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1 **Urban ecology, stakeholders and the future of ecology**

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32

33 ABSTRACT

34 The goal of our work is fourfold: to describe the diversity of scientific questions in
35 urban ecology, show how these questions are organized, to assess how these
36 questions can be built in close interactions with stakeholders, to better understand
37 the role urban ecology can play within ecological sciences. A workshop with
38 scientists from all relevant fields (from ecology to sociology) and stakeholders was
39 organized by the Foundation for Research on Biodiversity (FRB). Three types of
40 scientific issues were outlined about (1) the biodiversity of organisms living in urban
41 areas, (2) the functioning of urban organisms and ecosystems, (3) interactions
42 between human societies and urban ecological systems. For all types of issues we
43 outlined it was possible to distinguish both fundamental and applied scientific
44 questions. Overall, the human population is more and more urban. Cities have a
45 strong impact on the biosphere and increasing the share of Nature within towns is
46 more and more viewed as crucial for the well-being of town dwellers. Moreover, as all
47 types of ecological and evolutionary questions can be asked in urban areas, urban
48 ecology will likely be more and more influential in the development of ecology. The
49 future of towns, their biodiversity and the life of city dwellers is at stake. Depending

50 on research and the way its results are taken into account, very different towns could
51 emerge. Urban areas can be viewed as a test and a laboratory for the future of the
52 interactions between human and ecological systems.

53

54 *Key-words:* biodiversity, ecological engineering, ecosystem services, stakeholders,
55 research agenda, human sciences

56

57 **1. Introduction**

58 It is nowadays fashionable for ecologists to carry out studies in urban ecology. Nearly
59 all scientific institutions have a group of scientists working on this subject and more
60 than 14000 articles are currently published each year in this field (Fig. 1, see also the
61 same trend for urban ecosystem services in Luederitz et al., 2015) and these articles
62 represent about 14% of all articles published in ecology. This may seem quite
63 natural, but only 20 years ago the situation was totally different. Prior to 1995, only a
64 few articles (less than 100) were published each year in the field of urban ecology. It
65 was more usual for ecologists to work in pristine ecosystems such as tropical forests,
66 mountains, oceans (Niemelä, 1999)... The number of publications in urban ecology
67 increased slowly till 2000, and since then has increased exponentially. Many journals
68 specializing in urban ecology have been created: Landscape and Urban Planning
69 (1986), Urban Ecosystems (1997), Journal of Urban Ecology (2015).

70 The diversity of scientific issues being tackled has led to the observed
71 exponential growth of the number of articles published in urban ecology (Fig. 1). This
72 dynamism means that urban ecology is a quickly changing field, whose structure has
73 not yet stabilized. For these reasons we sought to build a research agenda for urban
74 ecology. As a consequence of the pervasive influence of humans on urban ecological

75 systems and the diversity of scientific issues concerning humans the agenda was
76 conceived right from its inception as a collaboration between scientists from various
77 fields and stakeholders involved in various aspects of town and city management
78 (from urbanists and urban planners to citizens). Stakeholders are essential to this
79 reflection because they know the issues directly at stake in the management of urban
80 areas, their biodiversity and ecosystems. They know the kind of knowledge they need
81 to help them make appropriate decisions. Besides scientists from a range of fields in
82 ecology, scientists from various fields of human sciences were an integral part of this
83 discussion. Indeed, as one important goal is to study in urban areas the coupling
84 between ecological systems and humans, human sciences are required to analyse
85 human aspects of this coupling.

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

96 **2. Building a research agenda**

97 The members of the working group, i.e. the authors of this article, originate from the
98 scientific board of the FRB, for the academic part of the group, and from the Strategic
99 Orientation Committee of the FRB that gathers stakeholders from all types of

100 activities, from industry to conservationist associations. In addition, a few experts in
101 urban ecology accepted to join the group. Taken together, half of the group was
102 composed of scientists with various ecological approaches (soil science, ecosystem
103 ecology, community ecology, ecological engineering, sociology, law science) and half
104 of practitioners (e.g. employee of territorial communities, landscape gardener,
105 member of a consultancy organisation). The general idea behind such an approach
106 to build a research agenda is that it is often pointed out that the results of science
107 tend not to be used and that the transfer of knowledge from scientists towards
108 stakeholders at the end of projects does not guarantee that their results will be used
109 (Phillipson et al., 2012). There are many ways to engage stakeholders in research
110 projects (Berkes, 2009). We think that involving stakeholders right from the start,
111 when scientific questions are delineated, should be fruitful. It should ultimately
112 facilitate the co-management of towns and their biodiversity using different types of
113 knowledge. We also think that this should increase the stakeholder capabilities to
114 understand the relevance of the more fundamental scientific questions and to foster
115 the development of the corresponding research actions.

116 The workshop was divided into three parts (see Fig. 2). During a first
117 workshop brainstorming techniques were used to allow the group members to
118 express the scientific issues related to urban ecology and biodiversity they
119 considered the most important. Between the first and second workshops, the
120 participants were asked to fill out tables to aid the construction of a more
121 comprehensive list of scientific questions. During the second workshop, this list was
122 discussed and methods and criteria for organizing the list were proposed. Between
123 the second and third workshop, the lead author transcribed and organized the list.
124 During the third workshop, the organization of the list was finalized and gaps in the

125 list were detected and remedied. The group met several times after the first three
126 workshops for further discussion and adjustment of the details of the article.

127 Developing a common list of questions required acquiring a common culture
128 and a common vocabulary because of the diversity of professional and scientific
129 backgrounds of the workshop participants. Half of each workshop was always used
130 for oral presentations (followed by discussions) either about scientific results or
131 operational projects involving urban ecological systems. Beyond building a list of
132 questions, our goal was also to analyse the consequences of the development of
133 urban ecology for the evolution of ecology as a science and for the future of towns
134 and their sustainability. The result of the corresponding discussions is synthesized
135 below after the description of the research agenda. Overall, the collective work was
136 relatively easy. At the beginning of the work, some definitions had to be clarified. For
137 example, what ecology is as a science was not obvious for non-scientists and for
138 scientists from other fields. Similarly, the diversity of ecological sub-fields had to be
139 described and explained. Initially, the scientific questions that were proposed had to
140 be sorted out and some of the questions were initially too vague or too broad to
141 constitute a valid scientific question that can be realistically addressed by a set of
142 experiments and measurements. However, it was relatively easy through discussions
143 to reach an agreement on the type of questions that were sought.

144 **3. The research agenda**

145 All domains of ecology can be studied in urban areas (Alberti, 2007; Collins et al.,
146 2000). This encompasses all types of organisms from microorganisms to large
147 mammals and all types of ecosystems: marine ecosystems, fresh waters, terrestrial
148 ecosystems, soils. This also encompasses all organization scales (population,
149 community, ecosystem and landscape ecology) and all sub-disciplines of ecology

150 (population genetics, evolutionary ecology, behavioral ecology, functional ecology,
151 ecophysiology...). The uniqueness of towns is the overwhelming influence of human
152 activities, i.e. the fact that towns lead to novel man-made ecological systems
153 (Kowarik, 2011). We thus first chose to organize questions according to three broad
154 areas (Fig. 3 and Tables 1 to 3): (1) the biodiversity of organisms living in urban
155 areas, (2) the functioning of urban organisms and ecosystems, (3) the interactions
156 between human societies and urban ecological systems. The first pertains to
157 population and community ecology, the second to functional and ecosystem ecology
158 and the third to various human and social sciences (sociology, economy, geography,
159 anthropology, philosophy...). The distinction between population and community
160 ecology on the one hand and functional and ecosystem ecology on the other hand is
161 classical in ecological sciences (Begon et al., 2005). The former corresponds broadly
162 to issues related to the dynamics of individuals within populations and species within
163 communities, while the later corresponds to issues based on fluxes of energy and
164 matter at various organization scale (from individuals to ecosystems). Social and
165 human sciences play an important role addressing issues (Table 3) about (1) the
166 perception by humans of biodiversity and Nature in urban areas, (2) the governance
167 of urban Nature and biodiversity, (3) ecosystem services and disservices provided by
168 urban ecosystems. Many issues are at the interface between the three broad
169 scientific areas (all three Tables). For example, it might be interesting to study how
170 biodiversity (e.g. species richness of plants chosen by stakeholders for a park)
171 influences ecosystem functioning (beyond the functioning of each plant species
172 separately), how this can be translated in terms of ecosystem services (e.g. carbon
173 storage) and how biodiversity and the provided services are perceived by citizens
174 (and whether there are differences between different categories of citizens).

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

200 and the fact that it is rarely relevant to segregate applied and fundamental ecology.

201 The main types of questions listed in the tables are outlined below.

202 *Urban biodiversity (Table 1)*. We first listed questions on how to monitor
203 biodiversity in urban environments. This led to rather fundamental questions about
204 the different methodologies to be developed but also to questions on the most
205 adequate methodologies to monitor urban biodiversity with the goal of managing this
206 biodiversity. The description of urban biodiversity is commonly justified by questions
207 on the impact of urban environment on biodiversity (Kowarik, 2011). This leads to
208 very diverse questions on the impact of all aspects of urban environment (from
209 pollution and the heat-island effect to the spatial structure of the town) on all types of
210 organisms (from micro-organisms to large mammals and trees). Again, these
211 questions can be rather fundamental but become applied when the ultimate goal is to
212 manage urban biodiversity. For example, the management of green spaces can be
213 adapted to favour various groups of organisms. Besides describing urban biodiversity
214 and designing means to favour it, many scientific questions arise about ecological
215 mechanisms underpinning biodiversity: population dynamics, interactions within
216 communities... We have only listed a few questions in this direction, but basically all
217 fundamental issues traditionally addressed about the dynamics of biodiversity can be
218 addressed in towns. This can involve testing general theories in an urban context,
219 e.g. theories about food web functioning, and testing whether the patterns usually
220 found in natural ecosystems can also be found in towns. It is obviously also important
221 to ask questions about the Darwinian evolution of urban biodiversity (Alberti, 2015).
222 What are the most important evolutionary pressures for urban organisms? Do towns
223 lead to converging evolutionary dynamics all over the world? Are there cases of rapid
224 evolution in urban environment?

225 *Functioning of urban ecosystems (Table 2)*. For the sake of clarity we have
226 separated questions on the functioning of urban vegetation from questions on urban
227 soils and aquatic ecosystems. As for biodiversity (Table 1), a first category of
228 questions is about the description of the functioning of urban vegetation (e.g.
229 photosynthesis, biomass production, uptake of mineral nutrients...) and urban soils
230 (e.g. mineralization, nitrification...) and the way urban conditions impact this
231 functioning (Pickett et al., 2008). Again, many of the questions are rather
232 fundamental because they aim at understanding basic ecological mechanisms. For
233 example, humans control or influence most water fluxes within towns and the
234 consequences of these altered fluxes on the growth of street trees are poorly known.
235 Indeed, the sources of water (e.g. rain water vs. various man-made water networks)
236 for these trees and their strategy (distribution of roots) to absorb enough water have
237 rarely been studied. In the same vein, many aspects of soil functioning remain to be
238 studied. For example, it is poorly known how soil management (urban soils are often
239 man-made) and the urban environment (e.g. local increases in atmospheric CO₂ due
240 to fossil fuel combustion or the urban heat island effect) impact soil microbial
241 communities and the functions they perform (mineralization, nitrification...). From
242 these questions about ecosystem functioning arise questions about the
243 consequences of this functioning in terms of provision of ecosystem services and
244 disservices. What are the types of service provided by urban ecosystems? How
245 much services are provided? Questions about the relations between human aspects
246 of ecosystem services are gathered in Table 3 (see below). But it is possible to ask
247 here (Table 2) questions about the purely ecological aspects of these services, i.e.
248 depending solely on the measurement of ecosystem functions. These questions
249 become much more applied if the possible ways to increase the provision of services

250 are addressed (Gómez-Baggethun and Barton, 2013). This leads to questions about
251 ecological engineering (Barot et al., 2012; Mitsch and Jørgensen, 2003). It could for
252 example be possible to increase the ability of a green space to reduce the heat island
253 effect by evapotranspiration through the choice of suitable tree species. It could be
254 possible to store more carbon in urban soils through suitable inputs of organic matter
255 or through particular ways to construct the soils. The same types of question can be
256 asked for totally artificial ecological systems such as green roofs. They have been
257 shown to provide services, but how to optimize the provision of services through the
258 design and management of these roofs and facades is not fully known.

259 *Urban systems as socio-ecosystems (Table 3).* Three types of questions have
260 been listed here at the frontier between ecological and human sciences: questions
261 about (1) the perception of Nature and biodiversity by city dwellers (Lo and Jim,
262 2010), (2) the governance of towns (Wilkinson et al., 2013), (3) ecosystem services
263 (Andersson et al., 2015). The proportion of humans living in cities is rapidly
264 increasing and, at least in some towns (Europe, North America, some parts of Asia),
265 the amount of Nature is tending to increase. The contact between humans and
266 Nature is therefore becoming proportionally more and more frequent within cities
267 (Shwartz et al., 2014). It is thus important to ask questions about the perception of
268 urban ecosystems and their biodiversity (Lo and Jim, 2012) and whether this may
269 also modify the overall perception of Nature by humans (Standish et al., 2013). This
270 leads to rather fundamental questions pertaining to sociology and psychology. These
271 questions become applied when research has a precise goal, e.g. finding ways to
272 increase the awareness of city dwellers of Nature. Many questions arise about the
273 governance of biodiversity in towns. The actual situation can be described and
274 analysed: What are the places and government authorities influencing urban

275 biodiversity? Are there specific legislations influencing urban biodiversity? The same
276 types of question may be addressed to help reach specific goals, i.e. to develop a
277 suitable governance to favour urban biodiversity. Besides the assessment of
278 ecological functions leading to ecosystem services (see Table 2) many questions
279 arise on the links between ecosystem services and the life of urban dwellers (Gómez-
280 Baggethun et al., 2013). First, it is important to develop sound methodologies to
281 assess services linked to human health, human psychological well-being and cultural
282 services. Some basic general questions also arise about services: Are there trade-
283 offs between the ecosystem services provided by urban ecosystems? Are there
284 differences in the access to services between socio-professional categories?
285 Second, the notion of ecosystem services is more and more viewed as a tool to
286 improve the management of ecosystems. However, the way to incorporate
287 assessments of ecosystem services in the governance of Nature is not
288 straightforward (Laurans et al., 2013) and research could be implemented on how to
289 better use the assessment of ecosystem services in the management of towns.

290 **4. Implementing the research agenda**

291 Some research areas require a particular attention. As usual in biodiversity sciences,
292 urban ecologists started by studying large organisms such as birds, mammals and
293 plants. There are currently an increasing number of studies in urban areas on insects
294 (Madre et al., 2013), soil invertebrates (Vergnes et al., 2017) or microorganisms
295 (Ramirez et al., 2014) and this trend will likely continue. In the same vein, scientists
296 often start by describing patterns, e.g. the distribution of organisms within towns, but
297 it is more difficult to determine the ecological mechanisms behind these patterns, e.g.
298 measuring dispersal and survival rates. However, ecology is precisely about linking
299 mechanisms to their consequences and more effort should be directed towards this

300 area of urban ecology. This is true for studies pertaining to population/ community
301 ecology but also for studies pertaining to functional ecology. For example, there are
302 few studies on the basic functioning of widespread urban types of vegetation such as
303 lawns and street trees. It is thus hardly known how the nitrogen budget of urban
304 lawns is balanced and the respective influence of soil micro-organisms and
305 atmospheric deposits on this budget. Similarly, while street trees are seen as
306 providing services (reduction in the heat island effect) and disservices (roots may
307 damage buildings and pavement)(Mullaney et al., 2015) the ecophysiology of these
308 trees is poorly known (but see David et al., 2018).

309 The services (and disservices) provided by classical urban ecosystems (parks,
310 street trees...) and by relatively new types of man-made ecosystems (green roofs,
311 vegetated facades) are being increasingly assessed (Lundholm and Cadotte, 2015;
312 Mullaney et al., 2015) and these services are often used as arguments to promote
313 these ecosystems. However, practices are often developing quicker than the
314 supporting scientific knowledge or independently of the existing knowledge so that
315 the real benefits of urban green infrastructures are still not fully documented and a
316 comprehensive approach of ecological engineering (Barot et al., 2012; Mitsch and
317 Jørgensen, 2003) is often missing. This is due to a common mismatch between the
318 research time scale on the one hand and the economic and political timescale on the
319 other hand. This probably impedes optimizing the design and management of green
320 infrastructures such as green roofs and vegetated facades. Developing such an
321 approach requires at least five research steps: (1) identifying the ecosystem services
322 that can be provided, (2) identifying the links between these services and ecological
323 functions, (3) determining the links between all features of green infrastructures and
324 ecological functions, (4) identifying links and trade-offs between services and

325 disservices, (5) assessing the various costs (especially environmental costs) of the
326 construction and management of these infrastructures (Barot et al., 2017). In the
327 case of green roofs, steps (1), (2) and (4) have at least partially been achieved
328 (Madre et al., 2013), while steps (3) and (5) have only been tackled very partially
329 (Dusza et al., 2017; Lundholm and Cadotte, 2015). This impedes the determination
330 of the best green roof substrate (e.g. artificial substrate vs. natural soil, clay content
331 or organic matter content), the best substrate depth, or the best plant combination to
332 store carbon, regulate stormwater, purify rain water or favour invertebrate
333 biodiversity. A key issue is that studying the long term dynamics (at least 10 years) of
334 man-made ecosystems such as green roofs is necessary to assess their
335 sustainability. However, such long-term studies are scarce.

336 One of the goals of ecology is to delineate general rules and theories.
337 However, there are hitherto very few general theories about urban biodiversity and
338 ecosystems. To our knowledge, the only general rule recognized in urban ecology is
339 that urbanization leads to biotic homogenization. At the global scale, because towns
340 are built to meet relatively homogenous human needs, they display homogeneous
341 physical environments (Clergeau et al., 2001) that tend to homogenize the town flora
342 and fauna (Schwartz et al., 2006). Worldwide, urban environments select organisms
343 that are adaptable to towns and often replacing native-species. These species tend
344 to be early-successional species with good dispersal abilities and are often
345 introduced by humans. Similarly, it is largely recognized that urbanization leads to
346 unique eco-evolutionary dynamics (Alberti, 2015): rapid feedbacks between
347 evolutionary and ecological dynamics likely modify community and ecosystem
348 functioning in urban environments. Much research is still required to describe and
349 analyse these dynamics. A recent study also suggested that vegetation growth is

350 enhanced in the urban environment of 32 major Chinese cities (Zhao et al., 2016),
351 but this should be tested further at the global scale in order to disentangle the
352 underlying mechanisms.

353 Our work focused on European towns. While the types of question we list are
354 relevant worldwide some of our thoughts and comments are mostly valid for
355 European towns and partially valid for North-American towns. A difficulty in
356 developing general theories for urban ecology is that modes of urbanization are
357 relatively diverse. In particular, urbanization dynamics are now relatively slower in
358 already developed countries than in developing countries (Seto et al., 2011). In
359 parallel, towns of the old world may be centuries-old or even millenaries-old while
360 towns of the new world and developing countries are usually much younger
361 (Ramalho and Hobbs, 2012). This leads to important differences in the structure of
362 towns, the type of building or the proportion of green spaces. These differences
363 between towns and countries will likely impact urban biodiversity and the functioning
364 of urban ecosystems. These issues deserve further research. In particular, much
365 fewer studies have been carried on the ecology and biodiversity of towns in
366 developing countries, e.g. in Africa, which is all the more regrettable as social,
367 environmental and biodiversity issues are huge in these towns (McHale et al., 2013).

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

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

372 Urban areas represent already ongoing experiments waiting for scientists to
373 study them. This can, for example, allow the testing in towns of theories developed
374 independently of urban ecology (Mc Donnell and Pickett, 1990). In particular, towns

375 display gradient of artificialization that can be studied as such (see for example Foti
376 et al., 2017; Zhao et al., 2016) and towns with different structures and characteristics
377 can be compared (Clergeau et al., 1998). For example, urban landscapes allow
378 studying the functioning of meta-populations and meta-communities of urban
379 organisms (Hamer and McDonnell, 2008; Vergnes et al., 2013) that depend on the
380 size and the connectivity between patches favourable to these organisms, e.g. green
381 spaces. Other ecological theories such as the intermediate disturbance hypothesis
382 can be tested in urban landscapes (Breuste et al., 2008) with the hypothesis that
383 species richness could be maximum at intermediate positions on the urban-rural
384 gradient. Towns also provide original situations that can be used in functional
385 ecology. For example, urban conditions often lead to higher temperatures and higher
386 CO₂ concentrations mimicking some aspects of climate changes that are difficult to
387 reproduce in long term experiments on vegetation and soils. Man-made soils in urban
388 areas also constitute original experiments. For instance, the soils of street trees
389 hardly receive any aboveground litter since soils are generally sealed a part from a
390 small opening around trees and since dead leaves are generally gathered and
391 exported. Overall, while new theories may not be required in urban ecology, urban
392 ecology should contribute to ecological theories (Niemelä, 1999).

393 Since the proportion of human urban dwellers is still increasing, urban ecology
394 constitutes a kind of acid test or showcase for ecological sciences, as already
395 emphasized in the particular case of ecological engineering (Mitsch and Jørgensen,
396 2003) and the general case of applied ecology (Barot et al., 2015). If ecologists
397 succeed in (1) understanding urban ecological systems, (2) making precise enough
398 predictions on these systems and their dynamics, (3) designing efficient ways to
399 manage these systems and (4) increasing the well-being of urban dwellers using

400 ecosystem services and biodiversity, they will demonstrate the value of their science
401 that is often underestimated and misunderstood. Indeed, it is important to convince
402 human societies to change their relation with the biosphere in a context where the
403 sustainability of this relation is threatened (Steffen et al., 2015). Urban ecology is also
404 becoming an important showcase for ecological engineering. Towns allow the
405 creation of totally man-made ecosystems that are inherently more diverse in terms of
406 the ecosystems services that can be provided than, for example, agricultural lands
407 that must above all produce food. This should favour the development of a real
408 ecological engineering of services and multifunctionality that goes far beyond the
409 mere management of ecosystems. For example, roof complex ecosystems could be
410 created to recycle wastewater and produce vegetables and fishes.

411 An important still ongoing evolution is that ecologists have first studied ecology
412 and biodiversity in towns, e.g. studying population of organisms as they would in any
413 natural ecosystem, but are more and more studying the ecology of towns as complex
414 ecological systems. In particular, research more and more tackles the complexity of
415 the nested structure of urban ecosystems (Breuste et al., 2008; Clergeau et al.,
416 2006). It is possible to study ecological processes at the scale of (1) a local green
417 space (e.g. demography of a plant population), (2) a network of green spaces (e.g.
418 the meta-population of a plant and fluxes of propagules between green spaces), (3)
419 the matrix between green spaces where some organisms live or spend a part of their
420 time, (4) a town and its urban-rural gradient (e.g. fluxes of plant propagules between
421 the rural and urban areas), (5) a network of towns (e.g. to study an invasive species
422 colonizing towns depending on town characteristics and distances between towns).
423 Of course, with the development of landscape ecology (Forman, 1995), ecological
424 sciences did not have to wait for the development of urban ecology to study such

425 complex systems. However, the way urban ecology analyses and understands
426 spatially complex ecological systems is influential beyond the mere community of
427 urban ecologists.

428 As shown by our tables (Tables 1-3) and by the functioning of our working
429 group, a particularity of urban ecology is that scientific questions quickly require the
430 intermingling of questions pertaining to natural sciences and human sciences. This
431 leads to the study of the complex feedbacks between urban ecosystems and human
432 societies, i.e. to study towns as complex social-ecological systems (Alberti et al.,
433 2003). This in turn leads to many new scientific questions at the interface between
434 various scientific fields. For the same reasons, research on urban ecosystems and
435 biodiversity nearly always involves stakeholders, from town citizens, to gardeners or
436 town councillors. This means that research is often orientated by these stakeholders,
437 which again leads to new scientific questions. Conversely, research results in urban
438 ecology tend to be quickly disseminated to the stakeholders, who in turn tend to use
439 them quickly. For example, implementing experiments on green roofs requires
440 working with the owners of the buildings supporting green roofs, and if results allow
441 designing efficient green roofs, the owners are likely to develop more green roofs on
442 new buildings. Overall this gives scientists important responsibilities and leads in
443 urban ecology to very quick feedbacks between sciences and the society. Again,
444 ecology has not waited for urban ecology to tackle issues related to social-ecological
445 systems and the involvement of stakeholders often leads to new ways to practice
446 science in many areas of ecology. Nevertheless, urban ecology is currently playing a
447 critical role in developing these aspects, which somehow contributes to the current
448 evolution of ecological sciences.

449 **6. Conclusion**

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

474 sustainability of the various options. Because the stakes are very high and because
475 of the pervasive entanglement of fundamental and applied issues, urban ecology
476 must also develop a strong ethic.

477 More and more humans are living in towns and urban planners are tending
478 towards an increase in the amount of Nature within towns, creating a situation
479 propitious for strong feedbacks between Nature and humans in urban areas. It is
480 therefore possible to see urban areas as a test and a laboratory for the future of the
481 interactions between human and ecological systems (Elmqvist et al., 2013; Standish
482 et al., 2013): (1) The perception of Nature by city dwellers is more and more forged
483 by what they perceive of urban ecosystems and biodiversity. Consequently,
484 understanding mechanisms behind this perception should help understanding the
485 general perception of Nature. Conversely, if urban dwellers see more clearly (for
486 example because of active education programs) their dependence on ecological
487 systems and biodiversity or the need for more Nature this could help protecting
488 biodiversity at the biosphere scale, for example because most policy makers are
489 town dwellers. In this context, citizen sciences dealing with biodiversity and
490 environmental issues are quickly developing within towns and could further help
491 changing the perception of Nature (Kobori et al., 2015). Indeed, citizen sciences
492 allow constructing a shared knowledge and may help convincing urban dwellers that
493 they depend on biodiversity and ecosystem services. It has also been suggested that
494 the increase in the proportion of urban dwellers is partially responsible for the
495 worldwide extinction of experience of biodiversity but that reintroducing biodiversity in
496 towns is a good leverage to fight this extinction of experience and make the case for
497 Nature conservation (Miller, 2005). This supports the possibility of an urban
498 reconciliation ecology (Francis and Lorimer, 2011). (2) The design and management

499 of towns can either leave an important space to biodiversity and Nature or totally
500 annihilate biodiversity, which is also the alternative at the biosphere scale. Thus,
501 understanding mechanisms behind the way the future of urban biodiversity is decided
502 could help understanding feedbacks between humans and ecological systems at the
503 biosphere scale. An advantage of studying these feedbacks at the town scale is that
504 they are probably quicker at this scale than at the global scale. (3) Urban areas
505 condense many environmental problems and have a huge impact on the biosphere
506 (e.g. consumption of resources and source of pollution) (Seto et al., 2012) so that
507 solving environmental problems in towns will also aid in solving environmental
508 problems at larger scales. (4) Urban areas also condense many social problems that
509 interact with environmental problems, e.g. Nature plays an important role in the
510 quality of life and there are social inequalities in the availability of green spaces and
511 Nature (Heynen et al., 2006). It is thus important to jointly solve environmental and
512 social problems in urban areas. To this end, gathering all the necessary knowledge
513 using ecological and human sciences is of paramount importance.

514 Finally, the diversity of scientific questions we have listed has been made
515 possible because of the joint action of stakeholders and scientists from various fields.
516 We believe that this type of collaborative work could help implementing the research
517 agenda through a mutual agreement on (1) the relevance of both applied and
518 fundamental scientific questions, (2) what is at stake behind those questions. The
519 whole process could, for example, help in raising research funding and favour the
520 direct involvement of stakeholders in research.

521 **Acknowledgments**

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523 that was essential for the functioning of the group and the organization of the
524 workshops.

525

526 **References**

527

528 **Table 1**

529 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?

530

531 **Table 2**

532 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 (CO₂, 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)

By street trees?

How to manage vegetation in urban areas to increase the provision of ecosystem services?

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. N₂O)?

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?	

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536 **Table 3**

537 List of questions on the coupled functioning of urban ecological systems and human
 538 societies

Fundamental issues	Applied issues
Perception of Nature in urban areas	
What is the perception of urban Nature and biodiversity by city-dwellers?	Why and how can the awareness of city-dwellers to Nature and biodiversity be increased?
What is the perception of green spaces (including lakes and rivers)?	Can the increase of city-dweller awareness to Nature 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 Nature 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 Nature and biodiversity in towns?	
Governance and public policies	
What are the places / government authorities for the governance of urban Nature and biodiversity at the town scale or at larger scales?	How can citizens be associated to the governance of urban Nature and biodiversity?
Can the governance of Nature 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 Nature 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 Nature and biodiversity?
What is the impact of the features of the governance of urban Nature on urban biodiversity?	What fiscal and economic levers could favour the development of urban Nature 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?
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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 Nature 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?

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543 **Fig. 1.** Number of publications in urban ecology and their percentage relatively to the
 544 total number of publications in ecology from 1980 to 2015. The Web of Science (Web
 545 of Science Core Collection) was used to search for articles mentioning “urban” AND
 546 “ecology” in the topics (i.e. in the title, abstract and keywords) to assess the number

547 of articles in urban ecology while the total number of articles in ecology was
548 assessed searching the same data base for “ecology” in the topics.

549

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

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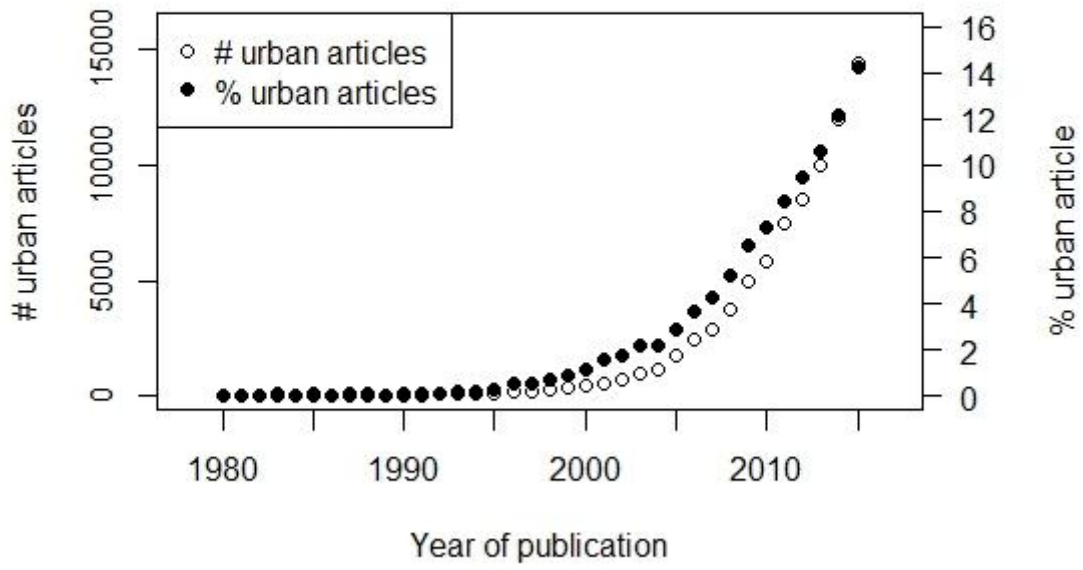
552 **Fig. 3.** Diagram describing interactions between humans, biodiversity and ecosystem
553 functioning in urban environments and displaying accordingly the organization of the
554 research agenda (See Tables 1 to 3) in three broad types of question and in
555 fundamental (understanding) and applied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

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558 Fig. 1

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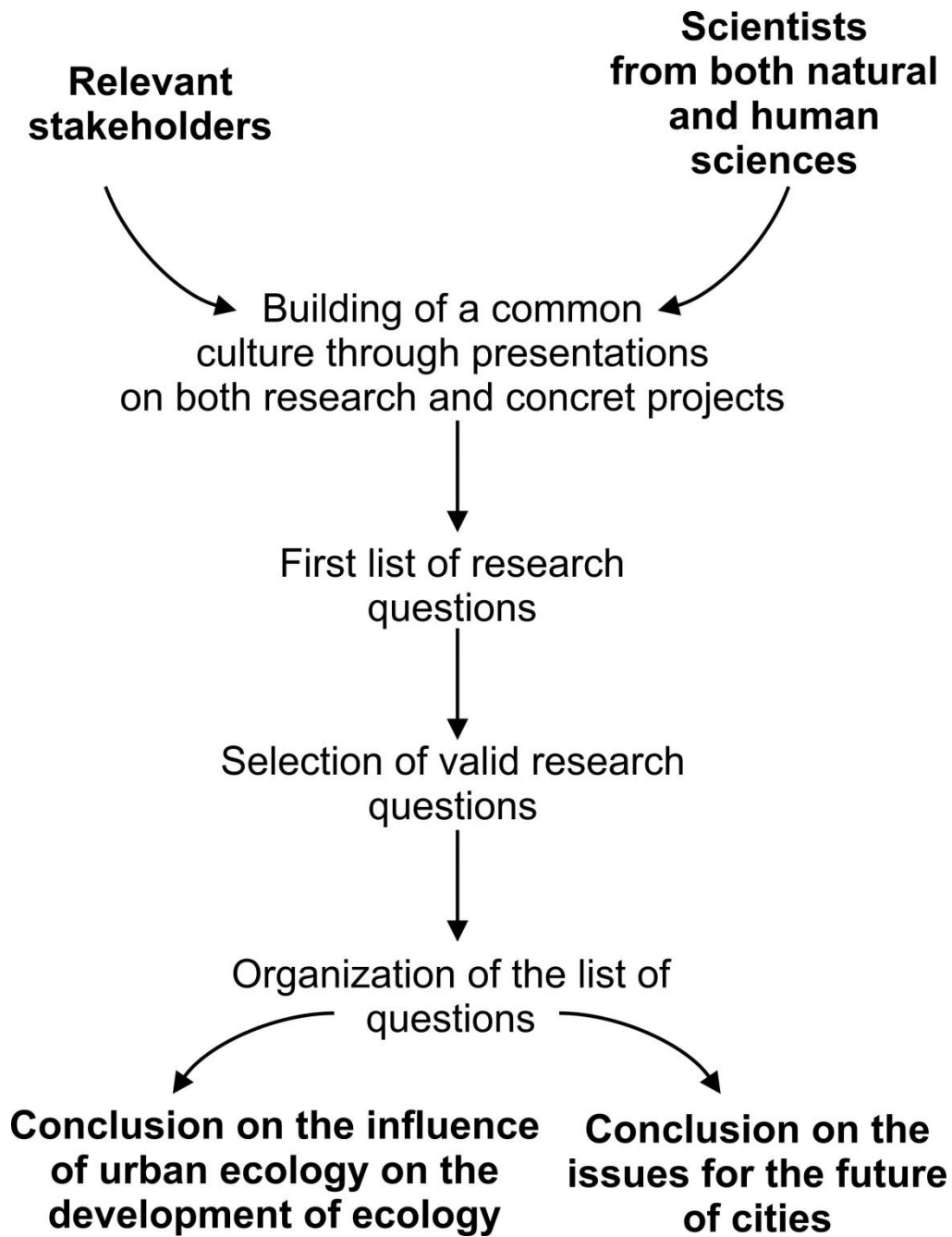
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563 Fig. 2

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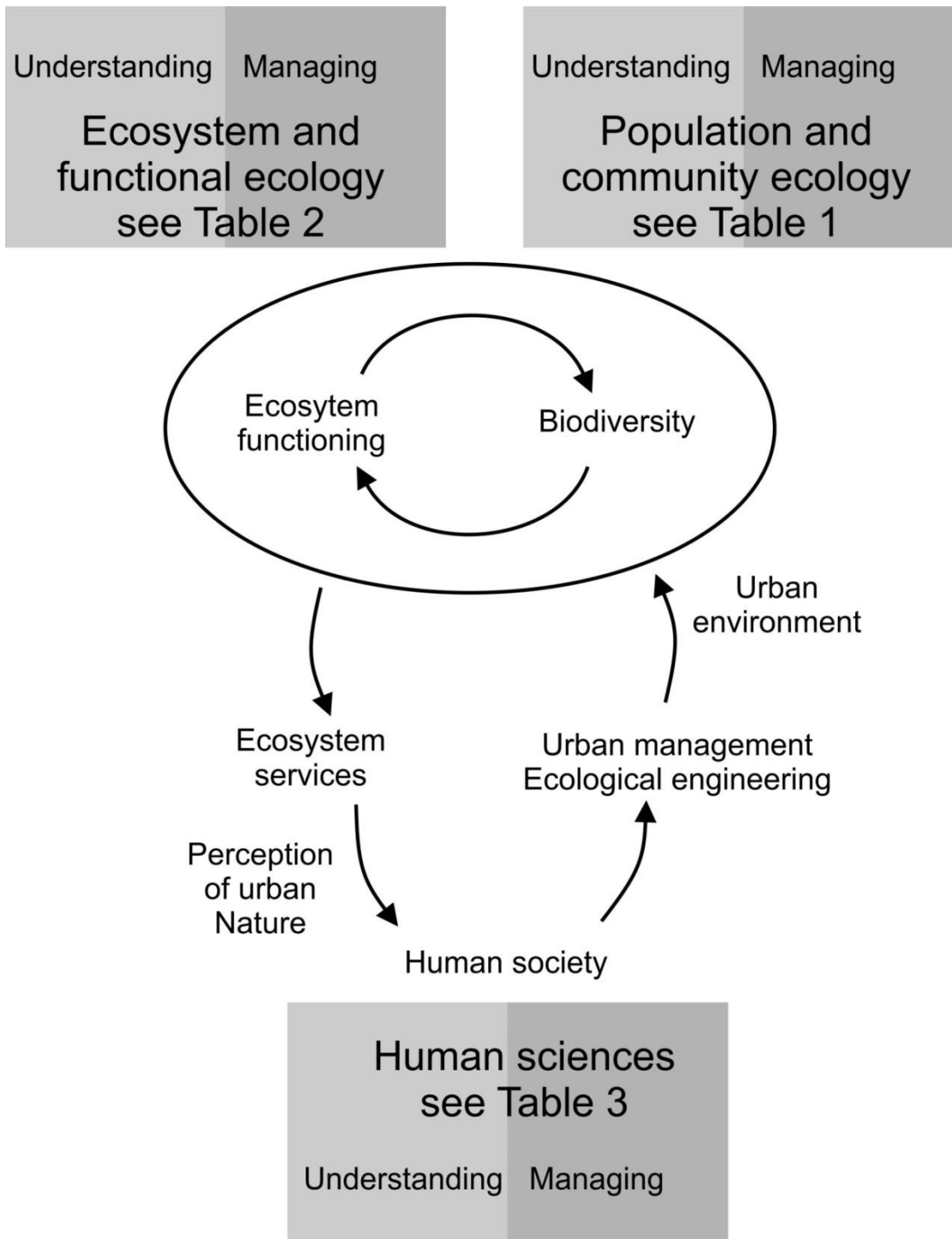


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567 Fig. 3

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