nationale Supérieure de Paysage, 78000 Versailles, France
[p] UMR SAD-APT (INRA, AgroParisTech), 75231 Paris, France
[q] Direction de l'environnement, Conseil Régional Hauts-de-France, 59019 Lille, France

HIGHLIGHTS

- A research agenda for urban ecology was built by scientists and stakeholders.
- Questions on biodiversity, ecosystems, interactions with humans are distinguished.
- For all types of issue it is possible to ask fundamental and applied questions.
- Urban ecology will likely be more and more influential in the development of ecology.
- The future of towns, their biodiversity and the life of city dwellers is at stake.

GRAPHICAL ABSTRACT



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ABSTRACT

The world human population is more and more urban and cities have a strong impact on the biosphere. This explains the development of urban ecology. In this context, the goal of our work is fourfold: to describe the diversity

* Corresponding author.
E-mail address: sebastien.barot@ird.fr (S. Barot).

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of scientific questions in urban ecology, show how these questions are organized, to assess how these questions can be built in close interactions with stakeholders, to better understand the role urban ecology can play within ecological sciences. A workshop with scientists from all relevant fields (from ecology to sociology) and stakeholders was organized by the Foundation for Research on Biodiversity (FRB). Three types of scientific issues were outlined about (1) the biodiversity of organisms living in urban areas, (2) the functioning of urban organisms and ecosystems, (3) interactions between human societies and urban ecological systems. For all types of issues we outlined it was possible to distinguish both fundamental and applied scientific questions. This allowed building a unique research agenda encompassing all possible types of scientific issues in urban ecology. As all types of ecological and evolutionary questions can be asked in urban areas, urban ecology will likely be more and more influential in the development of ecology. Taken together, the future of towns, their biodiversity and the life of city dwellers is at stake. Increasing the space for ecosystems and biodiversity within towns is more and more viewed as crucial for the well-being of town dwellers. Depending on research and the way its results are taken into account, very different towns could emerge. Urban areas can be viewed as a test and a laboratory for the future of the interactions between human and ecological systems.

1. Introduction

Ecology is defined as the science studying interactions between organisms and between organisms and their environment and consequences at all spatial and temporal scales including evolutionary consequences in the Darwinian sense. Biodiversity is a key concept for ecology because it denotes the diversity of life at all possible scales: genes, species and ecosystems. It is nowadays fashionable for ecologists to carry out studies on urban ecology and the biodiversity of urban areas. Nearly all scientific institutions have a group of scientists working on this subject and more than 14,000 articles are currently published each year in this field (Fig. 1, see also the same trend for urban ecosystem services in Luederitz et al., 2015) and these articles represent about 14% of all articles published in ecology. This may seem quite natural, but only 20 years ago the situation was totally different (Wu, 2014). Prior to 1995, only a few articles (less than 100) were published each year in the field of urban ecology. It was more usual for ecologists to work in pristine ecosystems such as tropical forests, mountains, oceans (Niemelä, 1999). The number of publications in urban ecology increased slowly till 2000, and since then has increased exponentially. Many journals specializing in urban ecology have been created: Landscape and Urban Planning (1986), Urban Ecosystems (1997), Journal of Urban Ecology (2015).

The diversity of scientific issues being tackled, the fact that the world population is more and more urban (54% in 2014, United Nations, 2014) and that urban areas have an increasing impact on the functioning of the biosphere (Seto et al., 2012; Zhu et al., 2019) likely explain the observed exponential growth of the number of articles published in urban ecology (Fig. 1). This dynamism means that urban ecology is a quickly changing field, whose structure has not yet stabilized. For these reasons we sought to build a research agenda for urban ecology. As a consequence of the pervasive influence of humans on urban ecological systems and the diversity of scientific issues in urban ecology concerning humans the agenda was conceived right from its inception as a collaboration between scientists from various fields and stakeholders involved in various aspects of town and city management (from urbanists and urban planners to citizens). Stakeholders are essential to this reflection because they know the issues directly at stake in the management of urban areas, their biodiversity and ecosystems. They know the kind of knowledge they need to help them make appropriate decisions. Besides scientists from a range of fields in ecology, scientists from various fields of human sciences were an integral part of this discussion. Indeed, as one important goal is to study in urban areas the coupling between ecological systems and humans, human sciences are required to analyse human aspects of this coupling.

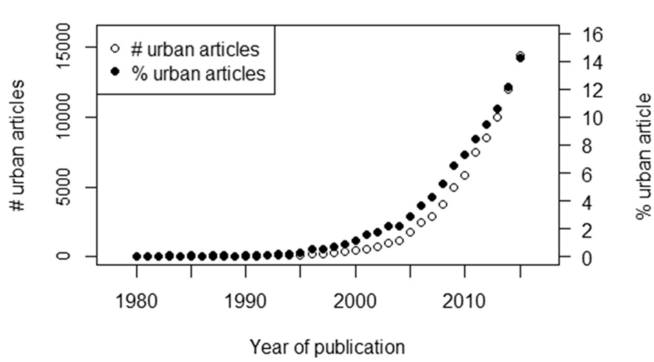

Fig. 1. Number of publications in urban ecology and their percentage relatively to the total number of publications in ecology from 1980 to 2015. The Web of Science (Web of Science Core Collection) was used to search for articles mentioning "urban" AND "ecology" in the topics (i.e. in the title, abstract and keywords) to assess the number of articles in urban ecology while the total number of articles in ecology was assessed searching the same data base for "ecology" in the topics.

The goal of our work was fourfold: (1) to describe the diversity of scientific questions that can be tackled in urban ecology, (2) to show how these questions can be organized and linked to each other, (3) to assess how research questions can be built in close interactions with non-scientists, (4) to better understand the role urban ecology can play within ecological sciences. In this way, this is close to other exercises aiming at building research agendas (Sutherland et al., 2013). However, the goal was not here to prioritize questions but rather to show the whole diversity of questions and their organization and to outline broad areas where many new questions are emerging. To achieve this goal a workshop gathering both scientists and stakeholders was organized by the Foundation for Research on Biodiversity (FRB). This allowed building a unique research agenda encompassing all possible types of scientific issues in urban ecology.

2. Building a research agenda

The members of the working group, i.e. the authors of this article, originate from the scientific board of the FRB, for the academic part of the group, and from the Strategic Orientation Committee of the FRB that gathers stakeholders from all types of activities, from industry to conservationist associations. In addition, a few experts in urban ecology accepted to join the group. Taken together, half of the group was composed of scientists with various ecological approaches (soil science, ecosystem ecology, community ecology, ecological engineering, sociology, law science) and half of practitioners (e.g. employee of territorial communities, landscape gardener, member of a consultancy organization). The general idea behind such an approach to build a research agenda is that it is often pointed out that the results of science tend not to be used and that the transfer of knowledge from scientists towards stakeholders at the end of projects does not guarantee that their results will be used (Phillipson et al., 2012). There are many ways to engage stakeholders in research projects (Berkes, 2009). We think that involving stakeholders right from the start, when scientific questions are delineated, should be fruitful. It should ultimately facilitate the co-management of towns and their biodiversity using different types of knowledge. We also think that this should increase the stakeholder capabilities to understand the relevance of the more fundamental scientific questions and to foster the development of the corresponding research actions.

The workshop was divided into three parts (see Fig. 2). During a first workshop brainstorming techniques were used to allow the group members to express the scientific issues related to urban ecology and biodiversity they considered the most important. Between the first and second workshops, the participants were asked to fill out tables to aid the construction of a more comprehensive list of scientific questions. During the second workshop, this list was discussed and methods and criterions for organizing the list were proposed. Between the second and third workshop, the lead author transcribed and organized the list. During the third workshop, the organization of the list was finalized and gaps in the list were detected and remedied. The group met several times after the first three workshops for further discussion and adjustment of the details of the article.

Developing a common list of questions required acquiring a common culture and a common vocabulary because of the diversity of professional and scientific backgrounds of the workshop participants. Half of each workshop was always used for oral presentations (followed by discussions) either about scientific results or operational projects involving urban ecological systems. Beyond building a list of questions, our goal was also to analyse the consequences of the development of urban ecology for the evolution of ecology as a science and for the future of towns and their sustainability. The result of the corresponding discussions is synthesized below after the description of the research agenda.

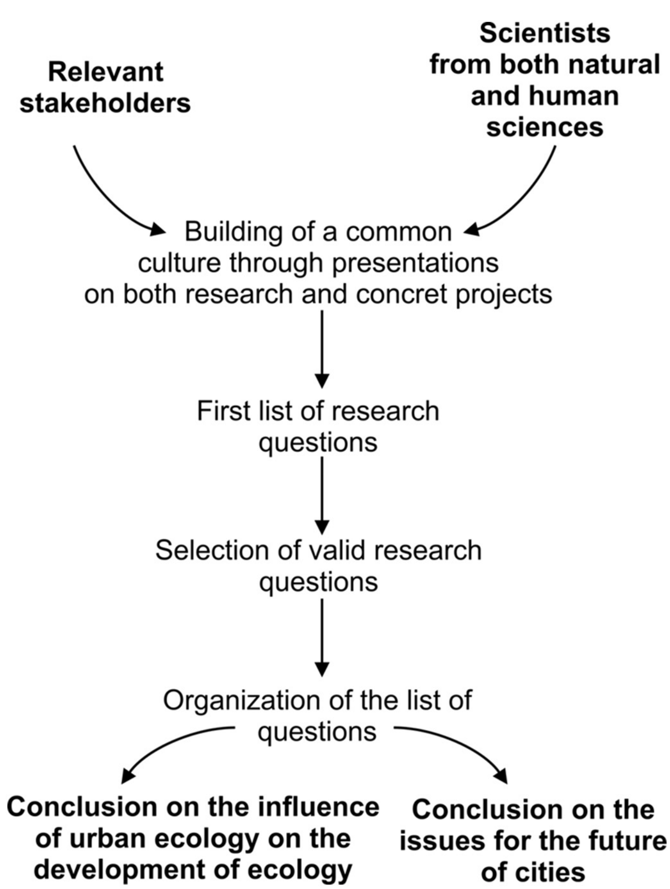

Fig. 2. General organization of the collective work used to build the research agenda.

Overall, the collective work was relatively easy. At the beginning of the work, some definitions had to be clarified. For example, what ecology is as a science was not obvious for non-scientists and for scientists from other fields. The meaning of the notions of biodiversity and ecosystems had to be explained for urban areas: clearly, in an urban context, biodiversity encompasses both wildlife and animals and plants that depend on human beings (e.g. plants planted in parks) and ecosystems can be either relatively natural ecosystems (some woods or lakes), human-made parks, street trees, or new human-made ecosystems such as green roofs. Similarly, the diversity of ecological sub-fields had to be described. Nevertheless, all members of the group were able to give their opinion and did propose scientific questions. This was favoured by work in small groups mixing both stakeholders and scientists during the two first workshops and by the possibility to freely propose questions thanks to a common online file. The stakeholders initially proposed many of the more applied questions we listed but also proposed more fundamental questions (see Tables 1 to 3). Initially, the scientific questions that were proposed had to be sorted out and some of the questions were initially too vague or too broad to constitute a valid scientific question that can be realistically addressed by a set of experiments and measurements. However, it was relatively easy through discussions to reach an agreement on the type of questions that were sought. We also had many discussions on the way to organize the research agenda (see Fig. 3) but all the members of the group agreed on the chosen organization and on the whole list of questions.

3. The research agenda

All domains of ecology can be studied in urban areas (Alberti, 2007; Bugnot et al., 2019; Collins et al., 2000). This encompasses all types of organisms from microorganisms to large mammals and all types of ecosystems: marine ecosystems, fresh waters, terrestrial ecosystems, soils. This also encompasses all organization scales (population, community, ecosystem and landscape ecology) and all sub-disciplines of ecology (population genetics, evolutionary ecology, behavioral ecology, functional ecology, ecophysiology…). The uniqueness of towns arises from the overwhelming influence of human activities, i.e. the fact that towns lead to novel man-made ecological systems (Kowarik, 2011). We thus first chose to organize questions according to three broad areas (Fig. 3 and Tables 1 to 3): (1) the biodiversity of organisms living in urban areas, (2) the functioning of urban organisms and ecosystems, (3) the interactions between human societies and urban ecological systems. The first pertains to population and community ecology, the second to functional and ecosystem ecology and the third to various human and social sciences (sociology, economy, geography, anthropology, philosophy…). The distinction between population and community ecology on the one hand and functional and ecosystem ecology on the other hand is classical in ecological sciences (Begon et al., 2005). The former corresponds broadly to issues related to the dynamics of individuals within populations and species within communities, while the later corresponds to issues based on fluxes of energy and matter at various organization scale (from individuals to ecosystems). Social and human sciences play an important role addressing issues (Table 3) about (1) the perception by humans of biodiversity and ecosystems in urban areas, (2) the governance of urban biodiversity and ecosystems, (3) ecosystem services and disservices provided by urban ecosystems. Many issues are at the interface between the three broad scientific areas (all three Tables). For example, it might be interesting to study how biodiversity (e.g. species richness of plants chosen by stakeholders for a park) influences ecosystem functioning (beyond the functioning of each plant species separately), how this can be translated in terms of ecosystem services (e.g. carbon storage) and how biodiversity and the provided services are perceived by citizens (and whether there are differences between different categories of citizens). Interestingly the

Table 1
List of questions on urban biodiversity.

Fundamental issues	Applied issues
Methods, measurements and indicators to study biodiversity	
How should urban biodiversity be described and monitored?	Can we define indicators that could help manage urban biodiversity?
How should indicators to monitor urban biodiversity be defined?	
How should long term observatories for urban biodiversity be set up?	
How can citizen sciences be used to study urban biodiversity?	
Impact of urban environment on biodiversity	
Is the biodiversity of the different types of ecosystem (e.g. aquatic vs. terrestrial) impacted in the same way?	
Are all types or organisms (e.g. mammals, birds, insects, fishes, soil fauna, and microorganisms) impacted in the same way?	
How do the characteristics of the urban environment impact biodiversity?	**How to increase biodiversity in urban environment?**
Impact of artificial light?	How to decrease the negative impact of artificial light?
Impact of various types of pollution in the air, soils and waters?	How to mitigate the impacts of pollution?
Impact of urban climate? (heat island …)	Is it possible to mitigate negative impacts of urban climate on biodiversity?
Impact of the spatial structure of towns? (connectivity, % of green spaces, size of towns…)	How to improve the structure of towns to increase biodiversity?
	How to reconcile high urban human densities and biodiversity?
	How to reconcile large urban projects (e.g. large shopping centres, towers) and biodiversity?
	How to develop green and blue networks to maximize biodiversity?
	Is it possible to use transport infrastructures to increase biodiversity?
Impact of construction type and the vertical structure of towns (e.g. houses, vs. small building vs. tall buildings)?	Is it possible to favour biodiversity through construction and rehabilitation projects?
Impact of the way constructions are built (e.g. type of materials) at various scales (from the building, to the town and the region)?	Is it possible to develop building materials that are more favourable to the biodiversity living on buildings?
	Is it possible to develop building materials that are less detrimental to biodiversity through their whole life cycle?
Impact of the management of green spaces?	How to optimize green space management for biodiversity?
Impact of urban agriculture?	How to optimize urban agriculture for biodiversity?
Impact of street trees?	How to optimize street trees (species, density, and management) for biodiversity?
Impact of green roofs and vegetated facades?	How to optimize green roofs and vegetated facades for biodiversity?
Underlying mechanisms	
Do species colonizing and living in towns have particular characteristics? (life cycle, dispersion ability, specialist or generalist species…)	
Do organisms have the same population dynamics in urban environments and in non-urban environments?	
Do communities have particular characteristics in urban environments? (total biodiversity, structure, functional diversity…)	
Do food webs have particular characteristics in urban environments?	
Does the urban environment lead to the local evolution of organisms?	
What are the most important selection pressures?	How should we take into account the evolution of organisms in towns for the well-being of city-dwellers? For example, in the case of disease vectors such as mosquitos.
What is the respective importance of plasticity and evolution in phenotypic changes?	
Do towns lead to converging evolutionary dynamics all over the world?	
Are there cases of rapid evolution in urban environments?	

structure of the research agenda (Fig. 3) emerged naturally during the workshops but has many similarities with the structure of urban ecology theorized by urban ecologists (see Fig. 4 in Wu, 2014).

We have also organized research questions according to their position on the gradient between purely fundamental and applied scientific issues: the first column of Tables 1 to 3 lists rather fundamental questions while the second column lists rather applied questions. It may appear as a surprise that purely fundamental questions can be asked on the ecology and biodiversity of urban areas. On the one hand, the pervasive influence of humans in urban areas does not impede asking scientific questions solely aiming at describing and analysing patterns and mechanisms. It is possible to study the structure of communities of organisms in urban areas and the underlying ecological mechanisms, e.g. dispersal and competition, whatever the human influence on these mechanisms. On the other hand, for nearly all fundamental questions, it was also possible to find corresponding more applied questions (Tables 1 to 3). For example, when communities of organisms have been described and factors of the structure of these communities have been identified it is possible to ask questions on the way urban environment (e.g. through the management practices within parks or through the abundance and distribution of green areas) can be improved to favour communities with higher species richness. The same logic applies to questions pertaining to human and social sciences. For example, fundamental questions can be asked on the perception of urban ecosystems and biodiversity and underlying social and psychological mechanisms. This questioning can also be transformed to ask questions about the best methods to increase the knowledge of urban citizens on urban ecosystems and increase their awareness about biodiversity and the importance of ecosystems for their well-being. Though we insisted during our discussions on the importance of asking standard fundamental ecological questions on urban ecological systems, this advocates, as others have done before (Barot et al., 2015), for a continuum between applied and fundamental questions in ecology and the fact that it is rarely relevant to segregate applied and fundamental ecology. The main types of questions listed in the tables are outlined below.

Urban biodiversity (Table 1)

We first listed questions on how to monitor biodiversity in urban environments. This led to rather fundamental questions about the different methodologies to be developed but also to questions on the most adequate methodologies to monitor urban biodiversity with the goal

Table 2
List of questions on the functioning of urban ecosystems.

Fundamental issues	Applied issues
Functioning of vegetation	
What are the impacts of the urban environment on vegetation? (photosynthesis, plant growth, uptake of mineral nutrients, uptake of water…)	
Impact of air pollution (CO_2, ozone, nitrogen oxides…)?	
Impact of climate (e.g. heat island)?	
Impact of soil pollution (e.g. heavy metals)?	
Impact of light pollution?	
Impact of soil management and soil age?	
Impact of human control on water fluxes (soil sealing)?	
What are the services provided by vegetation in urban areas? (quantitative and qualitative assessment)	**How to manage vegetation in urban areas to increase the provision of ecosystem services?**
By street trees?	Influence of the choice of planted species?
By parks?	Influence of watering?
By woods?	Influence of park management?
By green roofs?	Is it possible to optimize green roofs for the provision of services?
By rivers, canals and lakes?	
Are there trade-offs between services?	How to increase the provision of several services at the same time?
Functioning of soils	
What are the characteristics of urban soils?	
What are their dynamics?	
Do urban soils have a different functioning from non-urban soils? (e.g. mineralization, nitrification…)	
What is the impact of the urban environment (climate, management of parks…) on soil functioning?	
What are the services provided by urban soils?	**Can we manage urban soils to provide more ecosystem services?**
What is the capacity of urban soils to store carbon?	How can the storage of carbon be increased in urban soils?
What is the capacity of urban soils to release/avoid the release of other greenhouse gases (e.g. N_20)?	How can the capacity of urban soils to regulate fluxes of greenhouse gases be increased?
What is the capacity of urban soils to regulate water fluxes (stormwater)?	Is it possible to increase the capacity of urban ecosystems to regulate water fluxes?
	Can urban soils help recycling urban wastes (organic waste, sewage sludge)?
	How to create soils using building waste and other urban waste?
	How to optimize substrates for green roofs?
	How to optimize substrates for urban agriculture?
	Are there sanitary risks related to the recycling of urban wastes?
	Can we optimize the management of soils at the scale of towns and surrounding areas (e.g. fluxes of soils from crop lands to parks, fluxes of urban polluted soils…)?
	What role can play soil fauna in the creation of substrates for green roofs and urban agriculture and for waste recycling?
Functioning of aquatic ecosystems	
Do urban aquatic ecosystems have a different functioning from their non-urban equivalents?	Can we manage urban aquatic ecosystems to provide more ecosystem services?
What is the impact of urban environment on the functioning of aquatic ecosystems?	
How does the urban environment impact the mineral nutrient and dissolved organic matter contents of urban aquatic systems?	How can the sanitary quality of urban aquatic systems be improved?
How do human activities impact the sanitary quality of urban aquatic systems?	Can ecological engineering help improving the sanitary quality of urban aquatic systems?
What is the accumulation of xenobiotic substances and trace elements along the food webs of urban aquatic ecosystems?	

of managing this biodiversity. The description of urban biodiversity is commonly justified by questions on the impact of urban environment on biodiversity (Kowarik, 2011; Waite et al., 2019). This leads to very diverse questions on the impact of all aspects of urban environment (from pollution and the heat-island effect to the spatial structure of the town) on all types of organisms (from micro-organisms to large mammals and trees). Again, these questions can be rather fundamental but become applied when the ultimate goal is to manage urban biodiversity. For example, the management of green spaces can be adapted to favour various groups of organisms. Besides describing urban biodiversity and designing means to favour it, many scientific questions arise about ecological mechanisms underpinning biodiversity: population dynamics, interactions within communities… We have only listed a few questions in this direction, but basically all fundamental issues traditionally addressed about the dynamics of biodiversity can be addressed in towns. This can involve testing general theories in an urban context, e.g. theories about food web functioning, and testing whether the patterns usually found in natural ecosystems can also be found in towns. It is obviously also important to ask questions about the Darwinian evolution of urban biodiversity (Alberti, 2015). What are the most important evolutionary pressures for urban organisms? Do towns lead to converging evolutionary dynamics all over the world? Are there cases of rapid evolution in urban environment?

Functioning of urban ecosystems (Table 2)

For the sake of clarity we have separated questions on the functioning of urban vegetation from questions on urban soils and aquatic ecosystems. As for biodiversity (Table 1), a first category of questions is about the description of the functioning of urban vegetation (e.g. photosynthesis, biomass production, uptake of mineral nutrients…) and urban soils (e.g. mineralization, nitrification…) and the way urban conditions impact this functioning (Pickett et al., 2008). Again, many of the questions are rather fundamental because they aim at understanding basic ecological mechanisms. For example, humans control or influence most water fluxes within towns and the consequences of these altered fluxes on the growth of street trees are poorly known. Indeed, the sources of water (e.g. rain water vs. various man-made water networks)

Table 3
List of questions on the coupled functioning of urban ecological systems and human societies.

Fundamental issues	Applied issues
Perception of biodiversity in urban areas	
What is the perception of urban ecosystems and biodiversity by city-dwellers?	**Why and how can the awareness of city-dwellers to ecosystems and biodiversity be increased?**
What is the perception of green spaces (including lakes and rivers)?	Can the increase of city-dweller awareness to biodiversity help changing their relation to Nature in general?
What is the perception of soils?	Can the increase of city-dweller awareness to Nature help linking rural and urban people?
What is the perception of street trees?	How can be various audiences (age, socio-professional category) be targeted by these efforts to increase awareness?
What is the perception of ordinary biodiversity?	
Is the provision of services recognized? How is it perceived?	
Is biodiversity accepted in towns? Has this changed with time?	
How do these perceptions depend on sex, age, socio-professional category, size of the town, the level of development of the country?	
Can citizen sciences or urban agriculture help changing the perception of ecosystems and biodiversity in towns?	
Governance and public policies	
What are the places/government authorities for the governance of urban ecosystems and biodiversity at the town scale or at larger scales?	How can citizens be associated to the governance of urban ecosystems and biodiversity?
Can the governance of ecosystems and biodiversity in towns serve as a model of governance for human-Nature relations in general?	How can public policies and private activities be linked for the governance of urban biodiversity?
What are the differences in the governance of biodiversity between towns of different continents and countries with different levels of economic development?	What are the institutional, economic and legal obstacles to the development of urban ecosystems and biodiversity?
What is the impact of the features of urban governance on urban biodiversity?	What fiscal and economic levers could favour the development of urban ecosystem and biodiversity?
Are there specific legislations for urban biodiversity and ecosystems?	What levers could favour the development of innovative green infrastructures?
How does the legislation impact urban ecosystems and biodiversity?	How can the management of urban biodiversity over various spatial scales be improved while these scales depend on different administrative divisions and types of administrative divisions?
Ecosystem services	
How can ecosystem services be assessed in urban areas?	
How can the services and disservices linked to human health be assessed?	
How can the services linked to psychological well-being be assessed?	
How can cultural services be assessed?	
Can the costs avoided thanks to urban ecosystems be assessed?	
What is the demand for ecosystem services in urban areas?	
How can the assessment of ecosystem services in urban areas be used?	
Can the assessment of urban ecosystem services be used to guide the governance of towns?	What role can the assessment of ecosystem services and the optimization of their provision play in the design of sustainable cities?
Are there trade-offs between services (e.g. between aesthetic, cultural and regulation services?)	Is it possible to optimize the provision of ecosystem services by urban areas in a multi-functional approach?
Are there differences in the access to urban ecosystems and ecosystem services between socio-professional categories?	Can urban and peri-urban agricultures play a significant role in the provision of food?
	Can the assessment of ecosystem services be used to increase the health of city dwellers?

for these trees and their strategy (distribution of roots) to absorb enough water have rarely been studied. In the same vein, many aspects of soil functioning remain to be studied. For example, it is poorly known how soil management (urban soils are often man-made) and the urban environment (e.g. local increases in atmospheric CO_2 due to fossil fuel combustion or the urban heat island effect) impact soil microbial communities and the functions they perform (mineralization, nitrification…). From these questions about ecosystem functioning arise questions about the consequences of this functioning in terms of provision of ecosystem services and disservices. What are the types of service provided by urban ecosystems? How much services are provided (Wang et al., 2019)? Questions about the relations between human aspects of ecosystem services are gathered in Table 3 (see below). But it is possible to ask here (Table 2) questions about the purely ecological aspects of these services, i.e. depending solely on the measurement of ecosystem functions. These questions become much more applied if the possible ways to increase the provision of services are addressed (Gómez-Baggethun and Barton, 2013). This leads to questions about ecological engineering (Barot et al., 2012; Mitsch and Jørgensen, 2003). It could for example be possible to increase the ability of a green space to reduce the heat island effect by evapotranspiration through the choice of suitable tree species. It could be possible to store more carbon in urban soils through suitable inputs of organic matter or through particular ways to construct the soils. The same types of question can be asked for totally artificial ecological systems such as green roofs. They have been shown to provide services, but how to optimize the provision of services through the design and management of these roofs and facades is not fully known.

Urban systems as socio-ecosystems (Table 3)

Three types of questions have been listed here at the frontier between ecological and human sciences: questions about (1) the perception of urban ecosystems and biodiversity by city dwellers (Lo and Jim, 2010), (2) the governance of towns (Wilkinson et al., 2013), (3) ecosystem services (Andersson et al., 2015). The proportion of humans living in cities is rapidly increasing and, at least in some towns (Europe, North America, some parts of Asia), the space for ecosystems and biodiversity tends to increase within towns. The contact between humans and Nature is therefore becoming proportionally more and more frequent within cities (Shwartz et al., 2014). It is thus important to ask questions about the perception of urban ecosystems and their biodiversity (Lo and Jim, 2012) and whether this may also modify the overall perception of Nature by humans (Standish et al.,

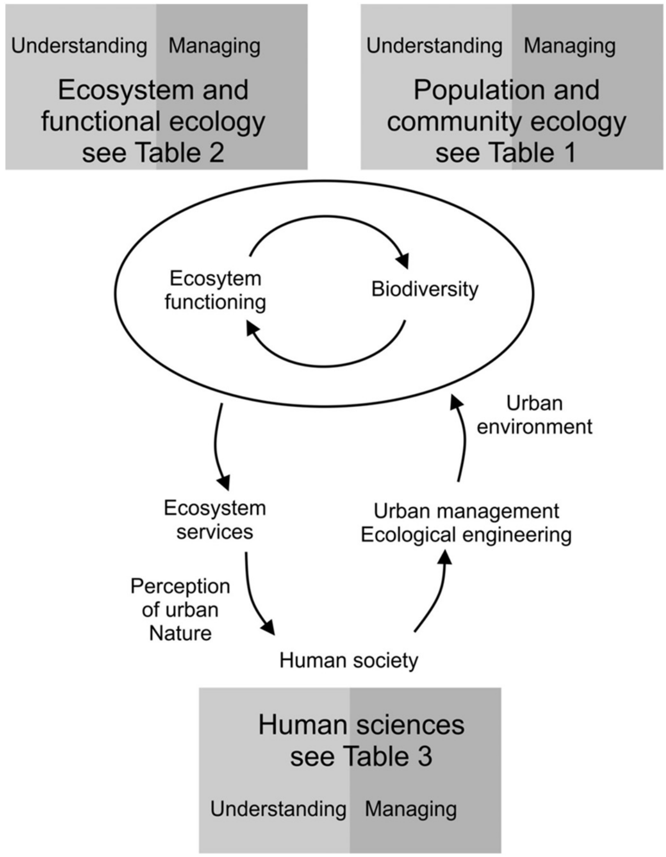

Fig. 3. Diagram describing interactions between humans, biodiversity and ecosystem functioning in urban environments and displaying accordingly the organization of the research agenda (see Tables 1 to 3) in three broad types of question and in fundamental (understanding) and applied (managing) issues.

2013). This leads to rather fundamental questions pertaining to sociology and psychology. These questions become applied when research has a precise goal, e.g. finding ways to increase the city dwellers awareness of Nature. Many questions arise about the governance of biodiversity in towns. The actual situation can be described and analysed: What are the places and government authorities influencing urban biodiversity? Are there specific legislations influencing urban biodiversity? How socio-economic factors shape urban ecosystems (Dobbs et al., 2017)? The same types of question may be addressed to help reach specific goals, i.e. to develop a suitable governance to favour urban biodiversity. Besides the assessment of ecological functions leading to ecosystem services (see Table 2) many questions arise on the links between ecosystem services and the life of urban dwellers (Gómez-Baggethun et al., 2013). First, it is important to develop sound methodologies to assess services linked to human health, human psychological well-being and cultural services. Some basic general questions also arise about services: Are there trade-offs between the ecosystem services provided by urban ecosystems? Are there differences in the access to services between socio-professional categories? Second, the notion of ecosystem services is more and more viewed as a tool to improve the management of ecosystems. However, the way to incorporate assessments of ecosystem services in the governance of ecosystems and biodiversity is not straightforward (Laurans et al., 2013) and research could be implemented on how to better use the assessment of ecosystem services in the management of towns.

4. Implementing the research agenda

Some research areas require a particular attention. As usual in biodiversity sciences, urban ecologists started by studying large organisms such as birds, mammals and plants. There are currently an increasing number of studies in urban areas on insects (Madre et al., 2013), soil invertebrates (Vergnes et al., 2017) or microorganisms (Ramirez et al., 2014) and this trend will likely continue. In the same vein, scientists often start by describing patterns, e.g. the distribution of organisms within towns, but it is more difficult to determine the ecological mechanisms behind these patterns, e.g. measuring dispersal and survival rates. However, ecology is precisely about linking mechanisms to their consequences and more effort should be directed towards this area of urban ecology. This is true for studies pertaining to population/community ecology but also for studies pertaining to functional ecology. For example, there are few studies on the basic functioning of widespread urban types of vegetation such as lawns and street trees. It is thus hardly known how the nitrogen budget of urban lawns is balanced and the respective influence of soil micro-organisms and atmospheric deposits on this budget. Similarly, while street trees are seen as providing services (reduction in the heat island effect) and disservices (roots may damage buildings and pavement) (Mullaney et al., 2015) the ecophysiology of these trees is poorly known (but see David et al., 2018).

The services (and disservices) provided by classical urban ecosystems (parks, street trees…) and by relatively new types of man-made ecosystems (green roofs, vegetated facades) are being increasingly assessed (Lundholm and Cadotte, 2015; Mullaney et al., 2015) and these services are often used as arguments to promote these ecosystems. However, practices are often developing quicker than the supporting scientific knowledge or independently of the existing knowledge so that the real benefits of urban green infrastructures are still not fully documented and a comprehensive approach of ecological engineering (Barot et al., 2012; Mitsch and Jørgensen, 2003) is often missing. This is due to a common mismatch between the research time scale on the one hand and the economic and political timescale on the other hand. This probably impedes optimizing the design and management of green infrastructures such as green roofs and vegetated facades. Developing such an approach requires at least five research steps: (1) identifying the ecosystem services that can be provided, (2) identifying the links between these services and ecological functions, (3) determining the links between all features of green infrastructures and ecological functions, (4) identifying links and trade-offs between services and disservices, (5) assessing the various costs (especially environmental costs) of the construction and management of these infrastructures (Barot et al., 2017). In the case of green roofs, steps (1), (2) and (4) have at least partially been achieved (Madre et al., 2013), while steps (3) and (5) have only been tackled very partially (Dusza et al., 2017; Lundholm and Cadotte, 2015). This impedes the determination of the best green roof substrate (e.g. artificial substrate vs. natural soil, clay content or organic matter content), the best substrate depth, or the best plant combination to store carbon, regulate stormwater, purify rain water or favour invertebrate biodiversity. A key issue is that studying the long term dynamics (at least 10 years) of man-made ecosystems such as green roofs is necessary to assess their sustainability. However, such long-term studies are scarce.

One of the goals of ecology is to delineate general rules and theories. However, there are hitherto very few general theories about urban biodiversity and ecosystems. To our knowledge, the only general rule recognized in urban ecology is that urbanization leads to biotic homogenization. At the global scale, because towns are built to meet relatively homogenous human needs, they display homogeneous physical environments (Clergeau et al., 2001) that tend to homogenize the town flora and fauna (Schwartz et al., 2006). Worldwide, urban environments select organisms that are adaptable to towns and often replacing native-species. These species tend to be early-successional species with good dispersal abilities and are often introduced by humans. Similarly, it is largely recognized that urbanization leads to unique eco-evolutionary dynamics (Alberti, 2015): rapid feedbacks between evolutionary and ecological dynamics likely modify community and ecosystem functioning in urban environments. Much research is still required to describe and analyse these dynamics. A recent study also suggested that vegetation growth is enhanced in the urban environment of 32 major Chinese cities (Zhao et al., 2016), but this should be tested further at the global scale in order to disentangle the underlying mechanisms.

Our work focused on European towns. While the types of question we list are relevant worldwide some of our thoughts and comments are mostly valid for European towns and partially valid for North-American towns. A difficulty in developing general theories for urban ecology is that modes of urbanization are relatively diverse. In particular, urbanization dynamics are now relatively slower in already developed countries than in developing countries (Seto et al., 2011). In parallel, towns of the old world may be centuries-old or even millenaries-old while towns of the new world and developing countries are usually much younger (Ramalho and Hobbs, 2012). This leads to important differences in the structure of towns, the type of building or the proportion of green spaces. These differences between towns and countries will likely impact urban biodiversity and the functioning of urban ecosystems. These issues deserve further research. In particular, much fewer studies have been carried on the ecology and biodiversity of towns in developing countries, e.g. in Africa, which is all the more regrettable as social, environmental and biodiversity issues are huge in these towns (McHale et al., 2013). We believe that it would be useful to build a research agenda for urban ecology using the approach we used for this article in the capital of an African country with local scientists and stakeholders.

5. Impact of urban ecology on the development of ecological sciences

The development of urban ecology is having a profound influence on the development of ecological sciences. We have shown that this influence is quantitative (Fig. 1) and outline below some qualitative aspects of this impact.

Urban areas represent already ongoing experiments waiting for scientists to study them. This can, for example, allow the testing in towns of theories developed independently of urban ecology (Mc Donnell and Pickett, 1990). In particular, towns display gradient of artificialization that can be studied as such (see for example Foti et al., 2017; Zhao et al., 2016) and towns with different structures and characteristics can be compared (Clergeau et al., 1998). For example, urban landscapes allow studying the functioning of meta-populations and meta-communities of urban organisms (Hamer and McDonnell, 2008; Vergnes et al., 2013) that depend on the size and the connectivity between patches favourable to these organisms, e.g. green spaces. Other ecological theories such as the intermediate disturbance hypothesis can be tested in urban landscapes (Breuste et al., 2008) with the hypothesis that species richness could be maximum at intermediate positions on the urban-rural gradient. Towns also provide original situations that can be used in functional ecology. For example, urban conditions often lead to higher temperatures and higher CO_2 concentrations mimicking some aspects of climate changes that are difficult to reproduce in long term experiments on vegetation and soils. Man-made soils in urban areas also constitute original experiments. For instance, the soils of street trees hardly receive any aboveground litter since soils are generally sealed a part from a small opening around trees and since dead leaves are generally gathered and exported. Overall, while new theories may not be required in urban ecology, urban ecology should contribute to ecological theories (Niemelä, 1999).

Since the proportion of human urban dwellers is still increasing, urban ecology constitutes a kind of acid test or showcase for ecological sciences, as already emphasized in the particular case of ecological engineering (Mitsch and Jørgensen, 2003) and the general case of applied ecology (Barot et al., 2015). If ecologists succeed in (1) understanding urban ecological systems, (2) making precise enough predictions on these systems and their dynamics, (3) designing efficient ways to manage these systems and (4) increasing the well-being of urban dwellers using ecosystem services and biodiversity, they will demonstrate the value of their science that is often underestimated and misunderstood. Indeed, it is important to convince human societies to change their relation with the biosphere in a context where the sustainability of this relation is threatened (Steffen et al., 2015). Urban ecology is also becoming an important showcase for ecological engineering. Towns allow the creation of totally man-made ecosystems that are inherently more diverse in terms of the ecosystems services that can be provided than, for example, agricultural lands that must above all produce food. This should favour the development of a real ecological engineering of services and multifunctionality that goes far beyond the mere management of ecosystems. For example, roof complex ecosystems could be created to recycle wastewater and produce vegetables and fishes.

An important still ongoing evolution is that ecologists have first studied ecology and biodiversity in towns, e.g. studying population of organisms as they would in any natural ecosystem, but are more and more studying the ecology of towns as complex ecological systems. In particular, research more and more tackles the complexity of the nested structure of urban ecosystems (Breuste et al., 2008; Clergeau et al., 2006). It is possible to study ecological processes at the scale of (1) a local green space (e.g. demography of a plant population), (2) a network of green spaces (e.g. the meta-population of a plant and fluxes of propagules between green spaces), (3) the matrix between green spaces where some organisms live or spend a part of their time, (4) a town and its urban-rural gradient (e.g. fluxes of plant propagules between the rural and urban areas), (5) a network of towns (e.g. to study an invasive species colonizing towns depending on town characteristics and distances between towns). Of course, with the development of landscape ecology (Forman, 1995), ecological sciences did not have to wait for the development of urban ecology to study such complex systems. However, the way urban ecology analyses and understands spatially complex ecological systems is influential beyond the mere community of urban ecologists.

As shown by our tables (Tables 1–3) and by the functioning of our working group, a particularity of urban ecology is that scientific questions quickly require the intermingling of questions pertaining to natural sciences and human sciences. This leads to the study of the complex feedbacks between urban ecosystems and human societies, i.e. to study towns as complex social-ecological systems (Alberti et al., 2003). This in turn leads to many new scientific questions at the interface between various scientific fields. For the same reasons, research on urban ecosystems and biodiversity nearly always involves stakeholders, from town citizens, to gardeners or town councillors. This means that research is often orientated by these stakeholders, which again leads to new scientific questions. Conversely, research results in urban ecology tend to be quickly disseminated to the stakeholders, who in turn tend to use them quickly. For example, implementing experiments on green roofs requires working with the owners of the buildings supporting green roofs, and if results allow designing efficient green roofs, the owners are likely to develop more green roofs on new buildings. Overall this gives scientists important responsibilities and leads in urban ecology to very quick feedbacks between sciences and the society. Again, ecology has not waited for urban ecology to tackle issues related to social-ecological systems and the involvement of stakeholders often leads to new ways to practice science in many areas of ecology. Nevertheless, urban ecology is currently playing a critical role in developing these aspects, which somehow contributes to the current evolution of ecological sciences.

6. Conclusion

We have emphasized many scientific issues that deserve research but what is eventually at stake is the future of towns, the life of city dwellers and urban biodiversity. Depending on the research that is carried out and the way its results are taken into account in designing towns, very different towns could emerge in the near future. One underlying general scientific, social and political issue is: Do we need to increase biodiversity in towns? For whom? With which goal? One possible model is the model of smart cities (Batty et al., 2012; Caragliu et al., 2011). The concept is still fuzzy and there is no strict contradiction between smart cities and the promotion of urban ecosystems and biodiversity. However, promoters of smart cities insist on Information and Communication Technologies (ICT) and the way to optimize traditional infrastructure (buildings, transportation…) and tend to forget about environmental problems and biodiversity, besides optimizing the use of energy. Technologies and specifically information technologies can potentially be used to foster biodiversity or to increase the provision of ecosystem services, however technologies are often viewed as a way to replace ecological mechanisms and all technologies have environmental costs, even information technologies. In fine, we must decide how much air conditioning will be optimized by ICT and how much the urban heat island will be attenuated by a profusion of green spaces, in the line of ecological engineering (Barot et al., 2017). We must also decide how much urban agriculture should be based on soft technologies and the principles of agro-ecology or ecological engineering and how much urban agriculture should go towards industrialized farming and hard technologies (e.g. vegetables cultivated in containers using LEDs as sources of light or vertical farms in towers). This is a matter of individual, cultural and political choice but science must document the consequences and the sustainability of the various options. Because the stakes are very high and because of the pervasive entanglement of fundamental and applied issues, urban ecology must also develop a strong ethic.

More and more humans are living in towns and urban planners are tending towards an increase in the amount of biodiversity within towns, creating a situation propitious for strong feedbacks between biodiversity and humans in urban areas. It is therefore possible to see urban areas as a test and a laboratory for the future of the interactions between human and ecological systems (Elmqvist et al., 2013; Standish et al., 2013): (1) The perception of Nature by city dwellers is more and more forged by what they perceive of urban ecosystems and biodiversity. Consequently, understanding mechanisms behind this perception should help understanding the general perception of Nature. Conversely, if urban dwellers see more clearly (for example because of active education programs) their dependence on ecological systems and biodiversity this could help protecting biodiversity at the biosphere scale, for example because most policy makers are town dwellers. In this context, citizen sciences dealing with biodiversity and environmental issues are quickly developing within towns and could further help changing the perception of Nature (Kobori et al., 2015). Indeed, citizen sciences allow constructing a shared knowledge and may help convincing urban dwellers that they depend on biodiversity and ecosystem services. It has also been suggested that the increase in the proportion of urban dwellers is partially responsible for the worldwide extinction of experience of biodiversity but that reintroducing biodiversity in towns is a good leverage to fight this extinction of experience and make the case for Nature conservation (Miller, 2005). This supports the possibility of an urban reconciliation ecology (Francis and Lorimer, 2011). (2) The design and management of towns can either leave an important space to biodiversity and ecosystems or totally annihilate biodiversity, which is also the alternative at the biosphere scale. Thus, understanding mechanisms behind the way the future of urban biodiversity is decided could help understanding feedbacks between humans and ecological systems at the biosphere scale. An advantage of studying these feedbacks at the town scale is that they are probably quicker at this scale than at the global scale. (3) Urban areas condense many environmental problems and have a huge impact on the biosphere (e.g. consumption of resources and source of pollution) (Seto et al., 2012) so that solving environmental problems in towns will also aid in solving environmental problems at larger scales. (4) Urban areas also condense many social problems that interact with environmental problems, e.g. ecosystems and biodiversity plays an important role in the quality of life and there are social inequalities in the availability of green spaces (Heynen et al., 2006). It is thus important to jointly solve environmental and social problems in urban areas. To this end, gathering all the necessary knowledge using ecological and human sciences is of paramount importance.

Finally, the diversity of scientific questions we have listed has been made possible because of the joint work of stakeholders and scientists from various fields. We believe that this type of collaborative work could help implementing the research agenda through a mutual agreement on (1) the relevance of both applied and fundamental scientific questions, (2) what is at stake behind those questions. The whole process could, for example, help in raising funding for research and favour the direct involvement of stakeholders in research. Modestly, our joint work between scientists and stakeholders has already led to the funding of a one-year post-doc in charge of a synthesis on the impact of urban forms on biodiversity and we are planning to organize a small call for proposals in the field of urban ecology. Our group has also published an outreach document describing the field of urban ecology and our research agenda. This will likely foster the implementation of this research agenda. More generally, our work is reproducible and could favour the development of other initiatives using the same approach for: (1) urban ecology focussing on particular cities and involving local stakeholders and scientists or (2) other fields of ecology or environmental sciences, e.g. agro-ecology.

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