On the early history of urban ecology in Europe[1]

Počátky výzkumu ekologie evropských měst

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Early investigations on the ecology of cities were in the tradition of natural history and focused on single biotopes. Of special interest were the plants and animals introduced into new areas directly or indirectly by man. In Central Europe, studies of anthropogenic plant migrations and cultural history were combined in a specific way, the so called Thellungian paradigm. The succession of vegetation on ruins after the bombing during the Second World War was studied in many cities. Ecological studies on whole cities started in the 1970s with investigations on energy flow and nutrient cycling. Today the term urban ecology is used in two different ways: in developing programs for sustainable cities, and in investigation of living organisms in relation to their environment in towns and cities.

K e y w o r d s : urban flora and vegetation, human impact, ecological studies, Thellungian paradigm

Introduction

Urban ecology is the investigation of living organisms in relation to their environment in towns and cities, as in ecological studies of forests or the sea. The ecological approach considers a city as an ecosystem, characterized by its history, its structure and function, including both biotic and abiotic components, and the cycling and conversion of energy and materials. Cities also have their own spatial organization and distinctive patterns of change through time, which result in patterns of species behaviour, populations dynamics and the formation of communities, each of which is specific to the urban environment. In policy and planning the term urban ecology is synonymous with "sustainable cities".

Early investigations looked for particular biotopes, for the nature in a city, not for the nature of a city as a whole. The initial studies were on castles and ruins or gardens and parks. Investigations on the peculiarities of urban flora and vegetation revealed a high species diversity and a dynamic development of vegetation. Ecosystem studies started in the 1970's.

The remarks presented here are mainly about studies on the urban flora and vegetation in Central and Western Europe.

Wild flora of castles and ruins

In all cities "ruderal" biocoenoses exist. "Ruderata" (from Lat. rudus: rubble, ruins) is the name for a specific habitat (Buxbaum 1721, Linnaeus 1751). The definition connects ruderal plants with their habitat: they grow in places strongly disturbed by man, but not cultivated, e.g., on rubble. Classical "ruderata" are ruins and waste lands, walls and pave-

[1] The innovative work of Slavomil Hejný inspired many urban ecologists. I use this opportunity to express my personal appreciation of his work.

ments. Plant remains from Roman "castra" and their surroundings have been studied; these localities often prove to be the nuclei of modern cities (Knörzer 1970). Studies include Celtic "oppida" (e.g. Küster 1992), Slavic cities (Opravil 1969, 1987, 1990, Wasylikowa 1978, Trzcinska-Tacik & Wasylikowa 1982, Wasylikowa et al. 1991) and Viking settlements (Behre 1983).

Castles are an ecological model of the changes in the environment and organisms that occur in settlements. Due to favourable microclimatic conditions and ruderal soils, plants and animals from warmer regions are spreading. In Berlin 60% of all non native plants come from such regions: this is true of archaeophytes as well as neophytes (Scholz 1960). The differences between the "Burgbergflora" and surrounding flora and vegetation were studied by botanists in the 19th century (Chatin 1861, Kirschleger 1862, Krause 1896). Around castles the number of species of wild flowering plants can be twice that in similar areas in the vicinity (Lohmeyer 1984).

The flora of ruins and walls has been studied for centuries, e.g., the flora of the Colosseum of Rome (Panarolis 1643, Sebastiani 1815, Deakin 1855, Celesti Grapow et al. 2001), walls in Palestine (Hasselquist 1762, Weinstein & Karschon 1976, 1977) and in Algeria (Jourdan 1866, 1872), and the walls of the churches of Poitiers (Richard 1888); for subsequent studies see Brandes (1992). Observations on the development of vegetation on the ruins of the Conseil d'Etat in Paris, destroyed during the last days of the Commune uprising, were published by Flammarion (1881) and Vallot (1884). Plant growth on walls is enriched when stones 'alien' to the locality of the town and old types of mortar are used. Modern Portland cement is harder and more resistant to weathering (Segal 1969). Wall plants have interested botanists for centuries (Fitter 1945). Gerard (1597) in his "Herball" mentioned several plants on the walls in London: *Parietaria judaica* "groweth neere to old walls in the moist corners of churches and stone buildings" (Woodell 1979).

Cultivated flora in gardens and parks

The existence of gardens worldwide is recorded in manuscripts, paintings and drawings from the time of Byzantium time to the present (e.g. Beuchert 1983, Willerding 1984). Ornamental plants, like lilies, roses and chrysanthemum have been cultivated for a long time. The first survey of the plants in German gardens was carried out by Conrad Gesner (in Cordus 1561). Introduced plants dominated over native ones. The history of introductions of ornamental plants is described by Kraus (1894), Wein (1914, 1943), Goeze (1916), Kowarik (1992) and Groeningen (1996). Plants introduced intentionally for horticultural use were planted first in monastery and peasant gardens and, nowadays in urban areas from which they have spread into the surrounding landscapes. The effect of escaped ornamentals on the flora around cities is documented by Kosmale (1981), Kunick (1991), Adolphi (1995) and Maurer (2002).

Botanical gardens are recorded from e.g. Pergamon, Athens, Byzantium and Toledo. The oldest European botanical gardens are those at Pisa 1543, Padua 1545 and Firenze 1545 (Chiarugi 1953), and north of the Alps those at Leiden 1577 and Leipzig 1580. Physic gardens were established to produce medicinal herbs, e.g. the Chelsea Physic Garden, which was established in London in 1673 by the Society of Apothecaries to grow and study the plants of their trade.

The well known drawings by Merian show gardens near cities. In Thünen's "Der isolierte Staat" (1826) is presented a theory of the relations between an ideal city and its surroundings in which intensively used gardens are situated close to the city.

Archaeological and palaeo-ethnobotanical studies have shown that fruit-trees were cultivated in early neolithic times. Under the Romans the number and performance of fruit-trees increased in Central and Western Europe. Vegetable cultivation was well developed in areas under Roman influence and improved during the Middle Ages. There is documentary evidence of the use of spice plants in the Roman era and the Middle Ages. Results of countrywide palaeo-ethnobotanical surveys given in Zeist et al. (1991) show differences in the species of cultivated plants in cities and villages.

In antiquity trees were planted around places of worship, during the Middle Ages in the squares in front of churches or town halls, and in Central Europe the trees were mainly *Tilia* species (Hennebo 1978). Since the 19th century trees have been an important element of urban planning (Stübben 1890). Around 1900 all big cities had trees planted along the streets.

Green roofs and roof gardens are known from ancient times (Babylon, Herculaneum) and many parts of the world (Japan: rice straw, Scandinavia with sod or turf). Roofs with self-established vegetation are described by Bornkamm (1961). The roof gardens in Berlin (Darius & Drepper 1985) became a well known feature of the city by the end of the 19th century and inspired architects.

During the medieval plague epidemics cemeteries were for the first time situated outside city walls. This was for hygienic reasons and because of the lack of space inside the city walls. Prior to 1900 publications on the flora of cemeteries only list ornamental plants (Unger 1870, Murr 1901) and spontaneously growing plants were only recorded over the last 25 years. A survey of the ecological investigations of cemeteries is given by Graf (1986).

Species diversity in urban habitats

The first recorded botanical ramble in the London region was on Hampstead Heath (Johnson 1629). Together with another report (Johnson 1632) it is the first list (72 resp. 97 species recorded) for a particular area with heath, bog and ruderal flora (compare Fitter 1945). The flora of Paris was repeatedly studied in the 17th and 18th century (Cornut 1635, Tournefort 1698, Vaillant 1727). Many famous botanists collected plants there (Jolinon 1997): among others, four members of the family Jussieu, Linnaeus, Rousseau, Buffon, Willdenow, Kunth, Bonpland and A. v. Humboldt.

The first printed urban floras were not restricted to a particular area "intra muros", but included areas distant from the centre, e.g. Jungermann's flora of Altdorf and Gießen (Jungermann 1615, 1623), Ray's flora of Cambridge (Ray 1660). Willdenow (1787) in his "Florae Berolinensis Prodromus" mentioned only 8 species "in urbe ipsa" (among a total of 822 species). Later there were publications with titles like "Intramuralornis" (Paquet 1874, Schalow 1877) and "Intramuralflora" (Vallot 1884). The number of publications on urban ecology – even on well known groups like birds and mammals – increased only slowly during the 19th century, but accelerated after 1900 and grew rapidly after 1950 (Jolinon 1997 for Paris).

Early publications refer to migration of plants (Anom. 1782; see Brandes 2001), which later became introduction and naturalization of non native plants or invasions. In early studies of plant geography (Willdenow 1792, Chapter "Geschichte der Gewächse" in his "Grundriß der Kräuterkunde") there are no references to urban conditions. It was Schouw (1823) in the first textbook on plant geography who introduced the term "plantae urbanae" for plants living near cities and villages, e.g. *Onopordum acanthium, Xanthium strumarium*. He added : "In most cases foreign origin is the cause why these plants are located only near cities and villages". In particular, he named the plants growing on walls, ruins, roofs and rubble, and weeds of gardens. Chamisso (1827) described the conditions and effect of man on the flora and fauna of settlements: "Wherever man settles, the face of nature is changed. His domesticated animals and plants follow him; the woods become sparse; and animals shy away; his plants and seeds spread themselves around his habitation; rats, mice and insects move in under his roof; many kinds of swallow, finch, lark and partridge seek his care and enjoy, as guests, the fruits of his labor. In his gardens and fields a number of plants grow as weeds among the crops he has planted. They mix freely with the crops and share their fate. And where he no longer claims the entire area his tenants estrange themselves from him and even the wild, where he has not set foot, changes its form."

This quotation is taken from an instructional work "Botany for the non botanists", which Chamisso wrote for the Culture Ministry. The subtitle of this book, written in the tradition of natural history, was "A survey of the most useful and harmful plants, whether wild or cultivated, which occur in Northern Germany, including views on botany and the plant kingdom". In scientific terms this is the introduction of non native species, changes in biotopes, synanthropy, hemerochory, apophyty and agriophyty. Introduction and naturalization of non native plants, the so called adventive plants, was first studied by Watson (1859) and de Candolle (1855).

The concepts and terminology of the Swiss botanist Thellung (1912, 1918/19) have influenced the Central European approach up to the present day. A number of similar earlier and contemporary attempts proved less successful (de Candolle 1855, Rikli 1903, Linkola 1916).

Thellung's achievement was not in the development of a new approach, but in producing a systematic summary of the basic concepts and methods, which were used, with some variations, in the "adventive floristics" of his time. He provided an exact definition of the terms according to prevailing usage (1918/19), in particular that of Rikli (1903). Thellung discussed and defined terms like native, introduced, aliens, casuals etc. in French, German and English and created a scientific (Greek) terminology. One is tempted to speak of a paradigm (Trepl 1990). However, it is descriptive and non theoretical, and not clearly defined. Scheuermann (1948) wrote that Thellung "opened up research in the field of alien plants". He combined natural science and cultural history in a specific paradigm, later criticized by natural scientists.

There are several summaries of the development of the concepts and terminology (Holub & Jirásek 1967, Kornas 1968, Schroeder 1969, Sukopp & Scholz 1997, Richardson et al. 2000), one of the aims of which was to standardize terminology. Thellung's terms are still used but all have been simplified (Schroeder 1969). A comparison of the Central European terminology with that used in studies on plant invasions is given by Pyšek (1995b).

The studies of the "Working Group on Synanthropic Plants" at the Botanical Institute of the Czechoslovak Academy of Sciences in Průhonice included plants on arable land, in particular so called "quarantine" weeds (Hejný et al. 1973, Jehlík 1998; see Pyšek 2001), as well as urban flora. Since Laus (1908) the vegetation of specific habitats has been studied, e.g. railway sites (Jehlík 1986), cemeteries (Pyšek 1988), road verges (Klimeš 1987) and factories (Pyšek & Pyšek 1988c). The distribution of plant communities in particular habitats was studied by Pyšek 1978 (Plzeň), Tlusták 1990 (Olomouc) and Pyšek & Rydlo (1984) in villages. The occurence of individual species in habitats was considered in detail in the papers by Pyšek & Pyšek (1988a for the city of Plzeň, 1988b for West Bohemian villages).

Historically, bombed sites have been important in the development of studies on urban flora. Less than 3 years after the blitz Salisbury (1943) described the plants that colonized the ruined houses in London. In many cities the war damage and its effects gave rise to studies of rubble flora and fauna (Erkamo 1943, Balke 1944, Lousley 1944, Scholz 1960, Pfeiffer 1960). Rubble offers warmer and drier conditions than natural habitats and is a suitable habitat for plants and animals from warmer regions of the world. Many plants that were previously rare became permanent members of the urban flora in war-damaged European cities.

Dispersal of organisms and vegetation development on rubble was studied extensively on rubble sites which differ in their environment from previously studied ruderal sites. As Pfeiffer (1957) wrote: "The recolonization of rubble, created in many cities due to the activity of bombers in the last war, has unintentionally become a tremendous natural experiment, which with respect to its size, must be compared to the colonization of new habitats created by volcanic activity."

A similar situation occurred many years earlier following the Great Fire of London in 1666, when Ray recorded a population explosion of *Sisymbrium irio*, which was subsequently named the London rocket. Soon it became established in towns over a wide area but is now extremely rare and one of the few urban species to be included in an early edition of the Red Data book for vascular plants (Perring & Farrell 1977); later it was removed because it is a non-native species (Wiggington 1999). After a century's absence it reappeared in London at the end of the second world war. Gilbert (1989) concluded that a number of today's common ruderals will show a similar decline in the future.

Plants spread during war – mainly with horse-fodder – were called polemochors (Gaudefroy & Mouillefarine 1871, Mannerkorpi 1944, Luther 1948). Thellung (1917) gave the name stratiobotany (polemobotany) to research on the development of new plant formations with characteristic flora and on changes in cultivation that result from war (see also Kupffer 1922, Pettersson 1944).

Studies on the dynamic character of vegetation on rubble resulted in the first peak in urban ecology studies. Every big city has its own naturalized plants (Gilbert 1992). Unlike floristic studies, ecological research focused on dispersal strategies of particular species, succession under various site conditions, and the formation of new plant communities. However, all these investigations were carried out on rubble, not on a city as a whole.

The city as a whole

Present urban biota and communites can be seen as a result of historic development. In Central Europe the re-establishment of forest vegetation after the last ice-age was incompleted when man began to influence the vegetation by disturbances on a local scale. Large scale disturbance, however, began with clear-cutting of extensive areas for agriculture and 2000 years ago with the development of cities.

The environment of cities is very different from that prevailing outside their limits. Nevertheless, in many cities fields and gardens have been present for many centuries. Today, however, cities usually consist of a mixture of densely settled areas in the historic center, remnants of agro-ecosystems ("encapsulated countryside") and even near-natural areas in urban forests, parks, and nature reserves.

Open spaces in cities are modifications of older habitats. The similarity between former and present habitat conditions decreases with time and along a gradient from the periphery to the center. Historic periods, like the pre-industrial, industrial and post-industrial, created specific site conditions and favoured different plant and animal communities in urban areas. Currently, parts of cities of different ages have different plant species and communities (Saarisalo-Taubert 1963, Aey 1990).

Early investigations revealed that even man-made sites have characteristic combinations of organisms. More exact analysis revealed a considerable variety of sites, organisms and communities in London (Fitter 1946, Gill & Bonnett 1973), Paris (Jovet 1954), New York (Kieran 1959, Rublowsky 1967), Vienna (Kühnelt 1955, Schweiger 1962), Polish cities (Falinski 1971), Saarbrücken (Müller 1972), Brussels (Duvigneaud 1974), Berlin (Kunick 1974), Birmingham (Teagle 1978) etc. The Man and the Biosphere Project 11 of UNESCO resulted in the first attempts at complex studies, e.g. Hong Kong (Boyden et al. 1981) or Tokyo (Miyawaki et al. 1975, Numata 1977). These studies deal with questions of health, human welfare and the connection between culture and nature.

Cities were compared to organisms, with the parks and gardens as the "green lungs" (Francé 1920 for Munich, Peters 1954 for Stuttgart). Pfalz (1910) described wild and planted habitats. Ecosystem studies of cities started in the 1970's with investigations of energy flow and nutrient cycling. Duvigneaud (1974) applied the methods of forest and lake analysis used in the International Biological Program (IBP) to analyse a big city. Taking Bruxelles as an example, the input and output of matter and energy were calculated, treating the city like a black-box. The inner differentiation of a city was looked along the lines of the Berlin model (Kunick 1974): densely built up zone, partly built up central areas, inner suburbs, outer suburbs.

Ecosystem studies used the methods of ecological assessments and "Produktlinienanalysen" (Newcombe et al. 1978, Maier et al. 1996, Baccini & Baader 1997, Simon & Fritsche 1998). Biogeochemical budgets, ecological footprints (Rees 1996) and summaries of citywide species richness are characteristic of this approach.

Flora and fauna

Investigations of the flora of whole cities, rather than single habitats, include lists of species and their systematic, biological, ecological and geographic analyses. The term flora first referred to garden plants. The "Flora Danica" (Pauli 1648) and the "Flora Marchica"

(Elsholz 1663) were the first books to include native and cultivated plants (Wein 1932). The higher number of species in cities compared to the surrounding countryside was first pointed out by Walters (1970) and Haeupler (1974). As a quantitative assessment, frequency (percentage of squares in which a species is recorded) was used by Kunick (1974). Numbers of species in cities were summarized by Falinski (1971), Pyšek (1989, 1993), Brandes & Zacharias (1990), Klotz (1990). Complete lists of urban floras are available for the following Czech cities: Prague (Špryňar & Münzbergová 1998), Brno (Grüll 1979), Plzeň (Pyšek & Pyšek 1988a), and Most (Pyšek & Hejný 2003). For a summary of the methods to study the flora and vegetation in urban areas see Pyšek (1995a).

In cities for which the history of the flora is known, the changes and their causes have been studied (Table 1). The changes reflect the economic and cultural history. The development of the ruderal flora "essentially runs parallel to the size and the intensity of trade and industry; it is a direct standard of the technical culture" (Naegeli & Thellung 1905: 226). The spatial structure of urban floras can be mapped on a grid of regular spatial units; Jackowiak (1998) reviews the published maps and atlases of city floras. The first atlases of a city's flora were for London (Burton 1983) and Duisburg (Düll & Kutzelnigg 1992). Based on 6000 vegetation relevés made in West Berlin, the hemeroby concept (Jalas 1955) was used to express the response of each species of the urban flora to the complex measure of human influence (Kowarik 1990). Human impact is made up of many factors, some of which (stress, disturbance) cannot be directly measured (Sudnik-Wojcikowska 1988). That city floras have specific features was shown by Gutte (1969) for Leipzig, Chemnitz and Dresden, based on the distribution of thermophilous plants and communities.

Table 1. – Historical analysis of the development of urban floras.

Author	City/region	Period
Strumpf 1969, 1992	Altenburg	1768, 1889–92, 1938, 1968
Scholz 1960	Berlin	1787, 1884, 1959
Brandes 1984, Hellwig 1990	Braunschweig	1650, 1830, 1876, 1990
Godefroid 2001	Brussels	1940–1971, 1991–1994
Zimmermann-Pawlowsky	Euskirchen	1910, 1983, 1985
Schwarz 1967	Gdansk	1825, 1866, 1941, 1965
Klotz 1984	Halle/S. a. Halle-Neustadt	1848, 1983
Linkola 1916	Karelia (56 settlements)	1600, 1850–1880, 1915
Klotz & Il'minskich 1988	Kazan	1900, 1983
Trzcinska-Tacik 1979	Krakow	1809, 1920, 1977
Gutte 1989	Leipzig	1830, 1846, 1867,
Gusev 1968	Leningrad	ca. 1760, 1960 (only ruderal flora)
Fijalkowski 1994	Lublin	1787, 1848, 1917, 1944, 1993
Thellung 1912	Montpellier	ruderal flora since 1570
Gödde 1982	Münster	1947, 1974, 1981
Michalak 1970	Opole	1882, 1904, 1946,1965
Jackowiak 1990	Poznan	1850, 1896
Sudnik-Wojcikowska 1987	Warszawa	1824, 1914,
Griese 1999	Wolfsburg	1985, 1998
Hetzel & Ullmann 1981	Würzburg	1947, 1980
Landolt 1991, 1992, 2001	Zürich	Middle Ages, 1839, 1905, 1990

Unger (1852) cites the ecological characteristics of ruderal plants: specifically those of the families of *Urticaceae*, *Amarantaceae*, *Polygonaceae*, *Solanaceae* etc., are growing near human settlements because of the high levels of nitrogen in the soil. Here the term ruderal is congruent with nitrophilous according to the definition of Warming (1902). "Fertilizer is known to replace heat" (Thellung 1914) is similar formulation for plants that need of heat and whose roots penetrate nutrient rich soils further than on nutrient poor soils in climatically unfavourable habitats (Hügin 1992).

The current distribution of plants in urban areas is determined by land use. Wittig et al. (1985) distinguished urbanophilous, urbanoneutral and urbanophobous species (see also Korsch 1999). The distribution of plants in urban areas of different ages has been investigated. Saarisalo-Taubert (1963) showed that the distribution of the "Begleitflora alter Siedlung" (flora accompanying old settlements) is determined by favourable edaphic and microclimatic conditions. They can be natives as well as introduced plants (Aey 1990). The spatial structure of the urban flora and fauna is subject to temporal changes due to dispersal (Sudnik-Wojcikowska 1987a, b) and retreat of species (Linkola 1933).

With the domestication of plants (Körber-Grohne 1987, Zohary & Hopf 1993, Hondelmann 2002) and animals (Benecke 1994) and the storage of food, some wild animals entered into a specific relationship with man (Povolny 1963, Kenward & Allison 1994) and many of them became cosmopolitan. For a long time, cities and cultural landscapes were seen as biologically impoverished. At first Hesse (1924) stated: "The garden and park landscape interspersing and surrounding cities and villages is rich in (animal) species according to the diverse plant world and the varied general character of this formation."

The intramural fauna dates from the beginning of cities in the Near East 7 to 10,000 years ago, and reached Central and Western Europe 1,000 to 1,300 years ago (Davis 1987, Reichstein 1987). Pests of stored foods occurred in ancient Egypt (2,900 BC) and in Europe since the 16th century (Stein 1986).

The literature on the animal life in cities is summarized by Klausnitzer (1993), Gilbert (1989), Erz & Klausnitzer (1998), Luniak & Pisarski (1994). The species richness of urban gardens is reported by Owen (1991).

Vegetation

The term "urban vegetation" includes all types of spontaneously occurring and cultivated vegetation in cities (Sukopp & Werner 1983). Recording of urban vegetation started in Berlin (Scholz 1956); a survey of the following investigations is given by Wittig (2002). Complete vegetation surveys of Czech cities are published for Brno (Grüll 1979), Plzeň (Pyšek 1978, Pyšek & Pyšek 1988c), Most (Pyšek & Hejný 2003), Sušice (Pyšek 1972), Chomutov (Pyšek 1975), Prague (Kopecký 1980–1984, 1986, 1990), Brno (Grüll 1981), Bechyně (Hadač 1982), Liberec (Višňák 1986), and Olomouc (Tlusták 1990). A survey of urban vegetation research in East-Central and East European countries is given by Mucina (1980). Pyšek & Pyšek (1991) demonstrated important differences between the ruderal vegetation of cities and villages. Numbers of plant communities in 39 European towns and 85 Czech villages were summarized by Pyšek (1993).

Although the considerable spatial and temporal variability in urban vegetation makes vegetation classification difficult, the deductive method is most promising (Kopecký &

Hejný 1978). Apart from vegetation mapping a semi-quantitative representation of vegetation is possible using the method of unit areas (Pyšek 1975, Pyšek & Pyšek 1987).

Phytosociological studies of ruderal vegetation need an ecological basis (Sukopp 1971, 1973, Kopecký 1980–1984). The effects of city soils and air, e.g. stress due to deicing salt, heavy metals, SO_2 and other harmful substances, have been studied (Antonovics et al. 1971, Bornkamm 1990, Darius 1996, Rebele 1996). Bornkamm et al. (1982) refer to international investigations and ecosystem studies on suburban forests (Faensen-Thiebes et al. 1991), which gave a new impetus to general ecology (Cornelius et al. 1999).

Urban flora and vegetation is poorly integrated into urban biocoenoses. They are non-equilibrium systems in which stochastic processes are more important than deterministic ones. Succession in urban biocoenoses, relative to that in non-urban ones, is subject to strong and extremely variable anthropogenic influences, which are strongly linked to site history. Hence, these communities do not experience directional succession but are dominated by chance and unpredictable events; there are no climax conditions. The initial species composition is important in their future development.

A major reason for the (relative) unpredictable nature of succession in urban ecosystems is the high frequency with which they are invaded by aliens species; the biogeographical spectrum of species in cities is very different from that of the surrounding countryside. The reason for this may be (a) the ease with which these biocoenoses are invaded, and (b) the favourable conditions for dispersal (introduction, transportation). Disturbances generally favour invaders and urban ecosystems are subject to disturbances. Towns are subject to invasion by alien species and the number is unpredictable (Trepl 1994).

Urban biocoenoses are an extreme example of communities produced by successive invasions and not by co-evolutionary development. In principle, the historic uniqueness of urban ecosystems, i.e. their combination of environmental factors and organisms, differentiate them from most natural ones, even those subject to strong disturbance.

Environmental conditions

Abiotic factors are an important component of the ecology of plants and animals (Humboldt 1807). The earliest studies showed that urban climate differed between cities and the surrounding countryside (Howard 1833). The heat requirements of ruderal plants are summarized in Sudnik-Wojcikowska (1998) and Hügin (1999). Urban heat islands are an important determinant of distribution of urban flora in Central European cities, whereas in Southern European cities it is ancient walls and ruins (Celesti Grapow et al. 2001).

Emission research ("Rauchschadenforschung") started with studies on the relation between the sulphur content of coal and damage by SO_2 (Stöckhardt 1850). Measures taken to reduce the damage caused by emissions are reported in Strabon in 7 BC (Meineke 1969) and in the Corpus Iuris Civilis (533/534 AD). Grindon (1859) and Nylander (1866) were the first to recognize the correlation between increasing air pollution and the retreat of epiphytic lichens. Sernander (1926) subdivided cities into zones according to the presence of certain lichens indicating different degrees of air pollution. Bioclimatology began in 1929 with studies on radiation and cooling (Kuttler 1993). Kratzer (1937, 1956) established another branch of urban ecology with his Berlin thesis on the urban climate. Regular recording of the first flowering of cherries started in Japan as early as 812; in England phenological investigations started in 1736 (Margary 1926, Sparks & Corey 1995).

Specific characteristics of soils in urban and industrial areas rarely received attention, except that of soil near smelting plants (Senft 1857). Archaeologists used high phosphate levels in soils as an indicator of settlements of hunters, fishermen and cattle breeders (phosphate mapping after Arrhenius 1931). For a long time, substrates in cities were regarded by pedologists as heterogenous and too young to develop into soils. Pedological studies in cities were not started before the 1970s and include Perth (Andrews 1971), Berlin (Runge 1975, Grenzius & Blume 1983), Washington (Smith 1976), and Halle (Billwitz & Breuste 1980). Recommendations for soil mapping in cities were published by Blume et al. (1989) and Burghardt et al. (1997). The International Working Group "Soils of urban, industrial, traffic and mining areas" was founded in 1998 (Burghardt & Kneib 2001).

Most biological studies of urban areas involve human health and welfare, e.g. control of disease, plants for medicines, air and water pollution, disposal of solid waste, treatment of contaminated soil. Thurnwald (1904) analysed the effects of city climate and professional life on physiological and psychic behaviour. Classical synopses are the books of Hellpach (1939) and Rudder & Linke (1940).

Most cities are located near rivers, the waters of which are changed by the increased run-off following urbanization of the catchment area and the resultant increase in impervious surface cover, chanellization, pollution and decline in richness of biotic communities (Paul & Meyer 2001). Methods of supplying drinking water and treating waste water were devised early in the establishment of urban agglomerations. Kolkwitz & Marsson (1902) devised biological indication of water quality, based on plant and animal indicator species and their capability to exist under different saprobic conditions.

Kolkwitz (1909, 1914) was the first to successfully rehabilitate a lake. He investigated the mass growth of algae in the Lietzensee, a lake in Berlin, and came to the conclusion that the factor regulating algal production was the almost continual supply of nutrients from the mud at the bottom of the lake. He successfully reduced the supply of nutrients by flushing out the nutrient-rich mud from the bottom of the lake with nutrient-poor water.

Urban ecology developed methodologically out of landscape ecology by intensively studying settlements (Sukopp 1990, Sukopp & Wittig 1998), which are regarded as ideal landscapes for such studies (Leser 1991). In geography landscape ecology is the study of the economy of nature (Naturhaushalt), i.e. the ecological aspects of mainly cultural and harmonic landscape. In pre-industrial times this concept also applied to cities, the direct and immediate expression of the natural-ecological conditions of an area. Modern cities are characterized by their worldwide connections and are uncoupled (disassociated) from the local surroundings with the consequence that the concept of a cultural landscape is only partly relevant. In ecology, on the contrary, landscape ecology is the investigation of several adjacent ecosystems; this concept can be applied to cities. In urban geography (Petermann 1903, Hard 1985, Lichtenberger 1998) the term urban landscape was developed around 1920 for a type of cultural landscape characterized by settlements. A major contribution to landscape ecology was the book "Design with nature" (McHarg 1969).

In urban history, ecological aspects increasingly played a role influenced by regional studies (Hauptmeyer 1987). Archaeological and archival studies of modern city centres made ecological analysis possible. Palaeoecology is especially suitable for revealing lifestyle, land use and demography (for Germany e.g. Meckseper 1985, Herrmann 1989). Palaeo-ethnobotany was developed by Unger (1851, 1852) and Heer (1865, 1883) and is reviewed by Willerding (1987). Urban archaeology of city centres lead, together with

early floras lists, to today's urban botany (Willerding 1986, Hellwig 1990, Landolt 1991, 2001). The cultivated plants and accompanying wild flora in gardens, fields and meadows in Pompei, which was destroyed in 79 AD, are documented in ikonographical, literal, archaeological, ethnobotanical and palynological records (Jashemski 1979). So another basis of urban ecology is urban archaeology.

First urban ecology syntheses were published by Weidner (1939), Rudder & Linke (1940) and Peters (1954), authors whose expertise was in biology, geography or medicine. Summaries are to be found in Gilbert (1989), Sukopp (1990), Wittig (1991, 2002), Klausnitzer (1993), Sukopp & Wittig (1998), Breuste et al. (1998), Friedrichs & Hollaender (1999), Kavtaradze & Fridman (2000) and Picket et al. (2001).

As a separate discipline urban ecology was established in the early 1970s with systematic studies of climate, soil, water and organisms. With growing interest in nature conservation in cities (e.g. Barker 1997) programmes focused on the mapping of biotopes appeared (Schulte et al. 1993). Hejný (1971) distinguished 68 habitat types in Prague. A total of 223 cities in Germany (all cities and many medium-sized towns) and 2000 villages and small towns have been biotope mapped (Schulte & Sukopp 2000). Although widely applied mainly in Germany such studies are mostly lacking application in other countries.

The term urban ecology was introduced by the Chicago school of social ecology within sociology (Park et al. 1925). In ecology, the term was formally defined in the 1970s, whereas the content had existed for centuries. Internationally, the institutionalization of urban ecology came with UNESCO's intergovernmental Man and the Biosphere (MAB) Programme in 1971.

Comparison with non European approaches

In many countries urban ecology research is less concerned with nature conservation, but more with sociological investigations under the heading of "human ecology". These investigations are conducted by sociologists and psychologists. In Japan relatively natural environments have been created by constructing of "native" forests with native trees, integrating research on the potential natural vegetation and traditional Japanese methods of creating "chinju-no mori" (shrine and temple forests). The introduction of "environmental forests" into various places – such as factories and power stations on reclaimed coastal land, schools, parks, streets, airports and harbours – has been increasingly successful. Restoration of natural environments by creating native forests has been carried out at such sites. By combining the traditional method of planting native trees in towns and villages with modern phytosociological and ecological diagnosis (map of present-day vegetation, report on the site conditions), and prediction (map of potential natural vegetation and habitats), new forests have been created in more than 120 locations throughout Japan (Miyawaki et al. 1987).

In Third World countries, more attention is given to agriculture or forestry in urban areas as well as water pollution, control of disease, and waste disposal in an attempt to improve the situation of the inhabitants (International Experts Meeting 1984).

When comparing European studies on urban nature conservation with contributions from North America, it is striking that the protection of game animals has almost no significance in the European programmes, where nature conservation is taken to refer to vertebrates that are not hunted, invertebrates and plants.

The widespread investigation and development of "urban forests" (McBride & Jacobs 1976, Grey & Deneke 1975, Rowntree 1986) in Anglo-American regions is not seen in Europe where the main concern is with the effect of man on forests near towns and cities. Inner-city areas are included only in Sweden and The Netherlands. For Düsseldorf Kürsten (1983) has studied roadside trees by using forestry methods and developed planning concepts.

Since 1970 there has been a gradual acceptance that nature conservation should include urban areas and their surroundings. Since the first quarter of this century pioneering naturalists and scientists, such as Paul Jovet (1954), emphasized the importance of biological diversity in human-dominated systems. This has paved the way for cities to become an important component of nature conservation (Barker 1997).

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Souhrn

Článek shrnuje historii výzkumu flóry, vegetace a jejich prostředí v lidských sídlištích. Nejstarší práce zabývající se ekologií měst se zaměřovaly na popis přírodních poměrů jednotlivých biotopů. V popředí zájmu byly rostliny a zvířata, které do těchto oblastí zavlekl člověk, ať už úmyslně či neúmyslně. Ve střední Evropě vyústilo specifické propojení studií věnovaných antropogenním migracím s kulturně historickými studiemi v takzvané thellungovské paradigma. Na zbořeništích vzniklých při bombardování ve druhé světové válce byla v mnoha městech studována vegetační sukcese.

Komplexní ekologické studie, zabývající se městem jako celkem, se objevily v 70. letech 20. století a byly inspirovány výzkumem zaměřeným na tok živin a energie. Dnes se termín městská ekologie (urban ecology) používá ve dvou různých významech: při vytváření programů trvale udržitelného rozvoje ve městech a ve smyslu ekologickém, tj. při studiu živých organismů v městském prostředí.

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