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PERSPECTIVE

Urban ecology principles: are urban ecology and natural area ecology really different?

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Abstract
Context To understand, even improve, the land of shrinking nature and spreading urbanization, a science applicable from remote natural areas to cities is needed.
Objective Today's scientific principles of urban ecology are articulated and compared with ecology based primarily on natural ecosystems; we either robustly merge the trajectories or watch them diverge.
Methods A literature review emphasizes that the field of ecology emerged from late 19th century and early 20th century research mostly in semi-natural environments, whereas urban ecology mainly developed from studying plants, habitat types, and ecosystem nutrient flows in late 20th century city environments.
Results Ninety urban ecology principles are identified and succinctly stated. Underlying the principles, 18 distinctive types of urban attributes are recognized in four major groups: land uses; built objects; permeating anthropogenic flows; human decisions/activities. The attributes or objects studied in "natural area" ecology and urban ecology differ sharply, as do the primary objects present in late 19th century and late 20th century cities. None of the 90 basic principles would have emerged from research on natural areas, and all are readily usable for improving urban and urbanizing areas.
Conclusion Incorporating urban ecology science into ecology's body of principles and theory now should catapult the field of ecology to the next level, and noticeably increase its usefulness for society.

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Introduction

Globally, natural areas are shrinking and becoming more remote, as urban environments and their effects expand swiftly and powerfully, almost tsunami-like (Forman 2008). Ecology principles based on natural ecosystem or area research seem sufficient for understanding less and less of the global surface. To provide universal understanding and robust applications, shouldn't the field of ecology incorporate urban ecology into its body of principles and theory now?

Ecological concepts have emerged from all major areas of the globe: croplands and pasturelands (agricultural ecology); woodlands/forests and deserts/grasslands (natural area ecology); freshwater, estuary and sea (aquatic ecology); and cities/suburbs (urban ecology). Ecologically, the land of towns and villages remains a less familiar frontier.

More specifically, the field of ecology seems to have begun with 1860s–1890s studies of somewhat-natural aquatic and terrestrial environments (McIntosh 1985; Worster 1994). In contrast, urban ecology basically began a century later focused on built environments. The objects studied and, one may hypothesize, the principles generated seem really different.

Ecological principles, based mainly on natural area research, are highlighted in many ecology texts and handbooks (e.g., Ricklefs and Miller 2000; Odum and Barrett 2005; Schulze et al. 2005; Townsend et al. 2008; Cain et al. 2011). A synthesis of urban ecology principles in succinct form for ready application has yet to emerge, but can be dug out of recent major works (Konijnendijk et al. 2005; Alberti 2008; Forman 2008; Marzluff et al. 2008; McDonnell et al. 2009; Adler and Tanner 2013; Forman 2014; McPhearson et al. 2016).

The attributes or objects studied by natural area/ecosystem ecologists and urban ecologists provide insight into, and may be a useful indicator for, the different principles generated by the two linked, but seemingly diverging, fields. Furthermore, urban objects and attributes of late 19th century cities (Fig. 1) and late 20th century cities have markedly changed, suggesting that time of origin may have a large effect on today's body of principles.

Thus the objective is to understand the linkage between ecology and urban ecology by considering where and when the fields originated, and focusing on the objects or attributes studied and the principles generated. Three specific goals are to:

1. Highlight the different environments and subject areas studied by pioneers in natural area/ecosystem ecology and urban ecology.
2. Articulate urban ecology principles based on the recent half-century of research.
3. Contrast the predominant objects or attributes studied: (a) in natural areas, underlying today's field of ecology; (b) in late 19th century cities, if ecology or urban ecology had begun there; and (c) in late 20th century cities, where urban ecology basically began.

Beginnings in semi-natural areas and urban areas

Ecology in semi-natural ecosystems/areas, 1860s–1910s

In what types of habitat or location did the field of ecology begin? The following encapsulated sequence of steps in Europe and North America provides an answer. Each step is represented by a leading scientist(s) with nationality, date of a major work, and research habitat, location and/or subject (McIntosh 1985; Worster 1994).

1. Antecedents to ecology
   Carolus von Linnaeus—Sweden, 1762. Gilbert White—Britain, 1789. Alexander von Humboldt—Germany, 1807. Charles Darwin—Britain, 1849. Henry David Thoreau—USA, 1854
2. Ecology beginning in Europe
   The sea (marine medusae, plankton, biomass, evolution): Ernst Haeckel—Germany, 1866, 1891
   Marine oysterbeds (community, equilibrium): Karl Mobius—Germany, 1877
   Plant communities (physiology, symbiosis, succession): Eugen Warming—Denmark, also worked in the American tropics, 1895
   Vegetation classification (communities, phytosociology): Zurich-Montpellier "School", 1890s onward, including J. Braun-Blanquet, 1915 onward
   Plants (physiology, adaptation, plant geography): Andreas F. W. Schimper—Germany, also worked in the tropics, 1898
   Vegetation survey: Arthur Tansley—Britain, 1904, 1911
   By the 1890s in Europe, "…natural history and physiology combined and emerged quite suddenly as a recognized discipline of ecology." (McIntosh 1985). It combined four research areas: biological oceanography, limnology, plant ecology, and animal ecology.
   The British Ecological Society was founded in 1913.
3. Ecology beginning in North America
   Lake microcosm (animals, competition): Stephen A. Forbes—Illinois, 1880, 1887
   Grasslands (pastureland, weeds, woods): Charles E. Bessey—Nebraska, 1886
   Geographic zones (animals): C. Hart Merriam—Western mountains/deserts, 1894
   Vegetation dynamics (community as organism, succession, climax): Frederick E. Clements—Nebraska, 1905, 1916
   Dunes (succession, non-equilibrium): Henry C. Cowles—Chicago, 1909
   Forest dynamics (shifting mosaic): W. S. Cooper—Minnesota, 1913

Fig. 1 Late 19th century city street life. Note: probable city manure-collectors (woman and man, far right); many chimneys atop buildings for coal smoke which darkens winter's daytime air; mourning the horse loss (*upper left*); dead horse on cobblestone street (*left*); workers in mud around fire, perhaps roasting chestnuts (*lower left*); pedestrians (*bottom*); recreational skaters on river ice (*lower right*). Paris, 1874–1888. "L'hiver a Paris" etching by Felix Hilaire Buhot. From New York Public Library

Animal communities: Victor Shelford—Illinois, 1913
The Ecological Society of America was founded in 1915, mainly by plant and animal ecologists, with aquatic ecologists increasing thereafter.

Urban ecology, 1970s–1990s

Although various interesting definitions of urban ecology exist, I use the following scientific concept of urban ecology (Forman 2014): "interactions of organisms, built structures, and the physical environment where people are concentrated." The encapsulated origins of urban ecology are based on three reviews (Sukopp 2008; McDonnell 2011; Forman 2014).

1. Antecedents to urban ecology
   From the 1500s to the 1960s, key areas of ecology study (at scattered intervals) in urban environments were (Forman 2014): (a) floras, vegetation, and plant migration; (b) faunas and economically important animals; (c) organisms related to environmental conditions, soils, microclimate, and air pollution; and (d) organisms on World War II bombed sites and rubble surfaces.

In the 1920s, some Chicago sociologists used early 20th century ecology concepts to study urban social patterns and changes. This work is excluded here since scientific understanding, or developing principles of urban ecology, was neither a goal nor a result. Today, linking urban sociology with ecology, or focusing on the overlap area, is an important goal in some research projects (McDonnell 2011; Pickett et al. 2011; McPhearson et al. 2016), whereas many projects essentially recognize diverse human effects while focusing on the science of urban ecology (Marzluff et al. 2008; Sukopp 2008; McDonnell et al. 2009; Forman 2014). In the present analysis, if the sociology dimension (or another major urban discipline) were included, urban ecology and natural ecosystem ecology would probably be widely divergent fields.

2. Urban ecology beginnings in urban environments
   The field appeared to accelerate and begin coalescence in the 1970s, when multi-investigator multidimensional studies were added to the diverse pioneering and ongoing studies by individual

researchers.

Ecosystem studies of nutrient and material flows: Brussels, Berlin, Hong Kong—Nix 1972, Duvigneaud 1974, Stearns and Montag 1974, Boyden et al. 1981, Sukopp 1990

Vegetation and the ecosystem concept: Tokyo—Numata 1982

Urban trees and their roles: various North American cities—Rowntree 1986, Grey and Deneke 1992

Diversity and analysis of urban habitats: Britain—Gilbert 1991

Human ecology: Hong Kong, North America, etc.—Boyden et al. 1981, Steiner and Nauser (1993)

Vegetation/biotope mapping, changing flora and vegetation: Berlin, Northern & Central Europe—Sukopp et al. 1990, Pysek 1993, Schulte et al. 1993, Sukopp et al. 1995, Pysek 1995

In brief, the field of ecology began with studies in a wide range of semi-natural and natural areas or environments, including woodland, grassland, farmland, dunes, lake, and marine environment. On the other hand, urban ecology began in built environments with quite different attributes. Nevertheless, many of the objectives or types of urban studies seem similar to those done in natural areas (Grimm et al. 2008; Marzluff et al. 2008; McDonnell 2011; Pickett et al. 2011; Wu 2014). This suggests that early urban ecology research was more based on the ecology framework developed in natural areas than on the distinctive attributes of cities.

Principles of urban ecology

The science of ecology or urban ecology is described by concepts, principles, laws, models, hypotheses, and theories. Principles are highlighted here since they are supported by a "reasonable amount" of evidence, including empirical evidence, and typically apply to the bulk of, though not all, situations. The criteria used for identifying urban ecology principles are: (1) important subject; (2) widely applicable; (3) reasonable amount of evidence available; and (4) predictive ability. Some principles presented may imperfectly fulfill all four criteria, additional principles probably exist, and doubtless more will emerge as urban ecology accelerates.

Ninety urban ecology principles, based on the recent half-century of research, are pinpointed in succinct form (Table 1). The principles are listed in 11 groups (habitats, biodiversity, soil and organisms, water and organisms, greenspaces, etc.), widely familiar and used by ecologists and other disciplines. These groups help in visualizing the similarities and stark contrasts with natural area ecology in the following section. They also help identify potential linkages tying urban ecology and natural ecosystem ecology closer together.

Each principle (Table 1) appears to be mainly based on a particular attribute or object of urban areas. Thus an alternative organizational approach, grouping the principles by urban attributes, provides additional perspective. Eighteen key attributes are readily recognized, and conveniently fall into four major groups: land uses; built structures; permeating anthropogenic flows; and human decisions/activities. The fourth group is based more on people than on specific objects.

Land uses (22 principles) include: water-supply source area (1); development & suburban areas (6); residential areas (4); commercial & industrial areas (2); greenspace patches (6); green corridors & "stepping stone" sequences (3)

Built structures (19): buildings (4); roads & streets (3); pipes & pipelines (4); impervious surfaces (5); concentrated diverse structures (3)

Permeating anthropogenic flows (18): human-produced chemicals (9); human wastewater (3); human-produced noise & light (2); vehicles (4)

Human decisions/activities (31): past societal actions/activities (or general evolution of an urban area) (17); current societal actions/activities (8); individual decisions (6)

Considering the urban ecology principles relative to the 18 attributes highlighted provides valuable insight. Hardly any of the attributes is present or significant in natural areas. Thus, interestingly, probably no urban ecology principle would have emerged from research focused on natural areas/ecosystems.

In effect, four major features—land uses, built structures, permeating anthropogenic flows, and human decisions/activities—frame the ecology of urban areas. Urban ecology principles (Table 1) seem to be strongly based on the distinctive attributes of built areas, rather than mainly being extrapolations or modifications of ecological principles from natural areas. All 90 basic principles generated for

Table 1 Urban ecology principles developed since the field's 1970s origin

Habitats

1. More buildings and tall structures create both more habitats and hazards for organisms.
2. Hospitals, veterinaries, zoos, structures with food, and human wastewater greatly enrich microbial diversity and ecology.
3. Both rectilinear networks of different form and the arrangement of buildings strongly affect species distributions and movements.
4. A concentration of numerous tiny and diverse human-made objects creates high microhabitat diversity.
5. Trees and shrubs, typically in straight lines along streets and roads, with associated animals are increasingly stressed by more traffic and diverse related pollutants.
6. House plots (lots), street blocks, neighborhoods, cities, and urban regions support relatively different vegetation and associated animals at each spatial scale.

Biodiversity

7. Planted native and nonnative species, along with diverse spontaneous colonizers, coexist, interact, and together provide the benefits offered by limited urban plant cover.
8. Few specialist species and mostly environmental generalists predominate in cities, with some pre-adapted and some *in situ* city-adapted species present.
9. Despite widespread species-scarce sites, overall biodiversity is high, mainly due to high habitat diversity, native species inputs, plantings, and abundant nonnative species.
10. Plant and animal biodiversity is typically high in neglected sites, and (excluding zoos and botanical gardens) decreases with more design, planning, management, and/or maintenance.
11. Numerous low-population-size species, especially plantings and recent nonnative arrivals, coexist with, some common species, and few highly abundant species.
12. Species populations commonly exhibit high mortality, so unplanted rich native biodiversity largely depends on "species rain" inputs, especially from surrounding semi-natural areas.
13. Almost all rare native species seem doomed to local extinction due to concentrated human impacts, whereas rare nonnative species may disappear, persist, or spread.

Plants and vegetation

14. Shrubs are commonly limited in abundance, especially near walkways and public spaces, due to human security concern.
15. Despite considerable tree mortality, dead trees, branches and logs, along with their associated fauna, are normally scarce due to human removal.
16. Abundant flowers with pollinators commonly persist much of the year, due to urban heat and/or gardens and plantings with sequential flowering.
17. Seed dispersal is greatly facilitated by people and vehicle movement, plus stormwater runoff and accelerated airflow associated with built structures.
18. Green roofs (vegetation covered) and green walls help reduce urban heat buildup, stormwater runoff, and air pollution locally within an urban area.
19. Most vegetation patchiness and succession results from human activity, i.e., site clearance/alteration/construction and/or ongoing management/maintenance/repair.
20. Ecological succession from plant colonization to mature tree vegetation, or even complete young-tree cover, is rare due to site disturbance or land-use change.
21. While species composition and abundance constantly change, pulses of new species (e.g., after 1500 in Europe) provide novel species assemblages, which in turn change rapidly.
22. Plant populations typically exhibit high resistance, high resilience, or temporary existence in urban areas with widely fluctuating environmental conditions.

Animals/wildlife

23. Most wildlife species strongly respond to the species and arrangement of trees and shrubs, especially in areas with high impervious-surface cover.
24. Animals tolerate and communicate in endless urban noise—some loud, most low frequency.
25. Many terrestrial wildlife species are nocturnal, avoiding daytime people and traffic, and respond to diverse changing urban lights.
26. Pipes and streets facilitate widespread pest movement between and into buildings.

Table 1 continued

27. Pets respond strongly to human behavior and feeding, while only slightly affecting surrounding animals and plants.
28. Genetic adaptation and differentiation includes urban-rural population divergence, while selective forces include pollution, human-provided food, and low-frequency noise.
29. Wildlife distributions and routes are commonly rectilinear, mainly reflecting road, street, walkway, rail, and pipe infrastructure networks.
30. Streets and roads are barriers against, and conduits for, animal movement, in both cases with more traffic strongly decreasing movement rate.
31. Food webs are typically simplified, and their predator links reduced, with increasingly intensive urbanization.

Soil and organisms

32. Porous low-organic-matter soils, characteristic of fill sites, predominate near roads, streets, and buildings.
33. Low organic matter in widespread fill, plus soil compaction by former construction or present human activity, strongly limits the growth of woody plants.
34. Soil types are often only 1 to 100 m wide, commonly reflecting an area's history of construction and fill.
35. Vertical soil layers from place to place are highly variable in number, depth, and types/amounts of embedded anthropogenic objects.
36. Abundant diverse pipes, tunnels, foundations, and artifacts, plus their chemicals, strongly affect the growth and distribution of roots, soil microbes, and soil animals.
37. Diverse dense overlapping pipe-systems with leaks and overflows add chemicals and water to the soil, while maintenance and repairs keep the area in flux.
38. Widespread high soil pH from water running across concrete or mortar surfaces differentially affects mineral nutrient availability, growth of organisms, and species present.
39. Concentrated heavy metals, hydrocarbons, pesticides, and other organic compounds in soil, especially from nearby industry and transportation, decimate soil animals and microbes.
40. Aerobic decomposition typically improves contaminated soil, whereas water flowing through such soil commonly spreads toxins into groundwater and surface waterbodies.

Chemicals and organisms

41. Around built structures chemical flows are mainly rectilinear, but locally convoluted, enhancing or inhibiting organisms along the routes.
42. Chemical "flow throughs" rather than cycles predominate, with little recycling.
43. Photosynthetic CO_2 absorption and organic matter production are low due to limited vegetation cover, plus heat-and-pollution stressed plants.
44. Nitrogen and phosphorus from diverse sources blanket the urban area, producing highly eutrophicated terrestrial and aquatic ecosystems often dominated by one or a few species.
45. Cities are cauldrons of countless concentrated human-created chemicals, overwhelmingly with unknown effects on species and their biology.

Air and organisms

46. Heat flow, especially related to impervious surfaces, rather than organic food-chain energy flow, dominates most urban ecosystems.
47. Extensive impervious-surface areas have limited plant transpiration along with considerable evaporation (after rains), with the net result being rather little air cooling.
48. Air turbulence and vortices, related to the arrangement of built structures, effectively remove particles from surfaces and create pollutant and propagule-dispersal patterns.
49. Diverse air pollutants, especially from nearby motor-vehicles and industries, bathe and often inhibit the growth and survival of plants and animals.
50. Strategically located tree plantings, e.g., in parks, help reduce most air pollutants, locally improving air quality.
51. Trees cool air by shading wall, sidewalk and street, by transpiring water, and by accelerating airflow between tree crown and wall.
52. Abundant well-adapted urban-tolerant nonnative woody plants help cool and clean urban air.
53. In summer, heat volatilizes certain organic substances from the surfaces of roads and car parks, with the heat and resultant air pollutants inhibiting some nearby plants.

Table 1 continued

54. Concentrated fossil-fuel combustion makes the urban area a primary CO_2 emitter, with global-warming effects on organisms in rural and remote areas.

Water and organisms

55. The watertable commonly supporting surface waterbodies is normally lower and more variable than in surrounding areas, and groundwater is polluted/contaminated.
56. Wetlands are scarce, often due to former farmer activity, and typically contain locally uncommon species tolerant of human disturbance.
57. Stormwater runoff largely from impervious surfaces and low-friction pipes dominates water flows, and hardly any water cycling/recycling occurs within an urban area.
58. Stormwater runoff, which cleans urban surfaces and is piped or ditched to stream, pond, or wetland, causes pulses or fluctuations in water levels and pollutant concentrations.
59. Most local waterbodies have intensive human use and disturbance, considerable hard edge, and a quite limited littoral area of vegetation zones with rich aquatic fauna.
60. Many streams, ponds, and wetlands have lowered water levels in a wastewater sewage-system area, and are polluted in a septic-system area containing some defective systems.
61. Human wastewater with limited or no treatment, or combined-sewer-overflows, is channeled downslope/downriver, often creating local anaerobic water conditions.
62. Chemicals and microbes in human wastewater commonly seep into the soil, but constantly or periodically pour into and pollute local aquatic ecosystems.
63. Streams are commonly truncated, channelized, rock/concrete-lined, flashy, in low-flow condition, and/or lost into pipes, all of which limit fish and other aquatic species.
64. Urban streams and rivers, or estuary and sea, normally clean an urban area by carrying away numerous types of solid waste and chemical pollution.
65. Water quality is strongly determined by diverse human effects along and near stream corridors.
66. Water quantity (or hydrologic flow) and flooding of streams and rivers commonly increase with the proportion of developed land in upstream or headwater areas.

Greenspaces

67. Dissimilar large greenspaces in a city contain most of the interior and uncommon native species, and are major sources for species dispersal within the city.
68. The distribution of greenspaces, even tiny, within a built area has a strong effect on urban heat, water flows, and species movement.
69. Diverse types of urban agriculture provide a distinctive flora, abundant herbivore populations, and nutrient-rich soil and water.
70. Vacant plots (lots) are typically susceptible to infill construction, which reduces the benefits of vegetation and of "stepping stones" for species movement.
71. Lawns, with intensive human use, mowing, watering, and chemical maintenance, are widespread patches of water absorption, low-structure plant cover, and low species richness.
72. Vegetated corridors, from house-plot shrublines to wide greenways, are often connected in networks and facilitate species movement.
73. Species movement along green corridors is commonly limited by internal heterogeneity, low-quality sections, gaps/breaks, and the sequence of adjoining land uses.
74. Sequences of green (vegetated) "stepping stones" surrounded by development are effective routes for some wildlife movement, especially generalist species.

Residential, commercial, industrial areas

75. Residential high rises, low rises, single units, courtyard/patio houses, and informal squatter housing in a city serve as differing sources, sinks, and repellents for species movement.
76. A block of highly diverse and ever-changing house plots is ecologically tied together by some repetitive plantings/land uses, plus green street side and back-boundary corridors.
77. Within a house plot, concentrating diverse land uses, maintenance regimes, and tiny structures commonly increases species richness well above that in a nearby natural area.
78. Biodiversity is likely higher in informal settlements than in similar-density areas, due to concentrated microhabitats and little-maintenance sites with native and nonnative species.

Table 1 continued

79. Numerous nonnative species are transported by ship, aircraft, train, and truck to warehouses/storage sites, and then escape or are trucked to commercial and residential areas.
80. Commercial and shopping areas, with concentrated goods, people, food, garbage, and other organic materials, sustain surrounding scavenger and pest populations.
81. Many industrial sites contain uncommon species associated with raw materials, byproducts, or pollutants, yet have low species richness.
82. Many pest insects genetically adapt to heavy pesticide use around kitchens, houses, restaurants, and food markets, as well as standing water.

City and ring-around-the-city

83. Urban pollutants, commercial goods, vehicles, and people flow outward from a city, ecologically transforming surrounding areas.
84. Commuters, suburban nonnative species, and diverse farm and industrial effects from surrounding areas flow inward to the city, ecologically modifying urban areas.
85. Urban areas normally expand by combined bulges, satellite-city growth, strip development, and sprawl, with the first two urbanization processes being least environmentally damaging.
86. Suburbs are filters of flows/movements between rural and city areas, and also key sources of flows affecting both areas.
87. The patterns (curve shapes) along urban-to-rural gradients especially depend on the specific radii selected, locations of first and last points, and the ecological variables measured.
88. Urban-region natural resources close to a city, including freshwater supply, food market-gardening, clean air, recreation areas, and tourist spots, strongly enhance the city's ecology.
89. Outside the city, a water-supply reservoir with protected surrounding land is a "hotspot" of fish, wildlife, and biodiversity, due to its large area and concentration of diverse habitats.
90. Major natural and human-caused disturbances are often ecological and human disasters, due to intensive development plus limited resistance and resilience of a large dense population.

Principles are extracted from six major syntheses (Konijnendijk et al. 2005; Alberti 2008; Marzluff et al. 2008; McDonnell et al. 2009; Adler and Turner 2013; Forman 2014) and succinctly presented. Some broad-scale principles are included from the urban-region ecology list in Forman (2008)

understanding are readily applicable and useful for improving urban and urbanizing areas.

Attributes or objects in the ecology of natural areas

Using the long-term most familiar concept of ecology, i.e., interactions of organisms and the environment, the principles of ecology are well described in textbooks and handbooks (e.g., Ricklefs and Miller 2000; Odum and Barrett 2005; Schulze et al. 2005; Townsend et al. 2008; Cain et al. 2011). At the broadest scale, seven areas of ecology are commonly recognized: organisms and the physical environment; ecology of populations; interspecific interactions; community ecology; ecosystem ecology; evolutionary ecology; and landscape/conservation/global/applied ecology.

Numerous specific attributes or objects underlie ecological studies in natural areas. More than 160 objects/attributes, such as phosphorus, seeds, detritus, rainfall, herbivores, ponds, fire, insects and watershed, were identified in the five ecology references cited. Ecologists working in natural areas with no built structures analyze processes, construct models, and study organisms (plants, animals, microbes) interacting with these diverse 160+ objects. All of the attributes/objects are also present in urban areas, though often in limited amount or truncated form. As noted above, urban environments contain many other distinctive characteristics.

In brief, a rich array of principles in ecology textbooks and handbooks summarizes our understanding of natural areas or ecosystems. The principles mainly result from studying specific objects, processes, and models. The attributes or objects studied in natural ecosystems are a convenient surrogate for comparison with the following objects studied in urban ecology.

Attributes or objects of 1870s–1890s cities and 1970s–2010s cities

Suppose the field of ecology in the 1870s–1890s had begun in urban areas (Fig. 1), and then expanded to natural and semi-natural areas. The attributes or objects of late 19th century cities (Table 2) (Mumford 1961; Cronon 1991; McNeill 2000) differed markedly from those of natural areas then. Although some of these urban attributes/objects were also scattered in rural areas, none would have characterized late 19th century natural areas.

But also note the contrast between the major attributes of late 19th century and late 20th century cities (Table 2). The urban ecology of those two environments would be quite different. Furthermore, both lists of attributes differ sharply from those studied by ecologists in natural areas.

Discussion and conclusion

In the late 19th century, if the field of ecology had begun in cities, or concurrently in urban and natural environments, today's ecology would doubtless be broader, more robust, and more widely applicable. Also, if urban ecology had coalesced in the late 19th century and continued through a century of dramatic urban change (Table 2), it would be noticeably deeper and more highly developed today.

Overwhelmingly, today's urban ecology principles (Table 1), largely based on urban characteristics, are

Table 2 Key attributes and objects of late 19th century cities and late 20th century cities

Late 19th century cities
1. Mud, dust, soil compaction by wagons, carriages, horses
2. Manure piles, huge numbers of seed-eating sparrows & rodents
3. Main streets with cobblestones, tracks, trollies
4. Open street-center or shopfront stormwater drains, often with wastewater
5. Stream/river or estuary/sea as primary waste-removal cleaning system
6. Coal-burning smoke, dense particulate & SO_2 pollution
7. Diverse strong odors, 24-h often-loud noise
8. "Tough" spontaneous native & nonnative plants predominant
9. Vegetable gardens & animals in center of many city blocks
10. Dispersed pigs, chickens, other livestock, feed sources, dead animals
11. Widespread free-ranging dogs & cats
12. Widespread brick & wooden buildings, widely spreading fires
13. Factories, shops, & residences interspersed (mixed use)
14. Numerous apprentice shops with raw-materials, storage, products, wastes
15. Large open markets for food & goods
16. Widespread nightsoil and solid-waste accumulations, many small dumps
Late 20th century and early 21st century cities
1. Reinforced-concrete highways, bridges, sidewalks, large buildings
2. Tarmac/asphalt roads, streets, car parks
3. Motor cars, trucks/lorries, buses, traffic, & their products
4. Bicycles, motorized cycles
5. Extensive impervious surface directly connected to local waterbodies
6. Separate or combined stormwater & wastewater systems
7. Extensive infrastructural pipe systems for many services
8. Solid-waste trucks, large dumps, recycling/incineration facilities
9. Reservoir outside city with piped water-supply
10. Enclosed supermarkets and small food shops
11. High-rise buildings, skyscrapers
12. Subway/underground systems for people movement
13. Suburban sprawl, septic systems, commuter transport systems
14. Widespread lawns
15. Large palette of nursery-provided nonnative plants

qualitatively different from natural-area ecology principles based on natural features. Still, some urban ecology principles may be mainly quantitatively different from, or variants of, natural area principles.

As urban ecology expands, probably additional traditional ecological subjects will be incorporated in modified form. For instance in cities, vertebrate territories, dead wood habitats, communities of diverse-origin species, edge/ecotone patterns, allelochemics, soil animal movements and effects, population dynamics, competition, and evolutionary ecology remain as promising frontiers.

Urban ecology ahead will also explore patterns based on additional little-studied urban attributes. These frontiers include hydrocarbon-covered surfaces, water infiltration in impervious surface cracks, green wall effects on air pollutants, species movements relative to pipe systems, rare species and natural selection in soil-contaminated brownfields, ditch ecosystems, biodiversity relative to maintenance regime, species richness and movements in informal squatter settlements, animal movements and predation relative to lights, roadside discarded debris, microhabitat diversity of buildings, and many urban region patterns.

Future texts and handbooks on ecology are likely to become, for example, 20–25 % urban ecology. But they will also increasingly incorporate, and be enriched by, the ecology of cropfields/pastures and town/village-influenced land.

Furthermore, analyzing the linkages between ecological science and other major disciplines in urban areas provides valuable perspective. Ecological economics, road ecology, socio-ecology, ecological engineering, and ecological design/planning are good examples. Each contributes useful dimensions and insight to both ecology and the associated core discipline.

Finally, natural areas shrink and become more remote. Meanwhile built areas and roads spread, perforating and slicing up the land. Let's form a science of ecology that works everywhere, from city to remote natural ecosystem.

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